

FOSSIL GREBES FROM THE TRUCKEE FORMATION
(MIOCENE) OF NEVADA AND A NEW
PHYLOGENETIC ANALYSIS OF PODICIPEDIFORMES
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Podicipediformes is a cosmopolitan clade of foot-propelled diving birds that, despite inhabiting marine and lacustrine environments, have a poor fossil record. In this contribution, we describe three new grebe fossils from the diatomite beds of the Late Miocene Truckee Formation (10.2 ± 0.2 Ma) of Nevada (USA). Two postcranial skeletons and an associated set of wing elements indicate that at least two distinct grebe species occupied the large, shallow Lake Truckee during the Miocene. Phylogenetic analysis of morphological data supports a basal divergence between a clade uniting the dabchicks (*Tachybaptus*, *Limnodytes*, *Poliiocephalus*) and a clade uniting *Podilymbus*, *Rollandia*, *Podiceps* and *Aechmophorus*. Missing data, combined with a paucity of informative skeletal characters, make it difficult to place the Truckee grebes within either of these major clades. Given the weak projection of the cnemial crests compared with extant grebes, it also

remains plausible that these specimens represent stem lineage grebes. Although more material is needed to resolve the phylogenetic position of the Truckee grebes, our analysis offers insight into the tempo of grebe evolution by placing the Miocene taxon *Thiornis sociata* within the dabchick clade. *Thiornis sociata* provides a minimum age calibration of 8.7 Ma for the basal divergence among dabchicks. Based on the recovery of a nonmonophyletic *Tachybaptus* and placement of the Western Hemisphere '*Tachybaptus dominicus*' as the basal member of the otherwise exclusively Eastern Hemisphere dabchick clade, we resurrect the genus *Limnodytes* for this extant species (*Limnodytes dominicus*). Our results also nest the large, long-necked *Aechmophorus* grebes within the genus *Podiceps*, as the sister taxon to *Podiceps major*.

Key words: Podicipedidae, calibration, phylogeny.

PODICIPEDIFORMES is a clade of foot-propelled diving birds characterized by a specialized hindlimb skeleton, unique dense plumage and lobed toes. These birds lead an almost entirely aquatic existence and several lineages have become either flightless or flight-impaired (Livezey 1989). Grebes exhibit many unique behaviours including highly ritualized courtship displays (e.g. Huxley 1914; Storer 1963; Fjelds  1985) and a peculiar habit of ingesting their own feathers (Simmons 1956; Storer 1961; Piersma and Van Eerden, 1989). Podicipediformes comprises 22 recent species, although regrettably *Podilymbus gigas* (Giant Pied-billed Grebe), *Podiceps andinus* (Colombian Grebe) and *Tachybaptus rufolavatus* (Alaotra Little Grebe) went extinct during the last century (LaBastille 1983; Varty *et al.* 1985; Fjelds  1993; Hawkins *et al.* 2000). While all recently

extinct species exhibited restricted geographical ranges, which contributed to their demise, many extant grebe species enjoy very wide distributions, often ranging over several continents (Fjelds  2004). As a clade, Podicipediformes occurs today on every continent except for Antarctica and further occurs on many islands.

Podicipediformes has long been considered one of the most difficult of the traditional avian orders to place phylogenetically. Numerous morphological analyses have recovered a sister group relationship between Podicipediformes and Gaviiformes (Cracraft 1982, 1988; Mayr and Clarke 2003; Bourdon *et al.* 2005; Livezey and Zusi 2006, 2007; Smith 2010). This hypothesis has been criticized as an artefact of convergence between these two clades of foot-propelled diving birds, especially in the light of

fundamental differences such as the hypertrophy of the patella in grebes (versus absence in loons) and the lobed nature of grebe toes (versus webbed foot in loons) (e.g. Storer 1971, 2002). Recent molecular analyses have found strong support for a Podicipediformes + Phoenicopteriformes (grebes + flamingos) clade (van Tuinen *et al.* 2000; Chubb 2004; Cracraft *et al.* 2004; Ericson *et al.* 2006; Hackett *et al.* 2008; Pratt *et al.* 2009), for which the name Mirandornithes has been proposed (Sangster 2005). Subsequently, several morphological characters have been proposed in support of Mirandornithes, including an increase in the number of presacral vertebrae, prominent caudolateral projections on the ventral face of the cervical vertebrae, flattening of the pedal unguals and the presence of 11 primary feathers (Mayr 2004; Manegold 2006).

Grebes have a surprisingly sparse fossil record despite their broad geographical distribution, relatively dense bone structure and preference for lacustrine environments. Thus far, fossils have offered little insight into the morphology of basal Podicipediformes. Most records consist of isolated limb bones, and all formally described finds are from Neogene deposits (e.g. Murray 1967; Steadman 1984; Chandler 1990; Olson and Rasmussen 2001; Storer 2001). Fragmentary grebe remains from several Oligocene sites in Kazakhstan have been mentioned in the literature but await full description (Kurochkin 1976; Nesson 1992; Fjeldsø 2004). If correctly identified, these Kazakhstan records may represent the earliest occurrence of the clade. Fossils from the late Oligocene or early Miocene of Australia have also been mentioned in the literature (Vickers-Rich 1991). These fossils, however, remain undescribed, and the basis for assignment to Podicipediformes remains unknown. Currently, the oldest formally described taxon of Podicipediformes is *Miobaptus walteri* from the early Miocene (MN4—Feifar 1974; Rojik 2004) Dolnice locality near Cheb, Czech Republic (Švec 1982). Two partial humeri, a coracoid, a partial tibiotarsus and five partial tarsometatarsi have been assigned to this species (Švec 1982, 1984). Mlíkovský (2000) later referred a distal tibiotarsus from slightly older (MN3) deposits at Skyřice, Czech Republic, to *Miobaptus walteri*, but did not figure the bone or provide a list of characters supporting this referral.

By far the most complete fossil grebe described to date is the holotype of *Thiornis sociata* from the Miocene of Spain. This specimen, a nearly complete postcranial skeleton with feather impressions, was originally described as a gallinule by Navas (1922). Olson (1995) subsequently had the specimen further prepared and re-identified it as a grebe. Aside from *Miobaptus walteri* and *Thiornis sociata*, Miocene records are rare, and in many cases are in need of re-appraisal. Dimitrijevič *et al.* (2002) described a partial wing from the early Miocene of Serbia as a new species of grebe, *Miodytes serbicus*. Although Dimitrijevič

et al. (2002) provided comparisons with several groups of seabirds, no synapomorphies that unambiguously supported an assignment to Podicipediformes were listed. The strongly elongate phalanx II-1 lacking an internal indicus process would support placement in the clade Mirandornithes (Mayr 2004). Other features such as the deep fossa m. brachialis and the elongate sulcus proximal to this fossa are not present in grebes, but rather only in some Procellariiformes and Charadriiformes (Dimitrijevič *et al.* 2002). More material is desirable to better resolve the phylogenetic affinities of *Miodytes serbicus*.

A large number of fossil grebe species have been named based on fragmentary material from the Pliocene and Pleistocene. Many of these species are based on undiagnosable sets of remains and have served only to confound understanding of grebe diversity over time. Pronounced sexual dimorphism is common in extant grebes and is reflected in both the lengths and robustness of skeletal elements (e.g. Storer 1992; Bocheński 1994). Therefore, it is critical to consider large sample sizes from multiple populations to adequately assess the taxonomic significance of diagnostic characters (e.g. Bever 2009). This practice has not been common in comparisons of fossil grebes to extant species. When evaluated in the context of large data pools for extant species, many proposed fossil grebe species cannot be diagnosed from one another or from extant species. For example, '*Podiceps pisanus*' is known only from a distal portion of a humerus (Portis 1888; Regalia 1902), and '*Podiceps dixi*' is known only from a proximal fragment of a carpometacarpus (Brodkorb 1963). Neither of these specimens can be diagnosed from extant *Podiceps auritus* (Steadman 1984; Olson and Rasmussen 2001). Replacing simple descriptive diagnoses with phylogenetic diagnoses is the logical way to untangle such a legacy of taxonomic problems (e.g. Nesbitt and Stocker 2008; Boyd *et al.* 2009), but in the case of grebes would entail a substantial undertaking that is beyond the scope of this paper. Based on the fragmentary nature of many holotypes and the lack of differential diagnosis in most early descriptions, we suspect that re-examination of named grebe fossils would greatly reduce the number of valid taxa. While the specimens described in this paper may well represent new species, we opt to avoid contributing to the current morass, pending future taxonomic revisions.

