THE FOSSIL PELICANS OF AUSTRALIA

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Among the fossil bird bones obtained in the Lake Eyre basin of Australia, remains of pelicans are not rare in the Pleistocene assemblages and one representative of this group has appeared in the mid-Tertiary deposits (Stirton, Tedford, and Miller, 1961, p. 35). No other Tertiary pelicans are known for Australia, although Pleistocene occurrences under the names of *Pelecanus grandiceps* De Vis and *P. proavus* De Vis have been on record since the turn of the century. A single species, *P. conspicillatus*, occupies the continent of Australia today.

It is the purpose of this paper to evaluate all the fossil pelican material of Australia and to describe the Tertiary form which I first regarded (Stirton, *et al.*, *loc. cit.*) tentatively as generically distinct from *Pelecanus*, but which is now judged to be a strongly differentiated species of the modern genus.

In pursuing this study, I have had the benefit of the loan of the fossil pelican material in the Queensland Museum (Q.M.) through the kindness of the late George Mack and of Alan Bartholomai. For the loan of Recent skeletons of *P. conspicillatus* I am indebted to H. J. de S. Disney and H. O. Fletcher of the Australian Museum, Sydney (A.M.), to A. R. McEvey, of the National Museum of Victoria, Melbourne (N.M.V.), and to H. T. Condon of the South Australian Museum, Adelaide (S.A.M.). Other material studied is in the collections of the University of California Museum of Paleontology (U.C.M.P.) and the University of California Museum of Vertebrate Zoology (M.V.Z.). In the field work in Australia during which fossil and Recent skeletons were collected I was particularly aided by Paul F. Lawson of the South Australian Museum and by R. A. Stirton, Richard H. Tedford, Harry J. Bowshall, and Virginia D. Miller of our field parties. Support for the work on fossil vertebrates of Australia was received from the National Science Foundation, Washington, D. C., under grants G15957 and GB1990.

TERTIARY MATERIAL

The genus *Pelecanus* is represented by several described species from the Tertiary of Europe and India and by one species from North America (see Brodkorb, 1963, pp. 265–267). The only other generic name to be taken into account in the fossil record of pelicans is *Liptornis* of South America, which is based very unsatisfactorily on a neck vertebra which has not as yet been well compared ; its familial relations seem not to have been fully elucidated, if indeed this is possible.

† Deceased 9th October, 1965.

PELECANUS TIRARENSIS sp. nov.

(Text-figure 1*a*, *c*, *e*)

HOLOTYPE.—Right tarsometatarsus, the distal end complete except for some fracturing and loss of plantar surface of trochlea IV ; shaft fragmentary, but plantar area represented between facet for digit I and beginning of ridge distal to hypotarsus ; no. P13858, South Australian Mus. ; locality no. V5762, Univ. Calif. Mus. Paleo., Lake Palankarinna, Ngapakaldi Fauna, middle Tertiary, probably late Oligocene or early Miocene ; text-figs. 1*a*, *c*, *e*.

TYPE LOCALITY.—Etadunna Formation, west side of Lake Palankarinna in Turtle quarry (V5762) ; Lake Eyre region, South Australia ; pale green, fine-grained quartz sand 2–4 feet in thickness with lenses of green argillaceous sandstone, claystone lying below and above ; abundant associated turtle and fish remains and fragmentary bird remains, including metatarsus of a gull or tern.

DIAGNOSIS.—In contrast with *P. conspicillatus*, medial surface of metatarsal II shows large pit for medial ligament ; pit situated farther distally and anteriorly and encroaching farther on articular surface of trochlea, extending almost to bottom of its groove. Posteromedial border of articular surface of trochlea II more elevated from shaft of metatarsus, thus creating a pronounced trough above it ; trough well set off from ligamental pit by an intervening ridge. Outline of trochlea less rounded viewed medially. Distal foramen less elongate on plantar surface. Mass and lateral dimensions 10 to 15 per cent. less than in females of *conspicillatus* (see table 1).

