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Volume 2, Issue 1

February 2016

Pages 41–58

Original Article

New data on stiff-tailed duck evolution and dispersal from a new species of diving duck (Anseriformes: Anatidae: cf. Oxyurinae) from the Miocene High Rock Caldera in north-west Nevada, USA

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First published:7 October 2015 [Full publication history](#)**DOI:**10.1002/spp2.1029 [View/save citation](#)**Cited by (CrossRef):**[Check for updates](#)

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Abstract

A new species of diving duck from lacustrine deposits inside the middle Miocene High Rock Caldera in north-west Nevada (USA) appears to be more closely related to the stiff-tailed ducks *Oxyura* and *Nomonyx* than to other Oligocene and Miocene anatid taxa. The new species, *Lavadytis pyrenae* sp. nov., is represented by 24 fragments of humeri, tibiotarsi, tarsometatarsi, coracoids, a scapula and carpometacarpi, and several of the specimens are from juvenile individuals, indicating that the caldera palaeolake was a breeding site. The humerus has a 'closed' non-pneumatic ventral pneumotricipital fossa, lacks a capital shaft ridge, has a cranial carpal fovea and has a pronounced medial epicondyle on the tibiotarsus. Many of the osteological features present in this new species also occur (convergently) among derived diving duck clades and therefore suggest that this extinct species foraged by diving. This new species' phylogenetic position close to the extant species in *Nomonyx* and *Oxyura*, its middle Miocene age (16.1–14.6 Ma) and its geographical location in North America are consistent with molecular clock analyses placing the origin of the stem leading to *Oxyura* + *Nomonyx* at approximately 15.9 Ma in the New World. This new species could indicate

that the stem of the *Oxyura* + *Nomonyx* clade had reached the New World by the middle Miocene and that the diversification present among New World Oxyurini/Oxyurinae began temporally close to the climatic warming of the Middle Miocene Climatic Optimum.

Extant diving ducks are a non-monophyletic grouping that includes the stiff-tailed ducks (Oxyurini), sea ducks (Mergini) and pochards (Aythini; McCracken *et al.* 1999). Most analyses indicate that the diving habit (and the morphological specializations related to diving) evolved independently multiple times in anatid diversification (McCracken *et al.* 1999; O'Connor 2004; Worthy and Lee 2008; Worthy 2009). The origins of the separate diving duck radiations extend into the late Oligocene and early to middle Miocene (Alvarez and Olson 1978; Olson 1985; Worthy and Lee 2008; Worthy 2009; Zelenkov 2011, 2012).

Much of the recent palaeontological focus on diving ducks has been on taxa from New Zealand, Europe (i.e. *Mionetta*), Australia and Mongolia (Worthy and Lee 2008; Worthy 2009; Zelenkov 2011, 2012). In general, fossils from North America have not really been considered in those discussions, with the exception of some problematic taxa that were first described in the first half of the twentieth century and have not since been examined phylogenetically (e.g. *Dendrochen robusta* and *Querquedula integra*; Miller 1944; Zelenkov 2012). Despite the recent fossil descriptions of Old World taxa and related phylogenetic analyses, the phylogeny and evolutionary pattern of Anatidae and diving ducks in the late Palaeogene and early Neogene remains problematic. Adding to this uncertainty, molecular analyses have not yet included all anatid genera or even all diving taxa into a single analysis (McCracken *et al.* 1999). The closest attempt at a comprehensive treatment of anatids is the supertree created by Eo *et al.* (2009), but their results are still questionable, with many unresolved nodes and some results conflicting with previous work (i.e. some genera not being supported as monophyletic). Even the morphological phylogenetic work relies on constraint trees and other manipulations of the osteological data to produce cladograms more consistent with traditional taxonomy and molecular analyses (Worthy and Lee 2008; Worthy 2009). More research is necessary to fully resolve the phylogenetic relationships among all anatid taxa.

One of the better-known diving duck clades is the Oxyurini (included within the Oxyurinae). The term Oxyurinae has had variable treatment by various authors, but includes the Tribe Oxyurini, and we use the term Oxyurinae in the same sense as Worthy and Lee (2008) and Worthy (2009). The taxonomic composition of Oxyurinae varies across authors, and the closest relatives to the *Nomonyx* + *Oxyura* clade include *Heteronetta*, *Nettapus*, *Biziura*, *Thalassornis*, *Stictonetta* and even geese and swans (Livezey 1995; Worthy and Lee 2008; Eo *et al.* 2009; Gonzalez *et al.* 2009). Members of the Oxyurini include the monotypic genera *Heteronetta* from South America and *Nomonyx* from Central and South America, and the species of *Oxyura* from all continents except Antarctica (Livezey 1995; Johnsgard and Carbonell 1996). *Biziura lobata* from Australia had been placed within Oxyurini (Livezey 1995), along an oxyurine stem (positioned with *Thalassornis* in Worthy and Lee 2008), slightly outside of Oxyurinae (Gonzalez *et al.* 2009), or unrelated to Oxyurinae (McCracken *et al.* 1999). In addition, *Malacorhynchus* (along with *Stictonetta*) has been hypothesized as a close relative of the oxyurines (Worthy and Lee 2008). Worthy and Lee (2008) and Worthy (2009) have supported several fossil taxa (*Manuherikia*, *Dunstanetta*, *Mionetta* and *Pinpanetta*) as the closest outgroups to the Oxyurini along an oxyurine stem, closer than *Malacorhynchus*, and those fossils constrain the origin of the oxyurine stem in the late Oligocene. While molecular analyses do not indicate the same membership of the Oxyurinae, the results of molecular clock analysis place the split between *Nomonyx* and *Oxyura*

in the middle Miocene at ~15.9 Ma (Gonzalez *et al.* 2009) with the stem lineage extending further back in time.

The stiff-tailed ducks (Oxyurinae/Oxyurini) are thought to be a monophyletic grouping of diving ducks, but there has been little molecular sampling or analysis to establish their phylogenetic positions relative to other derived anatids, and the membership of extant species within the stiff-tailed duck grouping is still debated (McCracken *et al.* 1999; Worthy and Lee 2008; Worthy 2009). One of the few more comprehensive molecular studies including oxyurines is that of Gonzalez *et al.* (2009), and their analysis places Oxyurini as the sister group to Anserinae (Gonzalez *et al.* 2009) with *Biziura* as the sister taxon to that larger clade (Anserinae + Oxyurini). Their study did not sample *Heteronetta* (Gonzalez *et al.* 2009), and that taxon is missing from some of the more recent osteological phylogenetic work (Worthy and Lee 2008; Worthy 2009). In addition, the relationships among the extant species in the *Nomonyx* + *Oxyura* clade suffer from conflicting nuclear and mtDNA data (McCracken and Sorenson 2005). Despite those issues, there is a diversity of extinct waterfowl (Anseriformes) known from the late Palaeogene and early Neogene around the world that are pointing to a radiation of diving and stiff-tailed ducks (Oxyurinae) from the Oligocene into the early and middle portion of the Miocene (Olson 1985; Worthy and Lee 2008; Worthy 2009; Zelenkov 2011, 2012).

