

Descriptions and phylogenetic relationships of two new genera and four new species of Oligo-Miocene waterfowl (Aves: Anatidae) from Australia

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The Tertiary anatic fossils (Aves: Anatidae) from Oligocene and Miocene deposits in Australia are described. Most fossils derive from the Late Oligocene – Early Miocene (26–24 Mya) Etadunna and Namba Formations, respectively, in the Lake Eyre and Lake Frome Basins of South Australia. The local faunas from these two formations contain the same suite of anatic species. Two new genera, the oxyurine *Pinpanetta*, with three new species (*Pi. tedfordi*, 18 specimens; *Pi. vickersrichae*, 15 specimens; *Pi. fromensis*, 20 specimens), and the tadornine *Australotadorna*, for a large new species known from eight specimens, are established. Three anatic bones from the Waite Formation (c. 8 Mya) at Alcoota, Northern Territory reveal the presence of a tadornine that is neither *Australotadorna* nor an extant *Tadorna* species, and an indeterminate duck about the size of *Malacorhynchus*. Phylogenetic analyses establish *Pinpanetta* as a basal member of an oxyurine (stiff-tailed duck) radiation. Oxyurines are found to include the Recent *Stictonetta* and *Malacorhynchus* as basal members, along with the fossil taxa *Mionetta*, *Manuherikia*, and *Dunstanetta*, and the traditionally included Recent *Oxyura*, *Biziura*, *Thalassornis*, and *Nomonyx*. © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, 156, 411–454.

ADDITIONAL KEYWORDS: *Australotadorna* – Oxyurinae – phylogeny – *Pinpanetta*.

INTRODUCTION

The Tertiary fossil record for Australian avifaunas is relatively rich with faunas derived from Lower Oligocene and younger deposits (Rich *et al.*, 1991; Vickers-Rich, 1991). The most significant sources of Tertiary fossil birds include the Oligocene to Pliocene sequences of inland South Australia (Stirton, Tedford & Miller, 1961; Woodburne *et al.*, 1994) particularly those near lakes Palankarina, Pinpa, Ngapakaldi, and Yanda (Rich & van Tets, 1982; Pledge & Tedford, 1990; Rich *et al.* (1991; Vickers-Rich, 1991). The richest avifaunas derive from the Oligo-Miocene (26–24 Mya) fluvial–lacustrine sequences in the Lake Eyre Basin from the Etadunna and Namba Formations (Woodburne *et al.*, 1994; Alley, 1998). Faunal correlations indicate that the abundant vertebrate faunas in the Carl Creek Limestone (Archer *et al.*,

1997, 1999, 2006) from deposits at Riversleigh in north-western Queensland are in part of similar Oligo-Miocene age but extend through to the Middle Miocene. In the numerous sites around Riversleigh, mammals dominate, and birds although relatively few, have high diversity (Boles, 1993a–c, 1995a, b, 1997a–d, 1998, 1999, 2001, 2005a–c).

After these Late Oligocene – Early Miocene faunas, a substantial gap exists in the Australian record. Only two significant faunas for birds are known from the Middle–Late Miocene. The Middle Miocene 10–12 Mya Camfield Beds at Bullock Creek in the Northern Territory, although containing an abundance of aquatic and stream bank species (Murray & Megirian, 1992; Archer *et al.*, 1999; Megirian, Murray & Schwartz, 2004) has, relative to the Etadunna and Namba formations, a much smaller and less diverse avifauna with no waterfowl. Slightly younger, and also containing an important avifauna, is the Waite Formation (c. 8 Mya) at Alcoota (Murray & Megirian,

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1992). In both Bullock Creek and Alcoota, mihirung birds (Aves: Dromornithidae) dominate the avifauna and other birds are rare (Rich, 1979; Rich & van Tets, 1982; Rich *et al.*, 1991; Vickers-Rich, 1991; Murray & Vickers-Rich, 2004). Other prominent components of all these Tertiary avifaunas are flamingos and palaelodids together in Phoenicopteriformes (Miller, 1963; Rich *et al.*, 1987; Baird & Vickers-Rich, 1998) and pelicans, Pelecaniformes (Rich & van Tets, 1981). Since Vickers-Rich's (1991) review, there have been notable reports of ratites, Casuariidae (Boles, 1992) and megapodes, Megapodiidae (Boles & Ivison, 1999) from the South Australian deposits.

Waterfowl (Aves: Anseriformes) fossils are a significant component of various Australian Tertiary fossil faunas (e.g. Tedford *et al.*, 1977; Rich & van Tets, 1982; Pledge, 1984; Pledge & Tedford, 1990; Tedford & Wells, 1990; Rich *et al.*, 1991; Vickers-Rich, 1991; Tedford, Wells & Barghoorn, 1992; Boles & Mackness, 1994; Boles, 1997c). To date, the only waterfowl faunas to have been studied are some of Plio-Pleistocene age. All nine presumed extinct Plio-Pleistocene anatid species named by De Vis from Australian-wide deposits (De Vis, 1888, 1889, 1905) were referred to living species by Olson (1977). The extensive faunas of Pliocene age that mainly derive from the Tirari Formation exposed in sediments at Lake Palankarina (Mampurdu Member, Palankarina Fauna), and Lake Kanunka (Kanunka Fauna), and along the Warburton River (Toolapinna Fauna) in South Australia contain a few anseriforms (Tedford, Williams & Wells, 1986; Tedford & Wells, 1990; Tedford *et al.*, 1992), but most are extant species (pers. observ.) and are not covered here.

Fossil anseriforms are common in the Late Oligocene – Miocene lacustrine deposits of the Lake Eyre Basin in central Australia (Rich *et al.*, 1991; Vickers-Rich, 1991), but their identity and phylogenetic relationships have been neglected to date. Such data will be especially relevant to understanding the evolutionary origins of the modern fauna. Taxa such as the endemic and monotypic *Anseranas* (Anseranatidae), and among anatids, *Dendrocygna*, the anserines *Cereopsis* and *Cnemiornis*, *Biziura*, *Oxyura*, and *Stictonetta*, are primitive members of the Recent fauna (Frith, 1964; Madsen, McHugh & de Kloet, 1988; Livezey, 1986, 1989, 1996a, 1997a, b; Sibley & Ahlquist, 1990; Christidis & Boles, 1994; Sraml *et al.*, 1996; Worthy *et al.*, 1997; Sorenson *et al.*, 1999; Donne-Goussé, Laudet & Hänni, 2002; Dickinson, 2003; Callaghan & Harshman, 2005; McCracken & Sorenson, 2005). Similarly, *Malacorhynchus* is also considered relatively basal (Brush, 1976; Frith, 1977; Olson & Feduccia, 1980) with Fullagar, in Kear (2005: 442) suggesting this taxon

is a part of the old endemic component of Australia's avifauna with no close relatives. These taxa are all monotypic or of low diversity and combined with their basal position within Anseriformes could be presumed to have a long history in the region. However, to date there is no Australian fossil record for any of them.

Recently several fossils from the northern hemisphere have been referred to Anseranatidae. Olson (1999) described *Anatalavis oxfordi* from the Eocene London Clay of Europe, and referred it and *Anatalavis rex* (Shufeldt, 1915) from the Palaeocene Hornerstone Formation in New Jersey, USA, to Anseranatidae, although this attracted some debate (Dyke, 2001; Mayr, 2005). More recently, Mourer-Chauviré, Berthet & Huguéney (2004) described *Anserpica kiliani* from the Late Oligocene Créchy Quarry in France and referred it to Anseranatidae. None of the other Australian endemic taxa listed above have a fossil record elsewhere in the world. There is considerable overlap of Recent taxa between New Zealand and Australia with congeneric species in *Biziura*, *Malacorhynchus*, *Oxyura*, *Aythya*, *Anas*, and *Tadorna* (Turbott, 1990; Worthy, 2005), and with *Cnemiornis* considered the sister taxon to *Cereopsis* (Worthy *et al.*, 1997). From the extensive St Bathans Fauna of Early Miocene age, 19–16 Mya, in New Zealand (Worthy *et al.*, 2007), six anatids are known, but none are referable to Recent genera. A phylogenetic analysis of the New Zealand fossils *Manuherikia* and *Dunstanetta* (Worthy & Lee, 2008) suggests that these taxa are basal oxyurines, which together with *Biziura*, *Thalassornis*, *Oxyura*, *Stictonetta*, *Malacorhynchus*, and the European Early Miocene *Mionetta*, form either a clade or a grade of 'oxyurines' relatively basal within Anatidae.

It is therefore the aim of the present work to describe the species represented by waterfowl fossils from the Australian Oligocene – Miocene and to determine their phylogenetic relationships. This information is fundamental to an understanding of the evolution of the modern waterfowl fauna of Australasia and is potentially significant in the context of the global evolution of waterfowl. The occurrence of waterfowl in both the Etadunna and the Namba Formations will allow assessment of taxonomic similarity of the contained local faunas and so test previous faunal correlations and hypotheses of relative ages of these formations. Similarly, an understanding of the Oligo-Miocene Australian waterfowl faunas will reveal their relationships to those from the extensive Early Miocene New Zealand St Bathans Fauna. Lastly, this knowledge can contribute to ecological reconstructions of the biomes from which the fossil faunas derived.

METHODS

ABBREVIATIONS

Institutions: AM, Australian Museum, Sydney, Australia; AMNH, Fossil Amphibian, Reptile, and Bird Collections, Division of Paleontology, American Museum of Natural History, New York, United States of America; ANWC, Australian National Wildlife Collection, CSIRO, Canberra, Australia; BMNH, The Natural History Museum, London, United Kingdom; CM, Canterbury Museum, Christchurch, New Zealand; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington (formerly National Museum of New Zealand, Dominion Museum, and Colonial Museum), New Zealand; MV, Museum Victoria, Melbourne, Victoria, Australia; NTM, Museums & Art Galleries of the Northern Territory, Darwin, Australia; QM, Queensland Museum, Brisbane, Queensland, Australia; SAM, South Australian Museum, Adelaide, South Australia, Australia; UCMP, University of California, Museum of Paleontology, Berkeley, California, USA; USNM, Division of Birds, Smithsonian Institution, Washington D.C., USA.

Anatomical nomenclature: Names for specific bone landmarks follow Baumel & Witmer (1993) with English translations, or follow Howard (1929), thereafter. Some common terms are abbreviated as follows: L is left and R is right elements. L or R elements are sometimes prefixed with either 'p', 's', or 'd', to indicate that the either proximal, shaft, or distal parts, respectively, of the element is represented; tuber, tuberculum; LF, local fauna; Mya, million years ago, indet, indeterminate. Measurements: TL, total length; PW, proximal width; SW, shaft width; DW, distal width.

Anatomical abbreviations: a, acrocoracoid; ap, alular process; bc, bicipital crest; bf, brachial fossa; cdf, crus dorsale fossa (median crest); cf, cranial fossa; cg, capital groove; cr, capital ridge; csc, scapular cotyla of coracoid; dc, dorsal condyle; dcf, dorsal lobe clavicle facet; dcr, deltoid crest; dls, distal ligamental scar; dpf, dorsal pneumotricipital fossa; ds, distal synostosis; dsf, dorsal sternal facet; dt, dorsal tubercle; ec, ectocnemial crest; ecp, ectepicondylar prominence; ect, dorsal ridge carpal trochlea; ep, extensor process; fa, flexor attachment; fal, facet for anterior articular ligament; fcc, fovea carpalis caudalis (cuneiform fossa); fp, flexor process; hh, humeral head; hf, humeral facet of coracoid; icf, ventral carpal (infratrochlear) fossa; ict, ventral ridge carpal trochlea; ls, scars for attachment external ligament; M., musculus; ma, medial angle; mc, medial condyle; MII, os metacarpale majus (major metacarpal); MIII, os metacarpale minus (minor metacarpal); ol, osseus

lamina; p, procoracoid; pc, procnemial crest; pls, proximal ligamental scar; pp, pisiform process; ps, proximal synostosis; sa, supraspinatus attachment scar; spm, superficial pronator muscle attachment; ss, supracoracoidal sulcus; tb, tendinal bridge; tg, scapulotricipital groove; TII, TIII, and TIV, trochlea for metatarsi II, III and IV respectively; vc, ventral condyle; vcf, ventral lobe clavicle facet; vpf, ventral pneumotricipital fossa; vt, ventral tubercle.

COMPARATIVE MATERIAL

The comparative material examined is listed in the Supporting Information.

IDENTIFICATION OF FOSSIL MATERIAL

Fossil collections in the following institutions were searched for anseriforms of Oligocene and Miocene age from Australia: Australian Museum (AM), Museum Victoria (MV), Queensland Museum (QM), and South Australian Museum (SAM). A large collection of fossil avian material housed at AM, including material from the University of California Museum of Paleontology (UCMP) and the American Museum of Natural History (AMNH), which had been assembled for other purposes, was also examined. All specimens at these institutions provisionally identified as anseriforms were borrowed for this study. Those whose identities were established as anseriforms form the basis of this report.

PHYLOGENETIC ANALYSES

The phylogenetic analyses were aimed principally at determining the relationships of the three extinct Australian anatids sufficiently well known for phylogenetic evaluation. These analyses built on those described in Worthy & Lee (2008) and used similar methodologies. In the present analyses 61 terminal taxa were included. The New Zealand Miocene fossil taxa *Manuherikia lacustrina*, *Dunstanetta johnstoneorum* and the European Oligo-Miocene *Mionetta blanchardi* were retained in these analyses as they are near contemporaneous with the Australian fossils. *Gallus gallus* and *Anhima cornuta* were defined as outgroups, as Galliformes is the sister group to Anseriformes (e.g. Sibley & Ahlquist, 1990; Ericson, 1997) and Anhimidae is the basal anseriform family (Livezey, 1986, 1997a; Clarke *et al.*, 2005; Livezey & Zusi, 2007). An additional set of analyses were made including *Presbyornis*, the Palaeogene sister taxon to Anatidae (Ericson, 1997; Livezey, 1997c), to determine whether this dataset obtained a similar sister-group relationship, and to see whether its addition affected the relationships within Anatidae.

As found by Worthy & Lee (2008), preliminary analyses of this dataset grouped all divers in a single clade, whereas molecular and immunological evidence indicates this result is an artefact of homoplasy (see Worthy & Lee, 2008: fig. 8). This is the result of morphological convergence towards specialized diving that affects multiple parts of the skeleton (e.g. McCracken *et al.*, 1999), for example, loss of pneumaticity has evolved independently in oxyurines (*sensu* Worthy & Lee, 2008), and in mergines and aythyines (O'Connor, 2004). Hence backbone constraints that reflected well-supported genetic clades were employed. A major effect of these constraints is to enforce the separation of certain diving taxa in line with genetic evidence: *Oxyura* is a basal form and not closely related to mergines and aythyines. Other divers, such as *Biziura*, *Thalassornis*, and the fossil taxa will then associate with one of these separated diving groups, based on the phylogenetic data. Essentially three clades, each with basal polytomies, were enforced above *Anseranas*. The most inclusive clade comprised *Stictonetta*, *Cygnus* + *Branta* + *Anser brachyrhynchus*, *Dendrocygna*, *Oxyura*, and the 'middle clade'. The middle clade had a basal a polytomy of *Tadorna ferriginea*, *T. tadornoides*, *T. tadorna*, *Alopochen* and the 'upper clade'. The upper clade included aythyines (*Aythya affinis*, *A. novaeseelandiae*, *A. australis*), mergines (*Lophodytes*, *Somateria*), *Anas superciliosa*, and *Aix*. The polytomies in this constraint means that only very robust genetic clades were enforced: the branching order of most taxa within each level was still largely free to vary depending on the phylogenetic signal; and the remaining 36 ingroup taxa (not included in these backbone constraints) were completely free to associate as dictated by the phylogenetic character data.

The dataset employed by Worthy & Lee (2008) was extended by seven humeral and ten pelvic characters for a total dataset of 150 characters (145 osteological, five integumental). Characters were based primarily on those in Livezey (1986, 1996a) with some from Howard (1929), Raikow (1971), Worthy *et al.* (1997); see Worthy & Lee (2008: supporting information, appendix 1) and new characters in Appendix 1 herein. All characters were scored following original examination of specimens (Appendix 2), except data for *Presbyornis*, which was scored from data in Howard (1955), Ericson (1997, 1999, 2000), and Livezey (1997c). Missing data were identified as either: (1) inapplicable characters (coded as '-') which could not be objectively scored in a particular taxon because of extensive divergence obscuring homology, or (2) unknown characters (coded as '?') that were not preserved in the (often incomplete) specimens exam-

ined, but which potentially could be determined. Although distinguished in our matrix (Appendix 2), PAUP and MrBayes treat both types of missing data in the same fashion.

A total of 35 multistate characters varied as morphoclines and could potentially be coded as ordered (numbers 2 11 12 19 24 29 31 37 48 52 53 55 59 60 66 72 77 80 83 85 89 93 97 105 107 108 116 118 120 121 124 129 138 142 146). Preliminary analyses were performed with these characters as unordered or as ordered. The results were very similar (see Worthy & Lee, 2008), and so those reported here focus on the 'ordered' analyses.

The phylogenetic analyses used PAUP* 4.0b10 (Swofford, 2000). Parsimony analyses used heuristic searches with tree-bisection-reconnection branch swapping, and 1000 random addition replicates per search. Trees were rooted with outgroups forming a polytomy at the base of the tree. When calculating tree lengths, multistate taxa were treated as polymorphisms rather than as ambiguous. Bootstrapping used heuristic searches and the same options. Analyses were performed without and with molecular backbone constraints, but only those using constraints are reported here for the reasons outlined in Worthy & Lee (2008).

Bayesian analyses

The program MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) was used to determine posterior probabilities for clades in the tree. The analyses were performed with the same characters and ordering assumptions as above; however, the outgroup was restricted to *Gallus gallus* as multiple outgroups were not allowed. MrBayes does not have an explicit command to effect a backbone constraint, so this was achieved by the addition of a second character block. In this character block, taxa in the molecular backbone constraint were coded with dummy characters that enforced the six clades assumed in the backbone constraints. Ten binary characters supporting each of the assumed clades were sufficient to generate posterior probabilities of 1.0 for assumed backbone relationships. The remaining taxa were coded as missing data for all characters in the 'backbone' character block. The analysis was then performed with the morphological (1–150) and 'backbone' (151–210) characters partitioned into two datasets, with topology linked but all other parameters unlinked across the two character blocks. The signal in the 'backbone' character block was sufficiently strong to enforce the assumed backbone constraints, whereas the positions of all the other taxa (and resolution of the polytomies in the backbone constraint tree) were generated by the morphological data. The MrBayes file is in the online Supporting Information.

The following priors were used. Characters were assumed to have rate variability distributed according to gamma parameter (rates = gamma) with flat prior distribution (0–200). In the morphological dataset, only variable characters were assumed to be included (coding = variable), whereas in the backbone constraint data partition, only parsimony-informative characters were assumed to be included (coding = informative); these assumptions were consistent with the structure of the data matrix. Topology was linked across the two character blocks, but the rate variability parameter, rate matrix, and branch lengths were unlinked across the two partitions [unlink shape = (all) Statefreq = (all) unlink brlens = (all)]. Unlinking parameters between character blocks means the analysis (and retrieved signal) of the morphological data is not affected by the structure of the backbone matrix.

After preliminary analyses with varying generation times, burnin, and sampling frequency, the following Markov chain Monte Carlo parameters were used. Two independent analyses were run simultaneously to check for adequacy of convergence, each for 5 000 000 generations, sampled every 1000 generations. To improve exploration of tree topology space, the heating parameter was set to 0.22, six chains (one cold and five incrementally-heated) per analysis were used, and branch swapping was set at three times the default (nswaps = 3). The time to convergence for topology, stationarity, and all parameters was checked using TRACER v. 1.3 (Rambaut & Drummond, 2004); the first 1000 sampled trees were discarded as burnin. A standard ‘all-compact’ consensus tree, where all clades are shown regardless of posterior probabilities values, was produced by combining the post-burnin samples from both runs. Posterior probability values for a node are the percentage of sampled generations that have that node.

FOSSIL SITES

The specimens described below mainly derive from localities in two main depositional basins of Lake Eyre Basin. The western sub-basin was formerly identified as the Lake Eyre Sub-basin and the eastern one Tarkarooloo Sub-basin by Vickers-Rich (1991) and Woodburne *et al.* (1994), but they now are named the Tirari Sub-basin and Callabonna Sub-basin, respectively (Tedford *et al.*, 1986; Krieg *et al.*, 1990; Callen, Alley & Greenwood, 1995; Alley, 1998). Sites in the Tirari Sub-basin that have revealed anseriform fossils are at Lake Palankarinna 28°46–47'S, 138° 24'E and Ngapakaldi 28° 17'S, 138° 17'E; those from the Callabonna Sub-basin are at Lake Pinpa (= Pine Lake) 31° 8'S, 140° 13'E, Lake Namba, 31° 12'S, 140° 14'E, Lake Yanda, 31° 0.05'S, 140° 18.5'E, and those asso-

ciated with Billeroo Creek, 31° 6'S, 140° 14'E (Rich *et al.*, 1991; Vickers-Rich, 1991).

These sites often have identification codes or name equivalents, for example, the Lake Palankarinna site ‘Tedford Locality Site 2’, has the University of California Museum of Paleontology site code V-5375. These codes are included whenever known so that locality data is as fully cross referenced to specimen data as possible. From Lake Pinpa, many specimens derive from Sites A and C. Site A was located at the south-west end of Lake Pinpa, CURNAMONA (prov. ed.) sheet grid coordinates 318146 and Site C is an area on the western shore of the lake that ‘extends north from the E-W cross lake track to about the location of the base of my measured section of 1971, e.g. grid coord. 317148, CURNAMONA. . . sheet.’ (R. Tedford, pers. comm., 30 August 2006).

Several of the following specimens derive from expeditions organized jointly between various institutions identified by the prefix in collection codes as follows: QMAM, joint Queensland Museum – American Museum expeditions of 1971 (QMAM 47, 65, 66 and 74) and 1973 (numbers > 100) led by Dick Tedford; VSQ, a joint Victoria, South Australia and Queensland museums expedition.

