

# THE FOSSIL PELICANS OF AUSTRALASIA

by

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## ABSTRACT

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A review of all known Australasian fossil pelecoid material suggests that four species have occurred in the southwest Pacific region during the past 20 million years. The oldest, *Pelecanus tirarensis*, a small robust pelican from Miocene sediments of central Australia, has a distinctive trochlear arrangement of the tarsometatarsus. The younger material is all Pleistocene in age, and most of it can be referred to *P. conspicillatus*, the living Australian Pelican. An exception is *P. novaezealandiae*, originally described as a large New Zealand subspecies of *P. conspicillatus*; it is as different, however, from that species as is *P. onocrotalus*. *P. cadimurka*, n. sp., is distinctly smaller, being within the size range of *P. tirarensis*, but with a differently shaped tarsometatarsus, more closely resembling that of *P. conspicillatus*.

## INTRODUCTION

Pelicans, all in the genus *Pelecanus*, have a long history in Australia, occurring as early as the Miocene in terrestrial deposits of the Lake Eyre Basin, South Australia. Their first occurrence elsewhere in the world is contemporaneous with this antipodean record.

Pelican fossils were first reported from Australia by De Vis (1892) when he recognized *Pelecanus proavus* from Quaternary sediments of south-eastern Queensland. Later he set up an additional two species, *P. validipes* (in Brown, 1894) and *P. grandiceps* (1905). No further pelecoid remains were reported until Miller (1966) reviewed the De Vis material and described a number of new specimens collected during the 1950's on the Stirton expeditions of the University of California and South Australian Museum. Miller set up a new species, *P. tirarensis*, based on a mid-Tertiary fossil from the Lake Eyre Basin and referred all of the De Vis material except the lectotype of *P. grandiceps* and the holotype of *P. validipes* to the living Australian Pelican, *P. conspicillatus*. The same year

Scarlett (1966) designated pelican material found in New Zealand as a new sub-species of the Australian pelican, *P.c. novaezealandiae* (see Fig. 1).

Since the mid-1960's more pelican material has been collected. This paper reports on all the fossil pelican material from Australasia. *Pelecanus tirarensis* is quite distinct from all other pelicans, both fossil and Recent. Most of the Quaternary material, however, appears to belong to *P. conspicillatus*. Two forms, one small, *P. cadimurka* n. sp. and one large, *P. novaezealandiae* from New Zealand, appear to be distinct species. The diagnoses of *P. tirarensis* and *P. cadimurka* are based on features of their tarsometatarsi and of *P. novaezealandiae* on features of its synsacrum and femur. We found many elements to be similar in size and shape in several species of *Pelecanus*. The fossil specimens that lacked diagnostic features we have referred therefore tentatively on the bases of size, location and age to: *P. tirarensis*, small, central Australia, Miocene; *P. cadimurka* n. sp., small, central Australia, Quaternary; *P. novaezealandiae*, large New Zealand, Holocene; and *P. conspicillatus*, large, Australia, Quaternary, including the Recent.

## ABBREVIATIONS

The following abbreviations have been used in this paper: AM, Australian Museum, Sydney; AMNH, American Museum of Natural History, Ornithology Department, New York; AWMM, Auckland War Memorial Museum, Auckland; CM, Canterbury Museum, Christchurch; ANWC, Australian National Wildlife Collection, CSIRO Division of Wildlife Research, Canberra; NMV, National Museum of Victoria, Department of Ornithology, Melbourne; QM, Queensland Museum, Brisbane; SAM, South Australian Museum, Adelaide; UCMP, University of California, Museum of Paleontology, Berkeley; UCMVZ, University of California, Museum of Vertebrate Zoology; I.Z., Institute of Zoology, Chinese Academy of Sciences, Beijing (Peking). > = greater than, † = slightly greater than, @ = approximately, rf = referred.

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### DIAGNOSIS OF ELEMENTS OF *PELECANUS* REPRESENTED BY AUSTRALASIAN FOSSIL MATERIAL

Fossil material discussed below was assigned to the *Pelecanidae* because of the following combination of characters of these large birds:

**Quadrates:** Lacks distinct rounded pit for quadrato-jugal; entire ventral articular area with little relief, lacking deep pitting between articular surfaces for mandible and quadrato-jugal such as that present in the *Phalacrocoracidae*; anterior border of ventral articular surfaces nearly straight lacking any marked process on ventral end that projects medial to mandibular articulation; mandibular articulation parallel-sided over most of medial half; squamosal articulation also of low relief, oriented at 90° to ventral articular surface being compressed mediolaterally; main shaft compressed antero-posteriorly and lacking pneumatization.

**3rd Cervical Vertebra:** Prezygapophyses elongate and narrow; diapophyses about one half total length of vertebra with short pleurapophyses extending posteriorly; most dorsally protruding part of neural spine low, and on posterior one-third of vertebra lying posterior to end of parapophyses; diapophyses not bulbous and not extending lateral to prezygapophyses, but continue posterior from them so that vertebra remains nearly same width as anterior-most width to end of pleurapophyses; lateral margins only slightly concave; deep pit on ventral surface near anterior end; prominent bulbous ridge along midline of centrum over posterior half of centrum ends in two prominent blunt projections on either side of midline ridge.

**4th Cervical Vertebra:** Differs from 3rd only in that dorsal-most expansion of neural spine occurs just slightly posterior to midpoint and at same level as ends of pleurapophyses; ventral pit near anterior end deeper and more elongate; two ventral spines present and very low.

**Sternum:** (dorso-anterior end only). Lacks dorsal manubrial spine but broad-based ventral spine present, extending anteriorly, not dorsally; coracoidal sulci converge upon one another anteriorly, forming a small obtuse angle; dorsal lips of coracoidal sulci separated and markedly expanded medially, tapering to a fine point postero-laterally; coracoidal sulci narrow, parallel-sided and deep, being deepest near postero-lateral end; ventral lips of coracoidal sulci straight, not curved or indented.

**Scapula:** Scapular blade not parallel-sided near proximal end but rapidly narrows distally, becoming parallel-sided near midpoint without any further broadening; near distal end blade narrows to nearly one half of previous width, terminating rapidly in blunt process, not recurved; entire shaft of blade nearly straight, not anteriorly concave; proximal part of shaft quite deep (dorso-ventrally) becoming more flattened distally, with prominent muscle scar on dorsal surface well separated from the proximal end (about one third of the total length of the blade); furcular articulation on elongate process, extending proximally beyond glenoid facet.

**Coracoid:** Coracoidal fenestra small but complete and well separated from the internal border of the coracoid; scapular facet deeply excavated; glenoid facet not flattened but markedly concave latero-internally; medial and lateral boundaries of shaft nearly straight, not markedly concave or convex, nearly perpendicular to long axis of shaft over medial half and at small obtuse angle over lateral half.

**Humerus:** Proximal end differs in palmar view from other large birds including storks, cranes, gannets, cormorants, and darters in ligamental groove not extending from ventral edge as far dorsally, and in being a pit rather than a groove. A similar pit occurs also in albatrosses, but the proximal end is more bulbous and rounded in *Pelecanus*, whereas it is thinner and more angular in *Diomedea*. Distal edge, as in waterbirds, orientated at right angles to main axis of shaft and not obliquely with a wide, protruding entepicondyle as in land birds, penguins, and auks. Ectepicondylar spur absent as in most waterbirds except for those in the *Procellariiformes* and *Charadriiformes*. As in other *Pelecaniformes*, distal end curved over more in palmar direction than in other waterbirds. Within *Pelecanus* this is more pronounced than in other

extant genera of the order. The humeri of *Pelecanus* are also decidedly larger than those of other extant genera in the order.

**Femur:** Trochanter low, with both it and head extending an equal distance proximally; trochanter and head not grading smoothly into one another but separated by a distinct, broad channel; head large, about 60 per cent of the length of the trochanter; in lateral view, proximal border of trochanter only slightly, not highly arched with the most proximal extension lying slightly behind antero-posterior midpoint; no pneumatic foramen present near proximal end on anterior surface.

**Tibiotarsus** (Distal end only): Internal condyle extends far distad of external and is much more elongate than internal; single supratendinal bridge lacks any ligamental prominences on either medial or lateral ends and forms small acute angle with long axis of shaft; shaft lacks external flange just proximal to external condyle; in distal view, condyles deep, with internal slightly deeper than external; distal end slightly broader anteriorly than posteriorly but lacking any marked constriction near anteroposterior midpoint.

**Tarsometatarsus** (Distal end only): Trochlea II longer (extending further distally) than trochlea IV; in medial view, trochlea II not extending far posteriorly and lacking medial spike on posteriomedial border; trochlea II lacking medial groove extending over entire trochlea but notched distally and posteriorly; in distal view, medio-lateral axis through trochlea II-IV not straight but arched.

#### SYSTEMATIC POSITIONS OF AUSTRALASIAN FOSSIL MATERIAL

Australasian fossils referred to *Pelecanus* by De Vis (1892, 1905; in Brown, 1894), Archey (1931), Miller (1966), and Scarlett (1966) are summarized with our determinations in Table 1 and on Figure 1. We have re-examined most of this material and have added to it a number of new specimens collected over the past decade and a half.

##### *Pelecanus tirarensis*

Citation: Miller, A. H., 1966. Mem. Queensland Museum, 14 (5), 182, Fig. 1a, c, e.

Holotype: Distal end, right tarsometatarsus SAM P13858.

Locality and Age: Lake Palankarina Site 3, Turtle Quarry (UCMP V-5762), west side of lake, South Australia, Etadunna Formation, Miocene. 28°48'S, 138°24'E.

Comment: The holotype of *P. tirarensis* (SAM P13858) differs from the tarsometatarsi of living

pelicans (see Figure 2 and Tables 2, 3 and 4) in having:

(1) an elongate trough developed on the posterior margin of the medial surface of trochlea II, separated from the ligamental pit by a slender ridge that is orientated nearly due proximo-distally along trochlea; this ridge trends posteriorly towards distal end and broadens slightly; in all other species examined this area is occupied by an elevated, inflated ridge that continues all the way to the posterior border of the trochlea, when trochlea II viewed posteriorly; the presence of the trough in *P. tirarensis* produces a more gracile trochlea over much of its length, as pointed out by Miller (1966);

(2) a decidedly narrower anterior margin of trochlea II than posterior margin (in distal view) rather than both approaching the same width. Differs from *P. occidentalis* and *P. erythrorhynchos* in having a trochlea II that extends much further distally than trochlea IV; in *P. occidentalis* and *P. erythrorhynchos* trochlea II extends only slightly distad of trochlea IV; *P. conspicillatus* and *P. onocrotalus* have trochlear conditions very similar to those in *P. tirarensis*.

Miller (1966) noted also that the size of the ligamental pit on trochlea II is greater than that on other pelicans; in our sample of *P. conspicillatus* this character seems too variable to be of diagnostic value, and our largest specimen (ANWC BS1202) had a large ligamental pit approaching that of *P. tirarensis*. Miller further noted that the distal foramen was less elongate on the plantar surface than that in *P. conspicillatus*; examination of our sample of *P. conspicillatus* (n=20) bore this out, but in the sample of *P. erythrorhynchos* (n=5) the character varied from the condition in *P. conspicillatus* to that in *P. tirarensis*; *P. onocrotalus* and *P. occidentalis* have distal foramina as in *P. tirarensis*. From fragments of SAM P13858 available, we cannot verify the position of the origin of the plantar ridge on the posterior surface nor can we see this in Miller's illustrations. Thus, comparison of proportions of the shaft (length vs. width) based on the location of this feature seems impractical.