GEOLOGICAL CONTEXT AND PALAEOENVIRONMENT

Specimens described in this contribution were collected in a small (c. 150 m diameter) open pit diatomite mine (Quarry D, 39.526° N, 119.094° W) near Hazen, Nevada (Fig. 1). The most complete specimen (UMMP 74784) was uncovered at a horizon approximately 1 m below the

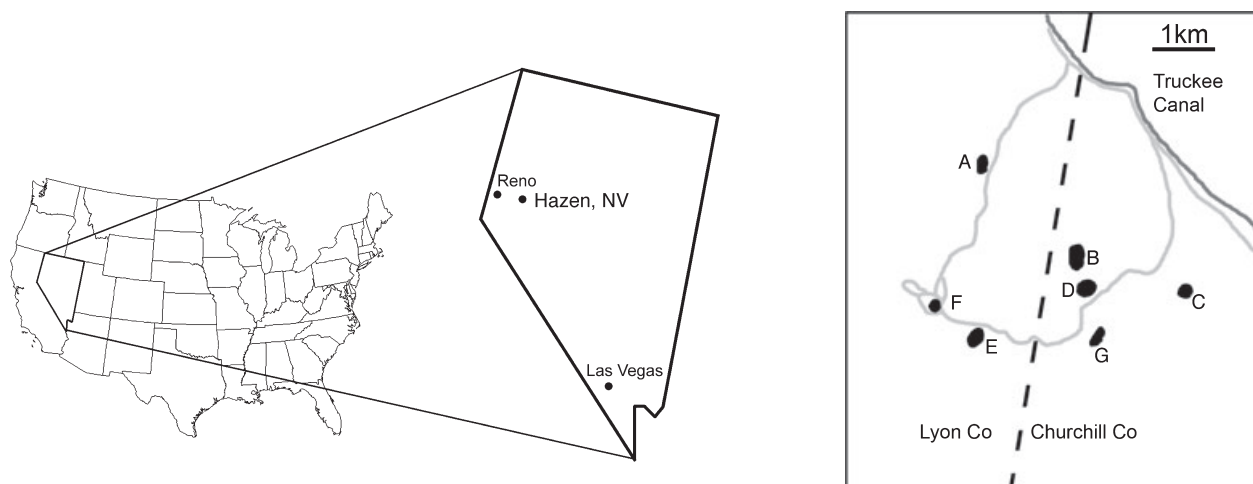


FIG. 1. Map showing the fossil locality. Right image and quarry localities after Bell (1994).

section described by Bell *et al.* (1985) and Bell (2009). Lacustrine deposits from the Hazen area were included within the Truckee Formation by Axelrod (1958) and Rose (1969). Pending formal revision of regional geology, we follow this practice. Trexler *et al.* (2000), however, noted that this part of Nevada had a complex late Miocene sedimentary history with multiple basins developing within a framework of both dextral slip and extensional faulting, as well as ongoing volcanism. Therefore, correlation of beds from basin to basin is difficult, and further study could result in modifications of the names applied to the Hazen diatomite beds. Regardless of nomenclature, the Quarry D section is precisely dated and much of its depositional history can be reconstructed.

Within the Hazen area, late Miocene sediments cover a basement of andesite and basaltic andesite flows. The onset of lacustrine sedimentation is contemporaneous with north-south faulting, and the development of several west-tilted grabens. Reconstructions by Houseman (2004) place these grabens on the southern margin of a late Miocene lake (Lake Truckee) as a series of narrow embayments. Most of these grabens share a similar history of initial, rapid westward tilting accompanied by infilling of coarse clastic sediments and occasional diatomite. Spatial distribution of clastic sediments suggests these narrow, deep embayments were surrounded by significant topographical relief and received high water throughput. Over time, many of these grabens became sediment filled, and tilting diminished to a point where clastic sedimentation ceased. Diatom accumulation continued from this time as an uninterrupted sequence of mostly benthic, pennate diatom laminae, including *Synedra*, *Nitzschia*, *Staurosira*, *Staurosirella* and *Navicula*, alternating with fine, darker terrigenous sediments and occasional volcanic ashes. Distribution of this younger sequence is consistent with regional expansion and shallowing of the lake over a more subdued topography.

Diatomites in the Quarry D section consist of pennate diatom laminae, indicating the basin remained a relatively shallow segment of Lake Truckee through the entire lake cycle. Further, delineation of late Miocene lake shoreline features, including marginal tufa deposits and basaltic andesite high ground, indicates this basin was probably periodically cut off from the northern main body of the lake during intervals of low water levels. $^{40}\text{Ar}/^{39}\text{Ar}$ dates obtained from tephra layers at the base of Quarry D yielded ages of 10.7 ± 0.2 and 10.2 ± 0.2 Ma (M.D. Houseman, unpublished data). Tephra sampled from adjacent areas have yielded younger ages (9.81 ± 0.20 : Perkins *et al.* 1998; 9.79 ± 0.12 and 9.75 ± 0.31 : Brown 1986). These dates approach the margin of error, but suggest that the Quarry D basin was likely the first to be tectonically active and lake formation may have begun there. The subsequent stratigraphical record within the basin suggests that movement along the basin bounding faults terminated quickly as faulting accelerated in surrounding areas. The Quarry D basin then remained relatively stable and tectonically passive, with sedimentation patterns little changed over a long interval.

Mapping suggests the avian fossil localities were located in the north-central part of the basin, about 1 km from the shoreline at the time the birds perished. Detailed diatom analyses of the beds near the fossil sites indicate a periphyton community dominated by *Nitzschia inconspicua*, *Staurosira construens*, *Staurosirella lapponica*, *Pseudostaurosira brevistriata* and several species of *Synedra* (principally, *S. tabulata*). Additionally, fragments of a *Surirella* form similar to *S. brebissonii* occur throughout the section. This diatom assemblage forms strongly laminated strata, with individual lamina approximately 0.3–0.5 mm thick. Scanning electron microscope images of individual lamina often show a mat-like texture, with tangled and interwoven clumps of *Nitzschia* and *Synedra*. The Quarry

D diatom assemblage is indicative of warm, slightly alkaline, shallow water, probably no more than a few metres deep. In particular, *Surirella* is known for a tolerance to elevated alkalinities (Kelly *et al.* 2005).

Over a wider geographical scale, diatom faunas from throughout the middle member of the Truckee Formation support a shallow depth and the presence of salt marsh vegetation for vertebrate-bearing lacustrine layers (Krebs and Bradbury 1984; Houseman 2004). The dominant components of the Lake Truckee fish fauna are two species known to tolerate elevated salinity: the stickleback *Gasterosteus doryssus* and the killifish *Fundulus nevadensis* (Griffith 1974; Guderley 1994). Rare trout, catfish and a possible minnow also have been reported (Baumgartner 1982; Bell 1994). Amphibians are represented by an undescribed anuran preliminarily identified to *Rana* (Lamm, pers. comm. 2009), and a salamander contained within a bird pellet. Reptiles are represented by an undescribed snake (Ruben 1971; Bell 1994, 2009), and mammals are represented by the tree squirrel *Sciurus olsoni* (Emry *et al.* 2005). At least eight fossil birds have been collected from the Truckee Formation including an undescribed cormorant (Phalacrocoracidae; see Bell 1994), a partial foot probably also representing a cormorant, two nearly complete songbirds (Passeriformes), the pelvis of an unidentified small bird, a currently unprepared skeleton of a mallard-sized waterbird and the grebe specimens described in this paper.

MATERIALS AND METHODS

Computed tomographic scanning

UMMP 74784 was scanned at Stony Brook University Medical Center using a GE Light Speed 16 medical CT scanner. The specimen was scanned along the coronal axis to generate 609 DICOM images at an image resolution of 512×512 pixels. The z-spacing (i.e. long axis of slab) is 0.325 mm, and the x- and y-spacing (i.e. sagittal and horizontal spacing, respectively) is 0.332 mm. Three-dimensional volumetric renderings of UMMP 74784 were made by rendering matrix transparent and bone opaque using the volumetric rendering program VGStudioMax 1.2.1. Scan images are available via Digimorph at: digimorph.org/specimens/fossil_podiciped.

Phylogenetic analyses

To test the phylogenetic relationships of fossil and extant grebes, we constructed a phylogenetic matrix of 49 morphological characters scored for 15 extant grebe species, the recently extinct *Podilymbus gigas*, the fossil

grebes described in this paper, and *Thiornis sociata*. Phoenicopteriformes were used as an outgroup.

All taxa were scored by direct examination of skeletal material, with the exception of *Thiornis sociata*, which was scored from a cast in the USNM collections in consultation with the description of the original specimen by Olson (1995). Characters of the integument were scored based on Storer (1967), Storer and Muller (2000) and Fjeldsø (2004). Morphological characters were drawn primarily from Bocheński's (1994) study of podicipediform osteology and from the matrix of Fjeldsø (2004). We excluded characters from both studies that exhibited high levels of intraspecific variation in multiple species (quantified in Bocheński (1994) for many characters). We treated four characters as ordered: (14) number of presacral vertebrae, (24) mediolateral compression of postacetabular pelvis, (25) extent of processus terminalis ischii, and (28) length of the cnemial crests of the tibiotarsus. Character definitions are provided in Appendix S1, scorings in Appendix S2 and specimens examined in Appendix S3.

Branch and Bound searches were conducted in PAUP*4.0b10 (Swofford 2003). Branches with a minimum length of 0 were collapsed. Multistate character scorings (e.g. 0&1) were used only for polymorphism. Bremer support was calculated manually in PAUP*4.0b10 by conducting successive Branch and Bound searches for trees of suboptimal lengths.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, NY, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NCSM, North Carolina Museum of Natural Sciences, Raleigh, NC, USA; UMMP, University of Michigan Museum of Paleontology, Ann Arbor, MI, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

SYSTEMATIC PALAEOLOGY

Order PODICIPEDIFORMES Fürbringer, 1888

Family PODICIPEDIDAE Bonaparte, 1831

Podicipedidae Species A

Referred specimen. UMMP 74784, articulated partial postcranial skeleton on slab (Figs 2–4). This specimen was previously referenced as *Phalacrocorax* sp. in Bell (1994). Measurements are provided in Table 1.

