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Running head: *Oligocene pedionomid from Australia*

A Plains-wanderer (Pedionomidae) that did not wander plains: a new species from the Oligocene of South Australia

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The remarkable fauna of Australia evolved in isolation from other landmasses for millions of years, yet understanding the evolutionary history of endemic avian lineages on the continent is confounded by the ability of birds to disperse over geographical barriers even after vicariance events. The Plains-wanderer *Pedionomus torquatus* (Charadriiformes) is an enigmatic, predominantly sedentary, quail-like bird that occurs exclusively in sparse native grasslands of south-eastern Australia. It is the only known species of its family (Pedionomidae), and its closest relatives are the South American seedsnipes (Thinocoridae). Here we describe a further representative of this lineage, *Oligonomus milleri* gen. et sp. nov. from the Late Oligocene of South Australia (26–24 Ma), which predates the earliest record of *P. torquatus* by ca. 22 Ma and attests to the presence of this lineage during Australia's period of isolation (50–15 Ma). Based on the morphology of the coracoid and the palynological record, we propose that *O. milleri* and *P. torquatus* were ecologically disparate taxa, and that

similar to coeval marsupials, *O. milleri* inhabited well-wooded habitats, suggesting that the preference for grassland in the extant *P. torquatus* and thinocorids is likely convergent and not ancestral. The speciation event leading to the evolution of the extant Plains-wanderer was probably triggered by the spread of grasslands across Australia in the Late Miocene-Pliocene, which this record predates. The presence of a pedionomid in the Late Oligocene of Australia strengthens the hypothesis of a Gondwanan divergence of the lineages giving rise to Thinocoridae and Pedionomidae.

Keywords: *Pedionomus torquatus*, Charadriiformes, *Oligonomus milleri* gen. et sp. nov., Australasian avifauna.

The extended period of geographic isolation spanning from complete separation of Australia from Antarctica to subsequent close proximity to the Indo-Malayan region (ca. 50–15 Ma; Hall 2009, Bijl *et al.* 2013) facilitated the evolution of Australia's iconic endemic biota (Boles 2006, Black *et al.* 2012). Nonetheless, the evolutionary history of many of Australia's endemic birds remains poorly understood, not least because identifying which components of the avifauna were already on the continent prior to isolation and which arrived later, especially from the north, has proven difficult (Boles 2006). The fossil record offers a unique opportunity to address whether the modern composition of Australia's avifauna is indeed reflective of ancient endemic speciation, or whether apparent endemic taxa may have originated, i.e. diverged, outside the continent in earlier times.

The Plains-wanderer *Pedionomus torquatus* is the only extant species within the Pedionomidae (Charadriiformes) and no fossil species have been hitherto recognised. *P. torquatus* is restricted to the open grasslands of southern and eastern Australia. It is now considered endangered as populations have been in decline since the arrival of Europeans

(Baker-Gabb 1996). The fossil record is sparse and limited to specimens from Quaternary cave deposits in Victoria and South Australia, with Plio-Pleistocene records being of uncertain age (Rich & McEvey 1980, Baird 1991). The first detailed description of the skull and postcranial skeleton of *P. torquatus* was that by Bock and McEvey (1969). Originally thought to be closely related to buttonquails (Turnicidae; Gadow 1891), subsequent research has shown *P. torquatus* closest relatives to be the morphologically similar South American seedsnipes (Thinocoridae; Olson & Steadman 1981, Baker *et al.* 2007, Mayr 2011, Gibson & Baker 2012, but contra Livezey 2010). Seedsnipes inhabit grasslands and alpine habitats of Patagonia and the Andean region (Fjeldså 1996).

Here we describe a fossil pedionomid from Late Oligocene (ca. 26–24 Ma) fluvio-lacustrine deposits of central Australia (northern South Australia), which greatly extends the known duration of this lineage on the continent, and adds to the still emerging knowledge of the Late Oligocene avifauna of northern South Australia (Miller 1963; Boles 2001; Boles & Ivison 2009; Worthy 2009). Palaeoenvironmental and historical biogeographic implications of the new taxon are discussed.

METHODS

The fossil material is deposited at the South Australian Museum, Adelaide, Australia (SAMA). Recent comparative material was obtained from the South Australian Museum; Museum Victoria, Melbourne, Australia (NMV); Natural History Museum Basel, Switzerland (NMB); Museum of New Zealand Te Papa Tongarewa (NMNZ); and the Senckenberg Research Institute, Frankfurt, Germany (SMF). Anatomical terminology follows Baumel and Witmer (1993).