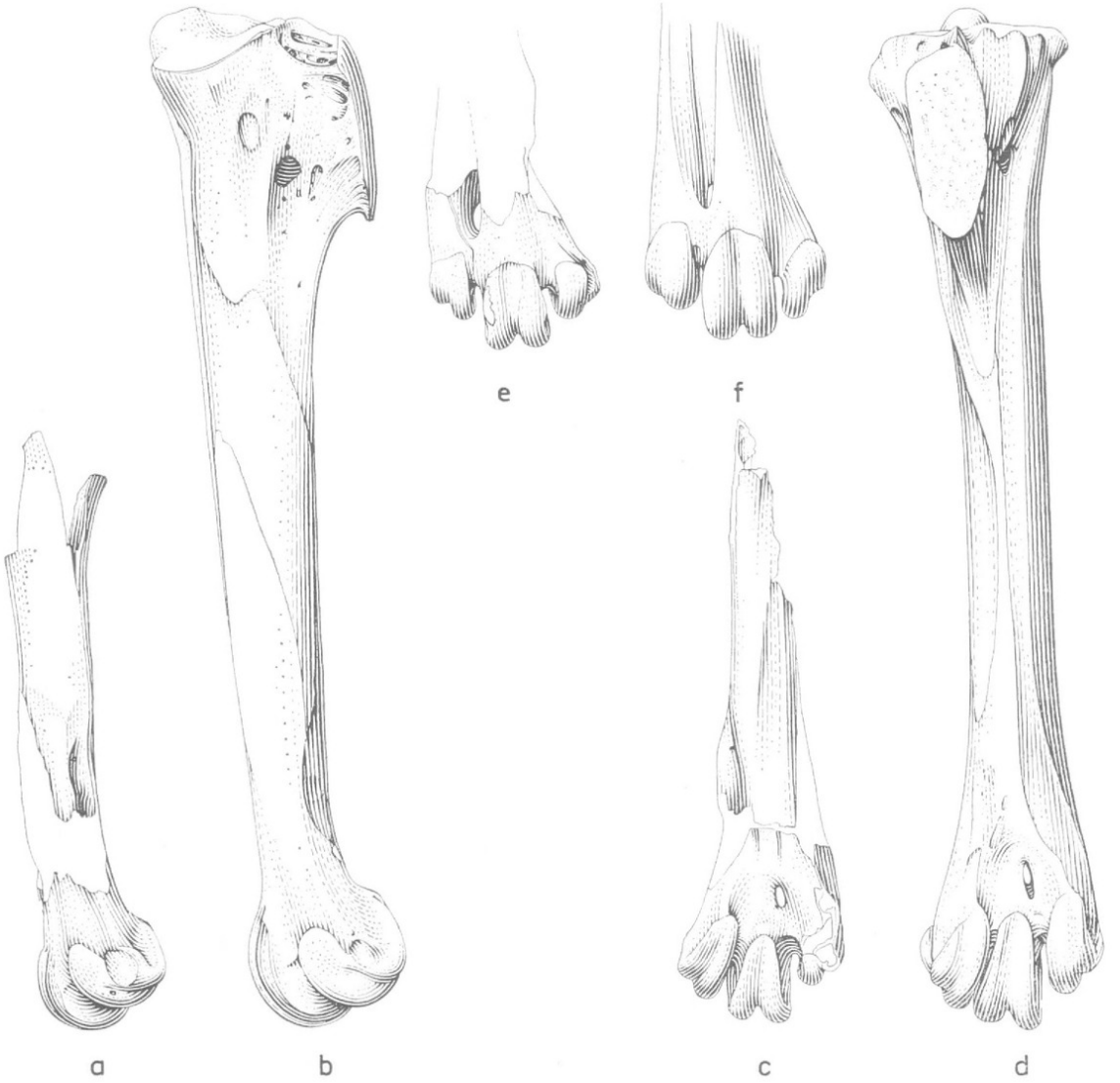
Table 1

MEASUREMENT IN MILLIMETERS OF TARSOMETATARSI OF PELICANS

——	Width across trochleae	Greatest antero-posterior dimension of trochlea III	Greatest antero-posterior dimension of trochlea II	Length from distal end scar digit I to base of hypotarsal ridge
Pelecanus tirarensis				
holotype	19·1	11·4	10·3	41·5
Pelecanus conspicillatus				
143245 M.V.Z. ♀	21·2	13·6	11·7	63·5
143248 M.V.Z. ♀	21·5	14·0	11·5	66·0
B11469 S.A.M. [♀?*] ..	22·0	13·7	12·0	63·5
S1206 A.M. [♀?*]	21·9	14·3	12·1	67·5
S1207 A.M. [♀?*]	22·0	14·2	12·1	66·0
143249 M.V.Z. ♂	24·3	14·7	12·9	69·0
W5982 N.M.V. ♂	24·6	15·1	13·0	75·5
Pelecanus grandiceps				
lectotype	—	16·9	—	—
56322 U.C.M.P.	—	16·6	—	—

* Sex suggested by size

Additional Features.—The fragments of the shaft of *P. tirarensis* which are present (see text-fig. 1) do not make perfect contact with the distal segment. On the shaft the articular surface for metatarsal I is clearly represented. It is more deeply excavated and more sharply flanged medially than in *conspicillatus*. The distance between it and the beginning of the plantar ridge that rises to the hypotarsus is one-third less than in *conspicillatus*, suggesting that the shaft and thus the entire tarsometatarsus was much shorter than in the modern species, and quite out of proportion to the slightly lesser size otherwise. However, the shaft fragments, although seemingly fitted together correctly, are not to be relied upon to register the total length with precision. The shorter shaft in relation to distal width approximates the condition in the modern short-legged brown pelican, *P. occidentalis*, although in the important matter of the configuration of trochlea II there is no similarity.



Text-figure 1.—Tarsometatarsi of pelicans, natural size. *a*, type of *Pelecanus tirarensis*, medial view; *b*, modern *P. conspicillatus*, no. 143245 M.V.Z., medial view; *c*, type of *P. tirarensis*, plantar view; *d*, *P. conspicillatus*, plantar view; *e*, *P. tirarensis*, anterior view; *f*, *P. conspicillatus*, anterior view. Drawings by Augusta Lucas.