Livezey's (1995) work on the phylogeny of Oxyurini only included species of *Oxyura*, *Biziura*, *Heteronetta* and *Nomonyx* and did not include any species outside of that grouping. In Livezey's (1995) analysis, he concluded that the likely centre of origin for the Oxyurini was in the Southern Hemisphere. That conclusion is consistent with the phylogenetic placement of the Australian and New Zealand Oligocene and Miocene fossils and a more basal position of *Malacorhynchus membranaceus* (from Australia) in some analyses (Worthy and Lee 2008; Worthy 2009). However, the molecular and morphological analyses of the *Nomonyx* + *Oxyura* clade (Livezey 1995; McCracken and Sorenson 2005; McCracken *et al.* 1999) indicate that the origin of the crown of that clade was in the New World (North and South America). Interestingly, the relationships among the species of *Oxyura* are not consistent across all trees and some tree topologies do not support a New World origin for that group of species (Eo *et al.* 2009; Gonzalez *et al.* 2009). The timing of dispersal of members of Oxyurini to the New World is not well constrained from that potential Australasian origin of the stiff-tailed duck lineage. Despite those conflicting data, a new species of diving duck from the middle Miocene High Rock Caldera in north-western Nevada adds diversity and expands the geographical range of known extinct stiff-tailed ducks into North America, indicating a more complicated biogeographical and evolutionary history of the group.

Geological setting

The High Rock Caldera is one of four overlapping calderas or caldera-like structures of the High Rock Caldera Complex (Ach and Swisher 1990). It is located in north-western Nevada (Fig. 1) and is related to the Yellowstone Hotspot (Coble and Mahood 2012). The High Rock Caldera lies between the Badger Mountain Caldera to the north-east and the Cottonwood Creek Caldera to the south-west (Fig. 1). The term High Rock Caldera was first used by Best *et al.* (1989) and affirmed by Ludington *et al.* (1996); however, the same caldera has been referred to as the Summit Lake Caldera (Noble 1988) and the Soldier Meadow Caldera (Ach and Swisher 1990). Adding further to the name confusion, Coble (2012) and Coble and Mahood (2012) referred to the caldera as the

Hanging Rock Caldera. We prefer the High Rock Caldera as it best suits the location and is the term most widely used. The north half of the High Rock Caldera is filled by lighter-coloured fluvial and lacustrine sedimentary rocks as well as lahars and thin, unwelded tuffs. The southern half is covered mostly by younger post-caldera andesitic and dacitic lavas (Ach **1988a**; Ach and Swisher **1990**). There are two main tuffs stratigraphically below the fossiliferous layer discussed here. The oldest is the Summit Lake Tuff with published ($^{40}\text{Ar}/^{39}\text{Ar}$) dates from sanidine crystals ranging from 16.58 Ma (Swisher **1992**), 16.45 Ma (Coble **2012**), to 16.43 Ma (Hausback *et al.* **2012**). These dates suggest that the Summit Lake Tuff may have been the eruption that formed the High Rock Caldera, in part because it is older than other tuffs and lavas that fill the caldera. The younger Soldier Meadow Tuff has produced a range of radiometric dates ($^{40}\text{Ar}/^{39}\text{Ar}$) including 16.29 ± 0.03 Ma (Swisher **1992**), 16.14 ± 0.01 Ma (Hausback *et al.* **2012**), 16.11 ± 0.02 and 16.10 ± 0.02 Ma (Coble **2012**). After the collapse of the High Rock Caldera, the caldera began to partially fill because of the partial collapse of the rim and additional, but minor, volcanic eruptions (Noble *et al.* **2009**). However, fluvial sediments, lahars and lacustrine deposits contribute to caldera fill Ach (**1988a**, **b**; RPH unpub. data).



Figure 1.

[Open Figure](#)

Generalized map of the location of avian fossil localities and the major volcanic structures of north-western Nevada (western USA). The type locality of *Lavadytis pyrenae* sp. nov. is 1936, and all other fossil avian material is from locality 1955, within the High Rock Caldera.

Sedimentary fill and other rhyolitic tuffs

The sedimentary fill crops out mostly in the northern half of the High Rock Caldera interior and includes shale, diatomite, sandstone, pebble conglomerates and a variety of tuffaceous deposits (Ach **1988a**, **b**; Ach *et al.* **1991**). Some of these sediments within the caldera are fossiliferous and have produced what is informally known as the Yellow Hills local fauna (Bromm and Hilton **2011**). The strata producing the vertebrate fossils are overlain by largely lacustrine deposits, perhaps correlative with beds in the Cottonwood Creek Caldera. Those stratigraphically higher lacustrine deposits are capped by a rhyolitic lava in Wall Canyon dated to 14.64 ± 0.07 Ma ($^{40}\text{Ar}/^{39}\text{Ar}$ total gas age), and that date provides a minimum estimate for the age of the vertebrate fossiliferous/lacustrine interval (Coble **2012**). At the other extreme, the sediments producing the vertebrate fossils lap onto a rhyolitic lava (Tra of Ach **1988b**) 0.5 km west of Stevens Camp that has been dated to ($^{40}\text{Ar}/^{39}\text{Ar}$) 16.30 ± 0.01 Ma (Hausback *et al.* **2012**), but all also are younger than the dates given for Soldier Meadow Tuff. These stratigraphically lower dates provide a maximum age constraint for the Yellow Hills local fauna. Meanwhile, a date based on sanidine crystals in ash-fall tuffs that are stratigraphically above the fossiliferous lahars north-east of Stevens Camp is slightly younger at ($^{40}\text{Ar}/^{39}\text{Ar}$) 16.14 ± 0.01 Ma (Hausback *et al.* **2012**). Other fossil localities within the caldera are not as well constrained. A tuff with petrified wood and embedded pumice north of the Yellow Hills has a date of 15.8 Ma (Hausback *et al.* **2012**), and that

deposit and date suggest that some of the High Rock Caldera fossils are younger than the 16.14 myr age of the lahars north-east of Stevens Camp. However, the vertebrate-bearing beds that are constrained between 16.14 and 16.30 indicate that the caldera was colonized soon after the Soldier Meadow Tuff eruption.

The fauna (and flora) from the fossiliferous deposits inside and near the High Rock Caldera represent organisms that were living in a volatile landscape and that at least some of the taxa represent posteruption colonizers in the area. The diverse vertebrate fauna termed the Yellow Hills local fauna (Bromm and Hilton [2011](#)) and associated palaeoflora (RPH unpub. data) indicate that the High Rock Caldera had a temperate climate. More than 600 vertebrate specimens have been collected in the High Rock Caldera, and those fossils represent at least 18 taxonomic families across mammals, reptiles, fish and birds. The fossil mammals include specimens of Amphicyonidae, Canidae, Felidae, Rhinocerotidae, Chalicotheriidae, Equidae, Camelidae, Mustelidae, Dromomerycidae, Merycodontidae, Tayassuidae, Merycoidodontidae (Oreodontidae), Mylagaulidae, Aplodontidae and Castoridae (Bromm and Hilton [2011](#)). Birds are represented by at least two species of Anatidae and a possible vulture (see below). Other vertebrates include a snapping turtle (Chelydridae) and a variety of actinopterygiid fish, possibly Salmonidae (Bromm and Hilton [2011](#)). Invertebrate fossils also have been collected and include insects, gastropods and bivalves. The diversity of fossils in the High Rock Caldera reflects a variety of past habitats (likely to include forest, lacustrine and riparian environments) within the caldera and nearby areas. Within this broader fauna and sedimentary deposits, one apparent shoreline deposit (Sierra College locality 1936) on the north side of a butte (detailed locality information is available to qualified researchers) capped by a Soldier Meadow-like lava (currently undated) contains only small vertebrate remains including fossils of beavers (Castoridae), dog (Canidae), small horse (Equidae), many badgers (Mustelidae) and the new species of stiff-tailed duck (Anatidae) described below. A fragment of an ulna and a proximal tarsometatarsus indicate that at least two additional species of birds (one a probable anatid and the other from possibly a vulture) were present at a nearby penecontemporaneous locality within the caldera (locality 1955, approximately 4.5 km from locality 1936; Fig. 1).