Locality and horizon. Open pit mine near Hazen, Nevada, located at 39.526°N , 119.094°W . Thick diatomites at this pit are provisionally considered part of the middle member of the Truckee Formation (see above). This horizon lies just below a tephra dated to 10.2 ± 0.2 Ma by $^{40}\text{Ar}/^{39}\text{Ar}$ spectroscopy which provides an

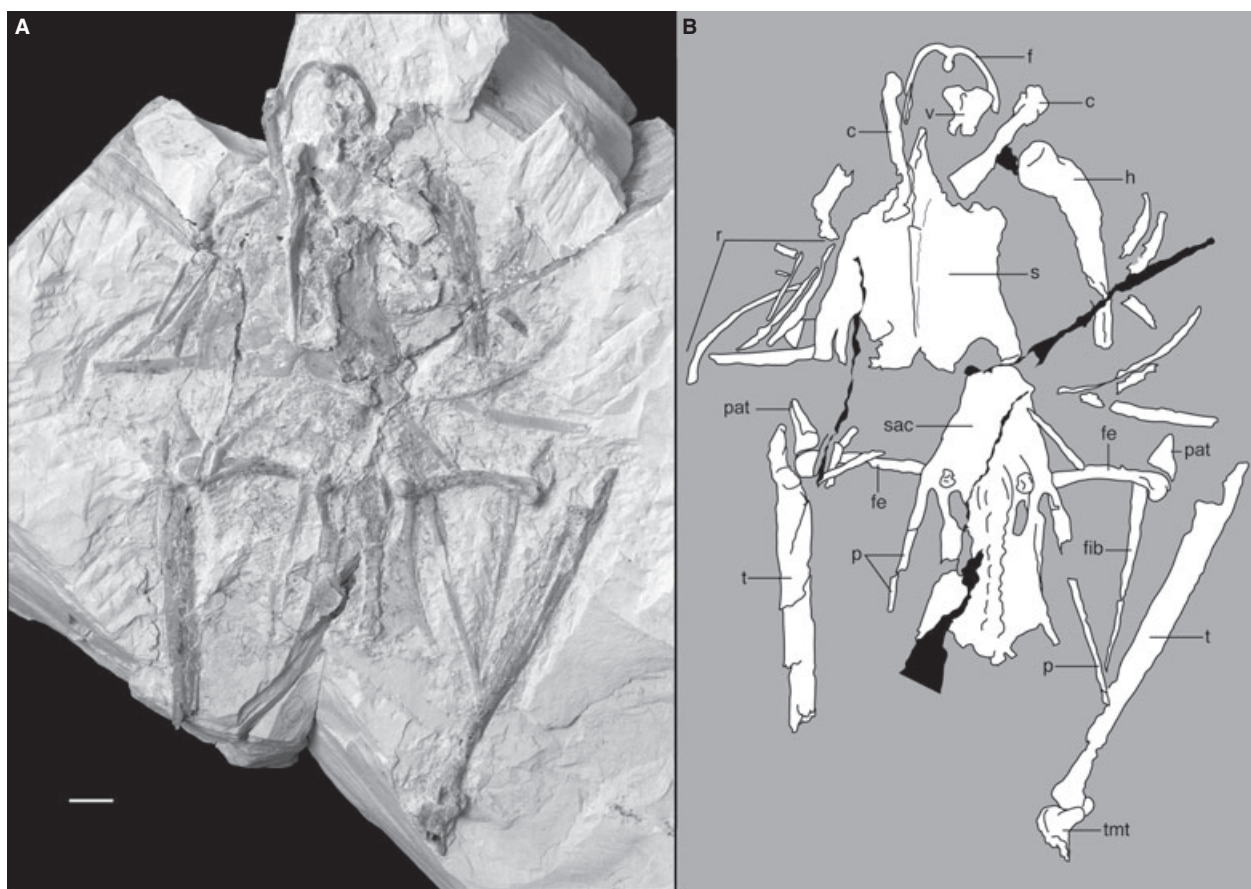


FIG. 2. UMMP 74784 (Species A). A, specimen in ventral view. B, line drawing of specimen. Black areas indicate breaks in the slab. Abbreviations: c, coracoid; f, furcula; fe, femur; fib, fibula; h, humerus; p, pubis; r, ribs; s, sternum; sac, sacrum; t, tibiotarsus; tmt, tarsometatarsus; v, vertebra. Scale bar in A represents 10 mm.

approximate age for the fossil. A second tephra much lower in the section is dated to 10.7 ± 0.2 Ma.

Preservation. The skeleton preserves all elements except for the skull, some cervical vertebrae, the distal portions of both wings and most of the pedal phalanges. The pectoral girdle and wing are slightly disarticulated and several ribs have been scattered. However, no obvious breaks or markings attributable to predation are identifiable. The quality of bone preservation and the diatom lamina of the slabs are surprising given inferred shallow water depths. We attribute this to the formation of protective biofilm coatings secreted by diatoms (Chang *et al.* 1998; O'Brien *et al.* 2008). Numerous disarticulated bones from small fish are scattered about the slab containing UMMP 74784. These are heavily concentrated in the area of the rib cage, with several fish elements overlaying the exposed ventral surface of the pelvis. We therefore interpret them as probable gut contents. A few elements occur outside the rib cage, but given the semi-disarticulated nature of the skeleton these may have been displaced by scavenging or water action.

Description. Species A is a moderate-sized grebe, close in size to large individuals of the extant *Podiceps auritus* (Horned Grebe

or Slavonian Grebe). Two articulated posterior cervical vertebrae are exposed near the furcula. Each vertebra bears a strong, flange-like processus ventralis. Three additional free posterior cervical or anterior thoracic vertebrae as well as the notarium can be identified in the CT imagery (Fig. 3), revealing that the remainder of the presacral vertebral column is intact within the slab. Fine details of morphology, however, cannot be observed for these vertebrae. The notarium appears to incorporate four thoracic vertebrae based on the number of rib attachments. The number of vertebrae forming the notarium varies from three to five in Podicipediformes, and intraspecific variation is common (Sanders 1967; Fjeldså 2004). Several ribs and processes uncinati are preserved. The latter are not fused to the ribs, as typical for diving birds (e.g. loons, penguins, diving petrels). Numerous ossified tendons can also be discerned in the CT imagery lying along the lateral surface of the neural spines. These ossified tendons extend to the cranial edge of the synsacrum and are identified as aponeuroses of the epaxial musculature based on comparisons with extant grebes (Vanden Berge and Storer 1995). Much of the synsacrum is exposed in ventral view, although a crack in the slab has damaged the cranial portion. The ventral surface of the synsacrum bears a shallow midline depression. Five sacral vertebrae bearing articular surfaces for



FIG. 3. CT reconstruction of UMMP 74784 (Species A) in dorsal view, showing elements hidden within the slab. Abbreviations: c, coracoid; f, furcula; fe, femur; fib, fibula; h, humerus; n, notarium; pat, patella; sc, scapula; t, tibiotarsus; tmt, tarsometatarsus. Scale bar in A represents 10 mm.

the ilia are present posterior to the foramen ilioischadicum, but all free caudal vertebrae including the pygostyle have been lost.

The sternum is exposed in ventral view and is craniocaudally short and mediolaterally wide as in extant grebes. The carina is well developed and projects cranially beyond the level of the sulcus articularis coracoideus. At the apex carinae, the carina is slightly expanded mediolaterally, forming a subtriangular surface that may have contacted the apophysis furculae in life. The trabeculae laterales are approximately the same width as those in *Podiceps*, whereas these processes are relatively wider in *Aechmophorus* and relatively narrower in *Tachybaptus*. As in all extant grebes, the caudal margin of the sternum bears an inverted triangular notch at the midline. Proximally, the coracoid bears both a dorsal and a ventral facies articularis sternalis, indicating it articulated tightly with the sternum in life as it does in extant grebes. The processus lateralis takes the shape of a weakly projected, thin, subtriangular crest. As in extant grebes, the coracoid lacks a processus procoracoideus and foramen nervi supratoracoidei. The extent of ventral projection of the processus acrocoracoideus (compared among Podicipediformes by Olson 1995)

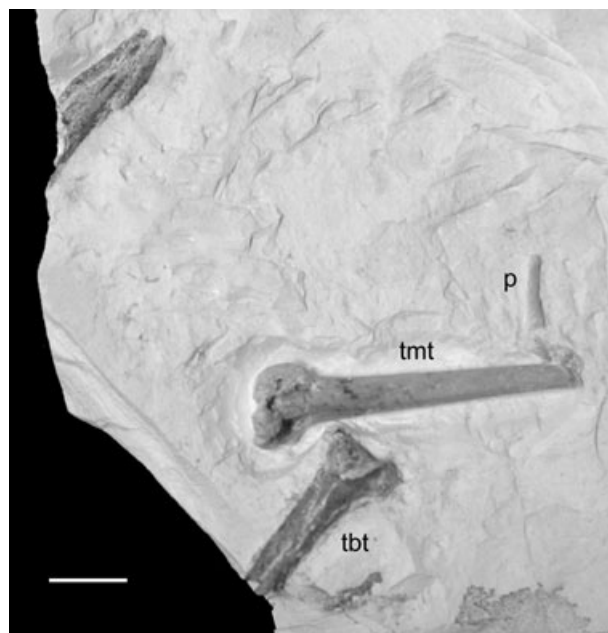


FIG. 4. Partial tarsometatarsus, metatarsal I and phalanx of UMMP 74784 (Species A). These elements are preserved on a slab originally continuous with the main slab but separated during collection. Abbreviations: p, pedal phalanx; tbt, tibiotarsus; tmt, tarsometatarsus. Scale bar in A represents 10 mm.

cannot be determined due to abrasion. In the CT imagery, both scapulae can be observed lying slightly out of articulation with the coracoids. As in extant grebes, the omal end of the scapula is unspecialized with a suboval facies articularis humeralis and a modestly projected acromion. The corpus scapulae is short, narrow, slightly curved and tapers to a pointed tip. Only the proximal portions of the humeri are intact. They are poorly preserved and do not differ notably from the humeri of extant grebes.