COMPARISONS.—Very little advance in knowledge of Tertiary pelicans has been made since the end of the last century. Lydekker (1891, pp. 37–45) reviewed the material known up to that time. Two species from the Pliocene of India, *P. cautleyi* and *P. sivalensis*, had been described by Davies (1880, p. 26). Both are based on distal ends of ulnae, although some fragments of other elements have been referred to them. Both were described as smaller than the living *P. roseus* of south-east Asia. Accordingly they cannot be compared with *P. tirarensis* which is known only from the tarsometatarsus, although they may have been in the same size range. *P. gracilis* Milne-Edwards (1867, p. 250) from the Oligocene (Aquitanian) of France was based primarily on the upper part of a tarsometatarsus ; nothing is known of the lower articular surfaces of the bone which would be critical in relating it to *tirarensis*. *P. gracilis* was a very much smaller, more slender-legged bird than *conspicillatus*, as Milne-Edwards' descriptions and figures show. *P. intermedius* Fraas (1870, pp. 281–283) from the Upper Miocene of Germany is based on a cranium and parts of the bill. Much other material has been referred to it (Lydekker, 1891, pp. 40–44 ; Lambrecht, 1933, p. 277), including tarsometatarsi, but these are not of proved association with the type material and moreover have not been described and critically compared. *P. fraasi* Lydekker (1891, p. 44) from the Upper Miocene of Bavaria was also based on a cranium, differing strongly in osteologic features from *intermedius*, but the lower leg bones of this species are unknown.

P. odessanus Widhalm[1] (1886, p. 6) from the Lower Pliocene of Odessa is based on a tarsometatarsus. The large size (tarsometatarsus 150 mm long) indicates a bird similar to *conspicillatus*, but if the description and figures are to be trusted, it differed rather radically from the configuration of *conspicillatus* and other modern pelicans in the shape of the trochleae and in the ridges and muscle scars of the metatarsus. It shows no approach whatsoever to the peculiar configuration of trochlea II seen in *tirarensis*.

P. halieus Wetmore (1933, p. 3) was described from the Hagerman Lake beds in Idaho. This has variously been regarded as Upper Pliocene or Lower Pleistocene. The species is based on the distal end of a radius and is not comparable, therefore, with the Australian Tertiary species ; it obviously was a much smaller bird.