The main vertebrate-bearing beds in the Lake Eyre Basin are in the Etadunna Formation in the Tirari Sub-basin, (Woodburne *et al.*, 1994), and in the Namba Formation of the Callabonna Sub-basin (Callen & Tedford, 1976; Tedford *et al.*, 1977). We follow Woodburne *et al.* (1994) in accepting a Late Oligocene 26–24 Mya age for the Etadunna Formation, and for the nomenclature of local faunas and fossil mammal zones. They correlated Zone A, the oldest mammal zone in the Etadunna Formation, or the Minkina LF, with the Pinpa LF of the Namba Formation, thereby suggesting a Late Oligocene age for this fauna. Secondly, Woodburne *et al.* (1994) correlated the superjacent Zone B, containing the Ditjimanka LF at Lake Palankarinna, with the Ericmas Fauna in the upper part of the Namba Formation. The youngest fauna in the Etadunna sequence is the Ngama LF from Mammalon Hill, Lake Palankarinna (Pledge, 1984). Woodburne *et al.*'s (1994) revised chronology based on magnetostratigraphy and biochronology has led to a considerably older age being attributed to these units than the previous Middle Miocene age that was based on palynological evidence (Callen & Tedford, 1976; Woodburne *et al.*, 1985), and is now widely followed (e.g. Archer *et al.*, 1997; Alley, 1998). Reassessment of pollen samples from the Namba Formation indicates a Late Oligocene – Early Miocene age for a rainforest flora from the base of the unit and a dry sclerophyll forest similar to Late Miocene – Pliocene floras elsewhere in its upper section (Martin, 1990).

Fossil anatids are known from only two sites in the Riversleigh deposits (19° 00'S, 138° 39'E): details of site localities are available from the University of New South Wales or Queensland Museum on request. A single bone derives from Sticky Beak Site, part of the System A sequence, considered to be of Late Oligocene – Early Miocene age as contained faunas have taxa in common with the Late Oligocene faunas from Lake Palankarina (Archer *et al.*, 1997). The other is from Ringtail Site, in the Ray's Amphitheatre Sequence on Gag Plateau, attributed to the System C assemblage. System C overlies System A deposits on Gag Plateau and so are younger, and were considered Middle Miocene in age, possibly 16–14 Mya and slightly older than the Bullock Creek LF (Archer *et al.*, 1997). The Riversleigh 'System' nomenclature has been replaced by Faunal Zones, with System A equating to Faunal Zone A, etc, (Travouillon *et al.*, 2006).

Map references are given as recorded by the collectors from the following sheets: CURNAMONA (prov. ed.) sheet is CURNAMONA, SH 54-14, provisional ed. 1964, Series R502, 1:250,000, 1973 reprint.

RESULTS

SYSTEMATIC PALAEOLOGY

ORDER ANSERIFORMES WAGLER, 1831

FAMILY ANATIDAE LEACH, 1820:

SWANS, GEESE, DUCKS

SUBFAMILY OXYURINAE PHILLIPS, 1926:

STIFF-TAILED DUCKS

The following fossil taxa are referred to Anatidae rather than Anseranatidae and Anhimidae by the following unique combination of humeral characters: 1, a wide caput humeri (head) with its distal margin caudally roughly at right angles to the shaft; 2, a relatively broad fossa pneumotricipitalis ventralis housed in an inflated crista bicipitalis; 3, a distinct dorsal pneumotricipital fossa. The following unique combination of humeral characters indicates that they are related to a clade termed Oxyurinae (*Oxyura*, *Nomonyx*, *Thalassornis*, *Biziura*, *Malacorhynchus*, *Stictonetta*, *Mionetta*, *Dendrochen*, *Manuherikia*, and *Dunstanetta*) by Worthy & Lee (2008): (1) a distinct capital shaft ridge that is directed towards the tuber. dorsale; (2) elevated dorsal tubercle; (3) an elongate crista deltopectoralis that is concave dorsally; (4) and a closed or nonpneumatic ventral pneumotricipital fossa. These characters are consistent with other traits. The fossils are much smaller than any anserine and derived relative to *Anseranas*, *Anhima*, and anserines with an elongate epicondylus ventralis (entepicondyle), extending distally nearly to

the same extent as the condylus ventralis (not markedly shorter). The new taxa are more derived than both anserines and dendrocygnines as (1) the capital shaft ridge is directed towards the dorsal tubercle rather than more ventrally, and has the same caudal elevation (is level with) the crus dorsale fossae (median crest), rather than being significantly more elevated or caudad, of the median crest; and (2) the humeri have a closed or nonpneumatic ventral pneumotricipital fossa. They are excluded from Tadorninae by having a closed ventral pneumatic fossa. They are excluded from Anatinae, including all anatines, aythyines, and mergines, by retention of the plesiomorphic characters of a distinct capital shaft ridge, and an elevated dorsal tubercle.

GENUS *PINPANETTA* GEN. NOV.

Type species: Pinpanetta tedfordi sp. nov.

Diagnosis: Oxyurines in which humeri have the following unique combination of characters: incisura capitis (capital groove) forming either a very shallow or no notch in proximal profile; ventral pneumotricipital fossa closed or nonpneumatic, not extending under median crest; dorsal pneumotricipital fossa narrower than ventral one; dorsal tubercle about as wide as long, not elongate; attachment of M. scapulothoracalis cranialis (supraspinatus) an elongate ridge, extending distally to point level with junction of bicipital crest and shaft; tuber. supracondylare ventrale (facet for anterior ligament) buttressed cranially; ectepicondylar prominence distinct; and attachment of pronator brevis is an isolated pit on ventral facies.

Etymology: After Lake Pinpa and the Pinpa Local Fauna from which many specimens derive, and for 'netta', duck in Greek.

Description and comparison: Within Anatidae, lack of a well-developed notch at the ventral end of the capital groove, as shown by *Pinpanetta*, is found only in dendrocygnines, anserines, and tadornines. *Thalassornis*, *Biziura*, *Oxyura*, *Nomonyx*, *Stictonetta*, *Malacorhynchus*, *Mionetta*, and *Manuherikia* are all more derived with their proximal profile interrupted by a distinct notch at the ventral end of the capital groove. The relatively narrow dorsal pneumotricipital fossa in *Pinpanetta* is shared with dendrocygnines, anserines, and tadornines. Within oxyurines, *Mionetta*, *Manuherikia*, *Thalassornis*, *Biziura*, *Stictonetta*, and *Malacorhynchus* also retain the narrow dorsal pneumotricipital fossa, but in *Oxyura* and *Nomonyx* the fossa is relatively wider. *Pinpanetta* shares the derived condition of a closed or nonpneu-

matic ventral pneumotricipital fossa with all oxyurines except *Stictonetta* and *Nomonyx*, in which taxa the fossa is pneumatic. In *Pinpanetta*, the attachment scar for *m. latissimus dorsi posterioris* commences proximal to and links to the end of the deltoid crest before extending down the shaft, as in *Anseranas*, some *Dendrocygna* species, and *Cereopsis*. This character state is therefore probably the primitive condition, and is shared with *Mionetta*, *Thalassornis*, *Oxyura*, and *Nomonyx*. In the assumed more derived states there is no connection of the scar with the deltoid crest, whether the scar begins anterior of the end of the crest, e.g. *Biziura* and *Manuherikia*, or commences level with its end e.g. *Stictonetta*, *Malacorhynchus*, tadornines, and most anatines. The tuber. ventrale slightly overhangs the ventral pneumotricipital fossa in *Pinpanetta*, rather than being directed proximally. This is a derived condition accentuated in most diving anatids, e.g. *Biziura* and *Oxyura*, and so differs from *Stictonetta* and *Mionetta* where the ventral tubercle is directed proximally. The dorsal tubercle is about as wide as long, as seen in *Anseranas*, *Dendrocygna*, anserines, and some oxyurines. The derived state (an elongate tubercle) is seen in other oxyurines (some *Oxyura* species, *Nomonyx*, *Stictonetta*, *Manuherikia*, and *Dunstanetta*), most tadornines and all anatines. An elongated attachment of the supraspinatus is derived relative to a short attachment characteristic of *Anseranas*, *Dendrocygna* species, and anserines. In *Pinpanetta*, the attachment is as elongate as in *Manuherikia*, *Thalassornis*, *Oxyura*, *Biziura* and *Malacorhynchus*, but it is much shorter in *Stictonetta*, *Nomonyx*, and *Mionetta*.

Distally, in *Pinpanetta*, the facet for the anterior ligament is cranially buttressed, as in *Mionetta*, *Manuherikia*, *Dunstanetta*, *Malacorhynchus*, *Stictonetta*, and *Nomonyx*, and so is derived relative to the unbuttressed state where the facet is parallel to the shaft in *Anseranas*, *Thalassornis*, *Biziura*, and *Oxyura*. The space between the facet for the anterior ligament and the dorsal condyle is wider than this facet, versus narrower in *Thalassornis* and *Dendrocygna bicolor*, which latter state is regarded as more primitive (Woolfenden, 1961). In *Pinpanetta*, the sulcus scapulo-tricipitalis (scapulo-tricipital groove) extends from the caudal surface around the distal margin, as in most oxyurines, tadornines and anatines, and is therefore derived compared to *Anseranas*, *Cnemionis* and *Biziura*, which either lack or have a barely defined scapulo-tricipital groove caudally, and to *Dendrocygna*, *Thalassornis* and some anserines, where the groove exists only on the caudal face. Although the epicondylus dorsalis is well developed and dorsally prominent level with the proximal margin of the dorsal condyle in *Pinpanetta*, a distinct ectepicondylar prominence of similar or relatively

larger size to that in *Malacorhynchus* is also present. A distinct ectepicondylar prominence is present in *Anseranas*, anserines and *Dendrocygna*, and so its presence in *Pinpanetta* is a retained plesiomorphy shared with *Thalassornis* and *Stictonetta*, but the derived condition (lack of ectepicondylar prominence) is found in *Oxyura*, *Nomonyx*, *Biziura*, most tadornines, and all Anatinae. *Pinpanetta* has the attachment of the pronator brevis (*sensu* Howard, 1929) in an isolated pit on the ventral facies of the ventral epicondyle, thus distinguishing it from *Thalassornis*, *Oxyura*, *Nomonyx*, and *Biziura* which have a derived state with the attachment area fused with the ventral margin of the facet for the anterior ligament. The brachial fossa is elongate, with well-defined margins, is separated from the ventral margin by a narrow rounded ridge, and lacks secondary deepening distoventrally, as in *Manuherikia*. In *Stictonetta*, the fossa is poorly defined and flat.

SPECIES *PINPANETTA TEDFORDI* SP. NOV. (FIG. 1)

Holotype: SAM P.41257, complete R humerus (Fig. 1A, F), reassembled from two pieces; shaft with some wear on distal margin of bicipital crest and on caudal shaft surface; light brown in colour.

Diagnosis: A species of *Pinpanetta* about the size of *Oxyura australis*, characterized by the following features: dorsal pneumotricipital fossa excavated below head; elongate deltoid crest with about 50% length extending distad of bicipital crest; ventral pneumotricipital fossa, from median crest, wider than its length measured from the ventral tubercle to the distal end of the bicipital crest – shaft junction; shaft narrows distally; facet for the attachment of anterior ligament directed distoventrally; and on ventral facies, attachment of pronator brevis positioned towards cranial facies, not centrally.

Etymology: For R. H. (Dick) Tedford whose efforts over many years have revealed much about the Namba and Etadunna Formations and their contained faunas and whose expeditions collected many of the following specimens.

Type locality: Young Bucks Quarry, site code RV-9002, Lake Palankarinna, 28° 47'S, 138° 24'E, Tirari Sub-basin, Lake Eyre Basin, SA, collected N.S. Pledge *et al.*, xii.1992.

Horizon: Stratigraphy/Age/Fauna: Etadunna Formation, Late Oligocene 24–26 Mya, Minkana LF, Zone A.

Distribution: Late Oligocene (24–26 Mya): Lake Palankarinna, Etadunna Formation, Minkana LF,

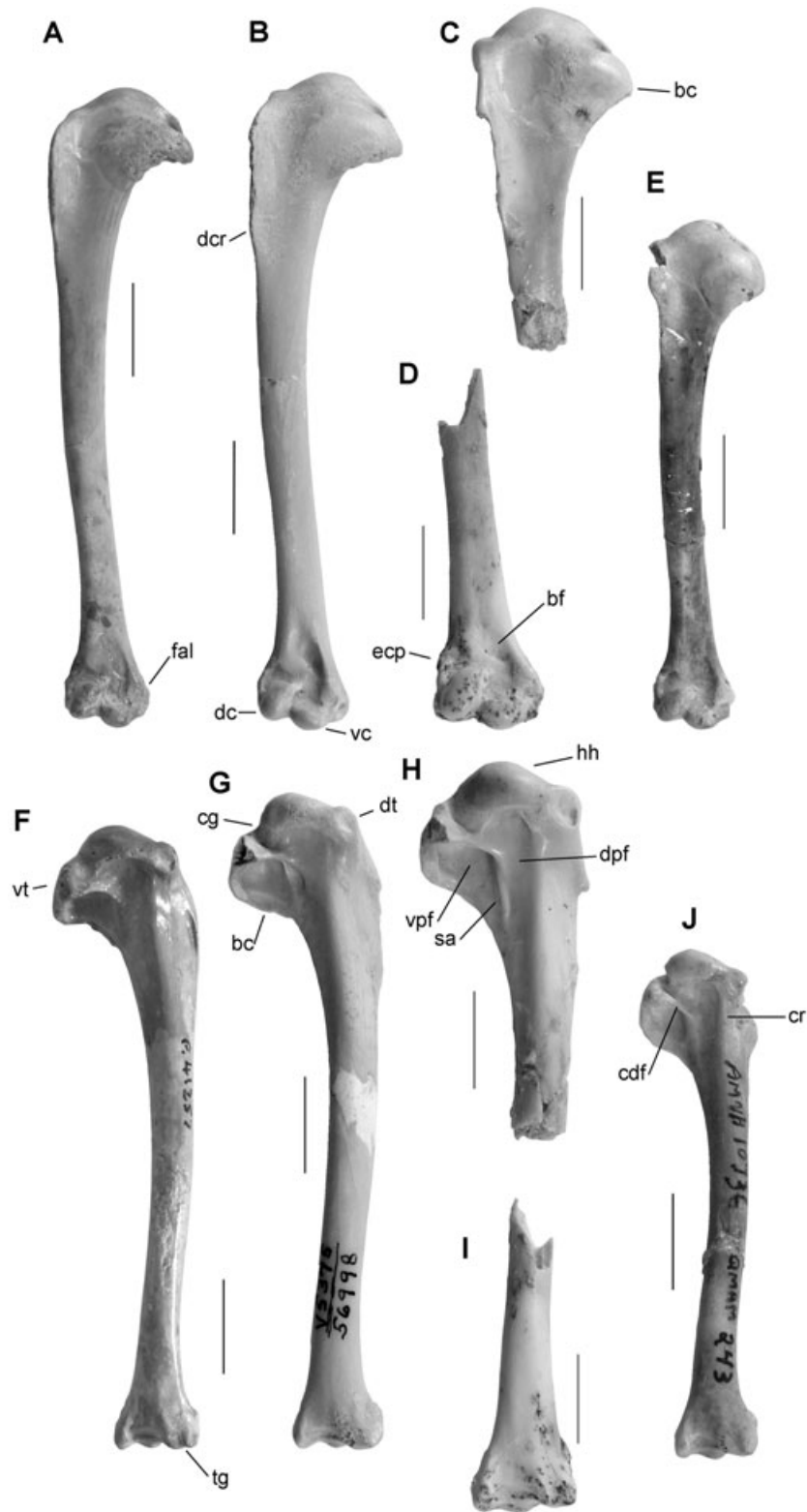


Figure 1. Right humeri of *Pinpanetta* species, A–E, cranial view, and F–J, caudal view. A, F, *Pinpanetta tedfordi* SAM P.41257, holotype; B, G, *Pi. tedfordi* UCMP 56998, paratype; C, D, H, I, *Pi. vickersrichae* SAM P.42703, holotype two nonarticulating fragments of one bone; and E, J, *Pi. fromensis* SAM P.43128, holotype. Scale bars = 10 mm. See main text for abbreviations.

Zone A and Ditjimanka LF, Zone B, Member 7; Lake Pinpa, Namba Formation, Pinpa LF.

Measurements of holotype: TL = 65.6 mm, PW = (maximum width from dorsal tubercle) 14.5 mm, SW = 4.0 mm, DW = 9.0 mm, depth dorsal condyle = 5.3 mm.

Paratypes: Lake Palankarina, Etadunna Formation: SAM P.42699, s+dR humerus, Neville's Nirvana, Minkina LF, Zone A, collection code VSQ 1978-40P. UCMP 46173, s+dL humerus, Tedford Locality Site 2, Ditjimanka LF, Zone B, Member 7, site code UCMP V-5375, collected by R. A. Stirton 1954, collection code RAS #4803. UCMP 56998, well preserved R humerus with the shaft broken and joined with some plaster infill caudally, Stirton Site 2, Ditjimanka LF, Zone B, Member 7, site code UCMP V-5375, collected by R. H. Tedford *et al.*, 1957, collection code RHT#450 (Fig. 1B, G).

Lake Pinpa; Namba Formation, Pinpa LF: SAM P.43133 (formerly AMNH 10957), dR humerus, collected by R. H. Tedford *et al.*, 1971 at Site C, collection code QMAM 151; SAM P.43130 (formerly AMNH 10835), d+sL humerus, collected by R. H. Tedford *et al.*, 1971 at Site C, collection code QMAM 252.

Referred material: Humeri – SAM P.23480, part pR humerus, Lake Pinpa, Namba Formation, Pinpa LF. SAM P.27846, dR humerus, west of site SIAM, Lake Palankarina, Etadunna Formation, Ditjimanka LF, Zone B. SAM P.41262, dL humerus, White Sands Basin, Lake Palankarina, Etadunna Formation, Ditjimanka LF, Zone B. QM F52743 (= AR17105), dL humerus, Ringtail Site, Gag Plateau, System C, Riversleigh.

Measurements: See Table 1.

Description and comparison: Humeri of *Pi. tedfordi* have the following additional features: dorsal pneumotricipital fossa variably excavated under the head,

slightly in holotype, marked in UCMP 56998 as in *Malacorhynchus*; pit for attachment of ligamentum collaterale dorsale on dorsal face of ectepicondyle, deep, divided by median ridge as in all anatids, although this median ridge is unusually weak in SAM P.41257; olecranal fossa well marked; brachial fossa elongate, aligned up shaft, in holotype c. 2.1 mm wide by 5 mm long with proximal dorsal margin barely extending past midshaft width, relatively deeper and extends closer to dorsal margin in other specimens, e.g. UCMP 46173, UCMP 56998, SAM P.43133.

Although distinguished from all oxyurines as indicated in the generic description, humeri of *Pinpanetta tedfordi* are most similar to those of *Oxyura* and *Malacorhynchus*. Both are distinguished from *Pi. tedfordi* by a marked notch at the ventral end of the capital groove and a shorter deltoid crest. *Oxyura* further differs as follows: relatively wider ventral pneumotricipital fossa and bicipital crest; distinct groove dorsad of median crest; attachment of pronator brevis fused with ventral facies of ventral epicondyle; and attachment of anterior ligament not buttressed anteriorly. *Malacorhynchus* humeri further differ by: lack of distal narrowing of the shaft; pocket of ventral pneumotricipital fossa much deeper; distal margin of bicipital crest more convex; facet for attachment of anterior ligament more distally directed; attachment of pronator brevis on ventral facies more central.

The New Zealand Early Miocene fossils *Manuherikia* and *Dunstanetta* share with *Pi. tedfordi* a distally narrowing shaft, but differ in the features listed above, notably with a marked notch in their proximal profile, a shorter deltoid crest, an elongate dorsal tubercle, a deeper ventral pneumotricipital fossa that extends under the median crest, and a relatively wider dorsal pneumotricipital fossa.

QM F52743, from Ringtail Site, System C, is one of only two confirmed anatid bones from the Carl Creek limestone at Riversleigh. It is slightly larger but otherwise indistinguishable from SAM P.43130 from the Namba Formation, which is one of the larger specimens attributed to *Pinpanetta tedfordi* (Table 1).

Table 1. Measurements (mm) of humeri of *Pinpanetta tedfordi*

Specimen	TL	PW from DC	SW min	DW	Depth DC
SAM P.41257	65.6	14.5	4.0	9.0	5.3
SAM P.42699	–	–	4.1	8.7	5.0
UCMP 46173	–	–	4.0	8.6	4.8
UCMP 56998	66.8	13.9	4.5	9.2	5.5
SAM P.43133	–	–	–	8.9	–
SAM P.43130	–	–	4.7	9.5	5.5
QM F52743	–	–	–	9.7	5.4

Abbreviations as in Methods; and DC, dorsal condyle; min, minimum.

The four distal humeri from the Lake Palankarina Etadunna Formation are also slightly smaller with DW ranging 8.6–9.2 mm. Given that distal humeri are relatively conservative in form with much more variation evident in the proximal end, it is possible QM F52743 could derive from a distinct species of *Pinpanetta*.

ANATID MAGN. *PINPANETTA TEDFORDI*

The following specimens are referred to *P. tedfordi* on the basis of size. There are three size classes of humeri of similar anatids present in the local faunas of the Etadunna and Namba formations, and three matching size classes of other elements; the intermediate-sized elements are all provisionally referable to *P. tedfordi*.

Ulna: SAM P.24227, dR ulna, Lake Yanda, CURNAMONA (prov. ed.) sheet, grid reference 328161, Namba Formation, Yanda LF, measurements – maximum DW = 6.0 mm. SAM P.41258, dL ulna, Young Bucks Quarry, Lake Palankarina, Etadunna Formation, Minkina LF, Zone A, measurements – SW = 3.6 mm; maximum DW = 6.4 mm. SAM P.41308, dR ulna, Neville's Nirvana, collection code VSQ 1978-74P, Lake Palankarina; Etadunna Formation, Minkina LF, Zone A, measurements – maximum DW = 6.2 mm, preserved length = 10.0 mm.

Description: These specimens have a typical anatid form, and other than a small carpal tubercle, preserve no phylogenetically informative features.

Carpometacarpus: AMNH 10772, pR carpometacarpus, Billeroo Creek, site 3, collection code QMAM 199, Namba Formation, Pinpa LF. AMNH 10899, pR carpometacarpus, Site C, Lake Pinpa, Namba Formation, Pinpa LF.

Description: These specimens tentatively referred to *Pi. tedfordi* are worn, precluding measurements, but are slightly smaller than AMNH 10748, which is referred to *Pinpanetta vickersrichae*. They otherwise differ from that specimen with the ridge extending caudally from the pisiform process higher and the minor metacarpal is not grooved at the fornix, in which features they are similar to specimens referred to *Pinpanetta fromensis*.