The pelvis is exposed in ventral view. Although it appears to be relatively broad, compression has affected its shape, and the true proportions cannot be reliably reconstructed. The pubis is thin and elongate, projecting far posterior to the caudal end of the ilium. A small projection from the ischium extends towards the pubis, constricting the foramen obturatum. This foramen typically remains open caudally in extant grebes, although it is sometimes completely closed by an ossified ligament in *Aechmophorus*. Although the ischium lacks its distal end, an impression on the slab suggests the ischium did not project as far posteriorly as the ilium.

The femur is anteriorly bowed and robust. Although the lateral surface of the shaft is embedded in matrix, its thickness can be determined from the CT imagery and is approximately 5 mm in diameter at midshaft. Midshaft cross section is >10 per cent femur length, as in most *Podiceps* species, *Poliocephalus poliocephalus*, and the flightless *Rollandia microptera*. More gracile proportions are seen in *Podilymbus*, *Tachybaptus*, *Rollandia rolland*, *Podiceps nigricollis* and *Podiceps occidentalis*, and the femur is markedly stouter in *Aechmophorus* and *Podiceps major* (Bocheński 1994). A large fovea indents the head of the femur as in extant grebes. At the intersection of the crista supracondylaris

TABLE 1. Measurements of maximum length (in mm) from Truckee grebe fossils.

	UMMP 74784	UMMP 74778	UMP 115962
Humerus	—	80.1 (r)/78.9 (l)	—
Ulna	—	69.3 (deformed)	67.5
Radius	—	71.1	c. 66
Carpometacarpus			32.8
Femur	35.5 (r)/33.9 (l)	—	c. 37
Tibiotarsus	78.8	—	97.2
Cnemial crest	10.2	—	13.2
Tarsometatarsus	—	—	52.9

medialis and crista supracondylaris lateralis, a strongly developed tubercle is present. Femur length to tibiotarsus length proportions fall within the range of extant *Podiceps*, whereas the femur is relatively more elongate in *Podilymbus* and *Tachybaptus* and shorter in *Aechmophorus*. The patella is wedge-shaped, with a gently concave articular surface for the cristae cnemialis lateralis of the tibiotarsus, a rugose proximal apex and a semicircular distal articular face for the femur. The long axis of the distal articular face is nearly as long as the proximodistal dimension, giving the patella a relatively short and squat shape. There is no perforation or furrow for the tendon of m. ambiens (a muscle lacking in grebes). The tibiotarsus is notable for the proportions of the cristae cnemialis cranialis. Although strongly projected compared with those of nondiving birds, the crest is proportionally shorter than in any of the extant grebes examined in this study. A small notch incises the distal edge of the medial crista bounding the trochlea cartilaginosa tibialis as in *Podiceps*, *Aechmophorus* and *Limnodytes*. Although the condylus lateralis is embedded in matrix, CT imagery reveals it lacks the distal notch observed in *Aechmophorus* and in some specimens of *Podiceps auritus*. Also observable in the CT imagery, the condylus medialis and condylus lateralis show an equal degree of anterior projection. The proximal half of the right tarsometatarsus is intact, but disarticulated from the tibiotarsus. A smaller portion of the left tarsometatarsus is preserved in articulation with the left tibiotarsus (Fig. 4). As in extant grebes, the tarsometatarsus is strongly mediolaterally compressed. Metatarsal I and a single pedal phalanx (tentatively identified as phalanx IV-2) are preserved adjacent to the right tarsometatarsus. No additional phalanges were uncovered by preparation in the region of the slab surrounding the tarsometatarsus.

Podicipedidae Species B

Referred specimen. UMMP 115962, semi-articulated specimen including the distal portion of the right humerus, right ulna, radius, ulnare, radiale and carpometacarpus, partial pelvis and complete right hindlimb, and several ribs (Fig. 5). Measurements are provided in Table 1.

Locality and horizon. Collected at the same locality as UMMP 74784, but from overlying beds and estimated to be c. 80 Ka younger based on varve chronology.

Remarks. This specimen shows proportional differences that indicate it belongs to a separate species from UMMP 74784. The tibiotarsus is >20 per cent longer than that of UMMP 74784, yet the femur is <10 per cent longer. Additionally, the cnemial crests are proportionally longer (13.5 per cent of total tibiotarsus length, versus 11 per cent in UMMP 74784).

Description. No diagnostic features of the humerus are visible. The ulna is fairly straight and robust, and the olecranon is extremely weakly developed. Both rami of the ulnare are exposed beneath the ulna, revealing that the ventral ramus (crus longum) is slightly longer than the dorsal ramus (crus breve). The carpometacarpus has a thin, straight metacarpal III and a narrow spatium intermetacarpale.

Even accounting for the effects of compression, the pelvis is relatively wide, more closely resembling that of *Tachybaptus* and *Rollandia* than the strongly mediolaterally compressed pelvis of *Podilymbus*, *Aechmophorus* and most species of *Podiceps*. Adjacent to the pelvis, a single caudal vertebra is preserved alongside impressions indicating the positions of three other caudal vertebrae that were lost in the splitting of the block. A portion of the pygostyle, which is reduced in size in grebes, is also intact. The femur is robust and strongly curved, but most details of the muscle insertions are obscured. As in Species A, the tibiotarsus has a relatively short crista cnemialis cranialis and patella compared with most extant grebes. The margins of the distal condyles of the tibiotarsus are sharply projected, although unfortunately it cannot be determined whether the condylus medialis and/or the condylus lateralis bore a distal notch. The tarsometatarsus is much longer than the femur and strongly mediolaterally compressed. As in extant grebes, the proximal margin of the tarsometatarsus projects dorsally so as to overhang the fossa infracotylaris dorsalis. The crista hypotarsi are prominently projected, but it is not possible to determine the number of canals due to crushing. As in extant grebes, trochlea metatarsi II is rotated and proximally displaced. The hallux is greatly reduced, comprising a short metatarsal, a thin proximal phalanx and a small ungual. The remaining pedal digits are elongate, nearly equalling the tarsometatarsus in length. Accounting for the missing ungual, the third digit is longest and the second digit the shortest. Only the ungual of the fourth digit is reasonably intact. It exhibits the long and flat shape seen in extant grebes.

Podicipedidae cf. Species B

Referred specimen. UMMP 74778, associated left and right humeri, right ulna and radius, and right radiale (Fig. 6). Measurements are provided in Table 1.

Locality and horizon. Collected at the same locality as UMMP 74784, but from overlying beds <30 m higher in the section and estimated to be <100 Ka younger based on varve chronology.