Given the stratigraphic relationships of the sedimentary deposits relative to various volcanic units and events, the maximum age for High Rock Caldera (Yellow Hills local fauna) vertebrates is ~16.3 myr and the youngest possible age is ~14.6 myr, although the stratigraphic position of the fossils suggests an age closer to the maximum than the minimum. Those dates constrain the High Rock Caldera/Yellow Hills fauna to the latest Hemingfordian North American Land Mammal Age (NALMA) to early Barstovian (Barstovian 1 to early Barstovian 2) NALMA (Pagnac [2009](#); Hilgen *et al.* [2012](#)). The boundary between the Hemingfordian NALMA and Barstovian NALMA is ~16 Ma and based on the first occurrence of the hemicyonid carnivore *Pliothocyon* (Pagnac [2009](#); Hilgen *et al.* [2012](#)). However, recently published data suggest that the Hemingfordian–Barstovian boundary may be older than previously recognized (Lander [2015](#)), and as a result, all of the fossils from the HRC may be derived solely from the Barstovian NALMA. Despite that potential biostratigraphic boundary shift, that range of absolute ages also overlaps with the Middle Miocene Climatic Optimum and sea level high in the middle Miocene (Hilgen *et al.* [2012](#)).

Abbreviations

VB, vertebrate bird specimen (for fossils) in the Natural History Museum at Sierra College, Rocklin, CA, USA; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA.

Osteological terminology follows Baumel and Witmer (1993) with English equivalents of many of the Latin terms used.

Systematic palaeontology

This published work and the nomenclatural act it contains have been registered in ZooBank:

<http://zoobank.org/References/0FA8E4AA-F590-4440-9959-E0A8DB5AB2B8>

Order ANSERIFORMES Wagler, 1831 Family ANATIDAE Leach, 1820
Subfamily cf. OXYURINAE Phillips, 1926 (*sensu* Worthy and Lee 2008) Genus
LAVADYTIS gen. nov.

LSID

urn:lsid:zoobank.org:act:ECDDDB059-940D-4810-B035-C2E5DAFCE203

Derivation of name

'Lava' is Greek for lava in reference to the fossil locality within a caldera. 'Dytis' is Greek for diver in reference to this taxon being a diving duck. 'Lavadytis' has a feminine (and masculine) nominative (and genitive) ending indicating the subject (i.e. 'lava diver').

Type species

Lavadytis pyrenae Stidham and Hilton; from the Miocene of Nevada (USA).

Diagnosis

Same as for the type and only known species, *Lavadytis pyrenae* (below).

Lavadytis pyrenae sp. nov. Figures 2-7



Figure 2.

[Open Figure](#)

Holotype humerus of *Lavadytis pyrenae* sp. nov. VB 42 in: A, caudal view; B, ventral view; C, cranial view; and D, dorsal view. Scale bar represents 10 mm. *Abbreviations* : bc, bicipital crest (damaged); dc, deltopectoral crest; dpf, dorsal pneumotricipital fossa; dt, dorsal tubercle; h, humeral head; vf, ventral pneumotricipital fossa.



Figure 3.

[Open Figure](#)

Distal humerus VB 67 referred to *Lavadytis pyrenae* sp. nov. in: A, dorsal view; B, cranial view; C, caudal view; and D, ventral view. Scale bar represents 5 mm.

Abbreviations : bf, brachial fossa; dc, dorsal condyle; of, olecranon fossa; pm, paired epicondylar pits; vc, ventral condyle; vl, attachment for the ventral collateral ligament.

**Figure 4.**[Open Figure](#)

Distal tibiotarsi of *Lavadytis pyrenae* sp. nov. VB 71 in: A, medial view; B, cranial view; C, lateral view; D, caudal view; and E, distal view. F–I are in cranial view. F, VB 70; G, VB 79; H, VB 73; and I, VB 72. Note the incompletely ossified supratendinal bridges in nearly all specimens. Scale bar represents 10 mm. *Abbreviations* : fg, groove for *m. fibularis*; lc, lateral condyle; mc, medial condyle; me, medial epicondyle; sb, supratendinal bridge; tc, trochlea for the tibial cartilage.

**Figure 5.**[Open Figure](#)

Tarsometatarsus VB 43 referred to *Lavadytis pyrenae* sp. nov. A–B, VB 43 in: A, plantar view; and B, dorsal view. C, E–F, details of the proximal end of VB 43 in: C, proximal view; E, dorsal view; and F, plantar view. D, G, proximal end of VB 75 in: D, proximal view; and G, plantar view. Scale bar represents 10 mm (A–B); and 5 mm in (C–G). *Abbreviations* : df, distal foramen; f, foramen; hr, hypotarsal ridges; lct, lateral cotyle; mct, medial cotyle; pf, proximal foramina; tr, ridge on the base of trochlea II; t2, trochlea II; t4, trochlea IV.

**Figure 6.**[Open Figure](#)

Coracoids (VB 65 and 86) and scapula (VB 66) referred to *Lavadytis pyrenae* sp. nov. A–D, coracoid fragment VB 65 in: A, dorsal view; B, lateral view; C, ventral view; and D, medial view. E–F, coracoid fragment VB 86 in: E, dorsal view; and F, ventral view. G–H,

scapula VB 66 in: G, medial view; and H, lateral view. Scale bar represents 10 mm.

Abbreviations : al, acrocoracohumeralis ligament scar; ap, acromion process; ct, coracoid tubercle; g, glenoid; n?, possible notch in the base of the procoracoid process; pcp, procoracoid process; sc, scapular cotyla; sf, supracoracoideus fossa.



Figure 7.

[Open Figure](#)

Carpometacarpi of *Lavadytis pyrenae* sp. nov. and the distal ulna of a potential anatid species. A–D, proximal carpometacarpus VB 69 in: A, ventral view; B, cranial view; C, ventral view; and D, dorsal view. E–H, proximal carpometacarpus VB 64 in: E, ventral view; F, proximal view; G, dorsal view; and H, caudal view. I, distal carpometacarpus VB 87 in dorsal view. J, distal ulna of the potential anatid (VB 92) in ventral view. Scale bar represents 5 mm. **Abbreviations** : af, alular digit facet; b, ossified bridge; ct, carpal tubercle; dr, dorsal rim of the carpal trochlea; ep, extensor process; f, foramen; mf, facet for the major digit articulation; nf, facet for the minor digit articulation; pp, pisiform process; vr, ventral rim of the carpal trochlea; ut, ulnar trochlea.