Referred Material: UCMP 60988: Distal end, right tarsometatarsus, Lake Palankarina, Site 6, UCMP V-5765, 28°46'S, 138°25'E, South Australia, Etadunna Formation, Miocene.

Comment: UCMP 60988 is very incomplete, lacking trochlea II and with articular surfaces of trochlea III and IV very worn so that the original surface cannot be defined on trochlea IV (see Figure 3). Thus, the diagnostic characters defining *P. tirarensis* cannot be evaluated sufficiently even though the distal foramen is small and ovoid, as in *P. tirarensis*, and the size is comparable (see Tables 2



and 3). We have therefore only tentatively referred it to this species.

UCMP 113115: Distal end, right tarsometatarsus, lacking distal end of trochlea II and totally lacking trochlea IV, Leaf Locality, UCMP V-6213 Lake Ngapakaldi, 28°18'S, 138°16'E, South Australia, Wipajiri Formation, late Miocene.

Comment: UCMP 113115 lacks those areas exhibiting characters diagnostic of *P. tirarensis*. Its size is comparable to that species (see Figure 3 and Table 3) and its distal foramen is of moderate size. We therefore only tentatively refer it to *P. tirarensis*.

AMNH 11494: Proximal end of right tarsometatarsus, lacking much of hypotarsus, Lake Pinpa, 31°08'S, 140°12'E, southeast of Lake Frome, Tarkarooloo Basin, South Australia, Namba Formation, Miocene.

Comment: AMNH 11494 is definitely pelecoid in that the proximal articular surfaces are deep; the intercotylar prominence is very prominent and is restricted to the anterior part of the proximal end; the hypotarsus viewed posteriorly, is triangular in shape with the longest portion on the internal side; there are two well defined calcaneal canals; the anterior surface of the shaft near the proximal end is deeply excavated with two large vascular foramina in this deep excavation. AMNH 11494 is smaller than the tarsometatarsi of *Pelecanus conspicillatus*, and differs further in that the lateral calcaneal notch is only slightly indicated and not deeply incised; the anterior border of the lateral articular surface does not form a sharp apex, but is rounded; the whole lateral articular surface is relatively broader; viewed anteriorly, the external foramen is smaller and not as enlarged as the internal foramen; the excavation of the anterior surface at the proximal end and further distad is relatively deeper; the tubercle for *tibialis anticus* is displaced onto the medial surface of the excavated area on the anterior surface rather than being more or less centrally located; the foramina on either side of the hypotarsus are relatively smaller than in *P. conspicillatus*.

Because AMNH 11494 is badly eroded, only the following measurements were practical: width across proximal end @ 18 mm; and depth across lateral articular surface and lateral calcaneal ridge of hypotarsus @ 14 mm. In *P. conspicillatus* these parameters are width:  $n = 10$ , range 22-24 mm, mean 23 mm, s.d. 1 mm; and depth  $n = 10$ , range 17-20 mm, mean 18 mm, s.d. 1 mm. Because of its size and age we refer AMNH 11494 tentatively to *P. tirarensis*.

QM F10703: Distal end of left tarsometatarsus, Crocspot 1, south end of Lake Palankarina, 28°46'S, 138°28'E, South Australia, Etadunna Formation, Miocene.

Comment: QM F10703 fits within the above description of the holotype, except that the proximodistal ridge does not broaden towards the distal end; we, therefore, refer it to *P. tirarensis*.

### *Pelecanus proavus*

Citation:

De Vis, 1892, Proc. Linn. Soc. New South Wales, 2(6): 444 Pl.24.

Holotype: No number (type lost), left tarsometatarsus.

Locality and Age: Darling Downs, 28°S, 150°E, Queensland, Quaternary.

Comment: *Tarsometatarsus*. Miller (1966) re-evaluated this left tarsometatarsus and assigned it to *P. conspicillatus*; the illustrations provided by De Vis (1892) are not helpful in making this assignment. Based on the illustrations, it appears that the distal foramen in *Pelecanus proavus* is not rounded, but is not as elongate as those in our sample of *P. conspicillatus*, being more like that in *P. onocrotalus*. This may be due to inaccurate illustration of damage to trochleae, which De Vis (1892) mentions.

De Vis' illustrations also indicates that there is little flare of the distal end of the tarsometatarsus of *P. proavus*, which most closely approaches the condition in *P. onocrotalus*. In most *P. conspicillatus*, *P. erythrorhynchus*, and *P. occidentalis* this flare, particularly on the internal margin of the shaft, is more pronounced.

The measurements made from De Vis' illustrations of the holotype suggest a medium-sized pelican, such as *P. rufescens* and *P. philippensis*. However, we are not entirely convinced that De Vis' illustrations are accurate because of the discrepancy between his measurement of the trochlear expansion and ours of the distal width of the illustration of the fossil, both of which appear to be the same measurement. De Vis (1892) originally recorded the 'width of the trochlear expansion' as 16.5 mm, but our measurements of maximum width of the distal end made from Figures 6a, 6b, Plate 24 were 18.0-18.6 mm (see Table 2).

Thus, at present until the original specimen is available we reserve judgment on the validity of *P. proavus*.

Carpometacarpus: De Vis (1892) assigned a proximal carpometacarpal fragment, QM F1141, to *P. proavus*, but we concur with Miller (1966) that it is not pelecoid.

Femur: De Vis (1905) assigned a distal right femur fragment (QM F3752, Lower Cooper Creek, South



Australia, Quaternary) to *P. proavus*. When we compared it with femora of large pelicans, *P. conspicillatus* and *P. onocrotalus*, we could find no appreciable differences (see Figure 4 and Table 5).

De Vis (1905) mentions that the fibular groove is more extensive in *P. proavus*, covering most of the fibular condyle and making it concave posteriorly further distad than in *P. conspicillatus*. Additionally, the ectepicondylar region in the extinct bird was supposedly comparatively narrow and rather deeply sunken between the trochlea and the ectepicondylar edge, the cavity formed extending distad nearly two-thirds of the length of the trochlea (De Vis, 1905: 17). These characters are so similar in some specimens of the modern Australian Pelican that this fossil is best referred to *P. conspicillatus*.

**Tibiotarsus:** De Vis (1905) assigned the distal end of a right tibiotarsus (QM F3753, Lower Cooper Creek, South Australia, Quaternary), damaged on the internal condyle, to *P. proavus*, noting that there was nothing to distinguish it from the extinct form. Our comparisons with other large pelicans including *P. conspicillatus*, have revealed no diagnostic characters that set his fossil tibiotarsus apart (see Figure 4 and Table 6), and thus it should be referred to *P. conspicillatus* as Miller (1966) suggested.

### ***Pelecanus conspicillatus***

#### **Citation**

*Pelecanus conspicillatus* Temminck, 1824 Planches col.Oiseaux 47: pl.276.

#### **New Synonymy of Fossil Forms**

*Pelecanus validipes*. De Vis, 1894 (in Brown, Proc. Parl. So. Aust., 2(25): 21, pl. 11, 5-6).

*Archaeocynus lacustris* (in part) De Vis, 1905 (Ann. Qld. Mus., 6:13).

*Pelecanus grandiceps*. De Vis, 1905 (Ann. Qld. Mus., 6: 16, Pl. V, Figs 1-3).

#### **Fossil Material Described by De Vis**

##### ***Pelecanus validipes***

**Holotype:** Distal end of a right tarsometatarsus, SAM 18412, Warburton River, South Australia, Quaternary.

**Comment:** Contrary to the comments made by De Vis (in Brown, 1894) we have found that (see Fig. 2):

(1) the middle trochlea (III) is not broader than that in *P. conspicillatus*;

(2) the hallucal depression is no better defined (in fact ANWC BS1363, *P. conspicillatus*, matches the condition in *P. validipes*);

(3) the dorsal sulcus is not any deeper nor the bounding ridges more well defined than in *P. conspicillatus*;

(4) the distal end of the plantar ridge is no straighter than in some *P. conspicillatus*; and

(5) *P. validipes* is within the size range of the living *P. conspicillatus* that we have measured (see Tables 2, 3 and 4).

Thus, we suggest that *Pelecanus validipes* be synonymized with *P. conspicillatus*.

##### ***Archaeocynus lacustris* (in part)**

**Relevant Syntype:** Fragment of 4th cervical vertebra (QM F5529), unknown locality.

**Comment:** Among a series of bones that De Vis (1905) named *Archaeocynus lacustris*, a new genus and species of swan, was a cervical vertebra that is not anatid, but pelecanid (see Fig. 3). The vertebra is quite eroded anteriorly and dorsally and thus preserves few useful characters. It is, however, of a pelican within the size range of *P. conspicillatus* (see Table 7) to which species it should be referred and removed from the Anatidae and the syntypes of *Archaeocynus lacustris*.

##### ***Pelecanus grandiceps***

**Lectotype:** Miller, 1966: QM F3751, left distal end of a tarsometatarsus, Lower Cooper Creek, South Australia Quaternary.

**Comment:** Miller (1966) in his review of Australian pelicans chose to retain this species as distinct from the extant Australian pelican, *P. conspicillatus* because of the following features of the lectotype tarsometatarsus: (1) large size; (2) 'presence of a deep pit on the plantar surface between the bases of trochleae III and II' (Miller 1966: 187); and (3) 'a greater breadth and flattening of the trochlear ridges on the anterior surface (of trochlear III)' (Miller 1966: 187).

QM F3751 (see Fig. 2 and Tables 3 and 4) only slightly exceeds in size the tarsometatarsi of *P. conspicillatus* in only one out of four measurements that are practical on the fossil. We doubt that this difference is significant. The deep pit on the plantar surface between the bases of trochleae II and III, present on QM F3751 is represented by only a tiny foramen on a specimen that Miller (1966) referred to this species (UCMP 56322, Lower Cooper Creek site 8, UCMP V-5860, South Australia, Quaternary) (see Fig. 3 and Table 4). In our sample of recent *P. conspicillatus* one specimen (ANWC BS1272) exhibited a distinct pit on the right tarsometatarsus and a pinhole foramen on the left tarsometatarsus. Thus, this character seems quite variable between and even within individuals and not particularly useful taxonomically for the genus

*Pelecanus*. The anterior ridges on trochlea III increase in breadth and flattening with size, and our largest specimens of *P. conspicillatus* approach or match that of *P. grandiceps*.

Thus, we suggest that *Pelecanus grandiceps* be synonymized with *P. conspicillatus*.

**Quadrates:** De Vis (1905) named a fragmentary left quadrate (QM F3749, Lower Cooper Creek, South Australia, Quaternary), *P. grandiceps*, because of qualitative differences as well as a distinctly larger size than *P. conspicillatus*. We agree with Miller (1966) that, in fact, this specimen is within the range of variability of the living *P. conspicillatus* (see Fig. 3 and Table 8), and we therefore refer it to this species.

**Coracoid:** De Vis (1905) assigned to *P. grandiceps* a left coracoid (QM F3750, Lower Cooper Creek, South Australia, Quaternary), lacking both dorsal and ventral ends but including most of the glenoid facet and part of the scapular facet. Although not preserving much that is diagnostic, the position of the coracoidal fenestra in the fossil form more closely approaches that in *P. onocrotalus*, where the coracoidal fenestra is displaced further laterad from the medial margin and thus is positioned nearer the centre of the coracoidal shaft than in most of our sample of *P. conspicillatus*. Because of the lack of a more complete bone, it is difficult to interpret the significance of this character, and because it is similar in size to those of modern *P. conspicillatus* (see Fig. 4 and Table 9) we refer it to this species as suggested by Miller (1966).

In conclusion, we can see no valid reasons for maintaining *Pelecanus grandiceps* as a species distinct from *P. conspicillatus*.