Coracoid (Fig. 2): SAM P.23477, R coracoid (Fig. 2A–C), Lake Pinpa, Namba Formation, Pinpa LF, measurements – medial length = 30.3 mm, SW = 3.6 mm, length scapular cotyla – acrocoracoid = 10.9 mm, length humeral facet = 6.5 mm, width humeral facet = 3.7 mm. SAM P.42672, cranial part R coracoid, lacking tips of acrocoracoid and procoracoid, Site 2, Billeroo Creek, 31° 06.205'S 140° 13.912'E. SAM P.42697, L coracoid lacking lateral angle, White Sands Basin, Lake Palankarina, collection code VSQ 1978-145, Etadunna Formation, Ditjimanka LF, Zone B, measurements – medial length = 29.2 mm, SW = 3.3 mm, length scapular cotyla – acrocoracoid = 9.8 mm, length humeral facet = 6.5 mm, width humeral facet = 3.6 mm.

Description: Acrocoracoid lacks pneumatic foramina; clavicle facet uniformly (over its depth) overhangs supracoracoidal sulcus, dorsal and ventral lobes not

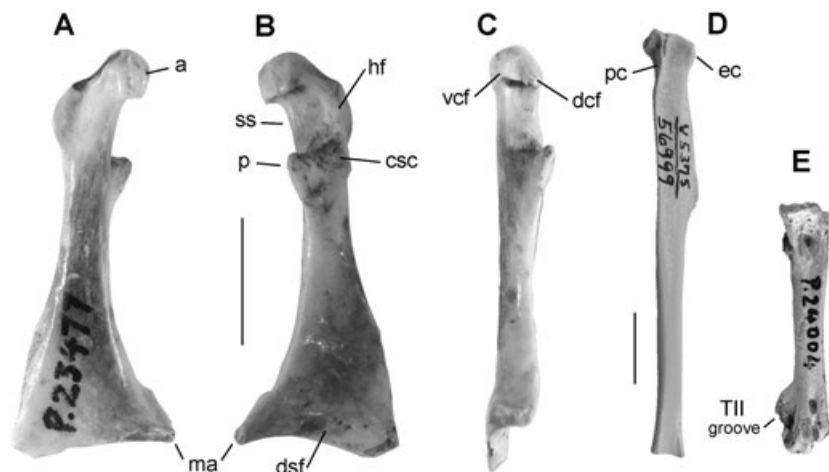


Figure 2. Referred elements of *Pinpanetta tedfordi*: A–C, right coracoid SAM P.23477 in A, ventral; B, dorsal; and C, medial aspect; D, left tibiotarsus UCMP 56999 in anterior view; and E, left tarsometatarsus SAM P.24004 in dorsal aspect. Scale bars = 10 mm. See main text for abbreviations.

separated by notch, ventral lobe markedly overhangs the medial shaft margin but not the shaft ventrally; acrocoracoid wider than high (dorsal view); humeral facet not undercut by secondary fossa in supracoracoidal sulcus, although in SAM P.42697 it is secondarily deepened; procoracoid at right angles to shaft, short, robust, not decurved ventrally, without foramen or notch; dorsal sternal facet broad, bound by ridge cranially in middle third of width only; sternocoracoidal impression shallow, no foramina; ventral surface blade with broad shallow depression; ventral sternal facet short, obvious, but not prominent ventrally; medial angle with distinct flange extending cranially along the medial shaft margin.

Comparisons: These coracoids are of appropriate size for humerus SAM P.41257 so are referred to *P. tedfordi*. Best exemplified by SAM P.23477, they are distinguished by a unique combination of traits that place them more derived than anserines. They are more derived than *Anseranas* and *Anhima* in lacking both a procoracoidal foramen and a pneumatic fossa in the dorsal surface of the sternal blade. They differ from all anserines, plesiomorphic tadornines e.g. *Miotadorna* and *Alopochen*, the fossil taxa *Dunstanetta* and *Matanas*, and from aberrant anatines e.g. *Cairina* and *Aix*, by the absence of pneumatic foramina within the acrocoracoid. They retain an intermediate derived condition of a shallow hollow on the ventral surface of the sternal blade (its absence is plesiomorphic, and a deep hollow, as in *Stictonetta* and *Dendrocygna*, is most derived). They share this derived shallow hollow on the ventral blade with other oxyurines (*Oxyura*, *Malacorhynchus*, *Mionetta*, *Manuherikia lacustrina*, and *Man. minuta*) and with *Nettapus*.

Coracoids of *Biziura* differ from *Pi. tedfordi* (SAM P.23477) with a more robust and less prominent procoracoid whose cranial margin slopes caudally rather than forming a right angle with the shaft, and in which the acrocoracoid overhangs the ventral facies of the shaft. Ventral overhang of the shaft by the acrocoracoid also distinguishes coracoids of *Oxyura* and *Stictonetta* from SAM P.23477, and also from *Manuherikia*, *Mionetta*, *Malacorhynchus* and *Nettapus*. Those of *Nettapus* differ from SAM P.23477 with a much more rounded acrocoracoid and a prominent ventral sternal facet. SAM P. 23477 is intermediate in size between coracoids of *Man. lacustrina* and *Man. minuta*, and shares with these taxa the presence of shallow fossa on the ventral surface of the sternal blade, absence of a pneumatic foramen in acrocoracoid, and the lack of a secondary sulcus beside the humeral facet in the supracoracoidal sulcus. It differs from *Manuherikia*, *Dunstanetta*, *Matanas*, and *Mionetta* in having a flange extending cranially from the

medial angle, and by lacking a notch in the clavicle facet. The broad overhang of the supracoracoidal sulcus by the clavicle facet and other features mentioned above are similar to those in *Malacorhynchus*; however, this taxon has a distinct notch in the clavicle facet (none in SAM P.23477).

Scapula: SAM P.41295, worn R scapula, Mammal Hill, Lake Palankarina, Etadunna Formation, Ngama LF, Zone D, Member 8. SAM P.42670, R scapula, lacking distal half blade, Site 2, Billeroo Creek, 31° 06.205'S; 140° 13.912'E. SAM P.42679, L scapula, lacking distal half blade, Site 4, Lake Pinpa, 31° 08.500'S; 140° 12.789'E.

Description: Typical anatid form, nonpneumatic, blade with parallel dorsal and ventral margins, acromion extends well cranial of coracoidal articulation but dorsal margin in line with dorsal margin of blade, not directed dorsally, glenoid facet laterally directed.

Tibiotarsus (Fig. 2): UCMP 56999, p+sL tibiotarsus (Fig. 2D), Tedford Locality Site 2, site code UCMP V-5375, Lake Palankarina, Etadunna Formation, Ditjimanka LF, Zone B, Member 7, measurements – preserved length 57.2 mm, PW = 6.6 mm, minimum SW = 3.0 mm, length of fibular crest = 16.4 mm. UCMP 57248, part L tibiotarsus missing the distal end and the cnemial crests, Site 12, site code UCMP V-5771, Lake Palankarina, Etadunna Formation, ?Ditjimanka LF, measurements – preserved length = 48.1 mm, PW = 6.9 mm, minimum SW = 2.8 mm, length of fibular crest = 15.0 mm. SAM P.36677, dR tibiotarsus, Young Bucks Quarry, RV-9002, Lake Palankarina, Etadunna Formation, Minkina LF, Zone A, measurements – DW = 6.3 mm, depth medial condyle = 5.6 mm, depth lateral condyle = 4.8 mm, SW = 2.8 mm. AMNH 10963, dR tibiotarsus, Lake Pinpa, Site C, Namba Formation, Pinpa LF.

Description: Available specimens do not preserve the cnemial crests. They have very flattened anterior facies with the cranial cnemial crest extended down the medial facies forming an elevated crest to a point level with the distal end of the fibular crest. The facies articularis medialis and the facies articularis lateralis have near equal depth (rather than the medial articular surface extending markedly caudad of the lateral one) and are separated caudally by a distinct notch. The impression for the medial collateral ligament is prominent and merged with the extension of the cranial cnemial crest. Shaft width at the proximal end of the fibular crest is noticeably narrower than that across the fibular crest, as seen in *Malacorhynchus*. The fibular crest is separated from

the proximal articular surface by a shaft section much longer than it is wide. On the caudal facies, the shaft is angular, not rounded over its length adjacent to the fibular crest. Most of these features are common to diving taxa. That the depths of the distal condyles do not differ markedly, and that condylar depth is less than width are features seen in diver anatids and so accord with features of the humeri.

Tarsometatarsus (Fig. 2): SAM P.24004, L tarsometatarsus (Fig. 2E), Snake Dam, Clayton River, south-east of Lake Eyre, Muloorina Station, SA, MARREE Sheet (1 : 250 000) 138° 06'E 29° 7.5'S, Etadunna Formation, measurements – TL = 33.4 mm, PW = 7.4 mm, shaft depth = 2.9 mm, SW = 3.8 mm, DW = 6.9 mm.

Description: SAM P.24004 has typical anatine-like proportions; trochlea for metatarsal II (TII) ends proximad of TIV, distal margin level with lateral intertrochlear notch; shaft wider than deep; extensor sulcus, deep, not extending distad of mid shaft length; well marked, raised, impressio ligamentum collaterale lateralis; TII strongly keeled caudal margin, deep medial groove; plantar exit of distal foramen occluded by affixed matrix, therefore form of exit not determined; hypotarsus worn, four ridges, base broader than half proximal width; form of tuberositas musculus tibialis cranialis is a pair of similar sized rugosities (as usual in anatids), medial one offset proximally half length of lateral one, and separated from it by a smooth area about as wide as one of the tubercles; distal foramen relatively large, opens from deep groove on anterior facies.

Several features of SAM P.24004 support the placement of *Pinpanetta* with oxyurines. In having a grooved TII it is more derived than *Anseranas* and *Dendrocygna* (they lack a grooved TII); its lack of a medial parahypotarsal fossa indicates that it is more derived than these taxa and the basal anserines *Cnemiornis* and *Cereopsis*; its broad hypotarsus is more derived than the narrow one of *Anseranas*, *Cnemiornis*, and *Cereopsis*; its short tarsometatarsus is derived relative to the elongate ones of *Anseranas*, anserines, *Dendrocygna*, and tadornines. In SAM P.24004, TIV diverges laterally from the alignment of the shaft and so differs from tarsometatarsi of *Biziura*, *Oxyura*, and *Nettapus* where the lateral profile is straight. SAM P.24004 is very similar to tarsometatarsi of *Malacorhynchus* and *Man. minuta*: no qualitative differences could be found. However, tarsometatarsi in these taxa do not differ in any appreciable way from those of small *Anas*, e.g. *Anas gracilis*, illustrating the conservative nature of this element in anatids and that it is phylogenetically relatively uninformative.

SPECIES *PINPANETTA VICKERSRICHAЕ*
SP. NOV. (FIGS 1, 3)

Holotype: SAM P.42703, R humerus in two parts (FIG. 1C, 1D, 1H, 1I), missing small part midsection of shaft, dorsal part deltoid crest, and tip of ventral tubercle. Bone pale with areas of orange staining.

Diagnosis: A species of *Pinpanetta* which differs from *Pi. tedfordi* in humeral characters as follows: larger (12–20% broader); deltoid crest shorter with 43–45%

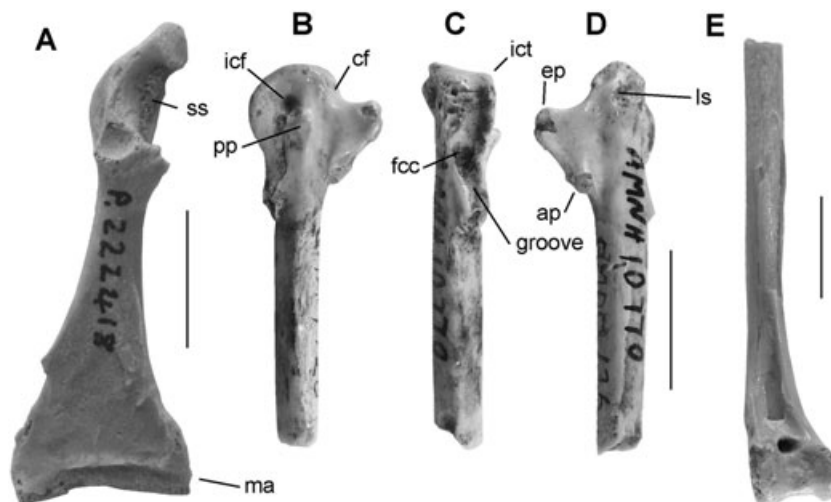


Figure 3. Referred elements of *Pinpanetta vickersrichae*: A, left coracoid MV P.222418 in dorsal aspect; proximal left carpometacarpus AMNH 10770 in: B, ventral; C, caudal; and D, dorsal aspects; E, distal right tibiotarsus SAM P.24529, in anterior aspect. Scale bars = 10 mm. See main text for abbreviations.

of length extending distad of bicipital crest; dorsal pneumotricipital fossa deeper, not excavated under head; capital shaft ridge more compressed; attachment scar of supraspinatus more prominent; shaft does not narrow significantly distally; and facet for attachment of anterior ligament directed distally and slightly dorsally (not distoventrally).

Etymology: For Patricia Vickers-Rich in recognition of the substantial contribution she has made to the knowledge of Australian palaeornithology.

Type locality: Kanunka Microsite, Lake Kanunka, Lake Eyre Basin, SA, collection code VSQ 1978-127; collected by Museum Victoria, South Australian Museum, Queensland Museum field party July 1978.

Horizon: Stratigraphy/Age: Etadunna Formation, ?Ngapakaldi LF, Late Oligocene 24–26 Mya.

Distribution: Late Oligocene (24–26 Mya): Lake Eyre Basin, Callabonna Sub-basin, Namba Formation, Pinpa LF (Lake Pinpa and Billeroo Creek), Yanda LF (Lake Yanda); Tirari Subbasin, Etadunna Formation, Ngama LF (Mammalon Hill, Lake Palankarinna), ?Ngapakaldi LF (Kanunka Microsite, Lake Kanunka).

Measurements of holotype: PW = 15.7 mm, length of deltoid crest = 20.7 mm, length head from dorsal tubercle = 11.8 mm, SW = 4.7, shaft depth = 4.1 mm, maximum DW = 11.3 mm, depth dorsal condyle = 6.6 mm.

Paratypes: Billeroo Creek, Well's Bog Site, near Lake Pinpa: SAM P.41321, a fragmented R humerus reassembled into distal and proximal parts, lacking the bicipital crest and ventral pneumotricipital fossa ventrad of the capital groove, collected by T. R. Rich *et al.*, 22 June 1978, collection code VSQ 1978-3, CURNAMONA (prov. ed.) sheet grid coordinates 319151, 31° 06'S 140° 14'E, Namba Formation, Pinpa LF. Tom Rich's field notes for 22 June 1978 have the following entry: 'In the afternoon, visited Wells Bog Site on Billeroo Creek. Here collected a bird humerus in several fragments plus the distal end of a tibiotarsus. This was out of the Namba Fm presumably. In addition we collected a *Sthenurus* claw from the Eurinilla Fm. as well as a lot of other Pleistocene material. This material was given the lot number VSQ 1978-3.' Aaron Camens and THW relocated this area in June 2007 finding Namba Formation exposed on the North side of Billeroo Creek with adjacent Pleistocene outcrops at 31° 06.205'S, 140° 13.912'E, so locating this site c. 1 km south-east of where previously recorded.

Lake Pinpa, Namba Formation: SAM P.43127 (formerly AMNH 10724), worn dL humerus, collection code QMAM 264, Site C, Pinpa LF; SAM P.43136 (formerly AMNH 11408), dR humerus, north-west side lake, near CURNAMONA (prov. ed.) sheet grid coordinates 317148 (R. H. Tedford, pers. comm. 30 Aug 2006), collection code QMAM 47, preserved length = 31.7 mm. The shaft of AMNH 11408 is stained dark grey and is infilled with red sand suggesting it was derived from the Ericmas LF.

Description and comparison: In addition to the diagnostic characters above, *Pi. vickersrichae* differs from *Pi. tedfordi* further as follows: ventral pneumotricipital fossa extends as a deeper pocket under capital groove; pit for attachment of pronator brevis is located closer to centre on the ventral facies, rather than more cranially. The orientation of the facet for the anterior ligament is related to habit with specialist diving taxa having it directed somewhat ventrally, e.g. *Oxyura* and *Mergus*. That *Pi. vickersrichae* could be a less specialized diver than *Pi. tedfordi* is also indicated by the humeral shaft not narrowing distally as seen for example in *Mergus* and *Oxyura*; however, the genera *Nomonyx*, *Stictonetta*, *Biziura*, *Malacorhynchus*, and *Mionetta* all lack distally narrow humeral shafts and *Biziura* is a good diver. In *Pi. vickersrichae*, the brachial fossa is well marked, aligned up the shaft, occupies about half shaft width, slightly less than in *Pi. tedfordi*, and is deepest distoventrally and separated from the ventral facies by a narrow ridge. *Pinpanetta vickersrichae* has a distinct dorsal ectepicondylar prominence of similar relative size to that in *Pi. tedfordi* and *Malacorhynchus*.

Measurements: See Table 2.

REFERRED MATERIAL *PINPANETTA VICKERSRICHAE*

Humerus: Lake Palankarinna: SAM P.22840, part dR humerus, Mammalon Hill, Etadunna Formation, Ngama LF, Zone D, member 8. Billeroo Creek: AMNH 10774, worn dL humerus, site 3, collection code QMAM 199, probably Namba Formation.

ANATID MAGN. *PINPANETTA VICKERSRICHAE*

The following specimens are referred to *Pinpanetta vickersrichae*, on the basis of expected size and given the observation that three size classes of humeri are referable to this genus.

Ulna: MV 222428, dL ulna, side of Billeroo Creek, CURNAMONA (prov. ed.) sheet grid coordinates 319151, collection code THR1977-206, Museum Victoria (MV) site number 2372, probably the Namba

Table 2. Measurements (mm) for *Pinpanetta vickersrichae*

Specimen	TL	PW from DC	SW min	DW	Depth DC
SAM P.42703 Holotype	–	15.7	4.7	11.3	6.6
SAM P.43136	–	–	–	10.8	6.1
SAM P.43127	–	–	–	10.6	6.3
SAM P.41321	–	–	5.0	c.10.5	–
SAM P.22840	–	–	–	–	6.2

Abbreviations as in Methods; and DC, dorsal condyle; min, minimum.

Formation, rather than the overlying Quaternary Eurinilla Formation; measurements – preserved length = 16.7 mm, maximum DW = 7.3 mm.

Description: The fragment has typical anatid form with no unusual features.

Carpometacarpus (Fig. 3B–D): AMNH 10770, pL carpometacarpus, Lake Pinpa, Site C, collection code QMAM 126, Namba Formation, Pinpa LF; measurements – PW = 9.3 mm.

Description: The dorsal margin of the carpal trochlea is worn precluding observation of the notch form, but otherwise it is unworn. The internal carpal fossa is deep, extending to level of extensor process from which it is separated by a rounded ridge. The extensor process is narrower than the ventral side of the carpal trochlea. A cranial fossa is present and the cuneiform fossa is relatively deep. The proximal synostosis is short and the minor metacarpal is grooved at the fornix. The flexor attachment is distad of the fornix. Dorsally, only a single proximally located ligamental scar is present. It further differs from *Pi. tedfordi* and *Pi. fromensis* in that the pisiform process is more prominent and the ridge leading caudally from the pisiform process is absent.

Coracoid (Fig. 3): MV 222418, nearly complete L coracoid missing only the ventral part of the clavicle facet on the acrocoracoid and the lateral process (Fig. 3A), Lake Yanda, collection code THR1984.2, Namba Formation; measurements – medial length = 35.2 mm, SW = 3.8 mm, length scapular cotyla – acrocoracoid = 12.8 mm. MV 222429, R coracoid missing about 25% of length from the sternal end, side of Billeroo Creek, CURNAMONA (prov. ed.) sheet grid coordinates 319151 [but see locality data under paratype SAM P.41321, above], collection code THR1977-206, MV site No. 2372, probably the Namba Formation, rather than the overlying Quaternary Eurinilla Formation; measurements – SW = 3.6 mm, length scapular cotyla – acrocoracoid = 12.7 mm, length humeral facet = 8.1 mm. AMNH 10991, cranial

end L coracoid, Lake Pinpa, north-west side, near CURNAMONA (prov. ed.) sheet grid coordinates 317148 (R. H. Tedford, pers. comm. 30 Aug 2006), collection code QMAM 47, Namba Formation, Pinpa LF; measurements – length scapular cotyla – acrocoracoid = 12.0 mm, length humeral facet = 7.3 mm.

Description: Acrocoracoid not pneumatic, dorsoventral plane aligned at c. 45° to plane of sternal end; clavicle facet does not overhang shaft ventrally, as it does e.g. in *Biziura* and *Oxyura*; supracoracoidal sulcus does not undercut humeral facet; scapular cotyla nearly circular and deep; procoracoid lacks foramen, cranial margin extends at right angles to shaft from mid point of cotyla; ventral sternal facet present, not protuberant; medial angle not acute, with medially bulbous flange above it. These specimens differ from that attributed to *Pinpanetta tedfordi* by their larger size and a less prominent clavicle facet that is either notched (MV 222418) or unnotched (AMNH 10991) with the dorsal part prominent over the supracoracoidal sulcus and the ventral part slightly protuberant of the medial margin but not overhanging the sulcus. The ventral facies beside the sternal articulation is flat, rather than a shallow hollow.

Tibiotarsus (Fig. 3): SAM P.24529, dR tibiotarsus preserved distad of the fibular crest (Fig. 3E), Tedford Locality (Site 2), RV 7250 (= V-5375), Lake Palankarinna, Etadunna Formation, Ditjimanka LF, Zone B, Member 7, measurements – least SW = 3.6 mm, DW = 7.7 mm, depth medial condyle = 9.4 mm, depth lateral condyle = 8.2 mm. SAM P.42701, dL tibiotarsus, Neville's Nirvana, Lake Palankarinna, collection code VSQ 1978-97, Etadunna Formation, Minkina LF, Zone A, measurements – least SW = 3.4 mm, DW = 7.7 mm, depth medial condyle = 8.5 mm, depth lateral condyle = 7.2 mm. SAM P.42702, dL tibiotarsus, western side, Lake Pinpa, collection code VSQ 1978-1, Namba Formation, Pinpa LF, measurements – least SW = 3.7 mm, depth lateral condyle = 7.8 mm. AMNH 10888, pL tibiotarsus, Lake Pinpa, Site C,

collection code QMAM 136, Namba Formation, Pinpa LF, measurements – preserved length = 25.8 mm, PW = 6.8 mm. AMNH 11498, dR tibiotarsus, Lake Pinpa, Site A, collection code QMAM 66, Namba Formation, Pinpa LF, measurements – preserved length = 20.3 mm.