LSID

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Derivation of name

'Pyrena' means 'fiery one' in Greek. 'Pyrenae' has a genitive feminine ending ('of fire' or 'of the fiery one'). The informal translation of the name of the species is as a 'fiery lava diver'.

Type specimen

VB 42, a proximal left humerus (Fig. 2).

Occurrence

The High Rock Caldera is in Humboldt County, Nevada, USA (Fig. 1). The shoreline deposit (locality 1936), on the north side of a butte within the High Rock Caldera (see above) that contains part of the Yellow Hills local fauna, including the holotype and referred specimens, dates from between 14.64 and 16.14 Ma, and is probably closer to 16 myr in age (see above). The fauna is from the latest Hemingfordian or Barstovian NALMA (Hilgen *et al.* 2012) and is close in age to the Middle Miocene Climatic Optimum.

Diagnosis

This species lacks a fossa for metatarsal I (an anatid synapomorphy), lacks a procoracoid foramen on the coracoid and has a ridge on the plantar base of tarsometatarsus trochlea II (a crown anatid

synapomorphy). The proximal humerus exhibits a bony (non-pneumatic) wall within the ventral pneumotricipital fossa that is a derived state found among most diving ducks (Worthy and Lee [2008](#)). It differs from other known anatids, and in particular various diving duck taxa, through a combination of primitive and derived characters (below).

Lavadytis pyrenae shares the absence of a capital shaft ridge (on the proximal humerus) with *Aythya*, *Nomonyx* and most species of *Oxyura* and thus differs from *Dendrochen robusta* Miller, [1944](#), *Pinpanetta*, *Manuherikia*, *Mionetta blanchardi* Milne-Edwards, [1863](#), *Sharganetta*, *Nogusunna*, *Protomelanitta* and *Dunstanetta* which have the ridge at least weakly developed (Worthy and Lee [2008](#), appendix 1 and data matrix; Zelenkov [2011](#)). The new species' *m. lattissimus dorsi anterioris* scar links to the deltopectoral crest unlike the state in *Aythya*. *Dendrochen robusta* (UCMP 37364) also has a craniocaudally thickened prominence on the dorsal supracondylar ridge of the humerus that is absent in the new species. The new species is similar to *Oxyura*, but differs from *Nomonyx*, *Aythya*, *Pinpanetta*, *Manuherikia*, *Mionetta blanchardi* and *Dendrochen robusta* in the presence of a facet for the ventral collateral ligament parallel to the humeral shaft rather than inclined distally (as in the other taxa: see Worthy and Lee [2008](#), appendix 1 and data matrix). The humerus of *Lavadytis* appears to have an overall shallower dorsal pneumotricipital fossa with less extension of the fossa under the humeral head than the state in *Oxyura*. The morphology of the ventral rim of the carpal trochlea of the carpometacarpus (in that it is thickened in the new species) differs from the state in *Oxyura* and *Dendrochen robusta* (UCMP 37374). The cranial carpal fovea is present in the new species, *Aythya* and *Oxyura*, and is absent in *Dendrochen robusta*. The *m. extensor carpi ulnaris* morphology differs from that in *Dendrochen robusta* and *Aythya* as the new species has two distinct rugosities. The new species shares several characters of the tibiotarsus with *Dendrochen robusta*, *Aythya* and *Oxyura* including the pronounced medial epicondyle and the weakly developed *m. fibularis* sulcus. *Lavadytis pyrenae* shares with *Aythya* and *Oxyura*, but not *Dendrochen robusta*, the presence of tibiotarsus condyles extending about equally far cranially. There is a procoracoid notch (possibly from a reduced procoracoid foramen) similar to that in *Tadorna*, but absent in diving ducks such as *Oxyura* and most anatids (Worthy and Lee [2008](#)).

Referred material

The material referred to *Lavadytis pyrenae* is all derived from the same fossil locality as the holotype, and the fossils placed in *Lavadytis pyrenae* represent all of the avian remains found at that locality. The bones are all clearly anatid based on phylogenetic characters, and many of the bones (from across the skeleton) exhibit characters found among diving duck groups and the Oxyurinae (see above and below). All of the specimens are consistent in their relative sizes with the range present in extant oxyurine species and individuals and suggest that all fossils derive from individuals of approximately the same size (and the same region of the phylogenetic tree). Lastly, the size and morphological variation within each skeletal element (e.g. distal humeri) are consistent with derivation from a single species. VB 42, proximal left humerus; VB 43, right tarsometatarsus; VB 63, right carpal trochlea of a carpometacarpus; VB 64, right carpal trochlea of a carpometacarpus; VB 65, cranial right coracoid fragment; VB 66, cranial end of left scapula; VB 67, distal left humerus; VB 68, distal left humerus; VB 69, proximal left carpometacarpus; VB 71, distal left tibiotarsus (juvenile?); VB 72, distal left tibiotarsus (juvenile?); VB 73, distal left tibiotarsus (juvenile?); VB 74, shaft of a left tarsometatarsus; VB 75, proximal right tarsometatarsus; VB 76, proximal left tarsometatarsus; VB 77, cotylar region of a right coracoid; VB 78, shaft of a right

tarsometatarsus; VB 79, distal left tibiotarsus fragment; VB 80, fragment of the proximal right carpometacarpus; VB 81, fragmentary distal left humerus; VB 86, partial left coracoid; VB 87, distal carpometacarpus; and VB 89, shaft of a left tarsometatarsus.

Description

Humerus

The head is prominent and projects much more proximally than the dorsal tubercle (Fig. 2). The head overhangs the dorsal pneumotricipital fossa. Both the humeral head and bicipital crest are damaged. There is no capital shaft ridge on the proximal end. The dorsal tubercle is relatively large and concave across its surface. The deepest part of the pneumotricipital fossa does not extend to the level of the caudal end of the head and does not extend dorsally. The area ventral to the deltopectoral crest is slightly concave.

The division between the paired pits on the dorsal epicondyle is weak in VB 68 and absent in VB 67 (Fig. 3). The ventral paired epicondylar pits are asymmetric with the cranial pit being very deep. The dorsal rim of the scapulothoracic fossa extends around the distal end of the bone. The brachialis scar ends at the same proximodistal level as the proximal end of the ventral collateral ligament scar. The ventral collateral ligament scar faces a bit more craniodistal in VB 81 than the more cranially facing condition in VB 67. The olecranon fossa is deep.

Tibiotarsus

The distal end has a short *m. fibularis* groove with a ridge adjacent to it on the lateral side that ends distally at the proximal end of the lateral attachment site of the extensor retinaculum (Fig. 4). The lateral attachment site of the extensor retinaculum is lateral to the supratendinal bridge. The medial attachment of the extensor retinaculum is immediately proximal to the supratendinal bridge. The supratendinal bridge appears to be complete only in VB 70 with a nearly complete bridge in VB 72, and a nearly absent bridge in VB 73 and 79 (Fig. 4). The incompletely ossified bridges indicate a juvenile ontogenetic stage and perhaps some degree of wear on the specimen, but VB 73 also exhibits a spongy surface texture across the fragment consistent with an early ontogenetic state (Watanabe and Matsuoka 2013). The area medial to the lateral attachment of the extensor retinaculum is concave. The lateral condyle is wider than the medial one, but they extend about equally far proximally. The medial epicondyle is large and visible in cranial view. The distal margin of the bone is concave in cranial view. The lateral epicondyle also is small but visible in cranial view. There is a pit at the cranial base of the medial epicondyle. Other than the small epicondyle, the lateral surface of the distal end is nearly flat. The tibial cartilage articulation flares medially beyond the shaft edge. There is a broad convexity in the articulation surface. It is not a ridge, but a raised area making the articulation neither flat nor concave.