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[1]Brodkorb (1963, p. 266) and Lambrecht (1933, p. 295) both misspelt this name, and the former, apparently not able to consult the original paper and following Lambrecht's incorrect reproduction of the name of the species, assumed Widhalm did not offer a proper binomial designation of the species, whereas he appears to have done so as follows : " . . . . unter den Namen seiner Vaterstadt als *Pelecanus odessanus*. fossilis *Widhalm* in die Gesellschaft seiner Artgenossen einzuführen " (original italicization and punctuation are preserved). Thus the species name *odessanus* is properly derived from Widhalm (1886) and not from Lambrecht (1933). I am indebted to Bobb Schaffer for assistance in locating the original Widhalm reference in the Osborn Library at the American Museum of Natural History and providing me with a photographic copy of it.

The foregoing review indicates that on present evidence *P. tirarensis* is distinctly different from all other known Tertiary pelicans based on the same parts of the skeleton, and that those species described from other elements show no particular features of size or build that would suggest identity with it. Moreover representatives of the three modern subgenera of pelicans, the brown, white, and Australian pelicans, show no approach to *tirarensis* in the shape of the second trochlea.

Discussion.—The Tertiary record of the family Pelecanidae is surprisingly scant and it has not been significantly augmented in recent years. The characteristics of *P. intermedius*, *P. fraasi*, *P. odessanus*, and *P. tirarensis* reflect a stronger differentiation of species in the genus in the Tertiary than that between the living species. The substantial divergences represented by the first three and the comparable divergence of *tirarensis* have led me to include *tirarensis* in this broad generic grouping, rather than separate it further as was my earlier inclination.

Unfortunately the functional meaning of the distinctive tarsal configuration of *tirarensis* cannot be assessed. One may assume that it reflects stronger ligaments on the medial side of the base of digit II than in the living species, but without an analysis of the musculature operating or bracing this toe nothing definite can be concluded about action. In general the structure suggests greater strength of the foot in bracing and grasping.

PLEISTOCENE MATERIAL

The Pleistocene pelicans of Australia bear two names proposed by De Vis (1892, 1906). He evidently proceeded on the general belief that all fossils should be designated as separate species, whether or not they differed significantly from their modern relatives. In view of this a careful appraisal of his descriptions and original materials seems necessary, for many of the late Pleistocene specimens he worked with may indeed be inseparable from the living *P. conspicillatus*. The specimens of the latter which we collected and borrowed (see table 1) serve fairly adequately to show its range in size and the variability of its osteologic characters. It must be realized that at the turn of the century, when De Vis worked, there was very little awareness of the problems of variability and a typological approach prevailed. Usually a comparative osteologist was content with the examination of a single skeleton of a given species.

De Vis (1892, p. 444) based the species *P. proavus* on the distal end of a tarsometatarsus from the Darling Downs beds in Queensland, and not as Brodkorb (1963, p. 267) indicates on a fragmentary carpometacarpus. The latter was mentioned by De Vis only in passing and he gave no differentiating characters for it and did not figure it. Among the material extant at the Queensland Museum, the tarsometatarsus is lacking and it is therefore to be concluded that it is lost. A crushed proximal end of a carpometacarpus is present and it evidently is the one

De Vis mentions. He says of this that it has " a large pneumatic foramen placed as in *Pelicanus* ; the bone is too much crushed and distorted to allow of a description of any value." The specimen, no. F.1141 Queensland Museum, does appear to have the foramen referred to, although it may be unnatural and resulting from the crushing. The shape of metacarpal I and its processes, which are fairly well preserved, differs radically from that of pelicans and is more suggestive of that of *Grus*. This fragment had best be regarded, then, as indeterminate and removed from any consideration as a representative of the Pelecanidae.