Description: These few tibiotarsi fragments are from a bigger bird than *Pi. tedfordi*. AMNH 10888 reveals an elevated cranial cnemial crest extending down the edge of the anterior facies in similar fashion to *Pi. tedfordi* (UCMP 57248), but unlike that species the depth of the medial articular surface is significantly deeper than that of the lateral articular surface. They have similar depth in *Pi. tedfordi* and in all specialist divers. SAM P.24529 shows that the shaft distad of the fibular crest is round in section, not flattened anteriorly as in diving ducks and *Pi. tedfordi*. The medial condyle is deeper than the lateral condyle, unlike in specialist diving taxa and *Pi. tedfordi* where these depths are about equal. Condylar width is less than their depths. The medial condyle had only a low central prominence. These tibiotarsi, if correctly associated with the humeri described as *Pi. vickersrichae*, indicate that this taxon was a less specialist diver than *Pi. tedfordi*.

SPECIES *PINPANETTA FROMENSIS*
SP. NOV. (FIGS 1, 4)

Holotype: SAM P.43128 (formerly AMNH 10736), R humerus (Fig. 1E, J), reassembled from two pieces, missing proximal part of the deltoid crest, and for which the head has been broken off and reattached, stained light brown.

Diagnosis: A very small duck, about the size of the New Zealand Miocene *Man. minuta*, distinguished from its congeners as follows: smallest member of genus; shorter deltoid crest with *c.* 35% length extending distad of bicipital crest; ventral pneumotricipital fossa as wide as long; dorsal pneumotricipital fossa relatively deeper, stepped down from capital groove, distally maintains groove dorsad of median crest; capital groove forms shallow notch proximally; shaft lacks distal narrowing; and facet for attachment of anterior ligament directed cranially, rather than distoventrally.

Etymology: After Lake Frome and Frome Downs Station, around or on which many of the fossil sites producing the fossils described here have been found.

Type locality: Lake Pinpa (= Pine Lake), 31° 8'S, 140° 13'E, Lake Eyre Basin, Callabonna (= Tarkarooloo) Sub-basin, SA, Site C, the area extending north from the E-W cross lake track to about the point marked by the CURNAMONA (prov. ed.) sheet grid coordinates 317148 (R. H. Tedford, pers. comm. 30 Aug 2006), collected by R. H. Tedford 1971, collection code QMAM 243.

Horizon: Stratigraphy/Age/Fauna: Namba Formation, Late Oligocene 24–26 Mya, Pinpa LF.

Distribution: Late Oligocene (24–26 Mya): Lake Pinpa, Namba Formation, Pinpa LF. Lake Palankarinna, Etadunna Formation, Minkina LF, Zone A; Ditjimanka LF, Zone B; Ngama LF, Zone D, Member 8.

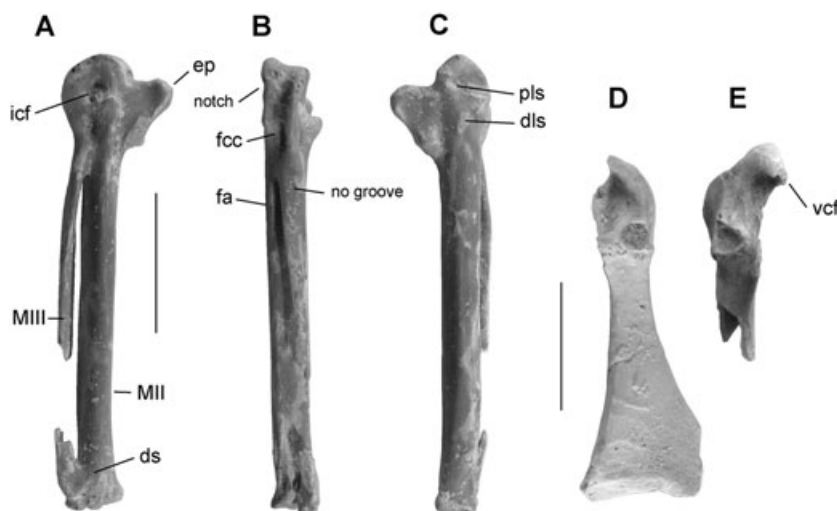


Figure 4. Referred elements of *Pinpanetta fromensis*: left carpometacarpus SAM P.42700 in: A, ventral; B, caudal; and C, dorsal aspects; D, right coracoid SAM P.41301 in dorsal aspect; and E, cranial part left coracoid MV P.222424 in dorsal aspect. Scale bars = 10 mm. See main text for abbreviations.

Measurements of holotype: TL = 50.85 mm, PW from dorsal tubercle = 11.0 mm, length deltoid crest = 14.4 mm, SW = 3.8 mm, DW = 8.3 mm, depth dorsal condyle = 4.8 mm.

Paratypes: SAM P.42675, pL humerus with worn ventral margin to bicipital crest, and SAM P.42676, dL humerus (DW = 7.8 mm, SW = 3.8 mm), both Site 2, Billeroo Creek, 31° 06.205'S; 140° 13.912'E; Namba Formation, Pinpa LF, collected by THW and A. Camens, June 2007.

Referred material: The following specimens are referred to *Pi. fromensis*: those other than humeri on the basis of expected size given the size of the humerus.

Humerus: SAM P.42674, dL humerus, SAM P.42677, worn dR humerus, both Site 2, Billeroo Creek, 31° 06.205'S 140° 13.912'E, Namba Formation, Pinpa LF. AMNH 10954, pL humerus; Lake Pinpa, Site C, collection code QMAM 151, Namba Formation, Pinpa LF, measurements – PW = 11.1 mm.

Description: The reconstructed holotype humerus of *Pi. fromensis* retains damage to the ventral side of the head resulting in loss of the floor of the capital groove and so preventing the form of the end of the capital incision from being determined. However, AMNH 10954 reveals the proximal profile to have a shallow notch, one deeper than the other *Pinpanetta* species. The deltoid crest is missing the proximal 5 mm but the remaining section is relatively high, extending 3.2 mm above the adjacent cranial surface. It is concave dorsally, and the attachment scar for m. latissimus dorsi posterioris links to its distal end before extending farther distally.

Pinpanetta fromensis differs from *Pi. tedfordi* and *Pi. vickersrichae* as follows: dorsal pneumotricipital fossa more deeply excavated, so capital groove opens to fossa from shelf, more excavated under head, and fossa forms a groove adjacent to median crest; deltoid crest shorter. It differs from *Pi. tedfordi* by the ventral pneumotricipital fossa being as wide as long and that the shaft diameter does not narrow distally.

Humeri of *Mal. membranaceus* are only slightly larger than *Pi. fromensis* and have a similar development of the dorsal pneumotricipital fossa, e.g. SAM B.39385; however, they differ as follows: ventral end of the capital groove with more distinct notch in proximal profile; ventral pneumotricipital fossa relatively wider; deltoid crest shorter, beside whose distal end the attachment scar for m. latissimus dorsi posterioris commences and passes distad of without connection; brachial fossa smaller; facet for attachment of anterior ligament craniodistally directed (rather than cranioventrally).

Humeri of the similar-sized *Man. minuta* of the St Bathans Fauna in New Zealand differ from those of *Pi. fromensis* as follows: dorsal tubercle distinctly elongate rather than about as wide as long; proximal profile at ventral end of capital groove distinctly notched; ridge for attachment of supraspinatus, although extending to level with end of bicipital crest in both taxa, is much less prominent, such that there is no distinct groove dorsad of median crest; intumescencia humeri less inflated cranially; deltoid crest less elevated from cranial surface; brachial fossa markedly deepened distoventrally rather than relatively flat and even depth.

The ventral tubercle extends at right angles to the ventral pneumotricipital fossa in *Pi. fromensis*. In all diving taxa, it is directed slightly distally to overhang the fossa, sometimes markedly, e.g. *Oxyura*. The deeper dorsal pneumotricipital fossa may be associated with a diving habit as it is deepened and broadened to an extreme in *Oxyura*; however, it is deep in *Malacorhynchus* which is not a specialized diving taxon. Most specialized divers have a distally narrow humeral shaft, e.g. *Oxyura*, *Aythya*, *Mergus*, a feature not seen in *Pi. fromensis*. Similarly, the facet for the attachment of the anterior ligament is directed cranially, rather than distoventrally as seen in specialist divers across diverse clades of anatids e.g. *Oxyura*, *Aythya*, and *Mergus*. These observations suggest that *P. fromensis* was not a specialized diver, and in this was similar to *Pi. vickersrichae*.

Ulna: SAM P.22837, L ulna, Mammalon Hill, Lake Palankarinna, Etadunna Formation, Ngama LF, Zone D, Member 8, measurements – preserved length = 44.7 mm, estimated TL = 46 mm.

The single available specimen is complete, but worn proximally so that the structure of the dorsal cotylar process and of the tuber. bicipitale ulnae in the incisura radialis is undeterminable. It has the following features: brachial fossa shallow; tuberculum for ventral collateral ligament not separated from ventral cotyla by deep groove (as in *Man. minuta*). It is smaller than ulnae of *Nettapus* with which it shares a shallow brachial fossa. If correctly associated with the humerus, this taxon has a comparatively short ulna.

Carpometacarpus (Fig. 4): SAM P.42700, L carpometacarpus (Fig. 4A–C), Neville's Nirvana, Lake Palankarinna, collection code VSQ 1978-40P, Etadunna Formation, Minkina LF, Zone A, measurements – TL = 31.8 mm, PW = 7.6 mm. AMNH 10938, L carpometacarpus lacking only the minor metacarpal, Lake Pinpa, Site C, Namba Formation, Pinpa LF, measurements – TL = 29.0 mm, PW = 7.1 mm. SAM

P.41261, worn L carpometacarpus, White Sands Basin, Lake Palankarinna, Etadunna Formation, Ditjimanka LF, Zone B, measurements – estimated length = 29.5 mm, PW = 6.5 mm. AMNH 10725, worn pR carpometacarpus, Lake Pinpa, Site C, collection code QMAM 264, Namba Formation, Pinpa LF. AMNH 10745, pL carpometacarpus, Lake Pinpa, Site C, Namba Formation, Pinpa LF, measurements – PW = 7.0 mm. AMNH 10748, worn L carpometacarpus, Lake Pinpa, Site C, collection code QMAM 243, Namba Formation, Pinpa LF, measurements – PW = 6.9 mm. AMNH 10951, pR carpometacarpus, Lake Pinpa, Site C, collection code QMAM 151, Namba Formation, Pinpa LF, measurements – PW = 6.7 mm.

The well-preserved specimens SAM P.42700 and AMNH 10938 enable the following character states to be determined: external rim of trochlea carpalis with a shallow carpal notch; both the anterior carpal fossa and cuneiform fossa are present, deep; internal carpal fossa deep, distinct foramen in base, separated from extensor process by rounded ridge; one ligamental facet for ligamentum ulnocarpo-metacarpale dorsale below the carpal rim (not two); short proximal synostosis or region from intermetacarpal space to proc. alularis (pollical facet); minor metacarpal not grooved at the proximal synostosis; flexor attachment marked by single scar distal of proximal synostosis of minor and major metacarpals; distal synostosis shorter than distal width; facets for digits II and III of approximate equal distal length. These specimens are slightly smaller than that of *Nettapus*, and bigger than those of *Man. minuta*.

Coracoid (Fig. 4): SAM P.41301, worn R coracoid (Fig. 4D), with the acrocoracoid, the tip of the procoracoid, the tip of the medial angle, and the lateral process missing, SAM North (a white sand locality), Lake Palankarinna, 28° 46.503'S; 138° 24.164'E, Etadunna Formation, Ditjimanka LF, Zone B. MV 222424, cranial part L coracoid preserved from the mid shaft (Fig. 4E), Lake Pinpa, (location code MV No. 2348), Namba Formation, Pinpa LF.

Together these specimens show the following: acrocoracoid not pneumatic, dorsoventral plane of acrocoracoid aligned nearly at right angles to plane of sternal end; both dorsal and ventral lobes of clavicle facet extensively overhang supracoracoidal sulcus; ventral clavicle facet does not overhang ventral shaft facies; supracoracoidal sulcus not excavated below humeral facet; scapular cotyla large and oval; procoracoid lacks a foramen; dorsal surface of the blade without pneumatic fossa; ventral facies flat; and ventral sternal facet present but not prominent of the ventral facies.

These coracoids are very similar to those referred to *Pi. tedfordi* and *Pi. vickersrichae*, but are smaller than both. Among extant taxa, SAM P.41301 is most similar to coracoids of *Nettapus pulchellus* and *Mal. membranaceus*, although it is smaller. It is more similar to *Malacorhynchus* and differs from *Nettapus* in the shape of the humeral facet, which is widest at about mid-length (not widest and rounded towards acrocoracoidal end as in *Nettapus*). Similarly, MV 222424 is very similar to both *Pi. tedfordi* and *Malacorhynchus* in the form of the clavicle facet that extensively overlaps the supracoracoidal sulcus.

Measurements: SAM P.41301 – estimated total medial length = 27 mm, SW = 3.2 mm; MV 222424 – length scapular cotyla-head = 8.3 mm; SW = 2.9 mm; length humeral facet = 6.0 mm.

Scapula: SAM P.42673, L scapula, Billeroo Creek, Site 2, 31° 06.205'S; 140° 13.912'E, Namba Formation, Pinpa LF, measurements – width acromion to humeral facet = 6.7 mm, shaft height = 2.2 mm.

Small anatid scapula, shaft with parallel dorsal and ventral margins, acromion not directed dorsally from shaft, coracoidal articulation globose and prominent, humeral facet laterally orientated.

Tibiotarsus: AMNH 10953, pL tibiotarsus, Lake Pinpa, Site C, Namba Formation, Pinpa LF, measurements – preserved length = 9.0 mm, PW = 5.8 mm. SAM P.42678, dL tibiotarsus with broken lateral condyle, Billeroo Creek, Site 2, 31° 06.205'S 140° 13.912'E, Namba Formation, Pinpa LF, measurements – SW = 2.5 mm.

These specimens are smaller than those referred to *Pi. tedfordi*, but have a similar morphology. They reveal that the medial and lateral articular facets of the proximal end have a similar depth (rather than the medial one extending markedly caudad of the lateral one), and that they are separated caudally by a distinct notch. The structure of the cnemial crests is not determinable.

Tarsometatarsus: AMNH 10838, worn dR tarsometatarsus, Lake Pinpa, Site C, Namba Formation, Pinpa LF, measurements – DW = c. 6.0 mm.

This specimen is referred to Anatidae as it lacks a fossa metatarsi I (metatarsal fossa) and the plantar exit for the distal foramen opens in a groove into the lateral intertrochlear notch, and is referred on size to *Pi. fromensis*. Trochlea metatarsal II does not extend distad of the lateral intertrochlear notch.

SUBFAMILY TADORININAE REICHENBACH 1849–1850: SHELDUCKS

The following taxon is referred to the tadorinines as the humerus has the following characters: (1)

proportions as in *Tadorna*; (2) elevated and elongate dorsal tubercle; (3) capital shaft ridge directed at area between dorsal tubercle and head; (4) dorsal pneumotricipital fossa narrow, not excavated under head; (5) ventral pneumotricipital fossa large, more than half proximal width, wider than long, pneumatic; (6) the osseous lamella extending from the caudal shaft surface around the distal margin of the ventral pneumotricipital fossa merges with the bicipital crest/base of fossa in ventral half of fossa; (7) deltoid crest dorsally concave; (8) facet for anterior ligament elevated, directed distally; (9) scapulotricipital sulcus a distinct groove caudally, extends around distal end; (10) distinct ectepicondylar prominence; (11) flexor process equal distal extent to dorsal condyle;

Character 1 is derived in tadornines with *Anseranas*, dendrocygnines, and anserines plesiomorphic with an elongate humerus. Character 3 is derived in tadornines relative to *Anseranas* and anserines where the ridge is directed towards the head. Character 5 is derived in tadornines with *Anseranas*, dendrocygnines, and anserines relatively plesiomorphic with a narrow fossa. Character 6 is considered an apomorphy of tadornines with the plesiomorphic state of the lamella remaining elevated from the floor of the fossa and extending up under the ventral tubercle in *Anseranas*, dendrocygnines, and anserines: anatines are more derived with the lamella merging with the floor of the fossa in the dorsal part of the fossa. Character 7 and the elevated dorsal tubercle are retained plesiomorphic features that distinguish tadornines from anatines that have derived states (deltoid crest convex or flat dorsally; dorsal tubercle not elevated off adjacent facies). Character 8 is derived relative to the unelevated state in *Anseranas* or the low elevation of the facet in anserines. Character 10 is a retained plesiomorphy with the prominence most developed in the tadornines (*Miotadorna*, *Alopochen*) that distinguishes tadornines from the anatines in which it is apomorphically lost.

Humeri of *Anseranas* differ greatly, for example, more elongate; capital shaft ridge directed towards the head; a relatively small ventral pneumotricipital fossa largely occluded by a broad osseous lamella extending from the caudal shaft surface; short flexor process; no scapulotricipital groove caudally or distally; and facet for anterior ligament not elevated. Those of anserines, geese and swans, are more elongate; the osseous lamella extending from the caudal shaft surface into the ventral pneumotricipital fossa remains elevated off the base of the fossa and extends up under the ventral tubercle; and the capital shaft ridge is directed towards the head. *Dendrocygna* species are all smaller; the dorsal tubercle is near circular; the osseous lamella extending from the caudal shaft surface into the ventral pneumotricipital

fossa is as in anserines; and the ventral pneumotricipital fossa is small, much less than half proximal width. Humeri of the oxyurines, *Biziura*, *Oxyura*, and *Malacorhynchus* differ in several ways but all have a closed or nonpneumatic ventral pneumotricipital fossa. *Stictonetta*, apart from the smaller size, differs with the capital shaft ridge directed towards the dorsal tubercle and so has a wider dorsal pneumotricipital fossa. All anatines differ by the derived loss of the capital shaft ridge and loss of elevation of the dorsal tubercle, and by the dorsal surface of the deltoid crest being flat or convex.

GENUS *AUSTRALOTADORNA* GEN. NOV.

Type species: Australotadorna alecwilsoni sp. nov.

Diagnosis: Humerus more robust than other tadornines, ventral pneumotricipital fossa larger, and caudal margin of bicipital crest in ventral view forming a single plane from ventral tubercle to junction with shaft rather than forming a marked angle with the proximal section at near right angles to the shaft.

Etymology: For its inferred ancestral relationship to the shelduck *Tadorna*, and that it derives from Australia.

Description and comparison: *Australotadorna* gen. nov. shares with tadornines the above features and that the capital groove forms only a shallow notch in the proximal profile, not a deep one as in most oxyurines and all anatines. The ventral pneumotricipital fossa is large and, with its internal diameter at about 46% of proximal width, is broader than that of all other tadornines. It is highly pneumatic and thus differs from *Miotadorna* where bone struts fill the fossa inside of the median crest. The capital shaft ridge is better developed and farther separated from the dorsal tubercle than it is in *Tadorna* species, but is in this similar to *Miotadorna* from New Zealand. As in *Miotadorna*, it has the dorsal tubercle separated from the capital ridge by a flaring groove extending onto the dorsal surface. *Alopochen* differs with a dorsal tubercle about as wide as long, rather than elongate, and by the capital shaft ridge being more directed to the dorsal tubercle. The latter results from a deeper and broader dorsal pneumotricipital fossa that extends under the head. *Chenonetta* and *Hymenolaimus*, two genera often associated with tadornines, have a much wider dorsal pneumotricipital fossa with the capital shaft ridge more weakly developed and directed towards the dorsal tubercle. The well developed ectepicondylar prominence is better developed than in *Tadorna* but similar to the development in *Miotadorna* and *Alopochen*. The brachial fossa was

secondly deepened distoventrally and did not extend closer than 3 mm of the dorsal shaft margin. Such a secondary deepened brachial fossa is seen in *Miotadorna* and *Alopochen*.

SPECIES *AUSTRALOTADORNA ALECWILSONI*
 SP. NOV. (FIGS 5, 6)

Holotype: SAM P.43141 (formerly AMNH 11499), L humerus (Fig. 5B, D, F), reassembled from several fragments with plaster infill in areas of shaft so that distal end is distorted ventrally; dorsal margin of deltoid crest lost, a 7 by 5 mm hole in ventral part of intumescencia humeri, distal margin of bicipital crest worn, and craniodistally part of the shaft proximal to the attachment of the anterior ligament extending through the brachial fossa is lost; light brown in colour.

Diagnosis: As for genus.

Etymology: For Alec Wilson, owner of Frome Downs Station who has freely allowed access to the fossil sites and helped palaeontologists over many years.

Type locality: Lake Pinpa (= Pine Lake), 31° 8'S, 140° 13'E, Lake Eyre Basin, Callabonna (= Tarkarooloo) Sub-basin, SA, north-west side Pine Lake, near grid coordinates 317148 on the CURNAMONA (prov. ed.) sheet (R. H. Tedford, pers. comm. 30 Aug 2006), collected by R. H. Tedford *et al.*, 1971, collection code QMAM 74.

Horizon: Stratigraphy/Age/Fauna: Namba Formation, Late Oligocene 24–26 Mya, Pinpa LF.

Distribution: Late Oligocene (24–26 Mya): Lake Pinpa, Namba Formation, Pinpa LF; possibly Lake Palankarina, Etadunna Formation (see below).