Tarsometatarsus

The intercondylar prominence is large and broad (Fig. 5). The medial cotyle is proximal to the lateral one. The proximal foramina are large. The lateral foramen is distal to the apex of the intercondylar prominence. The medial foramen is directly medial to the other foramen. The muscular ridges (for the *m. tibialis cranialis*) distal to the foramina also are similarly medially

displaced. The lateral side of the proximal sulcus is very tall relative to the medial side. The dorsal surface of the shaft is concave for about half of its length.

The medial proximal foramen opens medial to the hypotarsus on the plantar surface. There are weak ridges extending distal to the hypotarsus on the plantar surface. The hypotarsus is very broad. The medial side is at the medial edge of the shaft, and the lateral side is near the lateral edge of the shaft. The lateral proximal foramen opens plantarly at the lateral distal edge of the most lateral ridge of the hypotarsus. The hypotarsus has four ridges, and all have roughly the same length, although they progressively decrease in length laterally (Fig. 5). The medial side of the hypotarsus has a fully enclosed ligamental tube (preserved in VB 75: Fig. 5D), and there is a broken plantar ridge that is plantar to the tube with a concave lateral side for another tendon. The next more lateral tendinal canal (i.e. the middle of three) is a nearly fully enclosed tube, but a sliver of bone is still missing (possibly representing a subadult ontogenetic stage in VB 75). The most lateral tendinal canal is not enclosed at all. There is a thin ridge running down the plantar base of trochlea II.

Coracoid

The scapular cotyle is deeply concave, and the glenoid extends close to the caudal end of the cotyle (Fig. 6A). The glenoid is ovoid in outline and concave across its surface. The glenoid projects far laterally and has a concave ventral surface. There is no procoracoid foramen. The supracoracoideus fossa is concave. The acrocoracohumeralis ligament scar is a long arc that widens cranially. The acrocoracoid appears to have been very tall (craniocaudally long) relative to the length of the glenoid. It is likely that the acrocoracoid overhung the supracoracoideus fossa (the medial surface is missing on the coracoids present). It appears (in VB 65) that the acrocoracoid extended ventral to the ventral edge of the supracoracoideus fossa. The area ventral to the acrocoracohumeralis ligament is concave. The dorsal face of the caudal end of the coracoid is relatively flat. The procoracoid ends in a blunt point, and there is a slight concavity near its caudal base that may be a procoracoid notch (visible in VB 86). The ventral side of the procoracoid is concave nearly to the tip (preserved in VB 86). VB 77 is very worn, and the procoracoid is broken in VB 65 (Fig. 6).

Scapula

The acromion projects far cranially and has a craniocaudally elongate prominence dorsal to the coracoid tuber (Fig. 6G–H). The coracoid tuber is set off from the glenoid with a notch ventrally and a concave area laterally. Otherwise, the glenoid is relatively flat. Adjacent to the glenoid is a flat to slightly concave area. The shaft is broken caudal to that flat spot. The medial side of the scapula is nearly flat except for the area medial to the glenoid where it is concave.

Carpometacarpus

The extensor process is low (craniocaudally) versus its longer proximodistal length (Fig. 7). There is a foramen in the infratrochlear fossa. The pisiform process is distal to the proximal apex of the extensor process. There is a muscle scar caudal and just distal to the flexor process that widens distally and curves towards the base of the minor metacarpal. The pisiform process is a bit more pronounced and has a concave cranial face in VB 64 versus the condition in VB 69. There is a deep pit (fovea carpalis caudalis) at the distal edge of the carpal trochlea. The distal end of the

trochlea has a rectangular-shaped notch with the ventral rim of the trochlea extending distal to the very thin dorsal rim. The muscle scars overlap each other at the fornix. The distal end of the major metacarpal has a tendinal sulcus on it, and there is an enclosed tube for the passage of one of the interosseus tendons at the distal end of the bone.

Phylogenetically important characters

The acromion of the scapula extends distinctly cranial to the coracoid tuber (Worthy and Lee 2008, character 39: state 1). There is no pneumatic foramen on the cranial end of the scapula (Worthy and Lee 2008, character 40: state 1). The procoracoid foramen is absent in the specimen and the character is coded as in Worthy and Lee (2008) treated *Tadorna* with its broad shallow notch (character 42: state 3). The specimens of the new species do not preserve the acrocoracoid well, and it is likely (but not certain) that it did not have pneumatic foramina under the entire furcular facet on the acrocoracoid (Worthy and Lee 2008, character 43: likely state 0). The preserved part does not exhibit foramina, but a foramen or foramina could have been present in the damaged area or in other individuals. The character was coded (for the analysis below) as the state is currently preserved (state 0). The supracoracoideus fossa appears flat, and is not excavated under the humeral glenoid (Worthy and Lee 2008, character 46: state 0).

The capital shaft ridge is absent on the humerus, and the area where it would be in other taxa is a relatively flat area (Worthy and Lee 2008, character 51: state 1). The absence of that ridge means that the orientation of the ridge towards the distal end (Worthy and Lee 2008, character 52) cannot be discerned. The dorsal pneumotricipital fossa is a wide and shallow fossa that is greater or equal to the width of the ventral pneumotricipital fossa (Worthy and Lee 2008, character 53: state 2). The deltopectoral crest of the humerus has a cranially concave and rounded dorsal margin (Worthy and Lee 2008, character 54: state 0). Less than 30% of the length of the deltopectoral crest extends distal to the level of the junction of the bicipital crest with the humeral shaft (Worthy and Lee 2008, character 55: state 2). The dorsal tubercle of the humerus is elevated in comparison with the shaft (Worthy and Lee 2008, character 56: state 0). The ventral pneumotricipital fossa has an internal bony wall that forms a pneumatic recess, but this wall is more ventrally positioned than the condition in *Aythya* and *Dendrochen robusta* (Worthy and Lee 2008, character 58: state 1). The muscle scar for the *m. latissimus dorsi anterioris* on the caudal side of the proximal end of the humerus extends proximal to the distal end of the deltopectoral crest and joins the distal end of the deltopectoral crest before continuing distal to the crest (Worthy and Lee 2008, character 62: state 0). The flexor process on the distal end of the humerus is long, extending as far as the ventral epicondyle (Worthy and Lee 2008, character 63: state 1). The dorsal supracondylar tubercle in cranial view is just a low ridge with no distinct prominence on it (Worthy and Lee 2008, character 64: state 1). The attachment of the ventral collateral ligament is a facet that is parallel to the shaft and not projected cranially (Worthy and Lee 2008, character 65: state 0). There is a ventral rotation ('medial' in some authors' usage) to the facet that is common in diving ducks (Worthy and Lee 2008). The *m. flexor carpi ulnaris* originates from a pit that is separate from the ventral margin of the facet for the ventral collateral ligament (Worthy and Lee 2008, character 67: state 0). However, there is some variation in this morphology. VB 67 exhibits morphology closer to the derived state where the pit is part of the ventral margin of the attachment site of the ligament, but VB 81 is closer to the primitive state. The new species almost appears to have an intermediate character state of very close, but separate features. The brachial fossa is a

fossa with distinct margins (Worthy and Lee 2008, character 68: state 0).