The type of *proavus*, the tarsometatarsus, is described by De Vis in some detail, and from this and the figure it is quite clear that it represents *Pelecanus*. The differentiation from *conspicillatus* which he makes is based entirely on size : " the living species exceeds the extinct by one-fourth of the latter." The measurements which he cites appear to support this. The figures of the tarsometatarsus are apparently reproduced at natural size, although this is not stated, and one must acknowledge that there might have been some deviation from this in the engraving. One measurement De Vis gives is the " width across the trochlear expansion " as 16·5 mm. This apparently does not represent the maximum width across the trochleae and their lateral processes, which are obviously broken and incomplete, but rather the width proximal to that point at the level of the distal foramen. This measurement I can duplicate exactly by measuring on the figure. By contrast De Vis gives a single figure for the same dimension in *conspicillatus* as 20 mm. The two known females of the living form listed in table 1 measure 16·5 and 16·7 mm at this point, and the two males about 20·0 mm. Moreover, superposition of the metatarsus of female no. 143245 on the figure shows it to match almost perfectly in size. The other dimension given by De Vis, " the distance from the proximal end of the hallucal depression " to the end of the bone is not significant, for the proximal end of that scar is lacking in the fossil as figured. Again a superposition of the metatarsus of no. 143245 on the figure shows no difference in dimensions on the long axis of the bone. Moreover, I detect in the figure no aspects of shape that suggest differences from the modern bird.

I am therefore forced to conclude that *P. proavus* falls within the size range of the modern *P. conspicillatus* and that there are no characters differentiating the two. *Pelecanus proavus* must therefore be regarded as a synonym of *P. conspicillatus*.

In naming *P. grandiceps*, De Vis (1906, p. 16) described and figured a quadrate, a coracoid, and a tarsometatarsus, the latter two fragmentary. All the original material is before me for analysis and I find that De Vis' illustrations are natural size and reasonably accurate representations.

The quadrate of *grandiceps* in comparison with that of modern males is not larger as claimed. For example it is equalled or slightly exceeded by no. 11849 A.H.M., a pick-up modern skull from Cooper Creek, Australia, in the same dimensions

used by De Vis (p. 16). It is interesting that his rather unjustified extrapolation of the total head length of 21 inches is also exceeded in this modern bird, in which it is 22 inches long. In this particular study, De Vis must not have had at hand a large male of *conspicillatus*.

The configuration of the quadrate which he mentions in respect to the pterygoid articulation I find quite variable in the modern material, in some cases essentially duplicating the fossil. The difference in size of a foramen and the distinctness of certain ridges are variable features which are not meaningful, and the squamosal articulation is not in fact broader than in *conspicillatus* as was claimed.

The coracoidal fragment included in De Vis account is too incomplete, as De Vis says, " to supply further information " about this Pleistocene form. It was from a bird as large as males of the modern species and may have exceeded the examples at hand slightly in shaft width.

The distal end of the tarsometatarsus is indeed conspicuously large. I cannot be sure how De Vis took the length measurements of trochlea III which he cites, and I find it difficult to specify the degree of difference in dimension along the linear axis because of the incompleteness of the distal surface. The most significant measurement that can be taken is that of the greatest anteroposterior distance across trochlea III, which is 16·9 mm. Compared with the largest male of the modern species, which is 15·1 mm, this is a 12 per cent. difference and a greater difference than that between the smallest female and the largest male in the sample of seven available. This measurement in the fossil exceeds the mean for *conspicillatus* by more than three times the standard deviation and thus falls outside its range of variability. Other parts of the fossil metatarsus are similarly large as judged by general comparison with males of *conspicillatus*. For example the breadth of the facet for metatarsal I and the length of the distal foramen, though not precisely measureable, are of the order of 15 to 20 per cent. greater than in males of *conspicillatus*. Two aspects of configuration are worth noting, namely a greater breadth and flattening of the trochlear ridges on the anterior surface and the presence of a deep pit on the plantar surface between the bases of trochleae III and II. These features in combination seem sufficient to support the view that this tarsometatarsus represents a large species different from the modern pelican.

De Vis' name *grandiceps* rests, then, on three unassociated specimens, although they came from the same general Pleistocene locality of Cooper Creek. He designated no holotype and a type designation subsequently has not been published so far as I am aware. To conserve the existing name I designate the tarsometatarsal fragment, no. F.3751 Queensland Museum, as the lectotype of *Pelecanus grandiceps* and relegate the two other specimens which constituted De Vis' type material, namely the quadrate and the coracoid, to *P. conspicillatus*.