Remarks. This specimen is tentatively assigned to Species B. Based on preserved lengths of proportions of the ulnae, the

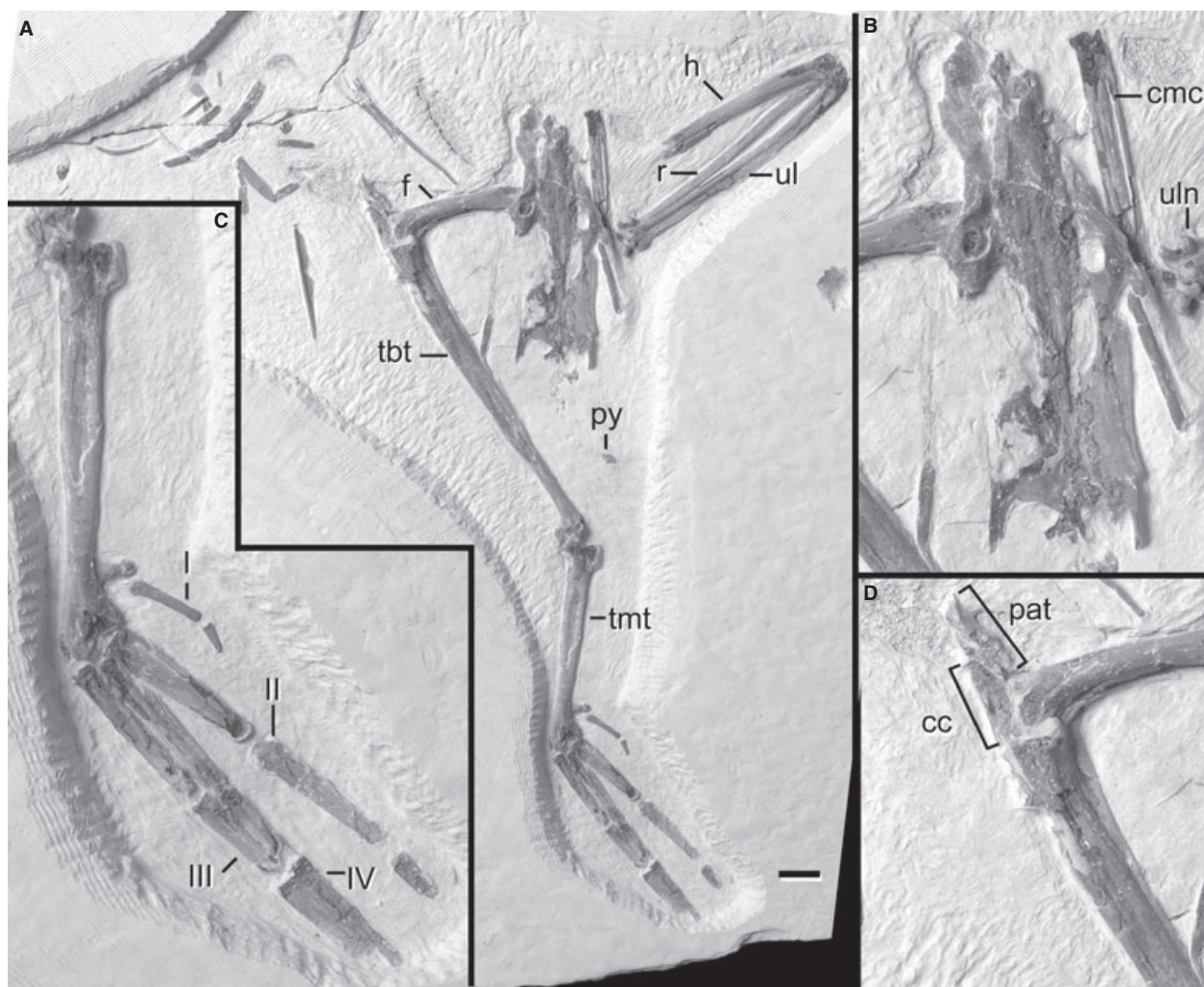


FIG. 5. UMMP 115962 (Species B). A, overview of specimen. B, close-up of pelvis. C, close-up of foot. D, close-up of knee region. Abbreviations: cc, cnemial crests; cmc, carpometacarpus; h, humerus; pat, patella; py, pygostyle; r, radius; ul, ulna; uln, ulnare; I–IV, pedal digits I–IV. Scale bar in A represents 10 mm.

individual represented by UMMP 74778 would be approximately 3 per cent larger than the individual represented by UMMP 115962. However, the undeformed radius indicates that the ulna is somewhat distorted and 9 per cent larger is a better estimate. This size disparity is well within the range of variation characteristic for sexually dimorphic extant grebe species (Fjeldsø 1982; Storer 2000). Indeed, because differences in major limb bone lengths can exceed 20 per cent (Bocheński 1994), an alternate referral to a very large individual of Species A cannot be fully ruled out.

Description. These elements were preserved in association and removed completely from the matrix during preparation. The humerus is apneumatic as in extant grebes and many other pursuit diving birds (e.g. loons, penguins, rails, see Smith 2012). The distal border of the crista bicipitalis lacks the notch observed in most extant grebes due to the less inflated intumescencia humeri. Individual variation occurs in this feature for *Podiceps*, so we do not

consider it diagnostic. Curvature of the shaft is similar to *Podiceps* as opposed to the straighter shaft in *Podilymbus* and *Tachybaptus* (see Murray 1967). The insertion of the ligamentum collaterale ventrale is a large, flattened surface, and the fossa m. brachialis is shallow. The processus flexorius is very weakly projected. The condylus dorsalis tapers to a sharp, slightly hooked point proximally. The radius bears a moderately developed tuberculum bicipitale radiale, and a slight elevation extending from this tubercle to the rim of the cotyla humeralis bounds a shallow depression (variably developed in extant *Podiceps*). The shaft of the radius is robust compared with similarly sized individuals of *Podiceps nigricollis* and *Podiceps cristatus* and has a subtriangular cross section with a sharp medial edge. Although the sulcus tendinosus appears unusually shallow, this condition is likely due to abrasion of the ridges bounding this sulcus. The ulna is best preserved at the articular ends. Proximally, the cotyla dorsalis tapers to a sharp cranial edge and has a hooked shape as in other grebes. A few faint papillae are present, but because the shaft is damaged, the total number of secondary feather insertions cannot be determined. At the distal



FIG. 6. UMMP 74778 (cf. Species B). A, right humerus in caudal view. B, right humerus in cranial view. C, left humerus in cranial view. D, left humerus in caudal view. E, right ulna in ventral view. F, right ulna in dorsal view. G, right radius in dorsal view. H, right radius in ventral view. Scale bar represents 10 mm.

edge, the incisura tendinosa is particularly well demarcated. The tuberculum carpalis is displaced further proximal relative to the condylus ventralis ulnae than in most extant grebes, a conformation also observed in *P. grisegena*, *P. cristatus* and *P. major* (Fig. 7). The depressio radialis is shallow.

PHYLOGENETIC RESULTS

An initial phylogenetic analysis including all taxa in the matrix yielded 384 most parsimonious trees of 95 steps. The strict consensus tree (Fig. 8) shows little resolution, with all grebe taxa collapsed into a large polytomy except for a clade uniting the two *Podilymbus* species and a clade uniting *Aechmophorus* with four of the sampled *Podiceps* species. A separate analysis including Species A but excluding Species B resulted in the resolution of two additional branches, supporting the monophyly of *Rollandia* and a clade uniting *Podilymbus* and *Rollandia*, but did not further resolve the relationships of the fossil (results not shown). A separate analysis including Species B but excluding Species A did not result in further resolution (results not shown). We attribute this lack of resolution to both a low overall number of phylogenetically informative characters available from the skeletal anatomy of grebes and the lack of preservation of key elements like the skull and hypotarsal canals in the Truckee fossils.

When the Truckee fossils are excluded, resolution improves substantially. Three most parsimonious trees

(MPTs) of 95 steps are recovered. The strict consensus tree (Fig. 9) supports a basal split between two major clades. One clade unites the dabchicks (i.e. *Tachybaptus*, *Limnodytes*, *Poliocephalus*) and the fossil taxon *Thiornis sociata*. Two characters are optimized as unambiguous synapomorphies of this clade: projection of the ilium far caudal to the caudal end of the ilium and presence of a red feathered head patch in the downy young (independently present in *Podilymbus*). The second, larger clade includes the 'golden grebes' (*Rollandia*), pied-billed grebes (*Podilymbus*) swan grebes (*Aechmophorus*) and the diverse assemblage of *Podiceps* species. This clade is only weakly supported by the ambiguous synapomorphy of a caudo-odorsally oriented fossa caudalis of the mandible. Projection of the labrum externum cranial to labrum internum of the sternum is optimized as an unambiguous synapomorphy of this clade, but must be considered noncomparable for several species where the labrum externum does not extend to the midline of the sternum. Within this clade, *Rollandia* and *Podilymbus* are recovered as monophyletic sister taxa. The subclade uniting these two genera is unambiguously supported by reduction of the apophysis furculae and presence of a hypotarsal canal for the tendon of m. flexor perforans digiti II (convergently present in *Tachybaptus*). A second subclade uniting *Podiceps* + *Aechmophorus* is unambiguously supported by the presence of a bare crown patch in the downy young and is ambiguously supported by an increase in cnemial crest length (*Podiceps occipitalis* exhibits the primitive shorter



FIG. 7. Comparisons of extant and fossil grebe material illustrating characters from the text and analysis. A, left coracoid of (A) *Aechmophorus clarkii* (AMNH 20027). B, left coracoid of *Podiceps nigricollis* (AMNH 19791) in ventral view. C, right ulna of *Tachybaptus ruficollis* (AMNH 24767) in dorsal view. D, right ulna of *Aechmophorus occidentalis* (AMNH 18666) in dorsal view. E, right tarsometatarsus of *Miobaptus walteri* (after Švec 1982), in proximal view. F, right tarsometatarsus of *Podiceps nigricollis* (AMNH 19791) in proximal view. G, right tarsometatarsus of *Podilymbus podiceps* (AMNH 10506) in proximal view. H, left tibiotarsus of *Podiceps auritus* (AMNH 23137) in lateral view. I, left tibiotarsus of Truckee Species A (UMMP 74784) in lateral view. Abbreviations: cc, crista cnemialis; fpdII, canal for tendon of flexor perforans digiti II; pl, processus lateralis; tc, tuberculum carpal. Not to scale.

state, possibly due to reversal) and an increase in the number of presacral vertebrae.