The dorsal rim of the carpal trochlea of the carpometacarpus has a distinct caudal notch (Worthy and Lee 2008, character 72: state 1), but the morphology is not as well preserved in VB 69 where it is worn, but still concave. The ventral rim of the carpal trochlea is thickened distally (Worthy and Lee 2008, character 73: state 1). The cranial margin of the carpal trochlea is concave (Worthy and Lee 2008, character 74: state 1). The caudal carpal fovea has a deep and high margin bounding it, and the fossa extends below the minor metacarpal (Worthy and Lee 2008, character 75: state 1). The infratrochlear fossa is deep and extends to or below the facies of the extensor process (Worthy and Lee 2008, character 76: state 1). The new species does not seem to have a state comparable to that for the ridge connecting the ventral rim of the pisiform process with the extensor process (Worthy and Lee 2008, character 77). The extensor process is perpendicular to the shaft of the carpometacarpus (Worthy and Lee 2008, character 78: state 0). The extensor process (in ventral view) of the carpometacarpus is short with its craniocaudal length being less than the craniocaudal width of the carpal trochlea (Worthy and Lee 2008, character 79: state 0). The length of the second (major) metacarpal distal to the facet for digit I to the intermetacarpal space is greater than the craniocaudal width of the fused bases of metacarpals II (major) and III (minor; Worthy and Lee 2008, character 81: state 1). The attachment of the *m. extensor carpi ulnaris* is as two distinct spots with one adjacent to the fornix (extending distally) and one proximal to the fornix (Worthy and Lee 2008, character 83: state 0). This is not the same as the two abutting scars present in *Oxyura* (Worthy and Lee 2008). The length (5.8 mm) of the synostosis of the metacarpals II (major) and III (minor) at the distal end of the carpometacarpus is less than the width (6.3 mm) adjacent to the intermetacarpal space (Worthy and Lee 2008, character 84: state 0). The facets for digits II (major) and III (minor) on the distal end of the carpometacarpus extend about equally far distally (Worthy and Lee 2008, character 85: state 1). The medial epicondyle is very prominent and visible in cranial view on the tibiotarsus (Worthy and Lee 2008, character 99: state 0). There is a shallow notch present (on VB 71) on the distal edge of the medial rim of the distal condyle of the tibiotarsus (Worthy and Lee 2008, character 100: state 1). The sulcus for the *m. fibularis* is poorly defined and bounded by a lateral prominence (Worthy and Lee 2008, character 101: state 2). The condyles of the tibiotarsus extend about equally far cranially (Worthy and Lee 2008, character 103: state 1).

The width of the base of the hypotarsus on the tarsometatarsus is about equal relative to the proximal width (Worthy and Lee 2008, character 107: state 1). The medial parahypotarsal fossa is absent (Worthy and Lee 2008, character 108: state 2). The groove that continues distally from the extensor sulcus on the dorsal surface of the tarsometatarsus is relatively shallow and does not extend beyond half the length of the bone (Worthy and Lee 2008, character 110: state 0).

Trochlea IV does not exhibit any lateral deflection relative to the distal half of the tarsometatarsal shaft (Worthy and Lee 2008, character 111: state 1). The fossa for metatarsal I is absent (Worthy and Lee 2008, character 113: state 1). Trochlea II is not expanded medially and is flat (visible in VB 89; Worthy and Lee 2008, character 114: state 1). The tarsometatarsus shaft is wider than deep at its proximodistal mid-point (Worthy and Lee 2008, character 116: state 0).

Comparison with *Dendrochen robusta*

Lavadytis differs in its phylogenetic characters from extant and known extinct taxa (above in the diagnosis). Here, we present a detailed comparison to the only other potential oxyurine taxon from the middle Miocene of North America known, *Dendrochen robusta*. This includes a discussion of

material housed in the UCMP that was collected with the type series of *Dendrochen*, but has been largely ignored by later workers. Overall, *Lavadytis* is smaller than *Dendrochen*.

Humerus

The capital shaft ridge is long and prominent in *Dendrochen*. The area distal to the scapulohumeralis scar is more concave in *Lavadytis* than in *Dendrochen*. The proximal end of the dorsal pneumotricipital fossa extends more proximal and more dorsal than in *Lavadytis*. Otherwise, the proximal humerus is similar between the two species. The dorsal supracondylar ridge is much more pronounced in *Dendrochen*, and it lacks the ventral hook present in *Lavadytis*. The shape and size of the distal condyles are similar between the taxa. The facet for the ventral collateral ligament is not cranially projected in *Lavadytis*, and the ventral collateral ligament facet in *Lavadytis* has a ventral deflection absent in *Dendrochen*. In cranial view, the cranial pit of the ventral paired epicondylar muscular pits extends proximal to the proximal end of the ventral condyle in both *Dendrochen* and *Lavadytis*.

Tibiotarsus

The medial epicondyle in *Lavadytis* is much more pronounced than the state in *Dendrochen*. In addition, the medial condyle in *Lavadytis* is mediolaterally thicker and more medially placed than the condition in *Dendrochen*. The medial margin of the articulation of the tibial cartilage is very medially expanded (into a 'wing') on the caudal surface of the tibiotarsus of *Lavadytis* that is absent in *Dendrochen*.

Carpometacarpus

Lavadytis has an extensor process with a lower height (compared to its length). *Dendrochen* lacks the small fossa at the proximal end of the base of the extensor process at the cranial end of the trochlea, while the new species has that fossa. There are other differences in the muscle scars (see '[Phylogenetically important characters](#)' above).

Other AVES

Referred material

VB 92 is a right distal ulna, and VB 58 is a proximal right tarsometatarsus. VB 92 and VB 58 are both from locality 1955 (in the High Rock Caldera) that is not the shoreline deposit (locality 1936 above) where *Lavadytis* was found. The ulna fragment is larger than what would be expected for *Lavadytis* based on elements in similar sized extant species, but is probably from an anatid. The tarsometatarsus fragment differs from *Lavadytis* in several important phylogenetic characters and clearly derives from another avian (non-anatid) lineage (see below). Thus, it appears that there is at least one additional anatid species in the Yellow Hills local fauna, and it is likely that the two bone fragments derive from two different species.

Description and comparison

VB 92 Ulna

The trochlea is very asymmetric with the dorsal rim coming far proximally and also curving ventrally a bit at its proximal end. The distal end is worn. The most interesting thing is that there is a notch between the carpal tuber and the trochlea on the distal end. The ventral rim of the trochlea extends distal to the dorsal rim. The ligament pit on the dorsal surface is very large, but shallow. The ulna fragment comes from an individual that it is likely to have been larger than *Lavadytis*, based on comparison of similarly sized elements from other anatid species.