#### Additional Material

**Quadrates:** UCMP 56321, left, Cooper Creek, Site 8, UCMP V-5860, 28°34'S 138°00'E, South Australia, Quaternary. Left quadrate nearly complete except for erosion along some articular surfaces. Together with those of other living species of pelicans, this specimen differs from that of *P. occidentalis* in that the pneumatic foramen lies on internal rather than external surfaces; the otic process is short rather than elongate giving the quadrate a remarkably different shape. Allowing for variability in modern populations of pelicans, only the much larger *P. onocrotalus* can be ruled out. The fossil quadrate is similar in size to quadrates of several living species, including *P. conspicillatus*, and thus we follow Miller (1966) in referring it to this species (see Fig. 3 and Table 8).

**Palatines:** UCMP 60702, fused palatines, Cooper Creek, Malkuni Waterhole 28°34'S 138°09'E, South Australia, UCMP V-5382, Quaternary. We follow

Miller (1966) in referring this specimen to *P. conspicillatus*.

**Vertebrae:** UCMP 56394, posterior half of 3rd cervical vertebra, Cooper Creek, Site 7, 28°33'S 138°10'E UCMP V-5859, South Australia, Quaternary. Miller (1966) assigned this specimen to *P. conspicillatus*. In size it matches measurements of several of the larger pelicans (see Fig. 3 and Tables 10 and 11), and we can find no diagnostic differences from any of these forms, including *P. conspicillatus*. Thus we refer it to this species.

**Sternum:** UCMP 60656, anterior fragment of sternum, Cooper Creek, Site 18, 28°35'S 138°08'E, UCMP V-6147, South Australia, Quaternary. Although larger than any of our sample of *P. occidentalis*, this specimen falls again in the range of the larger pelicans, except for perhaps *P. onocrotalus* (see Fig. 3 and Table 12), and is so fragmentary that definite assignment to any species is rather senseless. We follow Miller (1966) in referring it to *P. conspicillatus*.

**Coracoid:** QM F6669, fragment of a left coracoid, Lower Cooper Creek, South Australia, Quaternary. Although part of a collection made during the summer of 1901/2 by J. W. Gregory and his students during the Melbourne University Lake Eyre Expedition, we are not aware that De Vis and Miller have commented on this specimen in print. We refer QM F6669 (see Table 9) to *P. conspicillatus* as it is within the size range of this species and we can discern no qualitative differences.

UCMP 60487, fragment of a left coracoid, Cooper Creek, Site 8, UCMP V-5860, Quaternary. We refer this specimen to *P. conspicillatus* in agreement with Miller (1966).

**Ulna:** UCMP 56348, distal end of left ulna, Cooper Creek, Site 16, UCMP V-5868, South Australia, Quaternary. UCMP 60520, distal end of left ulna whose articular surfaces are eroded, Cooper Creek, Site 8, UCMP V-5860, South Australia, Quaternary. We agree with Miller (1966) in referring these specimens to *P. conspicillatus* (see Fig. 2 and Table 13).

**Cuneiform:** UCMP 60503, left cuneiform, Cooper Creek, Site 8, UCMP V-5860, South Australia, Quaternary; UCMP 60549, right cuneiform, Lake Kanunka, Site 2, UCMP V-5773, 28°23'S, 138°17'E, South Australia Katipiri Sands, Quaternary. We agree with Miller (1966) in referring these specimens to *P. conspicillatus* (see Fig. 2 and Table 14).

**Femur:** UCMP 604777, proximal fragment of right femur, Cooper Creek, Site 8, UCMP V-5860, South Australia, Quaternary. Miller (1966) assigned this specimen to *P. conspicillatus* but because of the lack of any diagnostic differences either in morphology or

size with most other large pelicans (see Fig. 4 and Table 15), we can only refer it to this species. *P. rufescens* and *P. occidentalis* appear to be distinctly smaller, and *P. crispus* (based on one specimen) has a flattened, not curved, trochanter (viewed laterally), which does not slope anteriorwards as it does in UCMP 60477.

**Tibiotarsus:** UCMP 60521, very fragmentary, distal right, tibiotarsus, Cooper Creek, Site 8, UCMP V-5860, South Australia, Quaternary. Because of the incompleteness of this specimen, little can be said of its affinities except to the family Pelecanidae. It falls within the size range of *P. conspicillatus* and several other large pelicans (see Fig. 4 and Table 6). Therefore, we refer it tentatively to *P. conspicillatus*.

**Humerus:** UCMP 60640, very fragmentary distal left humerus with only external and internal condyles and external margin preserved, Cooper Creek, Site 18, UCMP V-6147, South Australia, Quaternary. Miller (1966) placed it in *P. conspicillatus*. In size and shape it is similar to the humeri of *P. conspicillatus* and other large species of pelican (see Fig. 3 and Table 16). We therefore tentatively refer UCMP 60640 to *P. conspicillatus*.

**Scapula:** UCMP 56633, right scapula missing parts of the glenoid facet and furcular articulation, Warburton River, Marcus Locality, 27°55'S, 138°00'E, UCMP V-5569, South Australia, Quaternary. The distance between the furcular facets is very narrow, but this character is extremely variable even within *P. conspicillatus*. The angle at which the two furcular facets meet (in ventral view) is slightly greater than 90°, but this varies from an acute to slightly obtuse in *P. conspicillatus*. In our small samples it is slightly obtuse in *P. occidentalis* and *P. onocrotalus* and acute in *P. erythrorhynchus*. In size UCMP 56633 is similar to the scapulae of the larger species of pelican (see Fig. 3 and Table 17), and we therefore tentatively refer it to *P. conspicillatus*.

#### *Pelecanus novaeseelandiae*

**Citation:** *Pelecanus conspicillatus novaeseelandiae*. Scarlett, 1966, Notornis 13: 204, Fig. 1 1-11.

**Holotype:** Large part of a single skeleton including mandibular fragments, left quadrate, pelvis, right and left humerus, right ulna, right and left radii, right and left carpometacarpi, left scapula, right and left coracoids, right and left femora, right tibiotarsus, right and left fibulae, right and left tarsometatarsi, and several vertebrae, CM AV21355.

**Locality and Age:** Poukawa, Site I, Hawkes Bay, New Zealand, (39°45'S, 176°43'E) Quaternary, between 3500 and 4500 years B.P. The holotype was

found just below the Waimihia Ash, a band of airfall volcanic ash, that was deposited  $3440 \pm 70$  years B.P. (pers. comm. P. Horn 1979).

**Diagnosis:** Very large pelican. Differs from recent large pelicans in that its pelvis is distinctly broader and more robust (see Fig. 5 and Tables 2-6, 9, 13, 15-19) particularly across supratrochanteric processes; ilioischial foramen not extremely elongate, thus differing from *P. conspicillatus* and more resembling *P. onocrotalus*; proximal end of femur wider than largest of *Pelecanus*, although most other measurements overlap. Tarsometatarsus longer than femur as in *P. conspicillatus* and not shorter as in *P. onocrotalus*.

**Referred Material:** Partial skeleton (no number, now lost), Archey (1931), cave deposits near Lake Waikaremoana, North Island (38°47'S, 117°06'E); right coracoid (CM AV15089), right humerus (CM AV12264), left femur (CM AV12482) and proximal end, right humerus (CM AV13095), Marfell Beach, Lake Grassmere, South Island (41°42'S, 174°10'E); distal left tibiotarsus (AWMM AU5845.1), Puheke Beach, Kārikari Peninsula, North Island (34°55'S, 173°22'E); left tibiotarsus and fragments of a left ulna (private collection of Peter Horn), type locality Poukawa, Site N141/1; part of fused furcula and sternal keel (CM AV32001) type locality, Poukawa; all Holocene in age.

**Comment:** Scarlett (1966) noted most of the characters we have utilized to define the species, *Pelecanus novaeseelandiae*. Because his sample of modern pelicans was so small, he chose to recognise the New Zealand form as only a separate subspecies. With our additional samples, we believe that the New Zealand form is sufficiently distinct, especially in the robustness of the pelvis and proximal hind limb, that it rates separation as a species.

#### *Pelecanus cadimurka* n. sp.

**Holotype:** SAM P22501, left tarsometatarsus fragment lacking trochlea IV and with some erosion of posterior border of trochlea II (see Fig. 6).

**Locality and Age:** Kuttipirra (Katipiri) Waterhole, Cooper Creek Site 9, UCMP V-5861, 28°33'S, 138°06'E, South Australia, Quaternary.

**Etymology:** Cadimurka (Aboriginal), noun in apposition. Brown (1894:5) in reporting the presence of bones of extinct animals at several places along the Warburton River, mainly along the edges of large waterholes, writes that 'The natives account for the presence of these bones by saying that they belong to the cadimurka, a large fish which lives in the bottom of the waterholes, and which has consequently never been seen by them'. One of the bones picked up by Brown on the Warburton River



is the holotype of *Pelecanus validipes*, and the material of *P. cadimurka* has been subsequently found in the same area.

**Diagnosis:** Small pelican in the size range of *P. occidentalis* and *P. rufescens*, distinctly smaller than *P. conspicillatus* and all other living species of pelican (see Fig. 2, 6 and 7 and Tables 2, 3 and 4). Where comparable published fossil material exists, only *P. tirarensis* and *P. gracilis* are of similar size. In medial view trochlea II lacks a deep channel on posterior border of medial surface, thus differing from *P. tirarensis*. Trochlea II and III extend an equal distance distally, unlike in most other pelicans, including *P. occidentalis* and *P. conspicillatus* where III is distinctly longer. In distal view, trochlea II is relatively narrow with posterior and anterior borders of nearly equal width, differing from (1) *P. conspicillatus*, which tends to be broader overall and laterally expanded along the posterior border, (2) *P. tirarensis* where the anterior border is decidedly narrower than the posterior, and (3) *P. occidentalis*, which tends to be broader. Trochlea III is deep and not shallow as in *P. occidentalis*, thus more closely approaching the condition in *P. conspicillatus*. Trochlea III is relatively slender, and not as broad as in *P. tirarensis* (see Fig. 2). In posterior view, articular surface of trochlea II terminates in a distinct apex proximally and is not squared off as in *P. occidentalis*. The shape of the distal foramen is not long and slit-like as in *P. conspicillatus* but more closely approximates those of *P. onocrotalus* and *P. occidentalis*.

**Referred Material:** UCMP 60577-60578. Two distal fragments of right tarsometatarsi with all three trochlea represented, Lake Kanunka, Site 2, UCMP V-5773, 28°23'S, 138°17'E, South Australia, Quaternary. Both specimens are slightly smaller than any of our samples of *Pelecanus conspicillatus*, about the size of *P. tirarensis* (See Fig. 3 and Tables 2, 3 and 4). On trochlea II, the posterior channel that characterizes *P. tirarensis* is not present, thus eliminating this species. In UCMP 60578 there is a small posterior depression in this area, but this condition can be matched in our sample of *P. conspicillatus*. The distal foramen is intermediate in shape between those of *P. conspicillatus* and *P. tirarensis*, more like those of *P. onocrotalus* and *P. erythrorhynchus*, but this character may quite likely vary somewhat with broader sampling. The trochleae of UCMP 60577 do not appear to flare as broadly distally as they do in *P. conspicillatus* and *P. tirarensis*, more closely approaching the condition in *P. onocrotalus*. Because parts of UCMP 60577 have been eroded, however, a final evaluation of this character is advisable. In both specimens, trochlea II extends far distad of trochlea IV as in other large pelicans including *P. tirarensis*, distinguishing it from *P. occidentalis* and *P. erythrorhynchus*.