Relationships within the dabchick clade are poorly resolved. However, all trees support the nonmonophyly of *Tachybaptus*. '*Tachybaptus dominicus*' is recovered as sister taxon to a clade uniting the remaining *Tachybaptus* species, *Poliocephalus*, and the fossil taxon *Thiornis sociata* (discussed further below). Monophyly of *Poliocephalus* remains untested in our study, as only a single species was available for incorporation into our matrix. However, only two extant *Poliocephalus* species are recognized and the monophyly of the genus has not previously been questioned.

Finally, an analysis including only extant grebes yielded a single fully resolved tree of 95 steps with higher support

values for several branches (Fig. 10). This tree included further resolution within the dabchick clade, supporting the monophyly of *Tachybaptus ruficollis* and *Tachybaptus novaehollandiae* to the exclusion of *Poliocephalus* and '*Tachybaptus dominicus*'. Otherwise, the topology matches that of the analysis including *Thiornis*.

DISCUSSION

Phylogeny of the Podicipediformes

Most early hypotheses for grebe evolutionary relationships (e.g. Storer 1963; Fjeldsø 1985, 1988) were based on interpretations of certain characters as primitive, but

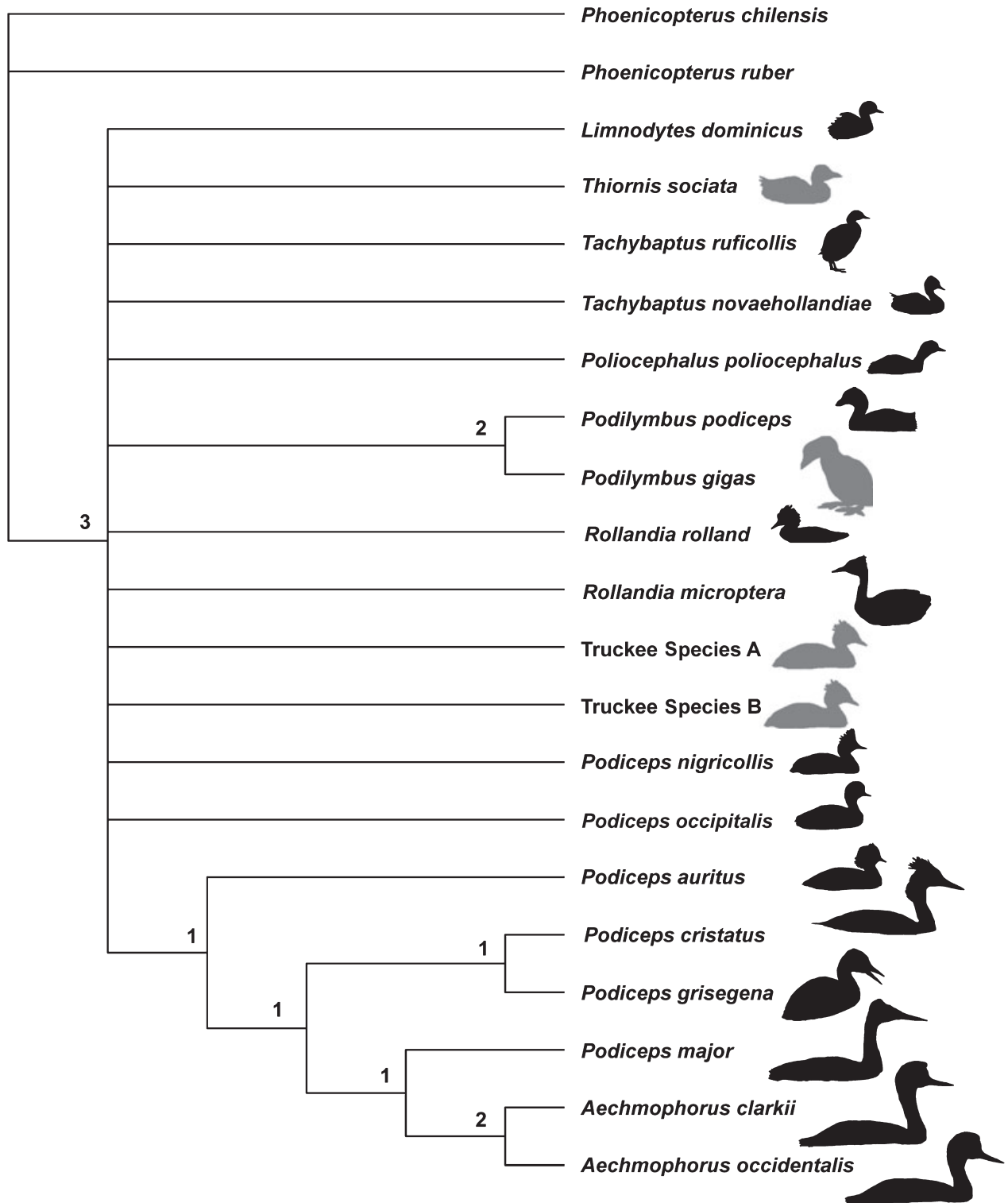


FIG. 8. Strict consensus of 384 most parsimonious trees (TL = 95, RC = 0.557, RI = 0.801) from the analysis of the morphological data set including all taxa. Extinct taxa are represented by grey silhouettes and extant taxa by black silhouettes. Bremer support values appear above branches.

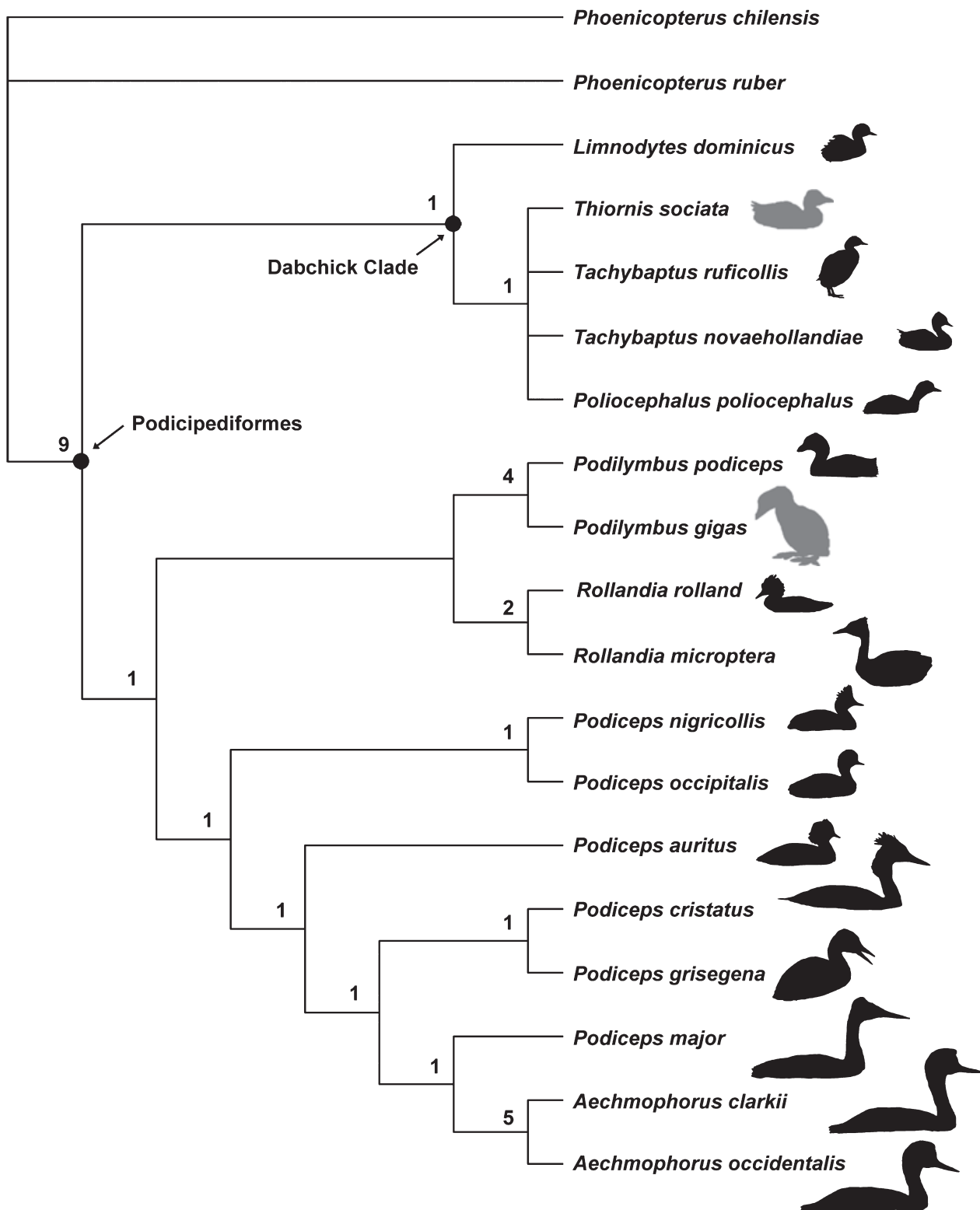


FIG. 9. Strict consensus of three most parsimonious trees (TL = 95, RC = 0.557, RI = 0.801) from the analysis of the morphological data set excluding fossil Species A and B. Extinct taxa are represented by grey silhouettes and extant taxa by black silhouettes. Bremer support values appear above branches.

were formulated outside of a cladistic framework. Considerable homoplasy is inferred for the morphological character most emphasized in precladistic classifications for grebes: the presence or absence of a bony canal in the hypotarsus for the tendon of m. flexor perforans digiti II (Fig. 7). The presence of this canal in some taxa (i.e. *Tachybaptus*, *Podilymbus*, *Rollandia* and some individuals of *Podiceps major*) was first considered evolutionarily significant by Storer (1960) and since has been used widely in classification schemes (e.g. Storer 1963, 2000). This canal, however, must have evolved convergently at least three times, in *Tachybaptus*, in the *Rollandia* + *Podilymbus* clade and in *Podiceps major*, given the results of the current analysis.