VB 58 Tarsometatarsus

The specimen (VB 58) is larger than that of *Lavadytis*. The intercondylar prominence projects much more proximally. The medial proximal foramen is very large and much larger than the lateral one. The proximal foramina are on either side of the mediolateral midline. The muscular ridges in the proximal end of the extensor fossa on the dorsal surface are displaced; the medial one is distal to the medial proximal foramen, but the lateral one is on the mediolateral midline. The dorsal sulcus is very deep proximally and the medial edge of it is much taller than in *Lavadytis*. The proximal cotyla also are not as offset as the state in *Lavadytis*.

The hypotarsus is very different from *Lavadytis*. The medial canal is caudal to the intercondylar prominence, not medial to it. In addition, there are two enclosed canals (tubes) on the hypotarsus. The medial canal also is plantar to the lateral one. The medial ridge of the hypotarsus extends very distal relative to the other two ridges. The lateral proximal foramen opens at the lateral distal corner of the hypotarsus, but the medial foramen is more distal and is medial to the medial hypotarsal ridge. The hypotarsal canals are quite wide. It is possible that this specimen derives from a species of vulture, but that hypothesis requires further study.

Phylogenetic analysis of *Lavadytis*: methods and results

The phylogenetic position of *Lavadytis* was assessed using TNT (Goloboff *et al.* 2008) on the matrix focused on diving ducks from Worthy and Lee (2008) and Worthy (2009). The character codings for *Lavadytis* (listed above in 'Phylogenetically important characters') were added to the matrix used in Worthy and Lee (2008) and Worthy (2009). All analyses were completed with 10 000 replicates and utilized ratchet, tree drift and TBR for searching. TNT and PAUP (Swofford 2003) utilize tree constraints differently in searches, and the molecular constraint tree used by Worthy and Lee (2008) for PAUP was not used here (in TNT). However, using some topological constraints based on those in Worthy and Lee (2008) resulted in broadly similar results to those discussed below (i.e. *Lavadytis* within Oxyurinae), but those results are not shown here as they do not significantly differ from the other (unconstrained) analyses (below). In addition, the molecular tree of anatids from Gonzalez *et al.* (2009) is consistent with the constraint tree used in Worthy and Lee (2008), but differs from their morphological results with Oxyurinae as the sister group to Anserinae. The characters were not ordered, in contrast to the methods of Worthy and Lee (2008), to reduce any assumptions about evolutionary pattern. The assumption that certain characters have to pass through an intermediate step in their evolution is not supported *a priori*, and thus, the character states are treated as independent in our analyses.

The result of an unconstrained analysis (all characters unordered and included, Galliformes as the

outgroup, and no constraint tree) overall resembles that produced with similar settings by Worthy and Lee (2008, fig. 8) with a monophyletic grouping of diving duck taxa and a paraphyletic *Aythya* at the base of the diving ducks. That analysis produced 53 most parsimonious trees (length 1167; see Fig. 8 for the consensus tree) that vary only in the position of different species outside of the diving duck grouping (with species in *Dendrocygna*, *Tadorna*, the geese, and others in less certain phylogenetic positions). In that unconstrained analysis, *Lavadytis* is placed within *Oxyura* (as the sister to *Oxyura vittata*), quite separate from the other Oligo-Miocene oxyurines who are more closely related to *Thalassornis* and *Biziura* (Fig. 8).



Figure 8.

[Open Figure](#)

Majority-rule consensus tree (of 53 most parsimonious trees of length 1167) from the phylogenetic analysis of the data matrix from Worthy and Lee (2008) with all characters unordered and no constraints on the analysis and with *Lavadytis pyrenae* sp. nov. included (in bold). Numbers above the branch are Bremer decay indexes, and the numbers below the branch indicate the percentage of most parsimonious trees that support that node (below 100% and above 50%). Nodes with Bremer decay numbers are supported in 100% of the parsimonious trees. See the text for details on the analysis and results.

An analysis with the same search parameters that excludes the diving-related characters identified by Worthy and Lee (2008) results in 90 most parsimonious trees with a length of 1014. In that analysis, the monophyly of the diving taxa is broken with the inclusion of *Anas* and other extant taxa placed closer to *Mergus*. However, the bulk of the diving taxa (species of Oxyurini and Aythini) continue to form a clade (see Fig. 9 for the consensus tree). For the most part, the variably placed taxa in the unconstrained analysis also are problematic in this analysis (e.g. the species of *Dendrocygna*; see the number of trees supported in the majority-rule consensus tree in Fig. 9). Despite the absence of a basal position of Oxyurinae relative to *Aythya* and *Mergus*, the phylogenetic relationships within each of the component diving clades are overall similar to that found using the constraints in Worthy and Lee (2008) and Worthy (2009).



Figure 9.

[Open Figure](#)

Majority-rule cladogram (of 90 most parsimonious trees of length 1014) based on an analysis of the data matrix from Worthy and Lee (2008) including *Lavadytis pyrenae* sp. nov. (in bold), but excluding the diving-related characters designated by Worthy and Lee (2008), and all characters unordered. Numbers above the branch are Bremer

decay indexes, and the numbers below the branch indicate the percentage of parsimonious trees that support that node (below 100% and above 50%). Nodes with Bremer decay numbers are supported in 100% of the most parsimonious trees. See the text for details on the analysis and results.

In both analyses, 100% of the trees produced (Figs 8, 9) fit *Lavadytis* closer to *Oxyura* / *Nomonyx* than to other members of the Oxyurinae (including other fossils). We do not consider the phylogenetic position of *Lavadytis* relative to other extinct taxa to be fully resolved, but the Nevada species appears to be more derived than the Oligocene and early Miocene basal oxyurines.

Discussion

There is a minimum of four *Lavadytis* individuals represented in the fossil assemblage (based on the presence of four left distal tibiotarsi), and there is a minimum of one individual of the second (potential) anatid species from a separate locality. The High Rock Caldera almost certainly was a breeding location for *Lavadytis* given the number of subadult bones found there. The tibiotarsi (with their incomplete or absent ossified supratendinal bridges) indicate the juvenile ontogenetic state of those individuals, but those same bones also lack any suture lines between the astragalus/calcaneum and the tibia, demonstrating that the individuals were not hatchlings or very young ontogenetically (Watanabe and Matsuoka 2013). The other skeletal elements from the fossil assemblage do not suggest juvenile states as they have a smooth periosteum and display fully fused skeletal elements (as in the carpometacarpi and tarsometatarsi). Some of those elements could be from adult individuals, but in general the wing elements become osteologically 'adult' before the hind limb completes its ontogeny (Watanabe and Matsuoka 2013). All fossil skeletal elements from the two fossil localities (*Lavadytis* from one and the other species from the other) could derive from six individuals (four of *Lavadytis*, one of the second possible anatid species and one from the potential vulture species). Given the preference of many oxyurines for nesting in emergent vegetation (Johnsgard and Carbonell 1996), the presence of juvenile ducks at the site probably indicates the past presence of reeds and other vegetation around the caldera lake (in addition to open water) during the time when this species bred. Extant species of Oxyurini can be resident, migratory or seasonally move within their geographical ranges (Johnsgard and Carbonell 1996), and therefore, the presence of the *Lavadytis* juveniles supports that the High Rock Caldera was within their breeding geographical distribution (which may have been equal to their entire distribution if they were residents). It is possible that the three juveniles could be siblings because three is within the range of hatchling success of a single nest among extant species of *Oxyura* (Johnsgard and Carbonell 1996).