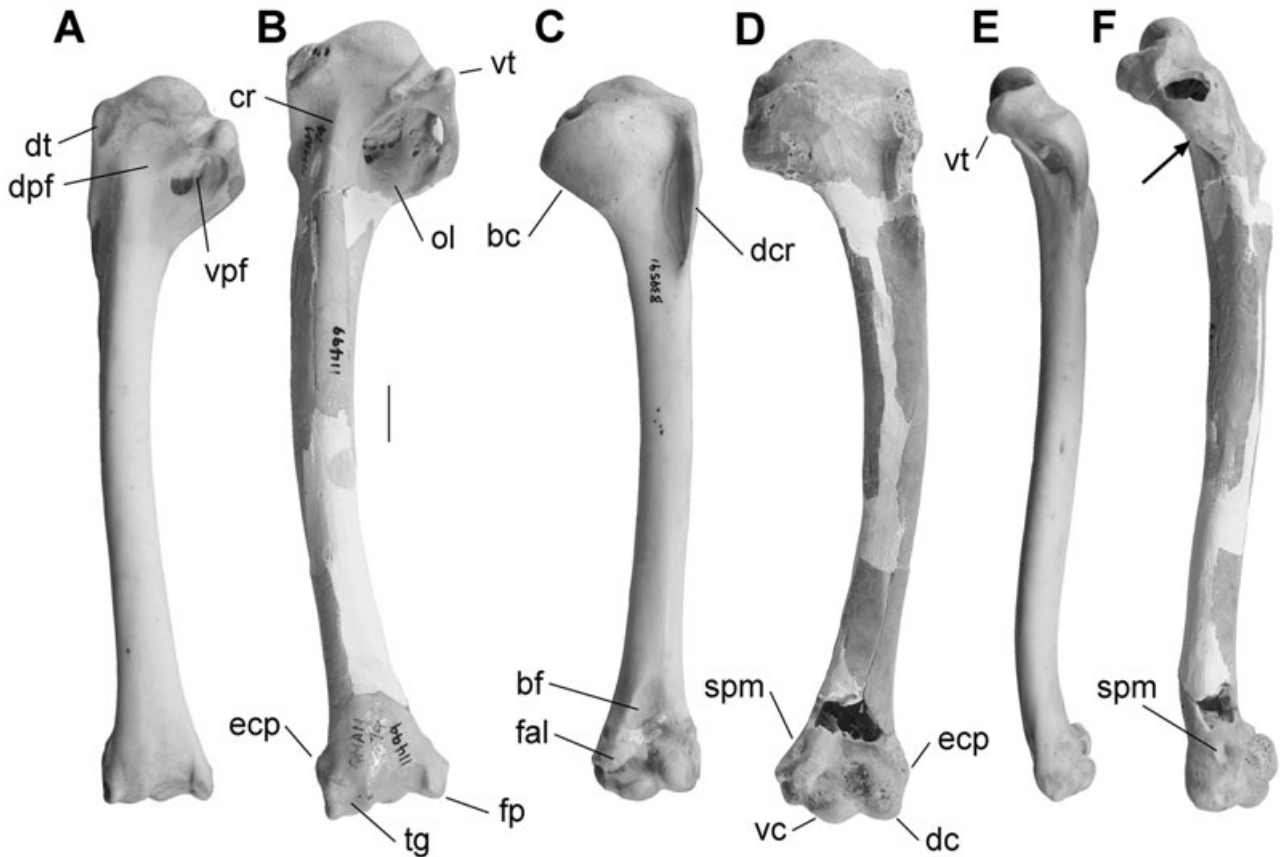


Figure 5. Left humeri of tadornines in caudal (A, B), cranial (C, D) and ventral (E, F) views: A, C, E, modern *T. tadornoides* SAM B.39591; and B, D, F, *Australotadorna alecwilsoni* (SAM P.43141). The arrow points to the planar caudoventral margin of the bicipital crest compared to the angled margin in *Tadorna*. Scale bar = 10 mm. See main text for abbreviations.

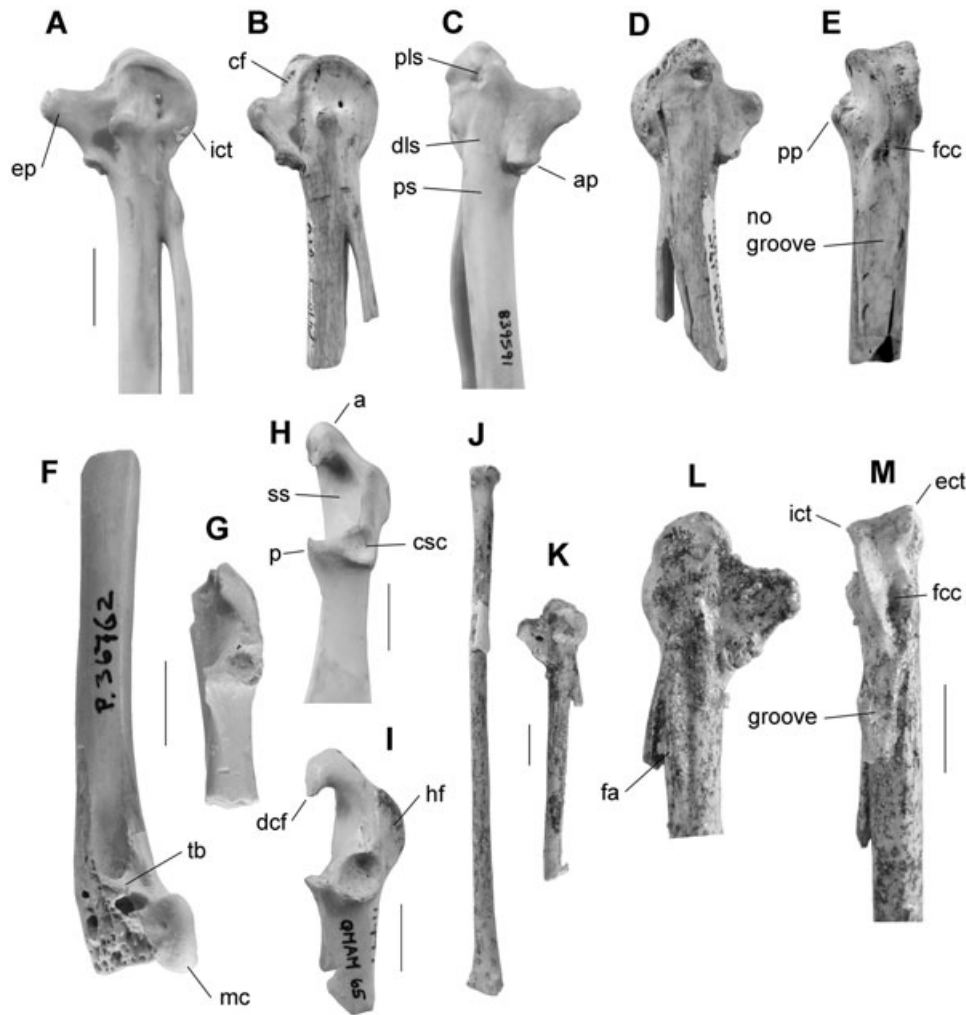


Figure 6. Fossil tadornine bones compared with modern *Tadorna tadornoides* SAM B.39591. *Tadorna tadornoides*: A, C, proximal right carpometacarpus; and H, dorsal view cranial half coracoid. Fossils referred to *Australotadorna alecwilsoni*: B, D, E, proximal right carpometacarpus; F, distal right tibiotarsus SAM P.36762 in anterior view; G, cranial part right coracoid (SAM P.24531) in dorsal aspect; I, cranial part right coracoid (SAM P.43137) in dorsal aspect. Fossils referred to an undetermined tadornine from Alcoota: J, left radius UCMP 65985 in dorsal aspect; and right carpometacarpus NT P.2913 in K, ventral; L, dorsal; and M, caudal views. Scale bars = 10 mm. See main text for abbreviations.

Measurements of holotype: TL = 132.4 mm (as preserved bent), estimated restored TL = 134 mm, PW (maximum from dorsal tubercle) = 28.7 mm, SW = 10.2 mm, DW = 22.4 mm, depth dorsal condyle = 12.6 mm.

Paratype: *Coracoid* (Fig. 6): SAM P.43137 (formerly AMNH 11497), cranial part R coracoid (Fig. 6I), Lake Pinpa, north-west side near CURNAMONA (prov. ed.) sheet grid co-ordinates 317148, R. H. Tedford, pers. comm. 30 Aug 2006, collection code QMAM 65, R. H. Tedford *et al.*, July 1971, Namba Formation, Pinpa LF. Measurements – preserved length = 38 mm, length humeral facet = 15 mm, SW = c. 7.5 mm.

Description and comparison
Humerus: As for genus.

Coracoid: SAM P.43137 preserves only the dorsal half of the cranial end so lacks the tip of the acrocoracoid, the ventral clavicle facet and the ventral half of the supracoracoidal sulcus. It is of appropriate size for *Australotadorna*, given the size of the humerus SAM P.43141. It has the following features: deep circular scapular cotyla, c. 7 mm in diameter; short supracoracoidal sulcus not undercutting the humeral facet; ridge separating supracoracoidal sulcus from humeral facet relatively short, broad and rounded; shallow fossa with small pneumatic foramina adja-

cent to the scapular cotyla on sulcus side of this ridge; dorsal clavicle facet markedly overhangs sulcus as sharp crest with pneumatic foramina under it; procoracoid short and robust, although tip lost; procoracoid lacking a foramen in it, although insufficient of the shaft, remains to determine if it had a notch as seen in *Cereopsis*; supracoracoidal sulcus extended as a groove along ventral side of procoracoid; ventral facies apparently flattened adjacent procoracoid, not very deep as in *Cereopsis*.

Although SAM P.43137 is of similar size to coracoids of *Anseranas*, it differs as follows: it lacks a procoracoidal foramen; it has a sharp dorsal lobe of the clavicle facet and pneumatic foramina in the supracoracoidal sulcus penetrating the acrocoracoid (both lacking in *Anseranas*). The pneumatic acrocoracoid suggests an affinity with anserines, but only *Cereopsis* has a similarly sharp overhanging dorsal clavicle lobe. Tadornines, e.g. *Alopochen* and *Miotadorna* also have pneumatic foramina under the clavicle facet, so their presence is a plesiomorphic feature. Whereas the fossil shares with *Cereopsis* a relatively broad, short, rounded ridge between the supracoracoidal sulcus and the humeral facet, a groove along the ventral side of the procoracoid is not seen in anserines but is in tadornines. The broad, rounded ridge cranial of the scapular cotyla differs from tadornines where it is narrower, but this may relate to the larger size of the fossil. Larger specimens of *Miotadorna*, e.g. NMNZ S.42315 have a short relatively inflated ridge approaching the condition seen in SAM P.43137. A shallow pneumatic fossa dorsally immediately cranial of the scapular cotyla in the fossil has its homologue in a small elongate pneumatic fossa on the supracoracoidal sulcus side of the ridge in tadornines, e.g. in *Tadorna tadornoides* and *Miotadorna*. The insertion on the shaft of the procoracoid is relatively shorter than in *Tadorna* and *Miotadorna* but breakage means its medial, ventral, and cranial extents are not determinable. In summary, SAM P.43137 is of appropriate size for *Australotadorna* and shares more features with tadornines than other groups of waterfowl, but it is distinguished by several apomorphies, such as a more circular scapular cotyla and shorter procoracoidal insertion. Their significance is obscure at present, but given that *Australotadorna* is several million years older than the next known tadornine, *Miotadorna*, such differences are likely to be plesiomorphic features.

Referred material: The following specimens are referred to *Australotadorna alecwilsoni* on the basis of their appropriate size and tadornine-like morphology.

Coracoid (Fig. 6): SAM P.24531, cranial part R coracoid (Fig. 6G), Tedford Locality, Lake Palankarina, Etadunna Formation, Ditjimanka LF, Zone B. Measurements – SW = 5.8 mm, length humeral facet $c.$ = 12.3 mm.

The specimen lacks the entire sternal blade, and the tip of the acrocoracoid including the clavicle facets. It has a standard anatid form: the scapular cotyla is circular and deep; procoracoid lacks a foramen; and the supracoracoidal sulcus does not have a secondary fossa below the humeral facet. Coracoids of Phoenicopteriforms, present in the Etadunna Formation, differ with a procoracoidal foramen. It is of similar size to coracoids of tadornines. The dorsal facies of the ridge leading from the humeral facet to the acrocoracoid is like that in SAM P.43137, short and broadly inflated. It is smaller than SAM P.43137; however, the size difference is within that seen in sexual dimorphism in modern anatids. SAM P.43137 is pneumatic below the dorsal clavicle facet but this cannot be determined in SAM P.24531. In summary, this specimen may be referred to *Australotadorna alecwilsoni* or a very similar taxon.

Carpometacarpus (Fig. 6): All from Lake Pinpa, Site C, Namba Formation, Pinpa LF, collected by R. H. Tedford *et al.*, 1971. AMNH 10728: pL carpometacarpus, PW = 16 mm. AMNH 10818, pL carpometacarpus (Fig. 6B, D, E), collection code QMAM 175, PW = 15.7 mm. AMNH 10864, worn pR carpometacarpus, collection code QMAM 175, PW = 14.6 mm.

These specimens preserve only the proximal half of the element. They are about the size of *Tadorna tadornoides* but have a shorter extensor process. They are tentatively referred to *Australotadorna* on the basis of size and that there is no evidence of another large anatid in the source fauna. They have the following features: shallow infratrochlear fossa, a deep cranial fossa, moderately deep cuneiform fossa, an elongate proximal synostosis, and the minor metacarpal is not grooved at the fornix. Only AMNH 10818 allows the morphology of the ligamental scars proximally on the dorsal surface. The proximal one is prominent, but a second, shallow and elongate distal scar usually found in tadornines is present only as an obscure elongate hollow, but polishing of the bone by windblown sand may have obscured its real form.

Scapula: UCMP 57156, R scapula, Lake Palankarina, Tedford Locality Site 3, UCMP V-5762, R. H. Tedford 1957, collection code RHT#465, Etadunna Formation, Minkina LF, Zone A, Member 4, measurements – acromion to ventral margin of humeral facet = 14.7 mm, depth of collum scapulae (blade) = 5.9 mm. UCMP unreg., R scapula, Leaf Locality, Lake

Table 3. Measurements (mm) and selected ratios (as percentages) of the fossil tibiotarsus SAM P.36762 compared to summary statistics [mean (range), standard deviation] for those for *Tadorna tadornoides* (five M, five F), and *Anseranas semipalmata* (one F, two M), all from SAM (catalogue numbers *T. tadornoides*: SAM B 39568, 39575, 39584-5, 39592, 39866, 39874, 39877-9; *Anseranas*, as below)

	SW	Caudal width distal condyles	Height medial condyle	Depth between distal condyles
<i>Tadorna tadornoides</i> <i>n</i> = 10	5.3 (5.1–5.8) 0.21	9.1 (8.7–9.6) 0.31	12.8 (12.1–13.5) 0.42	8.2 (7.5–8.5) 0.33
<i>Anseranas</i> , F, 39824	6.8	10.5	15.5	10.8
<i>Anseranas</i> , M, 36790	7.6	11.7	17.7	11.9
<i>Anseranas</i> , M, 48035	8	11.2	18.5	12.6
SAM P.36762	6.4	10	14.6	c. 8.4
	SW/CWD	SW/HMC	CWD/HMC	SW/DD
<i>Tadorna tadornoides</i> <i>n</i> = 10	57.77 (56.0–60.4) 1.35	41.22 (39.8–43.0) 0.32	71.36 (69.5–73.2) 1.21	64.83 (60.7–68.3) 2.48
<i>Anseranas</i> , F, 39824	64.96	42.94	66.10	63.87
<i>Anseranas</i> , M, 36790	64.76	43.87	67.74	62.96
<i>Anseranas</i> , M, 48035	71.43	43.24	60.54	63.49
SAM P.36762	64.00	43.84	68.49	76.19

Abbreviations: SW, shaft width; CWD, caudal width distal condyle; HMC, height of medial condyle; DD, depth between distal condyles; F, female; M, male.

Ngapakaldi, UCMP V-6313, collection code RAS #5294, Wipajiri Formation, Early Miocene, Kutjamarpu LF, measurements – blade depth = 5.2 mm.

UCMP 57156 is missing most of the blade. It has the general shape of anatid scapulae, particularly a compressed dorsal margin to the blade, acromion extending cranial of tuberculum coracoideum, and the coracoid tubercle prominent of a line joining the humeral facet and acromion. It is distinguished from *Anseranas* and anserines by the lack of pneumatic foramina either laterally or medially. In size, it is similar to that of *Tadorna tadornoides* and thus larger than scapulae of *Biziura*, *Oxyura*, *Dendrocygna*, *Malacorhynchus*, *Stictonetta*, and *Aythya* and other anatines. UCMP unreg., worn and lacking most of the blade and the acromion, is similar to UCMP 57156, but preserves little of diagnostic value.

Tibiotarsus (Fig. 6): SAM P.36762, dR tibiotarsus (Fig. 6F), White Sands/SAM North, RV-7247, Lake Palankarinna, Etadunna Formation, Ditjimanka LF, Zone B, Member 6.

Of typical anatid shape, SAM P.36762 is smaller than tibiotarsi of *Anseranas*, but is slightly larger and has a stouter shaft than *Tadorna tadornoides* (Table 3). It is thus smaller than anserines, e.g. *Cereopsis*, and larger than *Biziura*, *Stictonetta*, oxyurines, and all anatines. SAM P.36762 is also similar to tibiotarsi of *Tadorna* in qualitative features and differs from those of *Anseranas* as follows: short tendinal bridge; distal end with distal margin near

right angles to the shaft (not sloped distally); medial condyle forming notch with shaft at proximo-anterior junction (rather than a wide angle); and medial prominence small and occluded by medial condyle in anterior view (large, protuberant). It differs from those of *Dendrocygna* by larger size and greater medial inflection of the medial condyle. As it has tadornine features it is tentatively referred to *Australotadorna alecwilsoni*.

Measurements: See Table 3.

GENUS INDETERMINATE, MAGN. *TADORNA* SP.

Humerus: AMNH 10966, fragment pR, Lake Pinpa, Site A, R.H. Tedford 1971, Namba Formation, Pinpa LF, measurements – width of head = 16.0 mm, depth of head = 8.0 mm.

Description: This fragment preserves only the head and part of the dorsal tubercle. It is tentatively referred to Anseriformes as the caudal margin of the head is roughly at right angles to the presumed line of the shaft. The dorsal pneumatic fossa did not extend under the head. It is smaller than SAM P.43141 and of similar size to *Tadorna*, but nothing further can be determined.

ALCOOTA TADORNINE, GENUS INDETERMINATE,
MAGN. *TADORNA TADORNOIDES* (FIG. 6)

The following two specimens are referred to Tadorinae but in the absence of more diagnostic elements they are not named.

NTM P.2913: R carpometacarpus (Fig. 6K–M), Alcoota, quarry unknown, Alcoota Homestead, NT, 22° 52'S, 134° 27'E, Waite Formation, Miocene, c. 8 Mya, Alcoota LF. Measurements – PW = 16.7 mm, length to distal end intermetacarpal space = 64 mm, proximal synostosis wider (7.5 mm) than long (c. 6.5 mm).

NTM P.2913 lacks the synostosis metacarpalis distalis (distal synostosis) and the minor metacarpal. It has the following features: dorsal rim of the carpal trochlea distinctly notched; infratrochlear fossa shallow with base slightly above ventral facies of extensor process and lacking a large foramen in its base; proximal margin of extensor process at right angles to shaft; extensor process less than half proximal width; alular process distinctly distad of distal end of ventral rim of carpal trochlea; small distinct fossa dorsally adjacent to alular process; dorsal facies of carpal trochlea has two distinct ligamental attachments for the external ligament, one proximal, slightly elevated, caudally directed, and larger of pair, one distal and more elongate, level with the cuneiform fossa; cuneiform fossa extends deeper than the adjacent shaft facies; anterior carpal fossa present; the minor metacarpal at the proximal synostosis not grooved, has a prominent tuberosity on ventral margin centred on the synostosis; tuberosity for flexor attachment distad of the proximal synostosis; and cranial facies of the major metacarpal is convex.

This fossil is referred to Anatidae because of the apomorphic presence of a distinct notch in the dorsal rim of the carpal trochlea. The conformation of the ligament scars on the dorsal facies (distal one more elongate, larger than proximal one of pair, and level with the cuneiform fossa, proximal one slightly elevated and caudally directed) is an apomorphy for Tadorninae (including *Hymenolaimus*) and Anserinae (including *Cereopsis*): in all anatines the distal scar is smaller (second scar lacking in *Anseranas*). Both can be excluded from Cygnini by the lack of the apomorphic state for cygnines of a distally sloping extensor process, and from all anserines by markedly smaller size.

The carpometacarpus of *Anseranas*, which in females may be of similar size to the fossil, differs markedly as follows: the infratrochlear fossa has a large foramen in its base and is markedly elevated above the ventral facies of the extensor process; it lacks an anterior carpal fossa; it has a paired flexor attachment; the dorsal rim of the carpal trochlea has a very shallow or incipient notch; the cranial facies of the major metacarpal is markedly flattened; it has only a single scar for the external ligament attachment. *Cereopsis*, apart from being larger has a markedly more robust extensor process, more robust and ventrally directed pisiform process, and flattened

cranial facies to the major metacarpal. Most members of Anserinae (including *Cereopsis*) lack an anterior carpal fossa (exception, *Anser brachyrhynchus*) and most have a rounded or very weakly grooved minor metacarpal at the proximal synostosis (exceptions *Anser brachyrhynchus* and some individual *Branta canadensis*). However, the small distinct fossa adjacent to the alular process is seen in *Cereopsis*.

This fossil is similar in size to carpometacarpi of *Tadorna* and so larger than *Biziura*, *Oxyura*, *Stictometta*, *Malacorhynchus*, *Anas*, *Aythya*, and other anatines. Although it is of similar size to the Australian endemic *Tadorna tadornoides*, the latter has a more drawn-out tip to the extensor process, where proximodistal width increases evenly from the cranial tip of the process. Secondly, the minor metacarpal is distinctly grooved in *T. tadornoides* as in most tadornines including the Miocene *Miotadorna* from New Zealand (flattened in *Hymenolaimus*), but is not grooved in the fossil. The fossil differs further from *Tadorna* in that the alular process is distad of the carpal trochlea and by the presence of a small distinct fossa adjacent to alular process. It lacks the apomorphic state for *Hymenolaimus* of a very deep cuneiform fossa bound dorsally by an expanded dorsal rim of the carpal trochlea.

NTM P.2913 differs from the older fossils tentatively referred to *Australotadorna* as follows: extensor process longer (44 vs. 37% proximal width); alular process distally offset from distal end of carpal trochlea; depth at proximal synostosis less despite greater proximal width.

UCMP 65985: L radius (Fig. 6J), Alcoota, Paine Quarry, V6346, Alcoota Homestead, NT, 22° 52'S, 134° 27'E, collected by Woodburne *et al.*, 1963, Waite Formation, Miocene, c. 8 Mya, Alcoota LF. Measurements – TL = 128.6 mm, PW = 7.6 mm, DW = 8.7 mm.