**Comment:** Although these two specimens are somewhat intermediate in size between the holotype of *P. cadimurka* and the tarsometatarsi of *P. conspicillatus*, they appear to be qualitatively distinct from the latter as well as those of *P. tirarensis* and *P. occidentalis*. The specimens compare well with the holotype of *P. cadimurka* and thus will be referred to that new species. Miller (1966) had previously assigned both the above specimens to *P. conspicillatus*.

Our measurements from the De Vis figures of the holotype tarsometatarsus of *P. proavus* are within the ranges of those of the *P. cadimurka* material but because of a discrepancy between De Vis' and our measurements (see above) we doubt the scale of his figures and do not feel justified in referring the material of *P. cadimurka* to *P. proavus*. Furthermore, trochlea III is figured substantially longer than trochlea II in *P. proavus* and thus differs from the holotype of *P. cadimurka*.

UCMP 123382: Nearly complete 4th cervical vertebra, Cooper Creek, Site 8, V-5860, South Australia, Quaternary.

**Comment:** The vertebra is much smaller than any of *P. conspicillatus* in our sample (see Table 7) although very similar in shape. Also it is more gracile than those of *P. occidentalis*, which are antero-posteriorly compressed and more robust. It differs further from those of *P. occidentalis*, and is similar to those of *P. conspicillatus*, in lacking paired ridges over posterior half of ventral surface and in having a decidedly shallower pit just posterior to anterior articular surface of centrum on ventral surface. The vertebra may be, relative to total length, slightly broader across ventral surface of centrum on posterior half than in *P. conspicillatus*. It appears that this represents a species of pelican smaller than the extant and the Quaternary *P. conspicillatus*, and we have therefore referred it to *P. cadimurka*.

Not Pelecanidae. UCMP 69587. Proximal end, right humerus, Lake Kanunka, UCMP V-5773, South Australia, Quaternary.

**Comment:** Miller (1966) assigned this specimen to *P. conspicillatus*. Upon re-examination we find that the humerus is certainly within the size range of some living pelicans, but it shows considerable morphologic differences from all Pelecanidae. In UCMP 69587 the ligamental furrow is deeper. The bicapital furrow is deeply excavated instead of flat. In proximal view, the head narrows considerably near the external tuberosity, and is not bulbous.

In all of these characters, the fossil so closely resembles members of the Accipitridae that it should be transferred to this family. It appears to represent a giant raptor, larger than the living Wedge-tailed

Eagle, *Aquila audax* and more similar in size to the extinct New Zealand Eagle, *Harpagornis moorei*.

#### COMPARISON OF AUSTRALIAN FORMS WITH OTHER FOSSIL PELICANS

Brodkorb (1963) lists eight fossil species of pelicans, and recently Harrison and Walker (1976) have reported a ninth, *Pelecanus aethiopicus* from East Africa. Many of these are not directly comparable with most of the Australasian material except *P. novaezealandiae*, *P. intermedius* and *P. fraasi*, both from the Miocene of Europe, are known only from cranial material; *P. halieus* from the early Pleistocene of North America, a radius representing a bird the size of *P. erythrorhynchus*; *Liptornis hesternus* from the Miocene of Argentina, a lower cervical vertebra, whereas the Australian material is represented by higher cervicals.

*P. aethiopicus* from the Middle Pleistocene of East Africa is not directly comparable to Australian fossils as it is represented only by a proximal end of a tarsometatarsus and a scapula; scapulae of both *P. aethiopicus* and one Australian Pleistocene fossil pelican are so worn and broken that qualitative comparisons are futile, although they are clearly within the same size range.

The remaining fossil pelicans are at least represented by materials comparable to Australian specimens. *P. gracilis* (proximal humerus, femur, scapula, partial tarsometatarsus); *P. cautleyi*, (distal ulna); *P. sivalensis*, (distal ulna); and *P. odessanus* (coracoid, tarsometatarsus).

As Miller (1966) pointed out, *P. gracilis* from the early Miocene (Aquitainian) of Europe is decidedly smaller and more slender-legged than *P. conspicillatus*. Unfortunately, because nothing is known of the distal part of the tarsometatarsus, it cannot be compared with *P. tirarensis* or *P. cadimurka*, although it is clearly in this size range.

*P. cautleyi* and *P. sivalensis*, based on distal ends of ulnae from the Pliocene of India are smaller than the living *P. conspicillatus*, (Miller, 1966) and although within the size range of *P. tirarensis* and *P. cadimurka*, cannot be compared directly.

*P. odessanus* from the early Pliocene of Russia is similar in size to the living *P. conspicillatus*, thus larger than *P. tirarensis* and *P. cadimurka*. It differs from *P. conspicillatus* in the shape of the trochlea, ridges, and muscle scars of the tarsometatarsus (Miller, 1966).

#### STRATIGRAPHIC DISTRIBUTION OF PELECANIDAE WITHIN AUSTRALASIA

Fossil pelicans are known from three parts of the stratigraphic column in Australasia, and direct

correlation with sediments bearing pelecanid fossils elsewhere in the world is only approximate.

*P. tirarensis* occurs in the Etadunna Formation and possibly the Wipajiri Formation of the Lake Eyre Basin, Central Australia. The Etadunna Formation overlies fluvial rocks dated as Paleocene-Eocene because of contained plant remains. Unfortunately, none of the vertebrate bearing sediments has datable plant remains, and lithologic correlation must be used to tie the vertebrate bearing outcrops with subsurface geologic sections bearing such plant remains. Further correlation with plant-bearing marine sections to the south allow a tentative assignment of the Etadunna rocks to a mid-Tertiary, Oligo-Miocene age (Stirton *et al.* 1968). Correlation by use of fossil mammal remains with the Namba Formation, further to the southeast, which bears pollen basally, suggests a post Batefordian—Balcombian age of about 14-16 million years BP (Tedford, *et al.*, 1977). Based primarily on marsupial mammalian correlations, the Wipajiri Formation, which is channelled into the Etadunna, is thought to be of mid to late Miocene age. (See Rich, 1979 for a summary of the stratigraphy).

The remaining fossil pelicans of Australia have been collected from a number of sites along Cooper Creek, at Lake Kanunka (north of Cooper Creek), and along the Warburton River, all in the Lake Eyre Basin of northeastern South Australia; and on the Darling Downs of southeastern Queensland. All of these have been called Quaternary or Pleistocene in age. Locales along the Cooper and Warburton Rivers include fossils found both as 'float' on the surface and in place and are often associated with marsupials normally restricted to Pleistocene—aged sediments within Australia. Because many were collected out of a stratigraphic context, placement within the Pleistocene or even within the Recent is not certain. Dating of the Darling Downs vertebrates is based primarily on correlation using marsupial mammals, some species of which are entirely restricted to the Pleistocene, while others range from Pleistocene into the Recent.

New Zealand pelican fossils are known from several localities on both North and South Islands. All are no older than Holocene (see above).

#### DISCUSSION AND CONCLUSIONS

*Pelecanus conspicillatus* is the only extant pelican in Australasia. This has certainly not always been the case. During the last 2 million years, in the Quaternary, as many as 3 species were present in this biogeographic province, including: a small, gracile form, *P. cadimurka*, n. sp.; a very large, robust species, *P. novaezealandiae*; as well as a form

osteologically indistinguishable from the extant *P. conspicillatus*, *P. conspicillatus* and *P. cadimurka* were sympatric and contemporaneous in central Australia, a situation reflected by the modern broad geographic overlap of the small *P. rufescens* and the large *P. onocrotalus* in Africa. Likewise, the possible sympatry of *P. conspicillatus* and *P. novaezealandiae* is mirrored in the modern avifauna by the overlap of the large pelicans, *P. crispus* (the more gracile form) and *P. onocrotalus* (the more robust form) in the western Palaearctic. In fact, *P. novaezealandiae*, known only as a fossil from New Zealand, was contemporaneous with *P. conspicillatus* in Australia, suggesting probable overlap in distribution for such large mobile birds.

Only one other fossil pelican species is known from Australia, *Pelecanus tirarensis*, of Miocene age. It was a small form morphologically distinct from all later species.

Our review of all the Australasian fossil pelicans and comparison with all the recent pelicans support the inclusion in the synonymy of *P. conspicillatus* of: *P. validipes*, *P. grandiceps* and in part *Archaeocynus lacustris*. Although we agree with Miller (1966) that of the three specimens De Vis referred to *P. proavus*, one is not of a pelican and the other two may be referred to *P. conspicillatus*, the illustrations of the lost holotype suggest a pelican distinct from *P. conspicillatus*. Thus, determination of the status of *P. proavus* is impracticable unless the holotype is relocated. Provisionally the name should be retained. Our review has also demonstrated the necessity for recognizing as a new species of small and gracile pelican, *P. cadimurka*, and for elevating to specific status *P. novaezealandiae*, which Scarlett had named as a sub-species of *P. conspicillatus*.

As a result of this study, we have been impressed by the uniformity in skeletal morphology of the pelican species we examined, except for that of the New World Brown Pelican, *P. occidentalis*. Being the only diving pelican it is so distinctive in many aspects of its biology and morphology, that further study may well indicate it meriting separated generic status in *Leptopelicanus* Reichenbach 1852 (1853), *Avium* Syst. Nat.: 7.

#### REFERENCES

- ARCHEY, G., 1931. Skeleton of an Australian pelican found with moa bones, *Rec. Auck. Inst. Mus.* 1: 116-121.
- BRODKORB, P., 1963. Catalogue of fossil birds. Pt. 1 *Bull. Florida State Mus.*, 7: 179-293.
- BROWN, H.Y.L., 1894. Report of the Government Geologist for year ended June 30, 1894. Government Printer, Adelaide. 26pp.
- DE VIS, C. W., 1892 (1891). Residue of the extinct birds of Queensland as yet detected. *Proc. Linn. Soc. NSW.* 2(VI): 437-456.
- DE VIS, C. W., 1905. A contribution to the knowledge of the extinct avifauna of Australia. *Ann. Queensland Mus.*, 6: 1-25.
- HARRISON, C. J. O., and WALKER, C. A., 1976. A new fossil pelican from Olduvai. *Bull. Br. Mus. Nat. Hist. (Geol.)* 27, 4: 315-320.
- MILLER, A. H., 1966. The fossil pelicans of Australia. *Mem. Queensland Mus.*, 14: 181-190.
- NORTHCOTE, E. M., 1979. Determination of age and sex of long bones of Mute Swan *Cygnus olor*. *Ibis* 121: 74-80.
- RICH, P. V., 1979. The Dromornithidae, an extinct family of large ground birds endemic to Australia. *Bur. Min. Res. Bull.* 184: 1-196.
- SCARLETT, R., 1966. A pelican in New Zealand. *Notornis* 13(4): 204-217.
- STIRTON, R. A., TEDFORD, R. H., and WOODBURN, M. O., 1968. Australian Tertiary deposits containing terrestrial mammals. *Univ. Calif. Pub. Geol. Sci.* 77: 1-30.
- TEDFORD, R. H., ARCHER, M., BARTHOLOMAI, A., PLANE, M., PLEDGE, N. S., RICH, T., RICH, P., and WILLS, R. T., 1977. The discovery of Miocene vertebrates, Lake Frome area, South Australia. *Bur. Min. Res. Jour. Aust. Geol. Geophys.* 2: 53-57.