Comparative material

Scolopacidae: Spotted Sandpiper *Actitis macularius*, Ruddy Turnstone *Arenaria interpres*, Upland Sandpiper *Bartramia longicauda*, Sharp-tailed Sandpiper *Calidris acuminata*, Sanderling *C. alba*, Dunlin *C. alpina*, Curlew Sandpiper *C. ferruginea*, Stilt Sandpiper *C. himantopus*, Least Sandpiper *C. minutilla*, Red-necked Stint *C. ruficollis*, Subantarctic Snipe *Coenocorypha aucklandica*, Latham's Snipe *Gallinago hardwickii*, Black-tailed Godwit *Limosa limosa*, Asian Dowitcher *Limnodromus semipalmatus*, Eurasian Curlew *Numenius arquata*, Eurasian Woodcock *Scolopax rusticola*, Common Greenshank *Tringa nebularia*, Wandering Tattler *T. incana*, Terek Sandpiper *Xenus cinereus*. Rostratulidae: Australian Painted-snipe *Rostratula australis*, Greater Painted-snipe *R. benghalensis*. Jacanidae: Comb-crested Jacana *Irediparra gallinacea*, Northern Jacana *Jacana spinosa*. Pedionomidae: Plains-wanderer *Pedionomus torquatus*. Thinocoridae: Rufous-bellied Seedsnipe *Attagis gayi*, Grey-breasted Seedsnipe *Thinocorus orbignyianus*, Least Seedsnipe *T. rumicivorus*.

SYSTEMATIC PALAEOLOGY

Aves Linnaeus, 1758

Charadriiformes Huxley, 1867

Scolopaci Strauch, 1978; sensu Paton *et al.* 2003

Five families are included in the Scolopaci, the Pedionomidae (Plains-wanderer), Thinocoridae (seedsnipes), Rostratulidae (painted-snipes), Jacanidae (jacanas), and Scolopacidae (sandpipers and relatives) (Gibson & Baker 2012). Referral to this clade is based on the following combination of features of the coracoid: (1) facies articularis clavicularis ventrodorsally broad; (2) processus acrocoracoideus ventromedially protruding;

(3) foramen nervi supracoracoidei absent. Characters (1) and (2) are present in most Charadriiformes, and character (3) is characteristic of all Scolopaci (see Mayr 2011).

Pedionomidae Bonaparte, 1856

Referral to this family is based on the following combination of features: (1) absence of a recess in sulcus m. supracoracoidei, medially, below the facies articularis clavicularis (Fig. 1A, B); (2) impressio lig. acrocoracohumeralis well-marked and dorsoventrally broad (Fig. 1N); (3) cotyla scapularis deep and distinctly round with maximum diameter about half the length of the facies articularis humeralis (Fig. 1F, G); (4) lateral margin of facies articularis humeralis in dorsal view subangular instead of smoothly rounded (Fig. 1A, B); (5) processus procoracoideus elongated sternally, merging with margo medialis of corpus coracoidei at low angle (Fig. 1A); (6) ligamental attachment on dorsal surface at sternal end of processus procoracoideus well-marked and elongated (Fig. 1A, F); (7) shaft lacking abrupt widening towards impressio m. sternocoracoidei (Fig. 1A, compare with B, E).

Within Scolopaci, character (2) is also present in Rostratulidae and Jacanidae; (3) in Rostratulidae and Thinocoridae; (5), (6), (7) in Jacanidae; (4) in Thinocoridae, and (1) is only present in Pedionomidae.

***Oligonomus milleri* gen. et sp. nov.**

Holotype

SAMA P27976, left coracoid lacking sternal end, Fig. 1A, F, H, I, K.

Etymology

Genus name alludes to Oligocene and *Pedionomus*, masculine. Specific name after Alden Holmes Miller (1906–1965), American ornithologist and naturalist who accompanied R.A. Stirton on a fossil collecting expedition in South Australia in 1961, and described the first components of this late Oligocene avifauna (Mayr 1973).

Type Locality and Age

Steve's Site (locality number SAMA PL 8309 = University of California Museum of Paleontology RV-8447), located on the escarpment on the western side of Lake Palankarina, eastern Lake Eyre Basin, northern South Australia. Steve's Site is within member 7 of the Etadunna Formation (Faunal Zone B), which produces the Ditjimanka Local Fauna of Late Oligocene (26–24 Ma) age (Woodburne *et al.* 1994). This falls within the Etadunna land mammal age (Megirian *et al.* 2010). Additional locality information is available from the SAMA Palaeontology Section.

Measurements (mm)

Maximum length as preserved, 11.9; facies articularis humeralis – processus acrocoracoideus, 4.6; cotyla scapularis – pr. acrocoracoideus, 5.3; shaft width, 2.2.