The fossil is reconstructed with damage rebuilt in plaster in its proximal quarter. It differs markedly from *Anseranas* radii in having a more robust shaft and that the distal end lacks the abrupt widening, both dorsally and ventrally, from the shaft. Also, the depressio ligamentosa (ulnar depression) is centrally located on the ventral surface and bound by a large ligamental prominence ventrally, whereas in *Anseranas* the ulnar depression is in two parts divided by a median ligamental tuberosity. The fossil is smaller and straighter than anserine radii, but differs little from radii of *Tadorna* and is the size of a large *T. tadornoides*. It differs from *T. tadornoides* by the ulnar depression being deeper and more centrally located on the ventral facies and the sulcus tendinosus (tendinal groove) on the dorsal surface is deeper. Proximally, the capital tuberosity is relatively larger. The carpometacarpus (*NTM P.2913*) and the radius

(UCMP 65985) derive from the same local fauna, and are of appropriate size to come from a single species. Pending discovery of more diagnostic elements this taxon is not named.

OLIGO-MIOCENE INDETERMINATE ANATID FOSSILS

UCMP unreg.: L scapula, indet. small anatid; Leaf Locality, Lake Ngapakaldi, UCMP V-6313, collected by R. A. Stirton, collection code RAS#5274, Wipajiri Formation, Early Miocene, Kutjamarpu LF, measurements – length acromion to ventral side humeral facet = 7.7 mm, depth blade = 3.5 mm. The specimen has typical anatid form with a relatively short acromion.

MV 222431: R manus phalanx II.1, anatid indet., Neville's Nirvana, Lake Palankarina, MV site number 2396, I-V5367, Etadunna Formation, Minkana LF, Zone A, measurements – TL = 14.9 mm.

SAM P.42671: R manus phalanx II.1 lacking distal end, anatid indet., Site 2, Billeroo Creek, 31° 06.205'S; 140° 13.912'E, THW and A. Camens June 2007, Frome Downs Station, South Australia, Namba Formation, Pinpa LF.

SAM P. 42680: pL and dL radius, anatid indet., Lake Pinpa, Site 6, 31° 08.289'S; 140° 12.679'E, THW and A. Camens June 2007, Namba Formation, Pinpa LF.

AMNH 10935: pL radius, anatid indet., Lake Pinpa, Site C, Namba Formation, Pinpa LF.

UCMP 65978: pL carpometacarpus, anatid indeterminate cf. *Malacorhynchus membranaceus* SAM B.39384, Alcoota, Paine Quarry, UCMP V-6345, collection code RAS 5478, collected by Stirton 1962.

QM F52742 (= AR11004): dR femur with lateral condyle and fibular trochlea both eroded caudally and medial condyle eroded cranially, anatid indet., Sticky Beak Site (System A), Riversleigh, Queensland, Late Oligocene – early Miocene. Measurements: DW > 21.2 mm, SW = 8.7 mm. This specimen has a typical anatid shape and differs from *Anseranas* in two main ways: (1) the linea intermuscularis caudalis from the middle of the bone is aligned on the medial side, mesad of the nutrient foramen, and was directed towards the now missing femoral head (aligned laterally and directed towards lateral side in *Anseranas*); (2) the tuber. M. gastrocnemialis Lateralis is elongate (8 by 3.5 mm), not near circular. That this impression is relatively short and does not have a distinct bend in the proximal half indicates that it is plesiomorphic relative to anserines, exclusive of *Cereopsis* and *Cnemioornis*, and all other anatids, where the scar is more elongate to varying degrees and distinctly bent medially. In so far as preserved the specimen differs from *Cereopsis*, by a shallower popliteal fossa and a broader ridge separating that fossa from the tuber. M. gastrocnemialis lateralis. Little more can be said from this fossil other than that an anatid of similar size and evolutionary grade to *Cereopsis* existed in the System A faunas at Riversleigh.

RESULTS – PHYLOGENETIC ANALYSES

PARSIMONY ANALYSES

Parsimony analyses were made on the dataset with all characters unordered or with 35 characters ordered, in both instances employing the backbone constraint outlined in the Methods. In the ordered analysis, a strict consensus of the four shortest trees found, length 1269, consistency index (CI) = 0.2593, homoplasy index (HI) = 0.8125, retention index (RI) = 0.5950, is shown in Figure 7.

The monophyly of Anatidae was strongly supported (bootstrap 82%, Table 4 clade A). The basal

Table 4. Significant clades shown in Fig. 7, and the unambiguous apomorphies (UA) defining them. Only characters with a consistency index > 0.5 are listed

Clade	Taxon	Number UA	Character, State change (x to y), CI
A	Anatidae	21	4(0–1), 0.750; 26(0–1), 1.00; 30(0–1), 0.571; 87(0–1), 1.000; 89(0–1), 0.500; 91(0–1), 1.000; 107(0–1), 0.667; 109(0–1), 0.667; 113(0–1), 1.000; 115(0–1), 1.000; 146(1–2), 1.000.
B	Anatidae exclusive of anserines	9	None with CI > 0.5, but one significant ambiguous apomorphy 119(0–2), 0.500
C	'oxyurines'	6	119(2–0), 0.500

The characters are as in Worthy & Lee (2008) and Appendix 1. Abbreviations as in Methods.

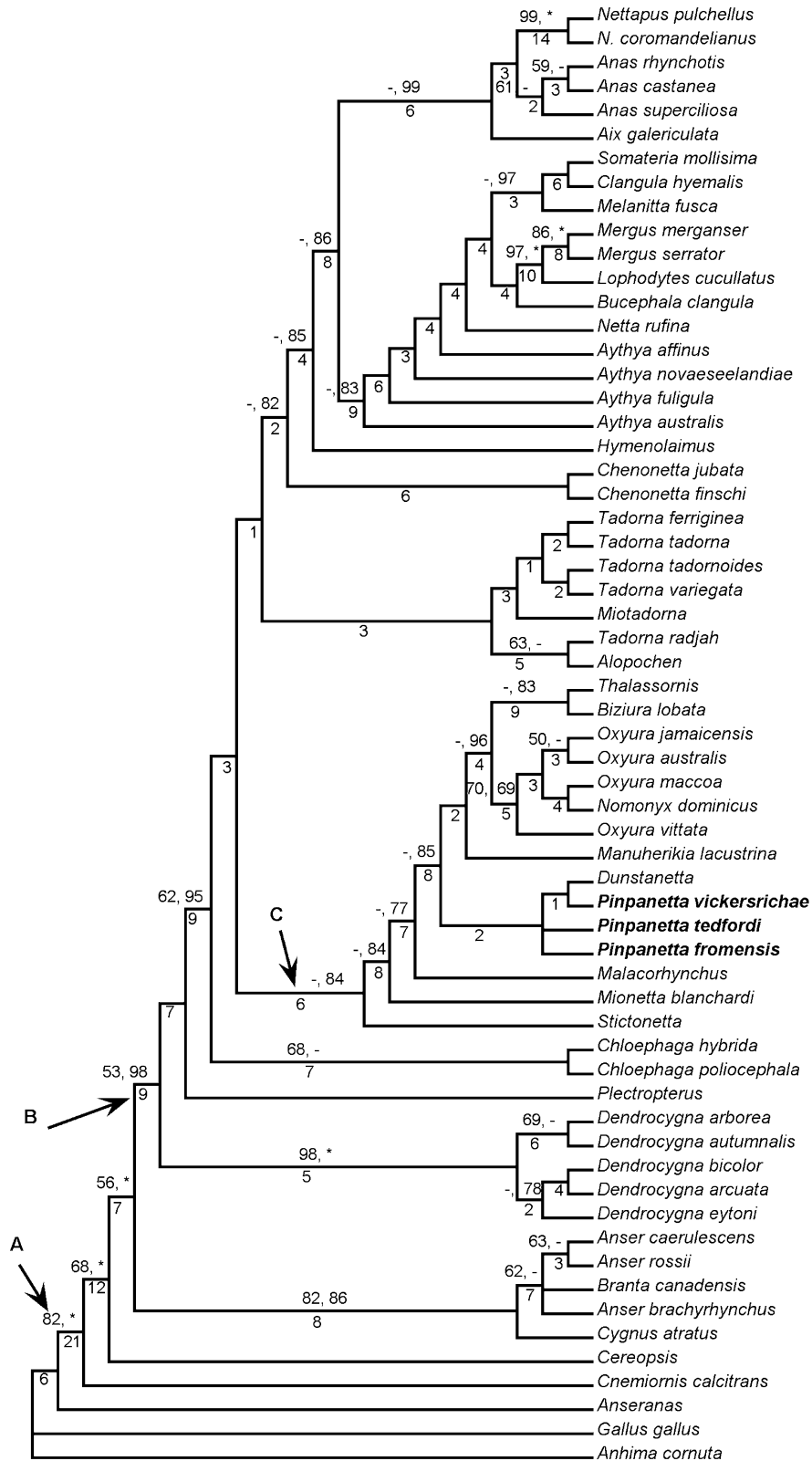


Figure 7. The strict consensus tree obtained from the parsimony analysis with 35 characters ordered. Support values above lines at each node show bootstrap > 50% and Bayesian credibility values > 70% (100% = *). Values below lines are numbers of unambiguous synapomorphies for each node. Clades A, B, and C are referred to in text and Table 4.

groups in Anatidae are two successive branches of Australasian anserines *Cnemiornis* [bootstrap support 68%, 12 unambiguous apomorphies (UA)] and *Cereopsis* (bootstrap support 56%, seven UA). The clade of the remaining anserines is strongly supported (bootstrap 82%, eight UA), although the precise positions of true geese (*Anser* and *Branta*) are unresolved. The sister clade to anserines (*Dendrocygna* and all other anatids) is weakly supported (bootstrap 53%, nine UA, Table 4 clade B); however, the *Dendrocygna* clade is itself well supported (bootstrap 98%, five UA). The position of *Plectropterus* next after *Dendrocygna* is also weakly supported (bootstrap < 50%, seven UA). In some preliminary analyses with fewer taxa, *Plectropterus* joined the base of the *Dendrocygna* clade, thus the conflict between *Plectropterus* forming an independent lineage or part of one including *Dendrocygna* explains the lack of significant bootstrap support for either clade. Above *Plectropterus*, all remaining anatids formed a clade with moderate support (bootstrap 62%, nine UA) whose basal branch of the two *Chloephaga* species had moderate support (bootstrap 68%, seven UA). Above *Chloephaga*, clades generally had no significant bootstrap support so their order has to be considered provisional. First was a fully resolved clade of oxyurine taxa (Fig. 7, Table 4 clade C). This clade successively included *Stictonetta*, *Mionetta*, *Malacorhynchus*, a clade containing the three Australian fossils (*Pi. tedfordi*, *Pi. fromensis*, and *Pi. vickersrichae* and *Dunstanetta*), *Manuherikia*, and finally a sister-clade relationship of *Biziura* + *Thalassornis* and a clade of *Oxyura* species and *Nomonyx*. This oxyurine clade had no bootstrap support > 50% for any node except for the clade of *Oxyura* species and *Nomonyx* (bootstrap 70%). *Oxyura* was, however, paraphyletic with *Nomonyx* embedded within it, although without bootstrap support > 50%. This oxyurine clade is supported by six UA of which Character 119 (syringeal bulla present to lost, CI = 0.5) is the most compelling. However, if *Plectropterus* and *Chloephaga* in reality branched after the oxyurines, a reversal in this character would be unnecessary. In an analysis with *Dunstanetta* excluded from the dataset (data not shown), although support for the oxyurine clade did not alter significantly, that for the clade more derived than *Malacorhynchus* improved to ten UA, bootstrap support < 50%. However, the association of taxa within this clade changed. *Biziura* + *Thalassornis*, now with bootstrap support of 58%, were sister to *Pinpanetta* species and together these were sister to *Manuherikia*. This clade was in turn sister to *Oxyura* species and *Nomonyx* whose bootstrap support increased to 78%. That up to 66% of characters have unknown states for *Pinpanetta*

species contributes markedly to the lack of support and the lack of resolution of the generic order in this clade.

Above oxyurines was a weakly supported clade comprising the tadornines *Alopochen*, *Miotadorna*, and *Tadorna* species (bootstrap < 50%; three UA) followed by successive branches to *Chenonetta* (the *C. jubata* and *C. finschi* pairing is supported by six UA) and *Hymenolaimus*. *Tadorna* was paraphyletic with *T. radjah* sister to *Alopochen* forming the basal tadornine clade. In order to further assess the effect of missing data, a bootstrap analysis with *Miotadorna* (42% missing data) removed, found increased support for all nodes between Clade A and the tadornine lineage (Fig. 7) (data not shown) indicating that this fossil significantly reduces nodal support. The most deeply nested part of the tree comprised a clade of anatines (bootstrap < 50%, six UA), comprising *Aix*, the three *Anas* species (bootstrap 61%), and the two *Nettapus* species (bootstrap 99%) as sister to a fully resolved clade of the aythyine and mergine divers that was supported by nine UA but had bootstrap < 50%. In this clade of diving taxa, *Aythya* species followed by *Netta* forming a basal grade, and the mergines formed two separate groups. *Somateria* formed a clade with *Clangula* and *Melanitta*, whereas the remaining mergines *Lophodytes* and *Mergus*, often treated as congeneric, associated in a well-supported clade (bootstrap 97%) with *Bucephala*.

In the analysis with all characters unordered, essentially the same topology was obtained as above in a consensus of 148 shortest trees of length 1230. However, it was less well resolved, with polytomies in *Dendrocygna* species and in the aythyine–mergine lineage. The oxyurine lineage fully resolved, but the order of taxa differed slightly from the ordered analysis, with *Malacorhynchus* following *Stictonetta* before *Mionetta*, then *Pi. vickersrichae*, *Manuherikia*, *Pi. tedfordi*, and *Pi. fromensis*, below the remaining taxa.

Importantly, in both analyses, the European Oligo-Miocene *Mionetta* and the extant monotypic *Stictonetta* and *Malacorhynchus* were basal to the Australasian Tertiary taxa, which, in turn were basal to the extant oxyurines *Biziura*, *Oxyura*, *Nomonyx*, and *Thalassornis*. An exception occurred in the unordered analysis, where *Dunstanetta* appeared within extant oxyurines, interpolated between *Oxyura*–*Nomonyx* and *Biziura*–*Thalassornis*.

To examine the effect of diving characters in the dataset, 21 characters (36 57 61 68 73 75 88 90 92–96 98 103–105 110 118 125 126) were omitted from the dataset and a parsimony analysis repeated as above, as was carried out by Worthy & Lee (2008). Thirty-five shortest trees, length 1099, were obtained. In the consensus tree (data not shown), *Cnemiornis* and *Cereopsis* remained basal to other anserines; *Plec-*

tropterus moved to basal to *Dendrocygna*; the oxyurines largely became polytomous, although *Oxyura* and *Nomonyx* remained a clade, as did *Pinpanetta* species. A completely resolved clade of tadornines sequentially with *Hymenolaimus*, *Chenonetta*, *Miotadorna*, *Chloephaga* and other tadornines, was found above *Mionetta*, sister to anatines.

The analysis that included *Presbyornis* and had *Gallus* alone as the outgroup, resulted in five shortest trees (length 1297, CI = 0.2560, HI = 0.8157, RI = 0.5933). *Presbyornis* was sister to Anatidae, forming a clade that was unresolved with respect to *Anhima* + *Anseranas* and the outgroup *Gallus*. There were no changes in topology within Anatidae. The clade *Anhima* + *Anseranas* had bootstrap support of 74%. The monophyly of Anatidae inclusive of *Presbyornis* had bootstrap support of 65%. Within Anatidae there was some minor alteration to bootstrap support for clades: Anatidae exclusive of *Presbyornis* increased to 92%, that exclusive of *Cnemiornis* declined to 62%, and that exclusive of *Cereopsis* improved to 61%. In more deeply nested parts of the tree, bootstrap support did not alter much except that for the clade of *Chloephaga* species improved to 80%.

BAYESIAN ANALYSES

A Bayesian consensus tree derived from 4001 trees sampled after the 1000 trees from the burnin period has credibility values (percentage posterior probabilities) as shown in Figure 7. The probability plot in Tracer plateaued by 250 000 generations, so the burnin discard of 1 000 000 generations was more than adequate. The two runs achieved stationarity and convergence: log likelihood statistics (LnL) after Burnin = 1,000,000 for Run 1 (mean = -4516.644, SD = 0.326, effective sample size = 930.672); Run 2 (-4517.587, 0.352, 816.292), and after 5 000 000 generations the average standard deviation of split frequencies for each tree was 0.030119, well within the recommended cutoff value of < 0.1.

In general, clades with high bootstrap values in the parsimony analysis also had high posterior probabilities; however, the latter were on average higher. There have been discussions of whether bootstrap might underestimate support, and Bayesian analyses overestimate support (Alfaro, Zoller & Lutzoni, 2003; Cummings *et al.*, 2003); however, those discussions have not discussed the different effects of missing data in the two methods. Bootstrapping is likely to be overly conservative when there are highly fragmentary taxa because the method randomly samples characters from the entire matrix. Thus, while the few known characters in a highly fragmentary taxon might all imply the same position, this taxon might

be sampled for none of these characters in many bootstrap replicates, leading to an overly uncertain position for that taxon (and thus, low bootstraps for relevant clades). In contrast, Bayesian analysis does not resample data, but instead perturbs parameters. In this process, even if a highly fragmentary taxon possesses few known characters, if those characters unanimously support the same phylogenetic position, perturbation of parameters is unlikely to change this result, leading to a high posterior probability. Therefore, where certain taxa have extensive missing data, Bayesian analyses may be more suited to evaluating clade support than is bootstrapping.

The Bayesian consensus tree differed in topology from the parsimony consensus tree only in areas with weak bootstrap support. *Plectropterus* moved to a basal position in the *Dendrocygna* lineage (61% credibility) rather than forming a discrete branch adjacent to *Dendrocygna*; *Dendrocygna* was monophyletic (100%) above *Plectropterus*; *Chloephaga* remained basal to oxyurines (95%); and *Miotadorna* separated from the crown tadornines and interpolated between them and *Chenonetta*, but also with little support (38%). The poor resolution of this fossil is certainly related to the significant amount of missing data. In the most deeply nested part of the tree, the anatines *Aix*, *Anas*, and *Nettapus* formed a clade sister to a clade of divers as before (99%). Within the diving lineage the two mergine lineages remained the same except that *Bucephala* disassociated from *Mergus*, and the aythyines moved from a basal grade to widely paraphyletic positions, some basal and others interpolated between the mergines.

High support was obtained for the nodes up to the pairing of oxyurines with more derived anatids suggesting that the topological sequence of anserines basal, then *Dendrocygna*, then oxyurines is phylogenetically significant. The clade of oxyurines had reasonable support (84%), as did the successively nested clades: *Mionetta* and remaining taxa (84%); *Malacorhynchus* and remainder (77%); the Australian and New Zealand Tertiary fossils and the extant traditional oxyurines (85%), and the extant traditional oxyurines *Oxyura*, *Nomonyx*, *Thalassornis* and *Biziura* (96%). This strongly suggests that the Australasian Oligo-Miocene taxa are more derived than the European Oligo-Miocene *Mionetta*, and further, that the extant *Stictonetta* and *Malacorhynchus* are basal oxyurines less derived than the Australasian Tertiary taxa. Considering the amount of missing data for the *Pinpanetta* species and *Dunstanetta*, these support values suggest the topology accurately reflects phylogeny.

The Bayesian analysis with *Presbyornis* included in the dataset was modified to improve stationarity and convergence by extending the run to 8 000 000

generations, burnin was extended to 2000 samples or 2 000 000 generations, and the heating parameter changed to 0.24. The log likelihood statistics (LnL) after Burnin for Run 1 (mean = -4622.029, SD = 0.257, effective sample size = 1467.957); Run 2 (-4622.072, 0.279, 1315.119); after 8 000 000 generations the average standard deviation of split frequencies for each tree was 0.029613. The overall topology of the obtained consensus tree was the same as the above tree, except that *Presbyornis* interpolated above *Anseranas*, as sister to Anatidae, with weak support (67%). Anatidae exclusive of *Presbyornis* was strongly supported (100%). Credibility values for more deeply nested clades along the main stem generally decreased slightly from the analysis without *Presbyornis*: that exclusive of *Cnemiornis* declined to 82%, that exclusive of *Cereopsis* declined to 88%, *Dendrocygna* and remaining anatids declined to 87%. Support for the clades of anserines declined slightly to 84% and that for *Dendrocygna* species remained unchanged at 100%. *Plectropterus* remained as sister group to *Dendrocygna* but with little support (54%). The clade of *Chloephaga* and all remaining anatids was strongly supported (96%), the clade of oxyurines as herein defined had moderate support (75%), as had the subclades *Mionetta* and remaining oxyurines (74%), and *Malacorhynchus* and remaining oxyurines (67%). The clade of traditional oxyurines (*Oxyura*, *Nomonyx*, *Biziura* and *Thalassornis*) and the Australasian fossil taxa also had moderate support (76%), and the traditional oxyurines formed the most deeply nested clade with strong support (98%). Above *Tadorna* and *Miotadorna*, the clade *Chenonetta*, *Hymenolaimus* and anatines had moderate support (73%); as did *Hymenolaimus* and anatines (77%); and anatines (77%). Within anatines, all diving taxa were united in a clade (75%) separate from a well-supported clade of nondiving taxa (100%). Within the divers, mergines formed two well-supported clades: *Melanitta*, *Clangula* and *Somateria* (97%); and *Mergus* and *Lophodytes* (100%). Most deeply nested in anatines, the two *Nettapus* species separated from *Anas* (100%). Generally, the addition of *Presbyornis* to the dataset reduced support throughout Anatidae, which is likely to be the result of missing data (24%) introducing significant conflict into the data.

DISCUSSION

DIVERSITY AND COMPOSITION OF THE AUSTRALIAN OLIGO-MIOCENE FOSSIL WATERFOWL

Deposits in Lake Eyre Basin have revealed the majority of Australian fossil waterfowl of Oligo-Miocene age (Rich *et al.*, 1991; Vickers-Rich, 1991; data herein) The Lake Eyre Basin is a large depositional centre

in central Australia with discrete sub-basins, the western Tirari Sub-basin and the eastern Callabonna (= Tarkarooloo) Sub-basin (Alley, 1998). Within these sub-basins, extensive lacustrine fluviodeposits, primarily the Etadunna Formation in the Tirari Sub-basin and the temporally equivalent Namba Formation in the Callabonna Sub-basin, attest to widespread shallow lakes from the Late Oligocene through the Early Miocene and have been significant sources of vertebrate fossils (Stirton *et al.*, 1961; Tedford *et al.*, 1977; Pledge & Tedford, 1990; Woodburne *et al.*, 1994; Alley, 1998). Waterfowl fossils are relatively common in both the Etadunna and Namba formations. The fossils described above reveal a minimum of four taxa in the Late Oligocene and earliest Miocene and another of Middle-Late Miocene age.