TABLE 1

Fossil specimens assigned to the genus *Pelecanus* from the Cainozoic of Australasia

Specimen Number	Element	Old Name	New Name	Specimens available to:		
				De Vis (1905)	A.H. Miller (1966)	PVR GFvT (this paper)
AMNH 11494	p. R. tarsometatarsus	—	rf. <i>tirarensis</i>	—	—	✓
Lost, De Vis	d. L. tarsometatarsus	<i>proavus</i> (holotype)	? <i>proavus</i>	✓	—	—
SAM P13858	d. R. tarsometatarsus	<i>tirarensis</i> (holotype)	<i>tirarensis</i>	—	✓	✓
SAM P18412	d. R. tarsometatarsus	<i>validipes</i> (holotype)	rf. <i>conspicillatus</i>	✓	—	✓
SAM P22501	d. L. tarsometatarsus	—	<i>cadimurka</i> , n. sp. (holotype)	—	—	✓
QM F1141	p. R. carpometacarpus	<i>proavus</i>	not pelican	✓	✓	✓
QM F3749	L. quadrate	<i>grandiceps</i>	rf. <i>conspicillatus</i>	✓	✓	✓
QM F3750	L. coracoid	<i>grandiceps</i>	rf. <i>conspicillatus</i>	✓	✓	✓
QM F3751	d. L. tarsometatarsus	<i>grandiceps</i> (lectotype)	rf. <i>conspicillatus</i>	✓	✓	✓
QM F3752	d. R. femur	<i>proavus</i>	rf. <i>conspicillatus</i>	✓	✓	✓
QM F3753	d. R. tibiotarsus	<i>proavus</i> (syntype)	rf. <i>conspicillatus</i>	✓	✓	✓
QM F5529	4th cervical vertebra	<i>Archaeocynus lacustris</i>	rf. <i>conspicillatus</i>	✓	—	✓
QM F6669	L. coracoid	—	rf. <i>conspicillatus</i>	—	—	✓
QM F10703	d. L. tarsometatarsus	—	rf. <i>tirarensis</i>	—	—	✓
UCMP 56321	L. quadrate	<i>conspicillatus</i>	rf. <i>conspicillatus</i>	—	✓	✓
UCMP 56322	d. L. tarsometatarsus	<i>grandiceps</i>	rf. <i>conspicillatus</i>	—	✓	✓
UCMP 56348	d. L. ulna	<i>conspicillatus</i>	rf. <i>conspicillatus</i>	—	✓	✓
UCMP 56394	3rd cervical vertebra	<i>conspicillatus</i>	rf. <i>conspicillatus</i>	—	✓	✓
UCMP 56633	R. scapula	—	rf. <i>conspicillatus</i>	—	—	✓
UCMP 60477	p. R. femur	<i>conspicillatus</i>	rf. <i>conspicillatus</i>	—	✓	✓
UCMP 60487	L. coracoid	<i>conspicillatus</i>	rf. <i>conspicillatus</i>	—	✓	✓
UCMP 60503	L. cuneiform	<i>conspicillatus</i>	rf. <i>conspicillatus</i>	—	✓	✓
UCMP 60520	d. L. ulna	<i>conspicillatus</i>	rf. <i>conspicillatus</i>	—	✓	✓
UCMP 60521	d. R. tibiotarsus	<i>conspicillatus</i>	rf. <i>conspicillatus</i>	—	✓	✓
UCMP 60549	R. cuneiform	<i>conspicillatus</i>	rf. <i>conspicillatus</i>	—	✓	✓
UCMP 60577	d. R. tarsometatarsus	<i>conspicillatus</i>	rf. <i>cadimurka</i> , n. sp.	—	✓	✓
UCMP 60578	d. R. tarsometatarsus	<i>conspicillatus</i>	rf. <i>cadimurka</i> , n. sp.	—	✓	✓
UCMP 60640	d. L. humerus	<i>conspicillatus</i>	rf. <i>conspicillatus</i>	—	✓	✓
UCMP 60656	Ant. sternum	<i>conspicillatus</i>	rf. <i>conspicillatus</i>	—	✓	✓
UCMP 60702	fused palatines	<i>conspicillatus</i>	rf. <i>conspicillatus</i>	—	✓	—
UCMP 60988	d. R. tarsometatarsus	—	rf. <i>tirarensis</i>	—	—	✓
UCMP 69587	p. R. humerus	<i>conspicillatus</i>	Accipitridae	—	✓	—
UCMP 113115	d. R. tarsometatarsus	—	rf. <i>tirarensis</i>	—	—	✓
UCMP 123382	4th cervical vertebra	—	rf. <i>cadimurka</i> n. sp.	—	✓	✓
				Scar- Archey lett PVR (1931) (1966) GFvT		
CM AV12264	R. humerus	<i>conspicillatus novaezealandiae</i>	rf. <i>novaezealandiae</i>	—	✓	✓
CM AV12482	d. L. femur	<i>conspicillatus novaezealandiae</i>	rf. <i>novaezealandiae</i>	—	✓	✓
CM AV13095	p. R. humerus	<i>conspicillatus novaezealandiae</i>	rf. <i>novaezealandiae</i>	—	✓	✓
CM AV15089	R. coracoid	<i>conspicillatus novaezealandiae</i>	rf. <i>novaezealandiae</i>	—	✓	✓
CM AV21355	partial skeleton	<i>conspicillatus novaezealandiae</i> (holotype)	<i>novaezealandiae</i>	—	✓	✓
CM AV32001	part of fused furcula and sternum	—	rf. <i>novaezealandiae</i>	—	—	✓
Lost, Archey	partial skeleton	<i>conspicillatus novaezealandiae</i>	rf. <i>novaezealandiae</i>	✓	✓	—
AWNM AV5845.1	d. L. tibiotarsus	—	rf. <i>novaezealandiae</i>	—	—	✓
Horn, no No.	L. tibiotarsus	—	rf. <i>novaezealandiae</i>	—	—	✓

TABLE 2

Measurements in mm of tarsometatarsi of recent and Australasian fossil pelicans

	Width of distal end				At proximal end of distal foramen				Depth of shaft			
	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd
FOSSIL												
<i>P. tirarensis</i>												
SAM P13858 type .....			19.6									
UCMP 60988 rf. ....						@12.0				8.3		
<i>P. cadimurka</i>												
UCMP 60577 rf. ....			18.5			14.2				8.8		
UCMP 60578 rf. ....			@19.3									
<i>P. novaezealandiae</i>												
CM AV21355 holotype .....			26.0			18.5				12.0		
Archey, lost, rf. ....			26.9 (Scarlett 1966)									
<i>P. proavus</i> from figures of holotype .....		>18.0-18.6				>14.8-15.2						
<i>P. conspicillatus</i> :												
SAM 18412 (holotype of <i>validipes</i> ) rf. ....			26.1			17.9				11.0		
RECENT												
<i>P. conspicillatus</i> .....	20	21-26	24	1.5	19	15-19	17	1.4	19	9-12	11	0.8
<i>P. crispus</i> .....	1		25		9		18		1		11	
<i>P. onocrotalus</i> .....	3	24-30	27	3.3	3	17-22	20	2.5	3	11-16	13	2.3
<i>P. erythrorhynchus</i> .....	5	22-25	23	0.9	5	12-18	15	3.2	5	10-11	10	0.6
<i>P. philippensis</i> .....	1		25		1		19		1		12	
<i>P. rufescens</i> .....	2	19-24			2	14-18			2	9-12		
<i>P. occidentalis</i> .....	9	17-21	20	1.4	9	12-16	14	1.0	9	6-9	8	0.8

TABLE 3

Measurements in mm of trochlea III of tarsometatarsi of recent and Australasian fossil pelicans

	Internal depth				External depth				Distal width			
	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd
FOSSIL												
<i>P. tirarensis</i>												
SAM P13858 holotype			11.3				11.2				9.4	
QM F10703 rf.			9.7				9.8				6.9	
UCMP 60988 rf.			>9.9				>10.3				@7.0	
UCMP 113115 rf.			@10.0				9.9				6.4	
<i>P. cadimurka</i>												
SAM P22501 holotype			9.2				9.6				>6.0	
UCMP 60577 rf.			>8.9				10.8				7.5	
UCMP 60578 rf.			11.5				12.0				7.2	
<i>P. novaezealandiae</i>												
CM AV21355 holotype			14.8				15.2				10.0	
<i>P. proavus</i> from figure of holotype											>6.8	
<i>P. conspicillatus</i> :												
SAM 18412 (holotype of <i>validipes</i> ) rf.			15.0				15.3				10.1	
QM F3751 (lectotype of <i>grandiceps</i> ) rf.			15.8				17.0				10.2	
UCMP 56322			15.3								10.1	
RECENT												
<i>P. conspicillatus</i>	19	12-16	14	1.0	20	13.17	15	1.0	17	8.10	9	0.6
<i>P. crispus</i>	1		14		1		14		1		10	
<i>P. onocrotalus</i>	2	14-17			3	14-16	15	1.3	2	9-10		
<i>P. erythrorhynchus</i>	5	13-14	13	0.4	5	13-14	14	0.4	2		9	
<i>P. philippensis</i>	1		14		1		14		1		9.5	
<i>P. rufescens</i>	2	11-14			2	12-14			1	7-9		
<i>P. occidentalis</i>	9	8-11	10	0.7	9	8-11	10	0.8	1		6	

TABLE 4

Measurements in mm of trochlea II and IV of tarsometatarsi of recent and Australasian fossil pelicans

	External depth of II				Anterior width of II				Internal depth of IV			
	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd
FOSSIL												
<i>P. tirarensis</i>												
SAM P13858 holotype			10.2				4.5					
QM F10703 rf.			9.1				4.0					
<i>P. cadimurka</i>												
UCMP 60577 rf.							5.7				10.2	
UCMP 60578 rf.			10.6				5.5				11.2	
<i>P. novaezealandiae</i>												
CM AV21355 holotype			12.9								13.0	
<i>P. proavus</i> from figure of holotype							>5.6					
<i>P. conspicillatus</i> :												
QM F3751 (lectotype of <i>grandiceps</i> ) rf.			>14.4									
SAM 18412 (holotype of <i>validipes</i> ) rf.			13.5				7.8				14.0	
UCMP 56322 rf.			13.9									
RECENT												
<i>P. conspicillatus</i>	20	11-15	13	1.0	17	6-10	7	0.7	20	12-15	13	0.9
<i>P. crispus</i>	1		13		1		7		1		14	
<i>P. onocrotalus</i>	3	12-15	13	1.4	2	7-8			3	14-18	15	2.3
<i>P. erythrorhynchus</i>	5	12-13	12	0.4	2		7		5	12-13	13	0.4
<i>P. philippensis</i>	1		13		1		7		1		14	
<i>P. rufescens</i>	2	10-13			2	6-7			2	11-14		
<i>P. occidentalis</i>	9	8-11	10	0.7	1		5		9	8-11	10	0.7

TABLE 5

Measurements in mm of distal end of femora of recent and Australasian fossil pelicans

	Width of distal end				Width across internal and external condyles			
	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd
FOSSILS								
<i>P. novaezealandiae</i>								
CM AV21355 holotype			36.2				28.4	
CM AV12482 rf.			>35				>28.3	
Archey, lost, rf.			38 (Scarlett 1966)					
<i>P. conspicillatus</i> :								
QM F3752 rf.			@29.0				24.4	
RECENT								
<i>P. conspicillatus</i>	15	30-37	32	2.2	15	24-29	26	1.7
<i>P. crispus</i>	2	35-37			2	27-29		
<i>P. onocrotalus</i>	2	33-35			2	26-29		
<i>P. erythrorhynchus</i>	9	28-33	31	1.9	9	24-27	25	0.9
<i>P. philippensis</i>	1		35		1		26	
<i>P. rufescens</i>	2	26-32			2	21-25		
<i>P. occidentalis</i>	5	20-26	23	1.8	5	16-19	19	2.1





TABLE 7  
Measurements in mm of fourth cervical vertebrae of recent and Australasian fossil pelicans