Differential Diagnosis

Within the size range of *P. torquatus*, from which it differs in: (1) dorsolaterally developed ligamental attachment area adjacent to dorsal portion of facies articularis clavicularis (Fig. 1B, L) absent; (2) sulcus m. supracoracoidei deeper (Fig. 1A); (3) dorsal margin that is the lateral portion of the canalis triosseus (triosseal canal) more elongated omal-sternally (Fig. 1A, compare with B); (4) processus acrocoracoideus more elevated omally (Fig. 1A, compare

with B, G). *Oligonomus milleri* agrees with other members of Scolopaci in these features (1–4), but differs from the coracoids of

–Scolopacidae, Rostratulidae, Thinocoridae, Jacanidae in: (5) absence of recess in sulcus m. supracoracoidei under facies articularis clavicularis. From

–Scolopacidae, Rostratulidae, Thinocoridae in: (6) shaft lacking abrupt widening sternally towards impressio m. sternocoracoidei; (7) ligamental attachment on margo medialis of corpus coracoidei located closer to sternal end; character (8) base of processus procoracoideus merging with margo medialis of corpus coracoidei at low angle (Fig. 1A, B, compare with E). From

–Scolopacidae, Jacanidae in: (9) length of facies articularis humeralis proportionally short, with cotyla scapularis about half its length (facies articularis humeralis more elongated in these taxa, Fig. 1D, E). From

–Scolopacidae and Thinocoridae in: (10) impressio lig. acrocoracohumeralis dorsoventrally broad (instead of mediolaterally elongated, Fig. 1O). From

–Rostratulidae in: (11) dorsal part of sulcus m. supracoracoidei deepened relative to ventral part (instead of evenly deep, Fig. 1M); (12) dorsal portion of facies articularis clavicularis with lesser sternal projection (Fig. 1M); (13) facies articularis clavicularis broader in omal-sternal direction (Fig. 1M).

Description

The holotype of *O. milleri* corresponds in size with the coracoids of larger individuals of *P. torquatus*. There is pronounced size dimorphism within this species, with females being larger than males. The coracoid of *Oligonomus* is missing its sternal end and most of the ventral portion of the facies articularis clavicularis (Fig. 1K). The bone is elongate, as evidenced by the very gradual widening of the shaft towards the sternal end (Fig. 1A, F).

Species of Rostratulidae, Thinocoridae, and most scolopacids (the taxon *Scolopax* being one exception) display different proportions: their coracoids are stout, with a proportionally short shaft in relation to the omal-sternal length of the omal extremity (Fig. 1E). As in *P. torquatus* and in species of Jacanidae, there is a smooth transition between the base of the processus procoracoideus and the margo medialis of the corpus coracoidei (Fig. 1A, B, D). The medial surface of the bone lacks a recess under the facies articularis clavicularis; this recess is present to varying degrees in all examined taxa of Scolopaci with the exception of *P. torquatus* (Fig. 1B).

One of the most notable differences from the coracoid of *P. torquatus* is the absence of a flat and wide ligamental insertion area on the dorsal side of the omal extremity, adjacent to the facies articularis clavicularis (Fig. 1B). In *O. milleri* and all other representatives of Scolopaci, there is a rather indistinct transition between the omal margin of the facies articularis humeralis and the dorsal portion of the facies articularis clavicularis (Fig. 1A, D, E). Compared to *O. milleri*, this area is nevertheless well developed in species of *Thinocorus* (Fig. 1C), but is not as prominent as in *P. torquatus* (Fig. 1B). Furthermore, the medial surface of the omal extremity (sulcus m. supracoracoidei), which bounds the canalis triosseus laterally, is shorter (in omal-sternal direction) and much shallower in *P. torquatus* (Fig. 1B, G), resulting in a reduced lateral depth of the canal in this taxon.

Most of the sternal end of the coracoid is missing, but the omal margin of the impressio m. sternocoracoidei is preserved and is slightly more medially situated than in *P. torquatus* (Fig. 1A, B).

DISCUSSION

By the Late Oligocene, pedionomids had attained a distinctive morphology of the coracoid compared to their closest relatives, the South American seedsnipes (Fig. 1A–C). Yet based on

outgroup comparisons with other members of the Scolopaci, the coracoid of *O. milleri* exhibits a more plesiomorphic morphology than that of *P. torquatus*. This is primarily evidenced by the narrower opening of the triosseal canal in the latter. The triosseal canal guides the tendon of the supracoracoideus muscle, one of the major muscles involved in flapping flight. In some groups of birds a reduction in the size of this muscle is correlated with diminished flight capabilities (Livezey 2003). While inferring a correlation between the morphology of the coracoid and the flying ability of a bird may be difficult, compared to species in closely related taxa (Thinocoridae, Jacanidae, Rostratulidae), we suggest the derived morphology of the coracoid of *P. torquatus* may indeed reflect its poor flight capabilities (e.g. Marchant & Higgins 1993). In contrast, *O. milleri* was probably a more adept and mobile flier, which can be inferred from the similarity in key features of its coracoid to those of migratory Scolopaci relative to their states in *P. torquatus* (features 1–4 in Differential Diagnosis).