Fjelds  (2004) conducted the first and only previous phylogenetic analysis of Podicipediformes. Fjelds 's (2004) results (Fig. 11) contrast with ours in four main respects: (1) a basal position for *Rollandia*, (2) lack of support for a dabchick clade, (3) monophyly of *Tachybaptus* (including '*Tachybaptus*' *dominicus*) and (4) monophyly of *Podiceps*. Although Fjelds  (2004) employed 82 characters in a preliminary analysis, the resultant tree from this initial analysis was not presented. Fjelds  (2004) subsequently discarded 12 characters that showed high homoplasy in the initial analysis, ordered several characters, weighted 20 characters and finally 'reapplied' the discarded characters to arrive at the tree shown in Figure 11. We are unable to assess which characters may contribute to differences between this analysis and our own because the weighting scheme was not explicit and codings for only 80 of the 82 characters defined in the character list appear in the matrix. Several numerical mismatches are also apparent based on number of states per character. Recreating the relationships shown in Figure 11 for all taxa overlapping between that tree and our analysis results in an increase in tree length of 11 steps.

One key factor that may explain difference between our results and those of Fjelds  (2004) is that the later study did not employ species-level outgroups, but rather a hypothetical outgroup constructed from comparisons with the fossil grebe *Thiornis sociata*, flamingos and other waterbirds. Rooting analyses using hypothetical ancestors can place problematic constraints on phylogenetic analyses (e.g. Bryant 1997). Morphologies in *Thiornis sociata* should not be interpreted as primitive *a priori* solely because this taxon is a fossil member of Podicipediformes. Doing so may negatively affect results by establishing polarities for characters based on preconceived notions of phylogeny, rather than allowing polarity to be established *a posteriori* by rooting the tree to a nonpodicipediform outgroup. In this particular case, *Thiornis sociata* is in fact recovered as a member of the grebe crown clade when it is treated as a distinct taxon (Fig. 9). The alternate hypothesis that this fossil taxon is a stem grebe requires

three extra steps. Whereas Fjelds  (2004) treated *T. sociata* as an ancestor to living grebes, Olson (1995, p. 139) recommended that *T. sociata* be 'carried in the nomenclaturally oldest and most widespread genus *Podiceps*'. Storer (2000), however, argued that because the fossil more closely resembles extant *Tachybaptus* than *Podiceps*, this change in taxonomy was unwarranted. Placement of *T. sociata* within *Podiceps* can be firmly rejected based on our phylogenetic results. At this time, however, we are not able to resolve whether *T. sociata* is sister taxon to *Tachybaptus*, *Polioccephalus* or these two taxa together. It therefore seems prudent to retain the genus *Thiornis* pending further resolution of this polytomy.

Olson (1995, p. 139) noted that despite being quite distinct from other avian clades, grebes are 'osteologically rather homogenous'. We agree with this assessment, having found relatively few morphological characters relevant to resolving the interrelationships of Podicipediformes. Independent evidence from molecular data would provide a test of the results reported here.

Limnodytes dominicus: implication for dabchick biogeography

Limnodytes dominicus has a complex taxonomic history. This small dabchick species has alternatively been assigned to the monotypic genus *Limnodytes* (Linnaeus), *Polioccephalus* (Peters 1931), *Podiceps* (Storer 1960; Howard and Moore 1991) and most recently *Tachybaptus* (Sibley and Monroe 1990; Storer 2000; Fjelds  2004). Review of the taxonomic literature also reveals two other past usages of the name *Limnodytes* outside of birds. Both are junior homonyms to *Limnodytes* (Linnaeus). *Limnodytes* was applied to a group of ranid frogs by Dum ril and Bibron (1841), but all these species have been reassigned to the genus *Hylarana* Tschudi 1838 (see Frost 2013). Marchal (1900) applied the name *Limnodytes* to a wasp, but this action was recognized as a taxonomic error and the genus changed to *Tiphodytes* by Bradley (1902). Thus, the use of *Limnodytes* for the small dabchick has seniority, and all competing uses have been recognized as invalid regardless.

Our analyses indicate that resurrection of the genus name *Limnodytes* for this species is warranted. Morphology-based analysis supports nonmonophyly of this species with other representatives of *Tachybaptus*. Although *Limnodytes dominicus* resembles the three living and one recently extinct species of *Tachybaptus* in its small size, dark colouration and general habits, this species lacks key character states that unite *Tachybaptus* including an accessory hypotarsal canal for m. perforans digiti II, chestnut patches on the neck, a yellow 'grin patch' at the rima oris and buff colouration in the plumage of the downy young.

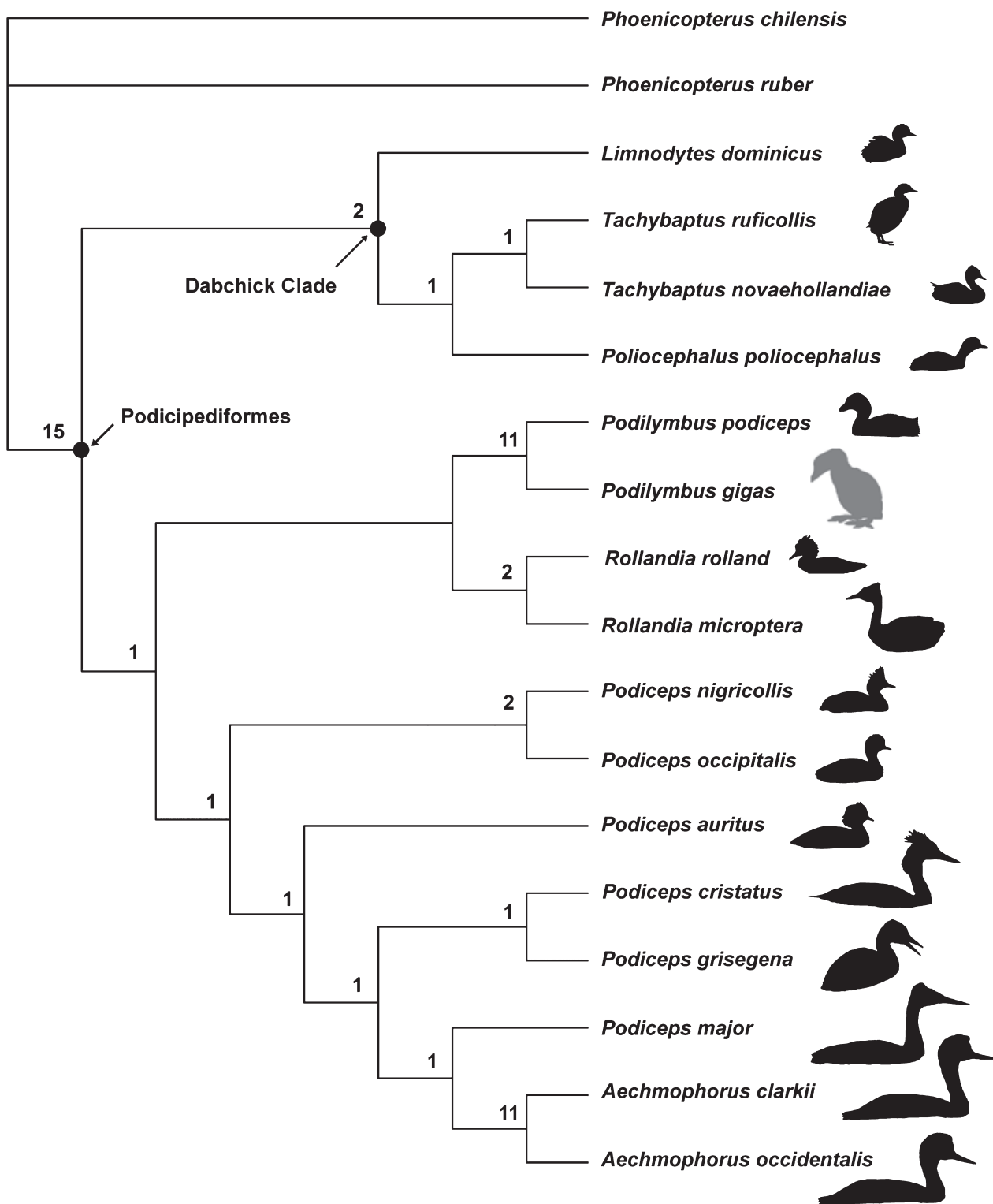


FIG. 10. Single most parsimonious tree (TL = 95, RC = 0.554, RI = 0.797) from the analysis of the morphological data set including only extant taxa. Bremer support values appear above branches.