	Length from prezygapophyses to posterior of neural arch				Width across prezygapophyses				Width across posterior of centrum				Width across postzygapophyses			
	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd
FOSSIL																
<i>P. conspicillatus</i>																
QM F5529 (syntype of <i>Archaeocygnus lucustris</i> ) rf.											‡12.1				‡19.9	
<i>P. cadimurka</i>																
UCMP 123382 rf.			32.4				15.6				8.3				@13.9	
RECENT																
<i>P. conspicillatus</i>	11	52-66	60	4.7	11	21-25	23	1.7	11	11-14	13	1.0	10	19-23	21	1.3
<i>P. crispus</i>	1		55		1		22		1		13		1		21	
<i>P. onocrotalus</i>	2	49-53			2	22-23			2	12-13			2	21-23		
<i>P. erythrorhynchos</i>	2	49-50			2	20-23			2	11-12			2	19-21		
<i>P. philippensis</i>	1		44		1		18		1		11		1		16	
<i>P. rufescens</i>	2	44-46			2	19-20			2	10-12			2	16-20		
<i>P. occidentalis</i>	1		37		1		17		1		9		1		16	

TABLE 8  
Measurements in mm of quadrates of recent and Australasian fossil pelicans

	Height from mandibular to squamosal articulation				Width across mandibular articulation				Width across orbital process			
	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd
FOSSIL												
<i>P. conspicillatus</i>												
QM F3749 rf. ....			33.9				27.0					
UCMP 56321 rf. ....			@31.5				>23.3			>24.6		
RECENT												
<i>P. conspicillatus</i> .....	11	28-36	32	2.3	11	22-27	26	1.9	11	24-30	28	2.1
<i>P. crispus</i> .....	1		32		1		24		1		26	
<i>P. onocrotalus</i> .....	1		40		1		30		1		30	
<i>P. erythrorhynchus</i> .....	1		29		1		23		1		24	
<i>P. philippensis</i> .....	1		33		1		24		1		27	
<i>P. rufescens</i> .....	2	29-33			2	20-25			2	22-26		
<i>P. occidentalis</i> .....	1		32		1		20		1		19	

TABLE 9  
Measurements in mm of coracoids of recent and Australasian fossil pelicans

	Width of shaft at coracoidal fenestra				Width from coracoidal fenestra to medial margin of shaft on posterior surface			
	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd
FOSSILS								
<i>P. conspicillatus</i> :								
QM F3750 rf. ....			@19.4				8.4	
QM F6669 rf. ....			17.4				7.0	
<i>P. novaezealandiae</i>								
CM AV21355 holotype .....			16.8				9.7	
CM AV15089 rf. ....			@17.5				8.7	
RECENT								
<i>P. conspicillatus</i> .....	13	14-19	16	1.7	13	6-9	7	1.0
<i>P. crispus</i> .....	2	17-20			2	7-9		
<i>P. onocrotalus</i> .....	2	18-19			2		9	
<i>P. erythrorhynchus</i> .....	9	14-18	16	1.0	9	6-9	7	1.1
<i>P. philippensis</i> .....	2	18-19			2	8-9		
<i>P. rufescens</i> .....	2	13-16			2	5-8		
<i>P. occidentalis</i> .....	5	11-13	11	0.7	5	5-6	5	0.4



TABLE 10

Measurements in mm of third cervical vertebrae of recent and Australasian fossil pelicans

	Width across prezygapophyses				Width of anterior articular surface of centrum				Length of left side of anterior articular surface of centrum			
	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd
FOSSIL												
<i>P. conspicillatus</i> UCMP 56394 rf. ....			24.9				16.1				9.8	
RECENT												
<i>P. conspicillatus</i> .....	9	22-26	24	1.4	9	11-14	12	0.9	9	7-11	10	1.5
<i>P. crispus</i> .....	1		23		1		12		1		11	
<i>P. onocrotalus</i> .....	2	23-26			2	11-12			2		10	
<i>P. erythrorhynchos</i> .....	2	21-23			2	11-12			2	9-11		
<i>P. philippensis</i> .....	1		18		1		10		1		8	
<i>P. rufescens</i> .....	2	19-21			2	11-12			2	8-10		
<i>P. occidentalis</i> .....	1		16		1		9		1		6	

TABLE 11

Measurements in mm of left prezygapophyses of third cervical vertebrae of recent and Australasian fossil pelicans

	Length				Width			
	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd
FOSSIL								
<i>P. conspicillatus</i> UCMP 56394 rf. ....			11.5				6.3	
RECENT								
<i>P. conspicillatus</i> .....	9	10-14	12	1.3	9	5-7	6	0.5
<i>P. crispus</i> .....	1		12		1		6	
<i>P. onocrotalus</i> .....	2		11		2	6-7		
<i>P. erythrorhynchos</i> .....	2		11		2	4-5		
<i>P. philippensis</i> .....	1		9		1		5	
<i>P. rufescens</i> .....	2	9-10			2		5	
<i>P. occidentalis</i> .....	1		10		1		4	

TABLE 12

Measurements in mm of sterna at coracoidal sulci of recent and Australasian fossil pelicans

	Depths across right dorsal and ventral lips at maximum expansion				Depths across left dorsal and ventral lips at maximum expansion				Minimum distance between sulci			
	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd
FOSSIL												
<i>P. conspicillatus</i> UCMP 60656 rf. ....			13.9				16.2				4.4	
RECENT												
<i>P. conspicillatus</i> .....	10	13-18	16	1.4	10	13-19	16	1.7	10	0-7	4.5	2.3
<i>P. onocrotalus</i> .....	1		21		1		19		1		10	
<i>P. erythrorhynchos</i> .....	5	9-16	12	3.0	4	8-16	12	3.9	5	4-11	7.5	2.7
<i>P. philippensis</i> .....	1		18		1		17		1		9	
<i>P. rufescens</i> .....	1		16		1		17		1		6	
<i>P. occidentalis</i> .....	9	7-9	8	0.5	9	7-9	8	0.6	9	7-11	9	1.2



TABLE 14  
Measurements in mm of cuneiforms of recent and Australasian fossil pelicans

FOSSIL	Width across			Height of ulnar			Width of ulnar			Height of opposite		
	n	range	$\bar{x}$	n	range	$\bar{x}$	n	range	$\bar{x}$	n	range	$\bar{x}$
FOSSIL												
<i>P. conspicillatus</i>												
UCMP 60503 rf.			19.2			13.5			10.2			18.2
UCMP 60549 rf.			17.5			13.9			9.2			17.6
RECENT												
<i>P. conspicillatus</i>	12	17-20	19	12	12-17	14	12	8-10	9	12	16-20	18
<i>P. crispus</i>	1		25	1		17	1		14	1		22
<i>P. onocrotalus</i>	2	21-23		2	16-18		2	10-12		2		19
<i>P. erythrorhynchos</i>	1		19	1		16	1		10	1		19
<i>P. rufescens</i>	2	17-18		2	13-14		2			2	16-19	
<i>P. occidentalis</i>	1		16	1		11	1		7	1		15

TABLE 15  
Measurements in mm of proximal end of femora of recent and Australasian fossil pelicans

	Width of proximal end				Depth of head				Depth of trochanter			
	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd
FOSSIL												
<i>P. novaezealandiae</i>												
CM AV21355 holotype .....			35.4				15.1				5.0	
Archey, lost, rf. ....			36.0 (Scarlett 1966)									
<i>P. conspicillatus</i>												
UCMP 60477 rf. ....			29.7				14.5				> 25.5	
RECENT												
<i>P. conspicillatus</i> .....	14	26-33	29	2.0	14	13-16	14	0.8	14	22-27	24	1.5
<i>P. crispus</i> .....	2	31-34			2	15-16			2	25-26		
<i>P. onocrotalus</i> .....	1		30		1		15		1		24	
<i>P. erythrorhynchos</i> .....	5		29	0.3	5	13-14	14	0.3	5	22-25	24	1.2
<i>P. philippensis</i> .....	1		32		1		15		1		23	
<i>P. rufescens</i> .....	2	24-29			2	12-14			2	19-24		
<i>P. occidentalis</i> .....	9	19-25	23	2.0	9	9-12	11	1.1	9	16-22	19	1.7

TABLE 16  
Measurements in mm of distal end of humeri of recent and Australasian fossil pelicans

	Length of external condyle				Depth of external condyle				Depth of internal condyle			
	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd
FOSSIL												
<i>P. novaezealandiae</i>												
CM AV21355 holotype .....			22.7				26.5				14.8	
CM AV12264 rf. ....			>22				>27				@15	
<i>P. conspicillatus</i>												
UCMP 60640 rf. ....			20.7				>21.1				13.1	
RECENT												
<i>P. conspicillatus</i> .....	17	19-25	22	1.6	18	22-27	25	1.5	18	12-16	14	1.1
<i>P. crispus</i> .....	2	23-24			1		28				16	
<i>P. onocrotalus</i> .....	2	23-28			2	24-30			2	15-17		
<i>P. erythrorhynchos</i> .....	5	20-22	21	0.6	5	24-26	24	1.2	5	14-15	15	0.2
<i>P. rufescens</i> .....	2	18-22			2	21-25			2	12-15		
<i>P. occidentalis</i> .....	9	15-20	18	1.5	9	17-22	21	1.4	9	11-13	12	0.8

TABLE 17  
Measurements in mm of scapulae of recent and Australasian fossil pelicans

	Total length				Width across glenoid facet				Width of shaft at distal end of glenoid facet			
	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd	n	range	$\bar{x}$	sd
FOSSIL												
<i>P. novaezealandiae</i> CM AV21355 holotype .....							23.7				14.7	
<i>P. conspicillatus</i> UCMP 56633 rf. ....			>101.8				@21.2				@13.8	
RECENT												
<i>P. conspicillatus</i> .....	9	114-140	126	9.2	11	20-25	22	1.2	11	11-17	14	1.3
<i>P. crispus</i> .....	1		134		1		24				16	
<i>P. onocrotalus</i> .....	2	129-137			2	24-25			2	16-17		
<i>P. erythrorhynchos</i> .....	5	121-133	126	5.5	5	20-22	21	0.8	5	13-20	16	2.9
<i>P. philippensis</i> .....	2	129-137			2	24-25			2	16-17		
<i>P. rufescens</i> .....	2	101-119	101		1		2		2		16	
<i>P. occidentalis</i> .....	10	81-103	97	6.5	8	14-18	16	1.3	10	8-13	11	1.3





TABLE 19

Log<sub>10</sub> ratios of width: length of synsacra and of ilio-ischiatic foramina of recent and Australasian fossil pelicans  
(cf. Table 18 and Northcote 1979)

	Synsacrum				Ilio-ischiatic foramen			
	n	range	$\overline{x}$	sd	n	range	$\overline{x}$	sd
FOSSIL								
<i>P. novaezealandiae</i>								
CM AV21355 holotype .....			0.47				0.31	
RECENT								
<i>P. conspicillatus</i> .....	12	0.47-0.51	0.49	0.01	20	0.33-0.48	0.40	0.04
<i>P. onocrotalus</i> .....	2	0.44-0.45			2	0.32-0.35		
<i>P. erythrorhynchos</i> .....	2	0.42-0.43			2	0.29-0.34		
<i>P. rufescens</i> .....	1		0.45		1		0.28	
<i>P. occidentalis</i> .....	1		0.42		1		0.31	