Several characters present in the skeleton of *Lavadytis pyrenae* are present convergently in the skeletons of different diving duck clades. Characters such as the non-pneumatic ventral pneumotricipital fossa of the humerus, loss of the capital shaft ridge and ventral deflection of the ventral collateral ligament facet are thought to be related to a diving lifestyle (Worthy and Lee 2008). However, having the skeletal characters of a diving bird does not mean that the bird is a diver, and that can be seen in *Malacorhynchus* who do not dive, but have a non-pneumatic ventral pneumotricipital fossa (Worthy and Lee 2008, appendix 1). Given the phylogenetic position close to extant diving birds and the presence of multiple derived osteological correlates of diving, it is quite likely that *Lavadytis pyrenae* was a diving duck in terms of its behaviour and not just its morphology.

The origin of diving ducks appears to extend back into the late Oligocene and early Miocene (Worthy 2009). Other than the late Oligocene specimens of *Mionetta* (and their tentative relationship to Oxyurinae), the three species of *Pinpanetta* from Australia are among the oldest fossils (24–26 Ma) attributed to the stiff-tailed duck lineage (Worthy 2009). The taxa *Dunstanetta* and *Manuherikia* from New Zealand are both from the 16 to 19 myr age range and exhibit diving features (Worthy and Lee 2008). Members of the other diving clades are present in the middle Miocene, including a merganser from Maryland (Alvarez and Olson 1978) and a variety of diving ducks from Mongolia (Zelenkov 2011, 2012). Overall, the fossil record indicates a radiation of diving taxa (and convergence in diving morphology) through this relatively warm temporal interval in the late Palaeogene and early Neogene (Fig. 10). The specimens of *Lavadytis* fit this broader evolutionary/phylogenetic pattern with its derived diving morphologies present at a slightly younger 14–16 myr age (likely near 16 myr, see above). It would also appear that diving ducks spread rapidly around the globe from their origins (potentially in the southern hemisphere) with records in North America, Australasia, Asia and Europe in the early and middle Miocene (Olson 1985; Worthy and Lee 2008; Worthy 2009; Zelenkov 2011, 2012). However, none of the recently described diving ducks from the Miocene of Mongolia have been analysed phylogenetically, and therefore, their relationships to this new species are unclear. They certainly will change the interpreted evolutionary landscape once they are further studied, and the Mongolian species may reflect a geographical bridge between the North American *Lavadytis* and more southerly occurring species.



Figure 10.

[Open Figure](#)

Phylogeny of extant and extinct stiff-tailed ducks. The topology of the phylogeny is identical to that in Figure 9, but the stratigraphic distribution of the extinct taxa has been added. Some of the extant genera have a fossil record, but only their phylogenetic relationships are shown here to emphasize the evolution of the stem taxa. The approximate duration of two global warming events are in grey and overlap the early branching of the phylogeny. *Abbreviations*: LOW, late Oligocene warming; MMCO, Middle Miocene Climatic Optimum.

Warming and an overall warmer global climate than today may have facilitated the intercontinental dispersal of ducks. Today, the species of *Nomonyx* and *Oxyura* occur or are quite commonly found in temperate to tropical environments between the tropics of Capricorn and Cancer, but individuals may breed or have their geographical distribution extend to near 50 or 60 degrees latitude in the New World (Johnsgard and Carbonell 1996). Thus, their occurrence at higher latitudes (closer to northern hemisphere land bridges) would have been facilitated during warmer temporal intervals (like that of the Middle Miocene Climatic Optimum). Unlike other groups of diving ducks, members of the *Nomonyx* + *Oxyura* clade prefer freshwater habitats, although they can be found in marine habitats, relatively close to shore (Johnsgard and Carbonell 1996). Given those habitat preferences and their current geographical distribution, it would seem more likely that a land bridge (rather than direct trans-oceanic dispersal) facilitated the journey of this lineage to the New World.

It is interesting to note that the oldest fossils tentatively assigned to Oxyurinae roughly cluster into two temporal groups, one with first records in the late Oligocene (*Mionetta* and *Pinpanetta*) and one in the middle Miocene (*Lavadytis* , *Manuherikia* and *Dunstanetta*). The known stratigraphical distribution of those taxa overlaps with two warm and warming temporal intervals, the late Oligocene warming and the Middle Miocene Climatic Optimum (Zachos *et al.* **2001**; Hilgen *et al.* **2012**). While the role of climate change is unclear in diversification, climate change impacts sea level and floral distribution and is itself influenced by tectonism and volcanism. In addition, the combination of tectonic, climatic and floral changes has been argued to have driven mammalian diversification through the Miocene (Kohn and Fremd **2008**). Those same environmental changes are likely to have impacted anatids in the same region, in particular with the disturbance created by volcanism (and other tectonism) across the western United States. Whether that pattern reflects diversification coincident with climate change or is simply a reflection of low temporal sampling of fossils through the late Oligocene to the middle Miocene will only be resolved with new fossils and further phylogenetic scrutiny of previously published material. The material of *Lavadytis* indicates that much about the evolution of oxyurines and early Neogene New World waterfowl is left to discover.

Acknowledgements

TAS is funded by the Chinese National Natural Science Foundation (NSFC41472025) and the Strategic Priority Research Program of the Chinese Academy of Sciences (CAS, XDB03020501). The fossils were collected under Bureau of Land Management permit N-78093 and Nevada State Museum permit #500 to RH. Patricia Holroyd provided access to collections in the UCMP. Nikita Zelenkov and Daniel Field provided helpful comments on an earlier draft of the manuscript.

We would also like to extend our appreciation to all the people below. Chris Henry (Nevada Bureau of Mines and Geology) provided many of the radiometric dates; the late Howard Schorn (UCMP) aided in the identification of many of the palaeobotanical specimens from HRC; Chris Farrar (US Geological Survey), Donald Noble and Paula Noble (not related, both at the University of Nevada, Reno); Julie Smith (former graduate student at California State University, Sacramento); and Walt Wright identified some of the petrified wood from HRC. The team of Sierra College Natural History Museum volunteers who helped to locate, excavate, collect, prepare and curate the wealth of fossils from the HRC includes Pat and Luke Antuzzi, Sue Ayres, Vicki and Gary Black, Annette Bromm, Tina Campbell, Charles Dailey, Chantal Decavel, Cindy McBride, Ed Coutts, Wendy Shaul, Jim Readle, Jared Walbert and Robin Wham. George Bromm curated all of the vertebrate fossils. Personnel from the United States Bureau of Land Management also contributed to the field work and study including Kathryn Ataman, Pat Barker, Penni Borghi, Thomas Burke, Erin Collins, Kenneth Collum, Kevin Dalton, Roger Farschon, Mark Gingrich, Peggy McGuckian, Rolando Mendez, Regina Smith and Dave Valentine, and individuals from the Nevada State Museum (James Barmore, Margaret Brown, Gene Hattori, Roz Works and Alena Woody) also provided valuable assistance with this broader project.

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