Additional Material.—Fragmentary remains of pelicans were obtained in early and late Pleistocene localities in the course of the recent field work in the Lake Eyre basin. Only one of these, a metatarsal fragment, is of the size of *P. grandiceps*. The following additional material all belongs to *P. conspicillatus*.

Early Pleistocene, Katipiri Sands, Lake Kanunka, Kanunka Fauna. Locality V5773, site 2, *in situ*, Univ. Calif. Mus. Paleo.: no. 60549, right cuneiform, complete ; no. 60577, distal end of right tarsometatarsus, the surfaces of trochlea II eroded ; no. 60578, distal end of right tarsometatarsus, trochlea II somewhat crushed ; no. 69587, fragment of proximal articulation of right humerus (float on surface).

Both metatarsal fragments are small. The only dimension that can be taken satisfactorily across adequately preserved surfaces is that of the anteroposterior dimension of trochlea III. One, no. 60578, is 12·3 mm and the other 11·3 mm. These are intermediate in the one case between *conspicillatus* and *tirarensis* and in the other case equivalent to *tirarensis*. This small size in itself is not sufficient grounds to view these as importantly different from modern *conspicillatus*, and affinity or approach to *tirarensis* is not supported by the shape of residual parts of trochlea II. In these matters of configuration these early Pleistocene fragments correspond with *conspicillatus*.

Late Pleistocene, lower Cooper Creek, Malkuni Fauna. Locality V5860, site 8, Univ. Calif. Mus. Paleo. : no. 56321, left quadrate, complete ; no. 60487, fragment of a coracoid ; no. 60477, proximal end of right femur ; no. 60520, distal end of left ulna ; no. 60503, left cuneiform ; no. 60521, distal end of right tibiotarsus. Locality V5859, site 7 : no. 56394, part of a cervical vertebra. Locality V5868, site 16 : no. 56348, distal end of left ulna. Locality V6147, site 18 : no. 60656, fragment of anterior end of sternum with coracoidal facets ; no. 60640, distal articular surface of left humerus. Locality V5382, Malkuni waterhole : no. 60702, fused palatines, essentially complete.

All this late Pleistocene material was found on the surface as outwash from the Katipiri Sands in the drainage channel of Cooper Creek. None of it departs in size or configuration from modern *conspicillatus*. A few elements slightly exceed the examples of males of the latter, but not to a degree to suggest the substantially larger *P. grandiceps*.

A fragment of a distal end of a left tarsometatarsus, no. 56322, from V5860, site 8, on Cooper Creek, is of essentially the same size (table 1) and configuration as the lectotype of *P. grandiceps* and thus is the only sure additional material of that extinct late Pleistocene form.

De Vis (1906, p. 17) assigned a tibiotarsus and a femur from lower Cooper Creek to *P. proavus*. These are before me and I cannot separate them from *conspicillatus*. The femur, on which he comments in particular, was I believe to some extent misinterpreted by him owing to the incompleteness of the condyles. All elements originally and subsequently ascribed to *proavus* therefore fall under *conspicillatus*.

SUMMARY

The record of fossils of the family Pelecanidae in Australia extends from the mid-Tertiary (late Oligocene or early Miocene) to the late Pleistocene. Most of the material is from the Lake Eyre basin. A new species of pelican, *Pelecanus tirarensis*, from the Tertiary, is described, a species differing from other pelicans chiefly in the configuration of the second metatarsal. It was shorter legged but otherwise only slightly smaller than the modern *P. conspicillatus*.

In the early Pleistocene the modern species occurred in the Lake Eyre region ; it may at that time have tended toward somewhat smaller size than today, but it shows none of the important features of *tirarensis*.

The late Pleistocene remains of pelicans are all of the species *conspicillatus* both in the Darling Downs locality and in the Lake Eyre region, with the exception of *P. grandiceps* De Vis based on a very large tarsometatarsus, one further fragment of which was found.

A review of nearly all of De Vis' fossil material reveals that his *P. proavus* is a synonym of *P. conspicillatus* and that his *P. grandiceps* was a composite. A lectotype for *grandiceps* has been designated and the remaining type material assigned to *conspicillatus*.

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