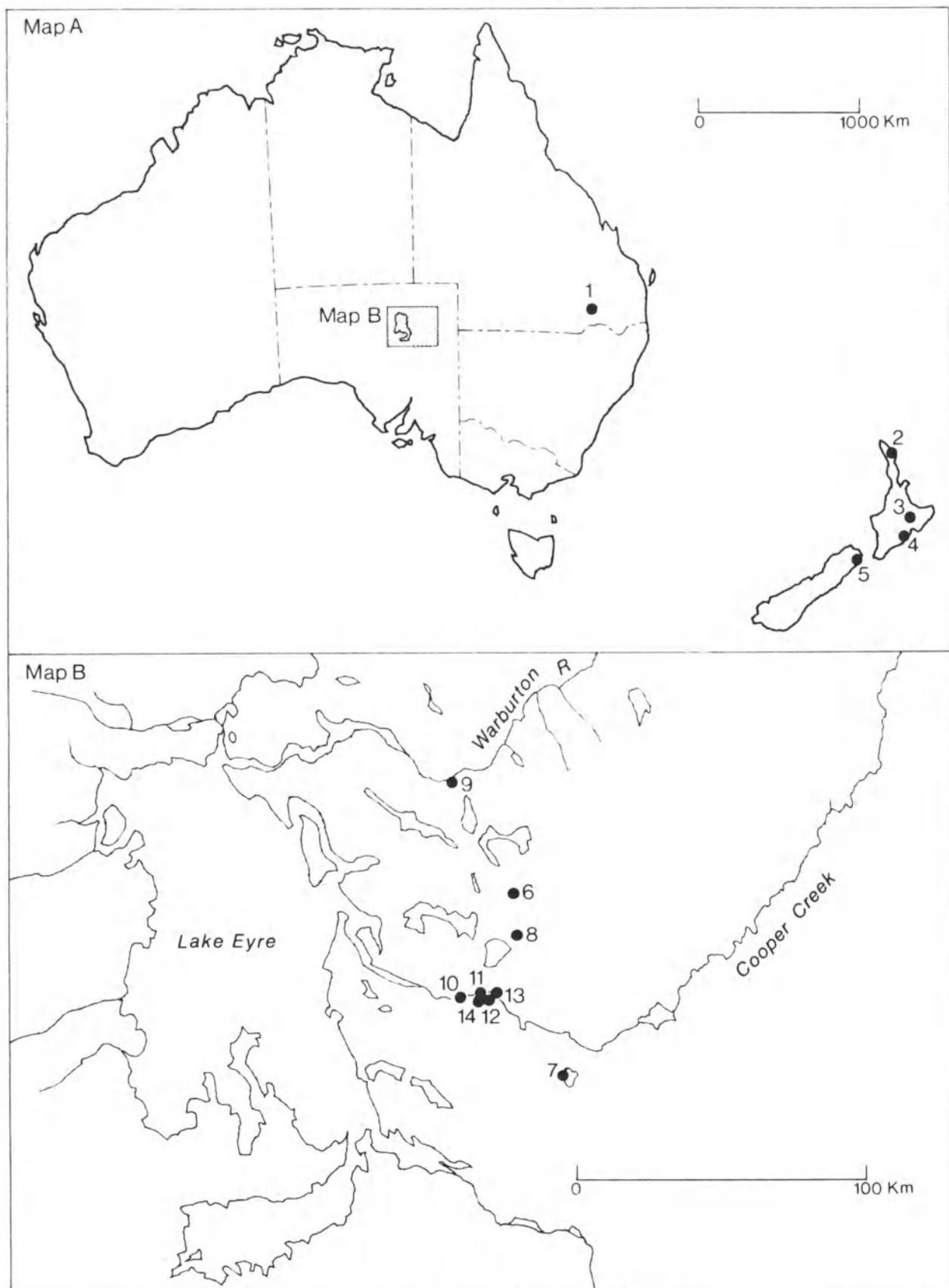


FIG. 1. Map of localities where fossil pelicans were found in Australasia. Map A: *Pelecanus proavus*, holotype (1); *P. novaezealandiae*, holotype (4), referred (2, 3 and 5); Map B: *P. tirarensis*, holotype (7), referred (6); *P. cadimurka* n. sp. holotype (10), referred (8, 13); *P. conspicillatus*, referred (8, 9, 11-14).

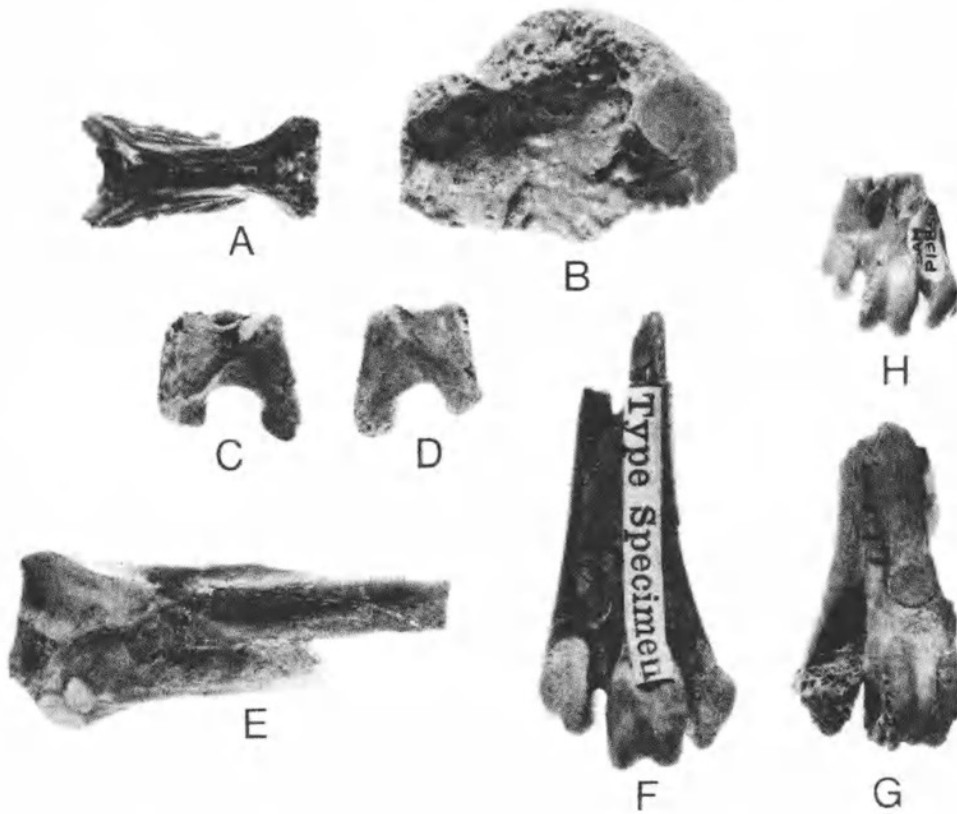


FIG. 2. Fossil pelicans of Australia. *Pelecanus* cf. *cadimurka*, UCMP 123382, fourth cervical vertebra (A); Accipitridae, UCMP 69587, proximal right humerus (B). *P.* cf. *conspicillatus*, UCMP 60503, left cuneiform (C); UCMP 60549, right cuneiform (D); UCMP 60520, distal left ulna fragment (E); *P. validipes*, holotype, SAM 18412, distal right tarsometatarsus (F); *P. grandiceps*, lectotype, QM F3751, distal left tarsometatarsus (G); *P. tirarensis*, holotype, SAM P13858, distal right tarsometatarsus (H). See scale for size.

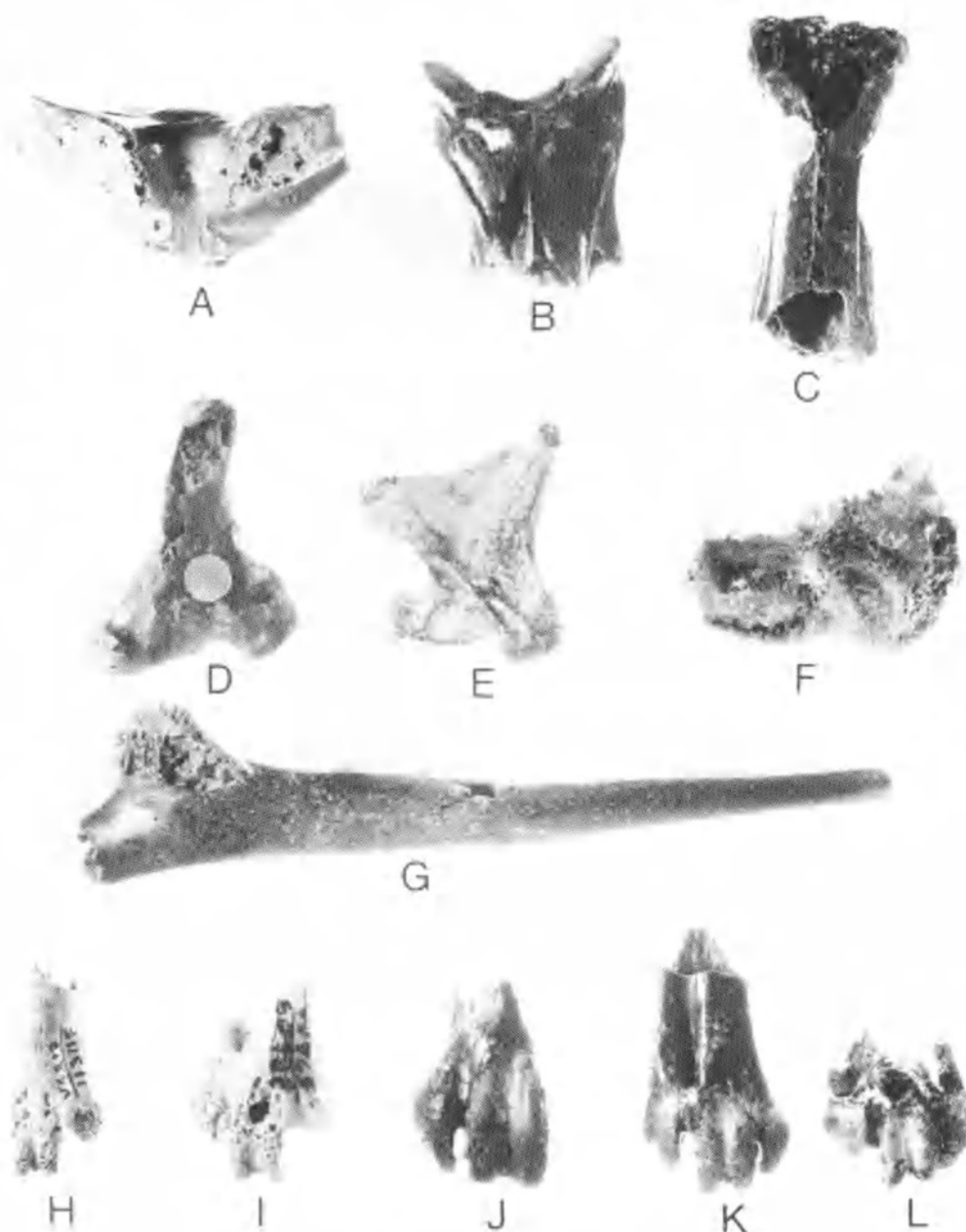


FIG. 3. Fossil pelicans of Australia. *Pelecanus* rf. *conspicillatus*, UCMP 60656, anterior sternal fragment (A); UCMP 56394 anterior 3rd cervical vertebra (B); *Archaeocynus lacustris*, syntype, QM F5529, 4th cervical vertebra (C); rf. *P. conspicillatus*, QM F3749, left quadrate fragment (D); UCMP 56321, left quadrate (E); UCMP 60640, distal left humerus (F); UCMP 56633, right scapula (G); *P. rf. tirarensis*, UCMP 113115, distal right tarsometatarsus (H); UCMP 60988, distal right tarsometatarsus (I); *P. rf. conspicillatus*, UCMP 56322, distal left tarsometatarsus (J); *P. rf. cadimurka*, UCMP 60577, distal right tarsometatarsus (K); UCMP 60578, distal right tarsometatarsus (L). See scale for size.