The largest taxon, *Australotadorna alecwilsoni*, is a large tadornine known with certainty by a single humerus SAM P.43141 from the Namba Formation at Lake Pinpa, South Australia. Seven more fragmentary fossils representing coracoids, carpometacarpi, and tibiotarsi from both Lake Pinpa and Lake Palankarinna are tentatively referred to this taxon. Another tadornine is reported from the Alcoota LF, c. 8 Mya, by two bones, but its affinities remain elusive until more diagnostic material is forthcoming. *Australotadorna* is dissimilar to the New Zealand Early Miocene (19–16 Mya) *Miotadorna* but together these taxa are the oldest tadornines in the world and support the origin of this group in Australasia. One possible exception is the mid-Oligocene fossil *Telornis impressus* Ameghino, which was interpreted as a tadornine by Agnolin (2004), but as it is based on a single distal humerus, this referral is tenuous. The discovery of *Australotadorna* in the 26–24 Mya sediments of the Etadunna and Namba Formation provides a new minimum age (base of Miocene) for the separation of true shelducks (tadornines) from all more derived anatines (including *Chenonetta* and *Hymenolaimus*, referred by Livezey, 1997a to Tadorninae). The presence of a pneumatic acroracoid in both *Australotadorna* and *Miotadorna*, unlike in modern *Tadorna* species, supports this feature being primitive in the group.

The majority of fossil waterfowl fossil bones belong to three species in the new genus *Pinpanetta*: *Pi. tedfordi* 28 specimens actual and referred; *Pi. vickersrichae*, 15 specimens; *Pi. fromensis*, 20 specimens). Parsimony and Bayesian phylogenetic analyses support placement of this new genus within an expanded Oxyurinae, *sensu* Worthy & Lee (2008). This oxyurine assemblage includes the traditional oxyurines (*Oxyura*, *Nomonyx*, *Biziura*), and *Thalassornis*, as derived members and the monotypic Australian *Stictonetta* and *Malacorhynchus* as basal members. It also includes the European Oli-

go-Miocene *Mionetta* and the New Zealand Early Miocene *Manuherikia* and *Dunstanetta* in relatively basal positions (Worthy & Lee, 2008). The present more expanded analyses (more characters, more ingroup taxa) find improved support for these relationships. Both parsimony and Bayesian analyses reported herein, either where all characters are unordered or where a subset of characters are ordered as morphoclines, support the placement of *Pinpanetta* in the oxyurine lineage in a position more derived than *Stictonetta*, *Malacorhynchus*, and *Mionetta* but basal to the New Zealand Tertiary fossils *Manuherikia* and *Dunstanetta* and to the extant oxyurines (*Oxyura*, *Nomonyx*, *Biziura*) and *Thalassornis*. Relationships within Oxyurinae are still provisional, however, as evidenced by low bootstrap support and instability in relationships if *Dunstanetta* is deleted from the dataset. Moreover, the effect of the exclusion of *Dunstanetta* from the analysis clearly reveals the destabilizing effect of missing data. When more complete data is available for the fossil taxa in this clade, support is likely to improve markedly.

In this study, as in those of Livezey (1986, 1995a, b, 1997a), homoplasy because of convergence related to diving was still a major factor to contend with (McCracken *et al.*, 1999; McCracken & Sorenson, 2005). As found by Wiens, Bonett & Chippindale (2005) in a study comparing phylogenies of salamanders derived from genetic and morphological data, in which pedomorphosis obfuscated phylogeny, removal of the homoplastic characters was not an effective solution. Instead, removal of diving characters led to an attraction of taxa characterized by large size and terrestrial habit, which is thus just homoplasy of a different set of characters. The constraint method used here that effectively overcame the formerly overwhelming homoplasy associated with diving habit, split *Oxyura* from aythyines and mergines according to strong independent genetic evidence (detailed above). This is a more effective method to overcome homoplasy, as no characters are excluded and all can contribute to a phylogenetic signal. It resulted in a more plausible tree with diving taxa separated, in which the fossil forms are free to associate by their phylogenetic signal. As a result, and given the larger dataset and different characters employed herein, it is not surprising that the phylogenetic relationships found differed markedly from those of Livezey (1986, 1995a, 1997a).

The radiation of *Pinpanetta* in Australia, in three species separated by size, is paralleled by the Early Miocene oxyurine radiation in New Zealand, with *Manuherikia* having two smaller species and *Dunstanetta* a larger one (Worthy *et al.*, 2007). Although the phylogenetic analyses embed *Dunstanetta* in

Pinpanetta, several apomorphies, such as an elongate humeral dorsal tubercle and a pneumatic coracoid distinguish *Dunstanetta*: the association may be an artefact of missing data as both taxa are relatively poorly known.

The geological age of *Pinpanetta* at 26–24 Mya, or on the Oligocene–Miocene boundary, does not increase the known age for the origin for oxyurines, as *Mionetta* derives from latest Oligocene deposits (Mourer-Chauviré *et al.*, 2004; Worthy & Lee, 2008). It does support a growing body of evidence that this group of ducks, whose fossil members were more recently included in Dendrocheninae (Livezey & Martin, 1988), dominated waterfowl faunas globally by the beginning of the Miocene (Worthy & Lee, 2008). Several of the extant monotypic and specialized taxa that characterize the Recent fauna of Australia and New Zealand, e.g. *Stictonetta*, *Malacorhynchus*, *Oxyura*, *Biziura*, are confirmed as relicts of this oxyurine radiation.

AN OXYURINE RADIATION – IS THERE A CONFLICT WITH GENETIC EVIDENCE?

Analyses based on molecular data that can address the phylogenetic relationships of the oxyurines as herein defined, or of them to other anatids, are so far of a limited and incomplete nature. I am not aware of any single published molecular study that has included together the taxa herein associated as oxyurines. Evidence from analyses of feather proteins found *Biziura* and *Oxyura* indistinguishable, *Malacorhynchus* quite unlike anatine species, *Stictonetta* near anserines and *Dendrocygna*, and an affinity of *Thalassornis* with *Dendrocygna* (Brush, 1976), but the study was poorly designed with taxon comparisons based on older phylogenetic assumptions. Combinations of *Stictonetta*, *Biziura*, *Oxyura*, *Nomonyx*, and *Malacorhynchus*, but not all together, have been included in two analyses of a small amount of sequence from cytochrome *b*, which suggest that *Biziura* is more closely related to anserines than to *Oxyura*, but with little or no bootstrap support (Sraml *et al.*, 1996; McCracken *et al.*, 1999). Interestingly, it has recently been demonstrated that cytochrome *b* is the most incongruent of a number of compared mitochondrial and nuclear genes, with major differences in clade sequence in topologies (e.g. Crowe *et al.*, 2006), so the oxyurine relationships found from cytochrome *b* analyses are likely to differ from those of more comprehensive studies. Moreover, homoplasy has been shown to significantly affect mtDNA datasets in anatids, even intragenerically within *Oxyura* (McCracken & Sorenson, 2005), and thus would be expected to be even more problematic

regarding the determination of deeper divergences. Weir & Schluter (2008) considered cytochrome *b* sequences to become so saturated, when older than 12 Mya, as to be unusable. Given that the oxyurine radiation dates to about 25 Mya, clearly analyses comparing the extant genera around this lineage, if based on fast-evolving genes like cytochrome *b* will be subject to considerable homoplasy. In summary, available molecular data do not provide strongly supported hypotheses for the relationships of the taxa associated as oxyurines by the present morphological analyses and are inadequate to contradict the hypothesis of an oxyurine lineage as advocated herein.

COMMENT ON INFERRED RELATIONSHIPS OF SOME RECENT TAXA

It was not the purpose of this paper to address the generic relationships of Recent anatids, but rather to determine the phylogenetic affinities of the fossils. Nevertheless, the results do suggest some different generic relationships than those currently accepted and advocated, for example (Livezey, 1997a; Dickinson, 2003; Callaghan & Harshman, 2005) and so require some comment.

Anserines

The basal position for anserines found by analysis of the present dataset is supported by the fossil record. The oldest putative anserines are some Middle Oligocene – Early Miocene taxa from Europe. *Cygnopterus affinis* from Belgium (MP 23–24), is generally considered to have anserine affinities (Lambrecht, 1933; Brodkorb, 1964; Howard, 1964; Cheneval, 1984; Olson, 1985). Cheneval (1984) identified it as a swan in Cygnini; however, Louchart *et al.* (2005) listed several differences that indicated *Cygnopterus* was an anserine, but ‘unrepresentative’ of swans. *Cygnopterus lambrechtii*, described from a distal humerus from the Middle Oligocene of Kazakhstan (Kurochkin, 1968), was synonymized with the flamingo *Agnopterus turgaiensis* Tugarinov, 1940, and thus is not an anseriform (Mlíkovský & Švec, 1986). The anserine affinities of the remaining *Cygnopterus* species were questioned by Mayr (2005, 2008), who noted especially that the referred coracoids of *C. alphonsi* are very similar to those of presbyornithids. Yet, the type tarsometatarsus of *C. alphonsi* is short and robust like those of anserines, unlike the elongate ones of presbyornithids. The phylogenetic affinities of *Cygnopterus* and its included species await re-examination of the material. All three *Cygnopterus* species were placed in Cygnopteridae by Callaghan & Harshman (2005). *Cygnavus formosus*, named on a distal tibiotarsus from the Lower Oligocene

of Kazakhstan, is possibly anserine, but the better known species *Cygnavus senckenbergi* from the Early Miocene of Europe (MN2a) is anserine (Kurochkin, 1968; Cheneval, 1987; Mlíkovský, 2002). *Guguschia* from Azerbaydzhan (Aslanova & Burczak-Abramowicz, 1968) had some similarities with *Cygnopterus* according to Louchart *et al.* (2005).

These are preceded by the basal anatids *Romainvillia* from the Late Eocene (Mayr, 2008) and *Paracygnopterus scotti*, from the Lower Oligocene of England (Harrison & Walker, 1979). *Romainvillia* has a distinct foramen for the supracoracoideus nerve and *Paracygnopterus* a distinct incision for this nerve (Mayr, 2005, 2008). A foramen for the supracoracoideus nerve is characteristic of Anseranatidae and its loss is said to characterize Anatidae (Livezey, 1986; Mayr, 2005). This is incorrect, as a distinct foramen is present in *Cnemiornis*, one is variably present in *Cereopsis*, and a distinct incision is found in remaining anserines. As dendrocygnines and other anatids lack such a foramen, the distribution of this character is strong support for the basal position of anserines in Anatidae.

A basal position for anserines (variously as either tribes or subfamilies) was generally accepted until the 1960s (e.g. Sharpe, 1899; Shufeldt, 1913, 1914; Phillips, 1923; Peters, 1931; Delacour & Mayr, 1945; Brodkorb, 1964), but following the influential work of Woolfenden (1961) and Johnsgard (1961, 1968, 1978), *Dendrocygna* took a position basal to anserines in most lists (e.g. Dickinson, 2003). Weak support for the basal position of *Dendrocygna* (three synapomorphies) was found by Livezey (1986). In subsequent studies, the position of *Dendrocygna* either was not addressed (e.g. Livezey, 1995b), or he found little support for this position. For example, he found *Cnemiornis* was the most basal taxon, and other Anserinae were sister to the remaining Anatidae, but if *Cnemiornis* was excluded from the analysis, the position of anserines was unresolved, with their position above or below *Dendrocygna* equally likely (Livezey, 1989). Similarly, the order of these taxa was unresolved in the majority-rule bootstrapped consensus tree obtained by Livezey (1996a) while investigating anserine relationships. Nevertheless, a basal position for *Dendrocygna* was adopted (Livezey, 1997a; Callaghan & Harshman, 2005).

The results of the present analysis show significant support (credibility values 100%) for a basal position of the anserines below *Dendrocygna*. In the present analyses, as previously advocated by Livezey (1996a, 1997a) both *Cereopsis* and *Cnemiornis* lie below anserines on the anseriform stem. This result was maintained even when diving characters were excluded, contra a previous analysis (Worthy & Lee, 2008) where these Australasian taxa

grouped with anserines when diving characters were excluded. These analyses confirm *Cereopsis* and *Cnemiornis* as basal anseriformes of approximately anserine grade.

Although the present results are derived from analyses constrained to be consistent with certain well-supported genetic results, most relationships were free to vary, and so the results are only partially consistent with genetic data. Results herein mirror those from electrophoretic comparison of proteins from a limited diversity of anatids (not including *Dendrocygna*) that found anserines basal to *Oxyura*, with anatines most derived (Patton & Avise, 1986). However, the position herein of *Dendrocygna* more derived than anserines is not consistent with genetic results. DNA–DNA hybridization data supported the early divergence of *Dendrocygna*, then successively *Oxyura* and *Stictonetta*, anserines and other anatids (Madsen *et al.*, 1988; Sibley, Ahlquist & Monroe, 1988). Analyses of mitochondrial DNA data also found *Dendrocygna* basal to anserines (Sraml *et al.*, 1996; Sorenson *et al.*, 1999; Donne-Goussé *et al.*, 2002). Although these relationships were weakly supported in each analysis (and were not enforced as backbone constraints here), they raise the possibility that convergence towards the large terrestrial morphotype between anserines and the unequivocally basal anseriformes *Anseranas* and *Anhima* has attracted anserines towards the base of the tree. Alternatively, because homoplasy related to base saturation has been shown to significantly affect mtDNA datasets in anatids (McCracken & Sorenson, 2005), it may well have affected intergeneric comparisons. True resolution of the branching order of early lineages of anatids awaits analyses of extensive nuclear gene data.

Thalassornis

In the present analyses, *Thalassornis* was found to be strongly supported as the sister taxon to *Biziura* and deeply nested within oxyurines. *Thalassornis* was retained in Oxyurinae by Delacour & Mayr (1945) following Eyton (1838) but more recently Johnsgard (1968) and Raikow (1971) advocated a taxonomic placement near *Dendrocygna*. Such a relationship was found by Livezey (1995a, 1996a, 1997a), although with weak support. Significantly, Livezey did not include oxyurines in these analyses, and in his initial analysis, Livezey (1986) found only a single apomorphy supporting the placement of *Thalassornis* below anserines. This character was the change from the external rim of the carpal trochlea on the carpometacarpus being unnotched to notched, which character is intragenerically variable in *Dendrocygna* (Worthy & Lee, 2008). The features that attract *Thalassornis* to *Dendrocygna*, e.g. reticulate tarsi, plain-coloured

downy young, tracheal structure, and certain skeletal features such as the straight dorsolateral margin of the quadrate (Johnsgard, 1968; Raikow, 1971) can be explained as shared plesiomorphies (Worthy & Lee, 2008), and are found in basal oxyurines as herein defined. In summary, the placement of *Thalassornis* with *Dendrocygna* is weakly supported by past use of morphological data, in contrast to the present result of a strongly supported sister relationship with *Biziura*.

Plectropterus

The present analyses found strong support for *Plectropterus* being included in the clade of *Dendrocygna* and more derived anatids, yet being more basal than tadornines and oxyurines, as herein defined. There is weak support for it being the sister taxon to *Dendrocygna*. Delacour & Mayr (1945) placed *Plectropterus* with the ‘perching ducks’ *Sarkidiornis*, *Cairina*, and *Nettapus*. Since then, this association has been usual, although Woolfenden (1961) concluded it was most similar to shelducks (Tadorninae). More recently, *Plectropterus* has been treated as a monotypic genus and subfamily of uncertain relationships (e.g. Dickinson, 2003; Kear, 2005). Livezey (1986), in a study using 120 morphological characters (five integumental, 115 skeletal) with a broad range of anatid genera, found *Plectropterus* to be monotypic and interpolate between *Stictonetta* and a more derived clade of tadornines and all anatines. More recently, Livezey (1996b) using a differential weighting scheme for various types of morphological characters, found a pairing of *Plectropterus* and the monotypic *Sarkidiornis*, that was, in turn, the sister group to a clade of tadornines and *Chloephaga*. In his taxonomic revision of Anatidae, Livezey (1997a) followed this topology and placed *Plectropterus* with *Sarkidiornis* as a tribe within Tadorninae. However, Livezey’s (1996b) analysis did not include any *Dendrocygna* species, so this alternate affinity was not explored. The present result of an attraction of *Plectropterus* to *Dendrocygna* may be a result of phylogenetic signal, but highly conservative characters such as the scutellated tarsi and asymmetrical syringeal bulla of *Plectropterus* (Livezey, 1996b) suggest not. *Dendrocygna* has reticulated tarsi like other basal anatids and, uniquely, a symmetrical bulla. This attraction may therefore result from homoplasy because of convergence towards a similar terrestrial morphotype, a possibility raised above for anserines. This suggestion is supported by the observation that in an analysis with diving characters removed, *Plectropterus* interpolated between *Dendrocygna* and anserines.

Tadornines

The present analysis finds support for a grade of taxa traditionally collected within Tadorninae. *Chlo-*

ephaga, unconstrained in the analyses, is more basal than the true shelducks (tadornines) in this grade, and may even be separated from them by the oxyurine clade, although there is only weak support for this. The mid-Oligocene fossil *Telornis impressus*, if correctly interpreted as a tadornine by Agnolin (2004), may give support for this basal position for *Chloephaga*. Within the clade of shelducks, *Tadorna* is paraphyletic, with *T. radjah* pairing with *Alopochen*. In parsimony analyses, *Miotadorna* lay within a clade of shelducks basal to *Tadorna*, but in the Bayesian analysis it separated from them, but without significant support. The significant amount of missing data for this taxon undoubtedly reduces support for the tadornine clades. Above the shelducks, the unconstrained *Chenonetta jubata* paired with *Che. finschi* supporting the generic synonymy of these taxa (Worthy & Olson, 2002), contra (Livezey, 1989, 1997a). The unconstrained position of *Hymenolaimus* as the most derived taxon in this grade of tadornines does not support Livezey's (1997a, b) conclusion, that this aberrant form is a tadornine. These data in contrast suggest that both *Chenonetta* and *Hymenolaimus* are outside of Tadorninae and would be better classed as basal anatines.

DIVING AND THE OXYURINE LINEAGE

Several features of the skeleton of *P tedfordi* indicate that it was a specialized diver, e.g. nonpneumatic and distally narrowing humerus and a flattened tibiotarsus. That the basal members of the oxyurine clade, *Stictonetta*, *Mionetta*, *Malacorhynchus*, are/were not specialist divers, suggests diving evolved just once within the clade. The fossil taxa indicate that this had happened by the latest Oligocene – Early Miocene. The slightly younger *Man. lacustrina* and *Dunsttanetta* from New Zealand were specialist divers (Worthy & Lee, 2008). In Europe, the smaller waterfowl from the latest Oligocene to the Middle Miocene were dominated by *Mionetta blanchardi* (Cheneval, 1983; Bochenki, 1997; Mlíkovský, 2002, 2003; Mourer-Chauviré *et al.*, 2004). This species lacked specialist diving apomorphies in its legs and is a basal oxyurine in these analyses. Other waterfowl taxa co-existing with *Mionetta blanchardi* are not nearly so well characterized; however, a size-equivalent of *Pinpanetta fromensis* and *Manuherikia minuta* is present, i.e. *Mionetta natator* (Milne-Edwards). A larger form, *Mionetta consobrina* (Milne-Edwards), is doubtfully distinct and may refer to larger specimens of *Mi. blanchardi* (Livezey & Martin, 1988), but neither have specialized diving features. Therefore diving, characteristic of the most deeply nested taxa in the oxyurines, evolved independently of other

diving anatids, e.g. the aythyines and mergines, necessarily just once within the lineage.

A decrease in the number of skeletal elements that are pneumatic within more specialized divers is a well-documented feature within anseriforms (O'Connor, 2004). However, the present results indicate that the nonpneumatic ventral tricripital fossa of the humerus evolved long before diving adaptations in oxyurines, and thus question whether it is functionally correlated with diving. *Stictonetta*, which is a specialized filter feeder in shallow water (Marchant & Higgins, 1990), not a specialized diver, is consistently found here to be the most basal oxyurine. It has a pneumatic humerus and also differs from other oxyurines in having reticulated tarsi like anserines and dendrocygnines. The fossil taxon *Mi. blanchardi* is the next most derived oxyurine above *Stictonetta* and its humerus is nonpneumatic, but its leg bones lack strong adaptations towards diving, such as dorsoventrally curved femora, flattened tibiotarsus, or shortened tarsometatarsus with trochlea II markedly proximally located. Similarly, *Malacorhynchus* has a nonpneumatic humerus, and is not a diver but a specialized surface dabbler. It is only in oxyurines more derived than these taxa that diving becomes prevalent and so a nonpneumatic ventral pneumotricripital fossa which characterizes Oligo-Miocene oxyurines may have predisposed this group towards a diving habit. In support of this suggestion are the results of a recent analysis of *Romainvillia* by Mayr (2008) that reveals this taxon to be the most basal anatid, and its tricripital fossa was not pneumatic.

In a study of pneumaticity of the post-cranial skeleton of anseriforms, O'Connor (2004) determined that specialized diving had to have evolved multiple times when he assumed Livezey's (1997a) phylogeny. Similarly, evolution of diving at least five times is inferred from the sequence Callaghan & Harshman (2005) adopted. They placed *Thalassornis* as a discrete tribe within Dendrocygninae, *Biziura* as a discrete lineage, *Oxyura* as a lineage basal to tadornines, and mergines and aythyines as separate deeply nested anatine groups. In contrast to the sequence advocated by Livezey (1997a) or Callaghan & Harshman (2005), the phylogenetic relationships found here (Fig. 7) reduces the number of times specialized diving necessarily evolved to just two: one in oxyurines and one in a clade of anatines that included both aythyines and mergines.

COMMENT ON CORRELATION OF LOCAL FAUNAS

The distribution of all three *Pinpanetta* species supports the previous broad biocorrelation of the Pinpa LF from the Namba Formation with the Minkina LF (Zone A), Ditjimanka LF (Zone B) and

Ngama LF (Zone D) of the Etadunna Formation (Woodburne *et al.*, 1994). The occurrence of the phoenicopteriform *Palaeodius wilsoni* throughout the Lake Palankarina sequence and at Lake Pinpa (Baird & Vickers-Rich, 1998) further supports these correlations. No other bird groups are sufficiently well known to add further data to these faunal comparisons.