Pedionomus torquatus inhabits open grasslands in southern and eastern Australia and does not occur in woodlands or treed areas (Marchant & Higgins 1993). The vegetation record for the Late Oligocene and Early Miocene of northern South Australia is fragmentary (Alley 1998), but pollen assemblages have been used to infer the presence of wetter forest elements in the area (Tedford *et al.* 1977, Truswell & Harris 1992). This is further reinforced by the presence of arboreal mammalian taxa, such as koalas (Phascolarctidae) and a diverse possum fauna (e.g. Pseudocheiridae) in the fossil record (Stirton *et al.* 1961, Rich 1991). The rarity of grass pollen grains does not support the inference of extensive grasslands in northern South Australia during the Late Oligocene, which are more likely to have spread across Australia in the Late Miocene or Pliocene (Martin 1990, Black *et al.* 2012). The presence of Pedionomidae in the Late Oligocene therefore predates the evolution of open grasslands, and suggests that *O. milleri* had different habitat preferences to *P. torquatus*. This finding

contradicts a previous hypothesis stating that this preference was ancestral to both seedsnipes and the Plains-wanderer (Fjeldså 1996), and instead suggests that habitat preference is convergent in these two taxa.

The uniqueness of the Australian fauna has been linked to its evolution in geographic isolation for over 30 million years after breakup from Antarctica and South America (Black *et al.* 2012). In flying birds, however, open water is often not a hurdle to dispersal, and in the absence of a chronologically complete fossil record, it is difficult to infer which components of the Australian avifauna are the result of divergence from a resident ancestor and which are derived from precursors that invaded from the north via the Indo-Malayan region during the Late Miocene, or even via Antarctica before complete glaciation (ca. 6 Ma; White 1994). The fact that only two pedionomids are known, both from Australia, one extant and one from the Late Oligocene, suggests that this represents another endemic Australian lineage. The speciation event leading to the evolution of the extant Plains-wanderer was probably triggered by the spread of grasslands across Australia during the Neogene.

The geographical range of the closely related seedsnipes of South America, in addition to the record here described, strengthens the hypothesis of a Gondwanan divergence of Thinocoridae and Pedionomidae from their last common ancestor, one possibly facilitated by the breakup of Australia from Antarctica and South America in the Early Eocene (Paton *et al.* 2003, Mayr 2011). However, the inferred flight capabilities of *O. milleri* do not rule out representatives of this lineage colonising Australia from Antarctica before the Late Oligocene, as the glaciation of Antarctica towards the Eocene/Oligocene transition may have played a role in this event (Mayr 2011).

The centre of diversification of crown group Charadriiformes still remains unknown, as extant distributions are often not reflective of past ones. Both stem group Charadriiformes, and representatives of most lineages within the crown group, have been described from the

Palaeogene of the Northern Hemisphere (Mayr 2009, De Pietri *et al.* 2011, De Pietri & Scofield 2014). Nevertheless, some early diverging charadriiform lineages, such as sheathbills (two species of *Chionis*, Chionidae) and the Magellanic Plover *Pluvianellus socialis* (Pluvianellidae), and even *P. torquatus* and Thinocoridae, persist only in the Southern Hemisphere (South America, Antarctica, and Australia). Although the record here described does not unequivocally inform on the centre of divergence of crown group Charadriiformes, it nevertheless attests to an evolutionary history of at least 26 Ma for pedionomids in Australia.

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Figure 1. Left coracoid of *Oligonomus milleri* gen. et sp. nov. from the Late Oligocene of South Australia in dorsal (A, F), ventral (H), medioventral (I), medial (K), and lateral (N) views. *Pedionomus torquatus* in dorsal (B, G) and medial (L) views. *Thinocorus rumicivorus* in dorsal (C) and medioventral (J). *Jacana spinosa* (D) in dorsal view. *Bartramia longicauda* in dorsal (E) and lateral (O) views. *Rostratula benghalensis* (M) in medial view.

Abbreviations: cs, cotyla scapularis; dtc, dorsal margin of canalis triosseus; fac, facies articularis clavicularis; fah, facies articularis humeralis; ila, impressio lig. acrocoracohumeralis; ims, impressio m. sternocoracoidei; laa, ligamental attachment area; pac, processus acrocoracoideus; ppc, processus procoracoideus; sms, sulcus m. supracoracoidei; toc, triosseal canal. Arrows point to the area below the facies articularis clavicularis. Scale bars equal 5mm.