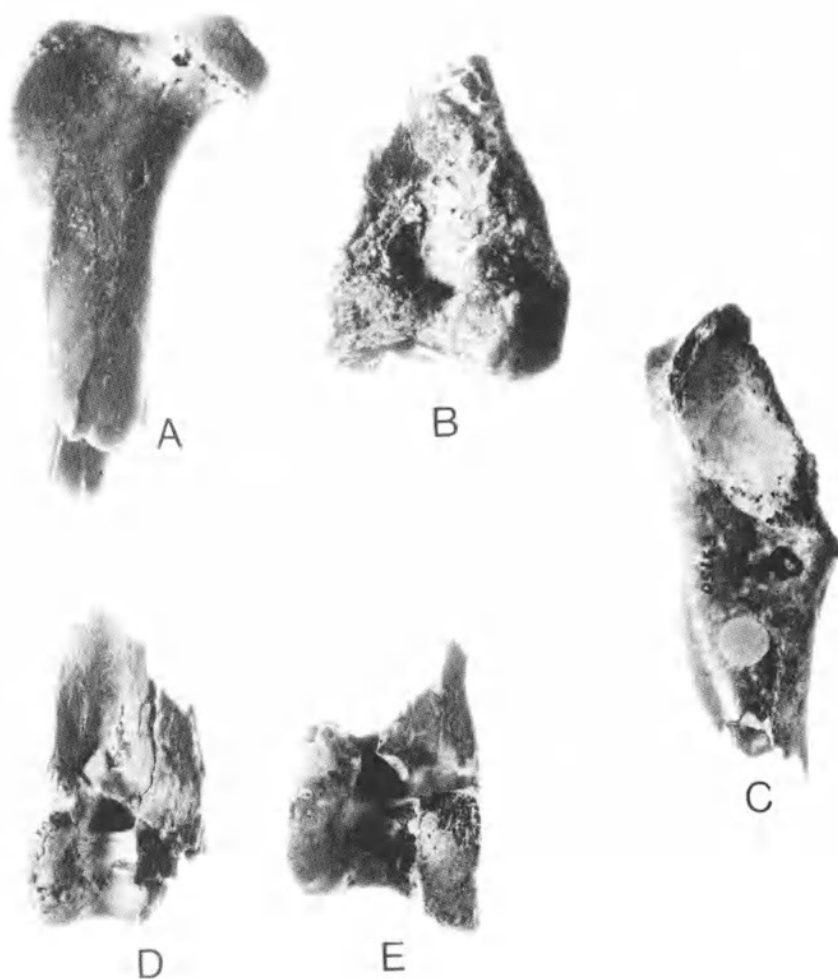


FIG. 4. Fossil pelicans of Australia. *Pelecanus* cf. *conspicillatus*, UCMP 60477, proximal right femur, (A); QM F3752, distal right femur, (B); QM FF3750, left coracoid fragment, (C); UCMP 60521, distal right tibiotarsus, (D); QM F3753, distal right tibiotarsus, (E). See scale for size.

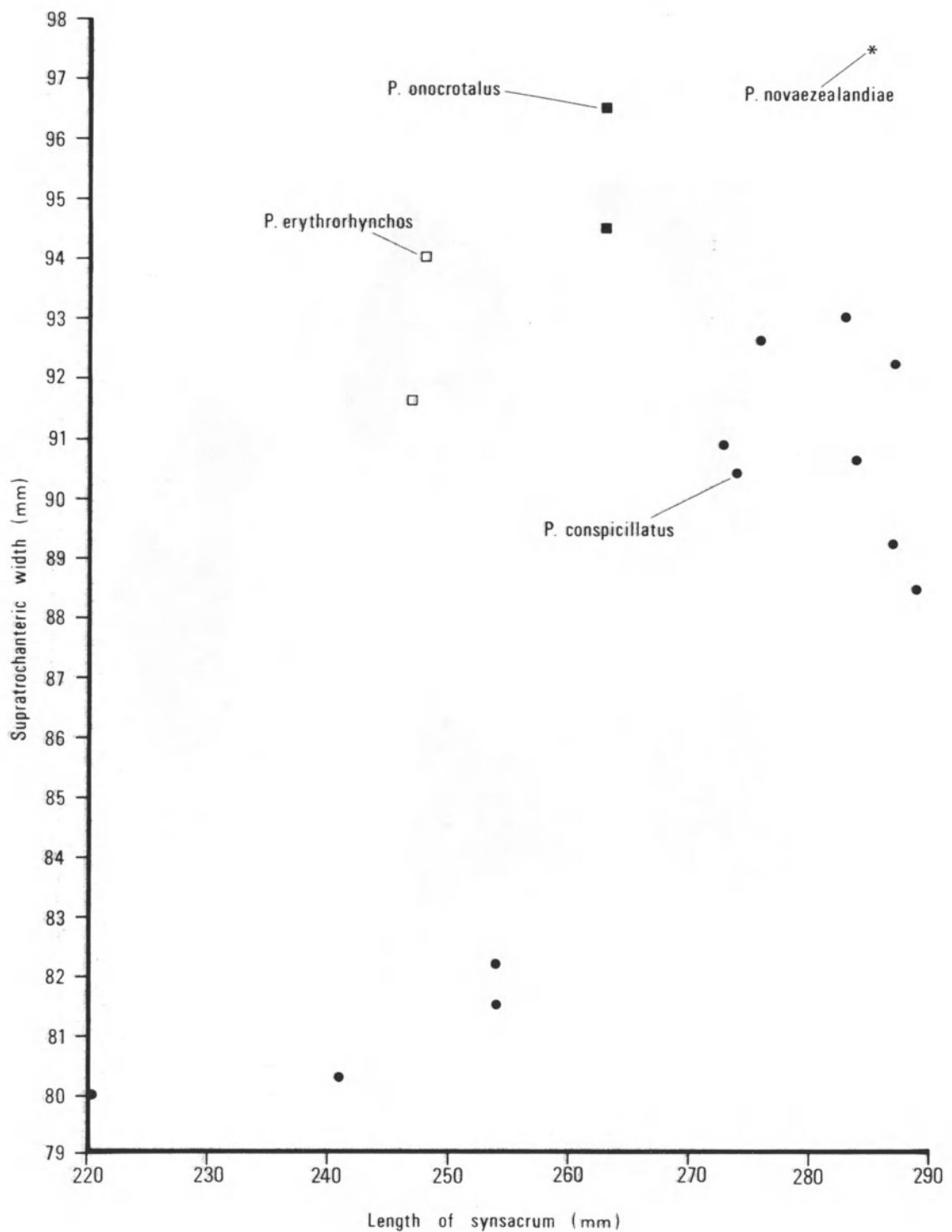


FIG. 5. Comparison of synsacral measurements of the large species of *Pelecanus*.

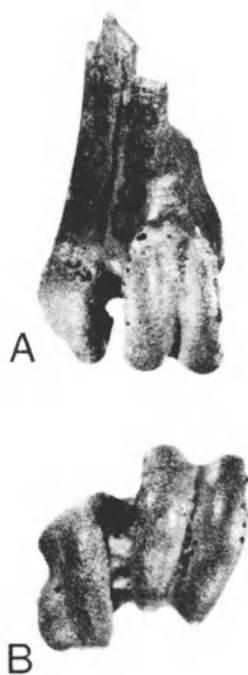


FIG. 6. Holotype of *Pelecanus cadimurka*, n. sp., SAM P22501, distal left tarsometatarsus. A. Anterior view. B. Distal view.

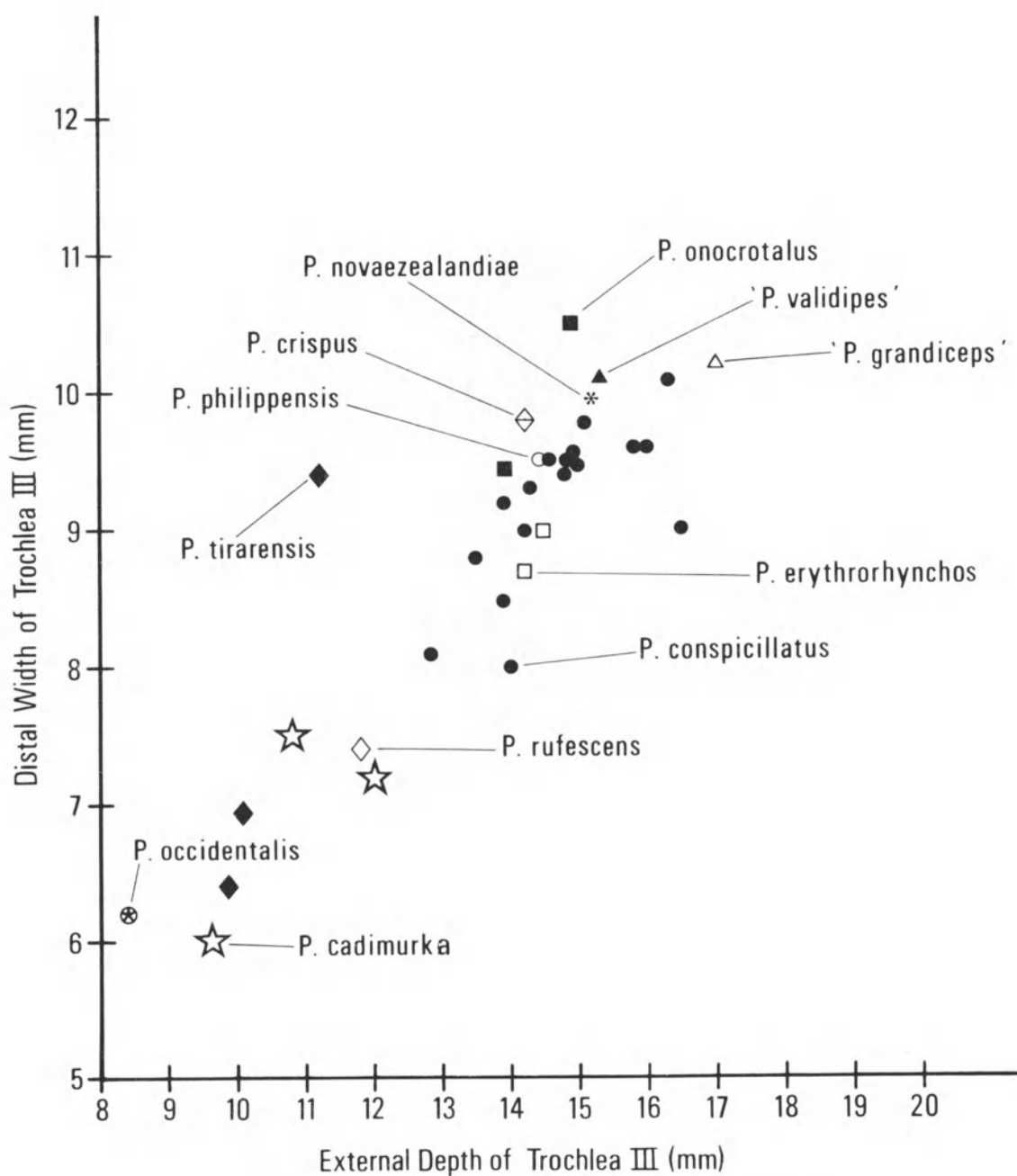


FIG. 7. Comparison of distal tarsometatarsal measurements of living and extinct species of *Pelecanus*.



1981. "The fossil pelicans of Australia." *Records of the South Australian Museum* 18, 235–264.

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