The recovery of *Pi. tedfordi* in Ringtail Site, from System C, at Riversleigh, if borne out by further specimens, presents a marked extension in geographic range of this taxon and also perhaps in time. System C sites, which equate to Faunal Zone C sites (e.g. Travouillon *et al.*, 2006), are considered to be Middle Miocene in age (Archer *et al.*, 1997) and slightly older than the Bullock Creek LF. The fossil *Pinpanetta* bone has several implications: Firstly, if its larger size is paralleled in further specimens by other morphological differences, then the Ringtail form would be a distinct species. Alternatively, if the presence of *Pi. tedfordi* is confirmed by further material in Ringtail Site, it would corroborate other faunal data that suggest an affinity with Faunal Zone B sites (Travouillon *et al.*, 2006). Ringtail Site is characterized by a number of aquatic taxa, especially numerous lungfish and turtles, and the platypus *Obdurodon*, which latter taxon is also present in System B sites (Archer *et al.*, 2006; Travouillon *et al.*, 2006). This aquatic component may mean the Ringtail fauna was deposited coeval with the limestone formation, whereas most other 'System C' sites on Gag Plateau are cave infill deposits which would necessitate their being somewhat younger. If so, the age of the Ringtail fauna could be closer to those of Faunal Zone B sites, which are intermediate between those of Faunal Zones A and C (Archer *et al.*, 1997). Sites from Faunal Zone A have a taxon found in the Ngama LF, uppermost in the Etadunna sequence and about 23 Mya, and six taxa otherwise known in the Kutjamarpu LF from sediments overlying the Etadunna at Lake Ngapakaldi (Archer *et al.*, 1997; Travouillon *et al.*, 2006). Some Faunal Zone C sites share taxa, e.g. *Neohelos* sp., with the Middle Miocene Bullock Creek LF, suggesting similar ages for their faunas. The Bullock Creek LF has no anatids to shed any light on this issue. Elsewhere in Australasia the fossil record does not support longevity of anatid species. The anatid fauna of the Early Miocene (19–16 Mya) of New Zealand contains at least five genera and six species, none of which persist into the Recent and, globally, no modern genera are unequivocally known earlier than the Late Miocene (Worthy *et al.*, 2007). This suggests that turnover in anatids is relatively rapid compared to other birds, as genera such as *Aegotheles* and *Collocalia*, *Menura*, *Cacatua*, and *Orthonyx* did persist from the Early–Middle Miocene

to the present (Boles, 1993a, b, 1995b, 2001; Worthy *et al.*, 2007). It therefore seems unlikely that a species of anatid would have persisted from 23–15 Mya. Together these observations suggest the age of Ringtail Site is likely to be closer to those of Faunal Zone B sites, perhaps about 20–18 Mya, and thus much closer in age to the Etadunna local faunas. If so the presence of an anatid species from, or very similar to one from, the Etadunna formation would be less surprising.

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APPENDIX 1

LIST OF CHARACTERS USED IN THE PHYLOGENETIC ANALYSES

Characters 1 to 133 are as given in Worthy & Lee (2008), except that character 63 was revised as follows:

63. Distal end, relative length proc. flexorius (= entepicondyle): 0, short, ends proximad to condylus dorsalis and condylus ventralis (in caudal view, a line across distal extreme of dorsal condyle at right angles to long axis of shaft passes well distad of entepicondyle, e.g. *Anseranas*); 1, long, distal extent roughly equal to that of the dorsal condyle.

Note: in most taxa, the entepicondyle, and the dorsal and ventral condyles have approximately equivalent distal extent. In *Anseranas*, *Branta*, and *Cygnus*, the dorsal and ventral condyles have equal distal extent and the entepicondyle is markedly shorter, so coded '0'. In *Cereopsis* and *Anser*, the dorsal condyle and entepicondyle have about equal length, and the ventral condyle extends slightly distad of a line

drawn across them, but here distal extent relative to the dorsal condyle is prioritized and they are coded '1'.

New characters

134. Humerus, dorsal pneumotricipital fossa excavated below head: 0, no; 1, yes.

135. Humerus, incisura capitis opens to dorsal pneumotricipital fossa: 0, at equal height; 1, groove elevated above (more caudal) the fossa and often separated from the fossa by a distinct ridge that transverses the groove.

136. Humerus, external tuberosity shape: 0, width roughly equals length; 1, elongate ovate.

137. Humerus, width of space between facet for anterior articular ligament and proximoventral apex of the dorsal condyle: 0, narrow, gap equal to or narrower than width facet; 1, wide, gap wider than facet. Derived from Woolfenden (1961).

138. Humerus, attachment of M. scapulohumeralis cranialis, or supraspinatus (Howard, 1929): 0, poorly defined short and wide; 1, elongate but ending distally well short of junction of bicipital crest and shaft; 2, elongate and robust, often elevated, ending distally level with or distad of junction of bicipital crest and shaft.

Note. This attachment scar straddles the median crest, i.e. the ridge between the dorsal and ventral pneumotricipital fossae, so when the dorsal fossa is large and wide as in some divers, e.g. *Clangula*, the ridge is larger and extends distally further. In this character care needs to be taken to differentiate the scar for the supraspinatus from this ridge.

139. Humerus, fossa olecrani (olecranal fossa): 0, shallow; 1, deep, well defined.

All *Tadorna* species were coded '0'.

140. Humerus, fossa pneumotricipitalis ventralis, lamina around the distoventral ventral margin from the caudal facies: 0, more than 1/2 occludes the fossa; 1, partially occludes the fossa and remains elevated off the base of the fossa and extends up under the ventral tubercle e.g. *Anser*; 2, extends into fossa where it merges with base of the fossa in ventral 1/2 of fossa; 3, extends into fossa and merges with base of fossa in dorsal 1/2 fossa; 4, incomparable as fossa closed/nonpneumatic.

Pelvis

141. Pelvis, relative length preacetabular region of synsacrum: 0, long, such that length to distal side of the costal process of the most caudal vertebrae sacrales > 40% length; 1, short, equivalent length < 40% synsacrum.

- 142. Fenestrae intertransversariae: 0, absent; 1, only in distal 1/2 of synsacrum caudad of acetabulum; 2, present in synsacrum over all length caudad of acetabulum.
- 143. Canalis iliosynsacralis: 0, absent, ilia fused dorsally entirely; 1, paired openings directed caudally.
- 144. Corpus ischii: 0, with no foramen opening laterally below the antitrochanter at its junction with the acetabulum; 1, with pneumatic foramen. Character 121, Worthy *et al.* (1997).
- 145. Antitrochanter: 0, with pneumatic openings medially to fossa renalis, or posteriorly into foramen ilioischadicum; 1, None.
- 146. Recessus caudalis fossae: 0, deep, e.g. *Gallus*; 1, shallow and pneumatic; 2, absent. Character 120, Livezey (1986).
- 147. Foramen ilioischadicum: 0, very short, much < 1/2 length ischium from foramen acetabulum; 1, about 1/2 length ischium from acetabular foramen; 2, long, > 1/2 length ischium from acetabular foramen.
- 148. Tuberculum preacetabulare: 0, very prominent with notch between it and ilium, e.g. *Gallus*; 1, less prominent, with no notch above it.
- 149. Pubis: 0, dorsally concave over length; 1, straight or flat. Character 115, Livezey (1986).
- 150. Pubis, section distad of articulation with distal ischium with flattened caudal expansion, typically rounded in lateral view and with diameter significantly greater than area immediately craniad of it: 0, not so; 1, yes, e.g. *Cygnus*. Character 117, Livezey (1986).

APPENDIX 2

DATA MATRIX USED IN THE PHYLOGENETIC ANALYSES

Gallus_gallus 0 - 1 0 1 0 0 0 1 0 0 1 0 0
 - - 0 - 0 1 1 - - 0 0 (01) 0 0 3 2 2 - -
 - 1 1 2 1 1 1 - 3 0 3 - 0 1 0 2 1 - - 2
 1 2 1 0 0 2 2 - - 1 0 0 0 0 0 0 0 (12)
 0 1 0 0 2 0 0 0 1 0 2 0 0 0 - 0 0 0 0 0
 0 0 ? 0 0 1 (12) 0 - 1 0 0 0 0 0 0 0 0
 0 0 1 0 0 0 1 0 0 2 0 0 0 1 0 0 0 2 (01)
 0 1 1 0 1 0 1 0 0 0 1 0 1 0 1 0 0 1 0 0
Anhima_cornuta 0 0 1 0 0 - 0 2 0 0 0 0 0 0
 0 - - 0 - 0 0 1 0 - 0 1 0 0 0 0 0 0 1 0
 0 0 - 1 0 0 0 0 0 0 0 0 0 0 0 2 0 0 0 0
 2 0 0 0 0 2 0 2 0 0 1 0 0 0 0 1 0 0 0
 0 2 0 - 0 - 0 1 0 1 1 0 0 0 0 0 0 0 0 0
 0 0 0 0 1 2 1 1 0 0 0 0 1 0 0 0 1 0 0 0
 1 0 0 2 0 0 0 0 1 2 3 0 0 0 0 2 0 0 0 1
 0 0 0 1 0 0 0 0 1 0 0 0 1 0 1 0 0

Anseranas 0 0 0 0 0 - 0 1 - 0 0 0 0 1 0
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 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0
 0 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0
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 0 0 0 1 0 0 0 0 0 0 0 0 1 0 1 0 0
Thalassornis 0 0 1 1 0 0 0 1 ? 1 1 1 0 1
 0 0 0 0 2 1 0 0 0 1 1 1 1 0 3 2 1 ? 0 1
 0 - ? 0 1 1 0 3 0 3 1 1 1 2 0 1 0 1 1 0
 0 0 1 1 2 2 1 0 1 0 0 1 1 0 0 0 0 ? 1
 ? 1 0 0 0 2 0 ? 0 0 1 3 1 - 2 1 1 1 1 1
 0 0 1 - 1 ? 1 1 1 1 2 1 2 1 1 0 1 0 1 1
 1 0 0 ? 0 1 ? 0 ? ? 1 ? ? 0 2 0 0 0 0
 0 0 0 2 1 4 0 2 0 0 1 2 1 0 1 0
Dendrocygna_arborea 1 0 1 1 0 0 0 1 3 1 0
 1 0 1 0 2 0 1 2 0 1 0 0 1 2 1 0 0 3 1 1
 1 0 0 0 - 1 1 1 1 0 3 0 1 0 1 1 2 0 1 0
 1 1 0 1 0 0 0 0 0 0 2 1 0 1 1 0 0 0 0
 1 0 1 1 1 0 0 0 0 0 0 1 1 3 1 0 1 0 1
 1 0 0 0 1 0 1 0 1 1 0 0 1 1 2 1 0 0 0
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 0 0 1 0 0 0 1 0 0 ? ? ? ? ? ? ? ? ?
Dendrocygna_autumnalis 1 0 0 1 0 0 0 1 2
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 1 1 2 0 1 0 1 1 0 1 0 0 0 0 0 (02) 1 0
 1 1 0 0 0 0 1 0 1 1 1 0 0 0 1 0 0 0 1
 1 3 1 0 1 0 1 1 0 0 0 0 1 2 1 0 1 1 0 0
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 0 2 2 1 0 1 0 ? 3 2 0 1 0 0 0 1 0 0 2 ?
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Dendrocygna_bicolor 1 0 0 1 0 0 0 1 2 1 0
 1 0 1 0 1 0 1 1 0 1 0 0 1 2 1 0 0 2 1 1
 0 0 0 0 - 1 0 1 1 0 3 0 1 0 1 1 2 0 1 0
 1 1 0 2 0 0 0 0 0 0 0 1 0 1 1 0 0 0 0
 0 0 1 0 1 0 0 0 1 0 0 0 1 1 3 1 0 1 0 1
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 0 1 0 0 1 1 1 0 1 0 1 1 1 0 2 2 1 0 1 0
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Dendrocygna_eytoni 0 0 0 1 1 0 0 1 2 4 0
 1 0 1 0 2 0 1 1 0 1 0 0 1 2 1 0 0 1 1 2
 0 0 0 0 - 1 1 1 (01) 0 3 0 1 0 1 1 2 0 1
 0 1 1 0 1 0 0 0 1 0 0 2 1 0 1 1 0 0 0
 0 0 0 1 0 1 0 0 0 1 0 0 0 1 1 3 1 0 1 0
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 1 0 0 1 1 1 0 0 0 1 1 1 0 1 3 1 0 0 0 1
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Dendrocygna_arcuata 0 0 0 1 0 0 0 1 2 4 0
 1 0 1 0 1 0 1 2 (01) 1 0 0 1 2 1 1 0 1 1
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Oxyura_vittata 0 0 1 1 1 0 0 1 3 2 2 2 0	5 0 0 1 0 0 1 0 1 2 0 4 1 1 0 0 1 2 2 0
1 0 0 0 0 2 0 1 (01) 0 2 2 1 1 1 3 2 1 0	1 0
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2 1 1 0 1 1 2 1 1 0 1 1 0 2 0 0 1 0 1 1	1 0 0 0 0 0 0 1 1 0 1 1 1 1 1 2 (12) 1 0
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0 1 1 1 1 2 1 4 ? ? ? ? ? ? ? ? ? ?	0 0 1 1 0 2 2 1 1 (23) 1 0 0 2 1 2 2 1 0
Oxyura_jamaicensis 0 0 1 1 0 0 0 1 3 2 2	0 0 1 1 1 1 0 1 0 2 1 0 2 1 1 0 1 1 1 0
2 0 1 0 0 0 0 0 0 1 (01) 0 2 2 1 1 1 3 2	0 1 0 1 1 0 1 2 1 4 1 2 1 0 1 2 2 1 0 0
1 0 0 1 1 2 2 0 1 1 0 3 0 2 0 1 1 1 1 1	Nettapus_pulchellus 0 0 2 1 1 0 0 1 3 4 2
0 2 2 1 2 0 1 1 2 2 1 0 1 1 0 2 1 0 1 1	1 0 1 0 2 0 0 1 1 0 1 0 1 0 1 1 1 2 2 2
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1 1 1 1 1 1 1 - 1 1 2 1 1 1 2 1 2 2 1	- 1 1 2 1 1 0 2 2 0 1 1 1 1 2 0 1 2 0 1
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Oxyura_australis 0 0 1 1 0 0 0 1 3 2 2 2	0 1 0 0 0 1 1 2 (01) 3 1 1 0 0 1 2 2 1 1
0 1 0 0 0 0 0 0 1 (01) 0 1 2 1 1 0 3 2 2	1
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Oxyura_maccoa 0 0 1 1 0 1 0 1 3 2 2 2 1 1	2 1 0 (01) 0 1 1 (01) 0 (01) 2 0 2 2 0 1
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Nomonyx_dominicus 0 0 2 1 0 0 0 1 2 1 2 2	0 1 1 1 2 0 0 1 1 0 0 1 1 1 1 1 0 0 0 1
0 1 0 0 0 1 1 0 1 0 0 2 2 1 1 0 3 2 2 0	1 1 0 2 0 0 1 1 1 2 (34) 1 0 1 0 2 2 0 0
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2 1 2 0 1 0 2 2 0 0 1 1 1 2 1 0 0 0 1 1	Cnemiornis_calcitrans 0 0 0 1 0 0 1 2 0 4
0 1 1 0 (12) 0 0 1 0 0 0 0 1 3 1 - 2 1 1	1 1 0 1 0 2 1 1 0 0 1 0 0 1 0 1 1 0 3 1
1 0 1 1 1 1 - 1 1 1 1 0 1 2 1 2 2 1 0 1	1 1 0 0 0 - 1 0 0 (01) - 2 0 - - 1 0 1
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Stictonetta 0 0 2 1 0 1 0 1 2 2 2 1 1 1	0 1 0 0 0 1 0 2 1 0 0 1 1 0 0 0 1 1 1 1
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2 0 0 0 2 1 0 1 1 0 1 2 0 1 1 0 1 1 0 1	0
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Biziura_lobata 0 0 1 0 0 0 0 2 2 1 0 2 0	0 1 1 0 0 0 0 0 0 1 (12) 0 3 1 1 (12) 3
1 0 1 0 1 1 0 0 1 0 1 1 1 1 0 3 2 1 1 0	1 0 1 0 1 0 0 0 1 1 1 1 1 0 2 1 0 0 (12)
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Anser_brachyrhynchus 0 0 0 1 0 0 0 1 0 4	0 0 0 1 2 1 1 1 1 0 0 1 1 2 2 1 0 0 0 1
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1 0 1 0 1 0 1 0 1 0 0 2 2 1 0 1 1 0 0 0	0 0 1 1 1 0 2 1 2 1 0 1 2 1 1 1 0
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1 1 0 1 0 0 0 0 0 2 1 3 1 1 2 3 1 0 1 0	1 1 0 2 0 1 0 1 1 1 1 1 2 1 1 0 2 2 2 0
1 0 0 0 1 1 1 1 1 0 3 1 0 0 1 1 2 2 1 0	0 0 1 1 2 0 1 1 0 3 0 1 0 1 1 0 1 1 0 1
0 0 1 1 1 1 2 1 0 1 1 0 2 4 0 1 1 0 4 3	1 0 1 0 0 0 1 1 0 2 1 1 1 2 0 0 1 0 1 1
(02) 0 0 0 0 0 1 0 0 1 1 2 0 1 1 2 2 0 0	0 1 0 0 0 0 1 2 1 3 2 1 2 3 1 0 1 0 1 0
1	0 0 0 0 1 (12) 1 1 2 1 0 0 1 1 2 2 1 0 0
Anser_caerulescens 0 0 0 1 0 (01) 0 1 0 4	0 1 1 1 1 2 0 2 1 0 0 2 (12) 1 1 1 0 1 2
1 1 0 1 0 2 0 2 2 1 1 0 1 1 0 1 1 0 2 1	0 1 0 0 0 1 1 1 0 2 1 2 1 0 1 2 2 1 0 0
1 1 1 0 1 1 1 1 1 0 0 3 2 1 0 1 1 0 0 0	Tadorna_radjah 0 0 2 1 2 0 0 1 1 4 1 2 1
0 0 1 0 1 0 0 0 0 0 0 2 1 1 1 1 0 0 0 0	1 0 2 0 1 1 1 1 1 1 1 2 1 1 1 1 1 2 0 0
0 1 0 0 0 0 0 0 0 0 1 3 0 0 2 3 1 0 1 0	0 1 1 2 1 1 1 0 2 0 1 0 0 1 0 1 1 0 2 1
1 1 0 0 1 1 1 0 0 0 3 1 0 0 1 1 2 2 1 0	0 1 1 0 0 1 1 0 2 1 1 1 2 0 0 1 0 1 1 0
0 0 1 1 1 1 2 0 0 1 1 1 2 3 1 1 1 0 3 3	1 0 0 0 0 2 0 3 2 1 2 3 1 0 1 0 1 0 0 0
2 0 0 0 0 0 1 0 0 1 1 2 0 (01) 0 2 2 0 0	0 0 0 1 2 1 1 1 1 0 0 1 1 2 2 1 0 0 0 1
0	1 1 0 0 2 1 1 0 2 1 1 1 0 2 2 1 1 0
Anser_rossii 0 0 0 1 2 1 0 1 0 4 1 1 0 1	0 0 1 1 2 0 1 1 2 1 0 1 2 0 0 0 0
0 2 0 1 1 1 1 1 0 1 0 1 1 0 2 1 1 0 1 0	Alopochen 0 0 0 1 2 1 0 2 3 4 1 2 1 1 0
1 0 1 1 1 0 0 3 1 1 0 1 1 0 0 0 0 0 1 0	2 0 1 2 1 1 1 0 1 0 1 1 0 2 1 2 0 0 0 0
1 0 0 0 0 0 0 2 1 1 1 1 0 0 0 0 0 1 0 1	- 1 0 1 1 0 3 1 1 0 1 1 0 0 1 0 2 1 0 1
0 0 0 0 0 0 1 3 1 0 1 3 1 0 1 0 1 1 0 0	0 0 0 1 (01) 0 2 1 1 1 2 0 0 1 0 1 1 0 1
1 1 2 0 1 1 2 1 0 0 1 1 2 2 1 0 0 0 1 1	0 0 0 0 1 2 0 3 2 1 1 3 1 0 1 0 1 0 0 0
1 1 2 0 0 1 0 1 2 3 1 0 1 0 ? 3 2 0 0 0	0 0 1 0 (01) 1 1 1 0 0 1 1 2 2 1 0 0 0 1
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Cygnus_atratus 0 0 0 1 0 1 1 2 0 4 1 1	1 0 0 0 0 0 2 1 2 1 0 1 2 0 0 0 0
0 1 0 2 0 2 2 1 0 1 0 1 2 1 1 0 0 1	Chloephaga_hybrida 0 0 1 (01) 2 0 1 1 1 4
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0 0 0 0 1 1 0 0 0 0 0 1 0 0 0 3 1 1	0 1 2 0 1 0 0 0 0 ? 0 2 1 1 1 2 0 0 0 0
1 1 1 0 1 0 1 0 0 0 1 0 0 2 1 0 1 1	1 1 0 1 0 0 0 0 1 2 1 3 1 1 2 3 1 0 1 0
0 0 2 1 2 2 1 0 0 0 1 1 1 0 2 0 0 1	1 0 0 0 0 2 1 2 1 1 1 1 0 0 1 1 2 1 1 0
0 1 1 5 1 1 1 0 3 0 2 0 0 0 0 0 1 0	0 0 1 1 1 0 0 0 2 1 0 0 2 1 1 1 1 0 2 1
0 1 1 1 1 0 1 2 1 1 0 1	0 1 0 0 1 1 0 0 0 2 1 2 1 0 0 2 1 1 0 1
Tadorna_ferriginea 0 0 0 1 0 0 0 1 2 4 1	Chloephaga_poliiocephala 0 0 1 (01) 2 0 1 1
2 1 1 0 1 0 1 1 1 1 1 1 2 1 1 0 2 2 2	1 4 0 2 0 1 0 1 0 1 2 0 1 1 0 2 ? 1 1 1
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1 1 0 2 0 0 0 1 0 0 2 1 1 1 2 0 1 1 0 0	1 1 1 - 1 0 1 0 0 0 0 ? 0 2 1 1 1 2 0 0
1 0 1 0 0 0 0 2 0 3 1 0 2 3 1 0 1 0 1	1 0 1 1 0 1 0 0 0 0 1 2 1 3 1 1 2 3 1 0
0 0 0 0 0 1 2 0 1 3 1 0 0 2 1 2 2 1 0 0	1 0 1 0 0 0 0 2 1 1 0 1 1 1 0 0 1 1 2 2
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Clangula_hyemalis 0 0 1 1 3 0 1 1 1 3 0 2	1 1 0 1 2 2 2 1 0 1 2 0 1 1 0 2 0 0 1 0
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