Limnodytes dominicus is furthermore unique among dabchicks in having a Western Hemisphere biogeographical distribution. All other dabchicks occur exclusively in

the Eastern Hemisphere. When a biogeographical character is mapped onto the cladogram using full Fitch optimization, the ancestral distribution for the dabchick

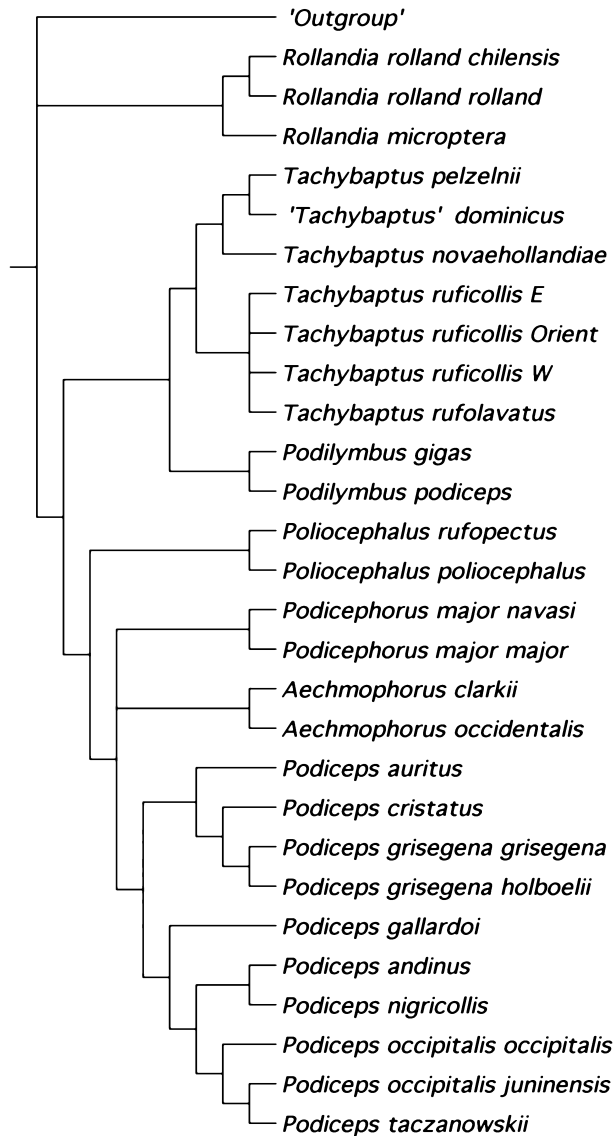


FIG. 11. Phylogeny of Podicipediformes proposed by Fjeldså (2004). See text and Fjeldså (2004) for details of analysis.

clade is reconstructed as South American. This reconstruction unambiguously supports a single dispersal event by dabchicks from the Western Hemisphere, where *Limnodytes dominicus* is the sole surviving representative, to the Eastern Hemisphere, where this clade of grebes exhibits greater diversity (five extant, one recently extinct species).

Given present sampling, biogeographical reconstructions support a New World, and more specifically South American, ancestral distribution for Podicipediformes. A South American ancestral distribution for grebes has been proposed before (Fjeldså 2004). However, we believe it would be premature to draw conclusions based on these reconstructions because some extant grebe species were not sampled here, and because molecular signal and

complete taxon sampling is desirable to improve resolution and independently test the results presented here.

Miobaptus walteri: a stem or crown grebe?

Results of the phylogenetic analysis call attention to lingering questions regarding the affinities of early grebes. The Early Miocene *Miobaptus walteri* is the oldest described grebe and, perhaps in part due to its antiquity, has been considered to represent a primitive lineage (Švec 1982). We did not include *Miobaptus walteri* in our analysis because we were unable to examine the material directly, and few characters in our matrix can be coded from the original descriptions. We note, however, that any consideration of the phylogenetic affinities of this taxon must rest heavily on the inferred homology of the hypotarsal canals. All extant grebes possess at least three large hypotarsal canals, which house the tendons of m. flexor digitorum longus, m. flexor hallucis longus and m. flexor perforans et perforatus digiti II (Hudson 1937; Fig. 7). Several extant species additionally possess a small fourth canal, identified by Storer (1963) as the passage of the tendon of m. flexor perforatus digiti II.

Miobaptus walteri possesses a canal in the position occupied by the m. flexor perforatus digiti II canal (when present) in extant grebes. However, Švec (1982) identified this canal as the passage for the tendon of m. flexor hallucis longus and considered the presence of a separate canal for this tendon unique (and plesiomorphic) for *Miobaptus* among Podicipediformes. Švec (1982) noted that the tendons of m. flexor digitorum longus and m. flexor hallucis longus are fused in extant grebes (see George and Berger 1966) and therefore inferred that both tendons occupy a single canal in Podicipedidae. However, Hudson's (1937) dissections of *Podiceps nigricollis* suggest that this interpretation of the extant grebe hypotarsal canals is incorrect. Although the tendons of m. flexor digitorum longus and m. flexor hallucis are fused in extant grebes and other taxa exhibiting the type IV deep flexor tendon arrangement of Gadow (1893), this fusion generally occurs near the mid-point of the tarsometatarsus (Hudson 1937). Thus, the tendons of m. flexor digitorum longus and m. flexor hallucis longus may occupy separate proximal hypotarsal canals, despite their fusion distal to these canals.

Although it is impossible to conclusively demonstrate the identity of the tendons occupying the hypotarsal canals in *Miobaptus walteri* without soft tissue preservation, it is most parsimonious to assume that the fourth canal in *Miobaptus walteri* represents the passage for m. flexor perforatus digiti II. A canal for m. flexor perforatus digiti II is optimized as primitively absent in Podicipediformes, so as reinterpreted here, the canal actually

supports interpretation of *Miobaptus walteri* as a crown rather than stem taxon. However, because this character has a homoplastic distribution in our data set, additional material is desirable to confirm the precise phylogenetic affinities of this important fossil taxon. Further complicating interpretations of polarity, extant flamingos lack this canal, but the putative stem flamingo *Palaelodus* appears to have retained it (Mayr 2004).

Calibrating grebe divergences

Podicipediformes appears to be one of the youngest 'ordinal' clades of living birds based on their stratigraphical record and phylogenetic relationships. Whereas most traditional avian orders first appear during or prior to the Eocene (Olson 1985; Blondel and Mourer-Chauviré 1998; Mayr 2005; Ksepka and Boyd 2012, figure 5), there is as yet no fossil evidence of Eocene grebes and potential Oligocene records remain unverified. Probable stem members of Phoenicopteriformes, the sister clade to Podicipediformes, are known from the early Oligocene (Palaeolodidae and *Elornis*; see Milne-Edwards 1867–1871; Mayr and Smith 2002), along with a putative late Eocene record of *Agnopteris hantoniensis* (summarized by Mayr 2009). However, the precise relationships of these potential stem flamingos have not yet been phylogenetically tested, and it remains possible some of these fossil taxa represent basal lineages that fall outside the grebe-flamingo split, or alternatively represent basal stem grebes (Mayr 2009).

DNA sequence-based divergence estimation studies incorporating fossil calibration points have produced greatly varying interpretations of the timing of the grebe radiation. One recent study utilizing data from five nuclear genes supported an Oligocene age for the Phoenicopteriformes-Podicipediformes split (Ericson *et al.* 2006), indicating strong concordance between the molecular data and the fossil record. In contrast, a study based on mitochondrial data (Brown *et al.* 2008) supported a far older age for stem Podicipediformes, with the preferred tree placing the Phoenicopteriformes-Podicipediformes split in the Cretaceous or earliest Paleocene (95 per cent confidence interval). The nuclear study included only one grebe species and therefore did not address the age of the crown radiation. The mitochondrial study included two extant grebe species, *Podilymbus podiceps* and *Podiceps 'caspicus'* (= *Podiceps nigricollis*) and reported ages ranging from Late Cretaceous to Oligocene to be within the 95 per cent posterior credibility interval for the *Podilymbus-Podiceps* divergence (Brown *et al.* 2008). In our results, the *Podilymbus-Podiceps* divergence is more highly nested than the basal divergence within crown clade grebes and so the molecular study suggests crown grebes are much older than supported by the fossil record.

Although the two divergence estimation studies cited above incorporated avian fossils as calibration points, at the time these studies were conducted no phylogenetically constrained grebe fossils were available for inclusion. Calibrations within the clade of interest are key to accuracy of divergence analysis (e.g. van Tuinen and Hedges 2004; Ho and Larson 2006; Hug and Roger 2007; Sauquet *et al.* 2012). Although many divergence dating studies within Aves have applied fossil calibrations (e.g. Ericson *et al.* 2006; Baker *et al.* 2007; Brown *et al.* 2008; Pacheco *et al.* 2011), few fossils used as calibrations have been phylogenetically vetted (Ksepka *et al.* 2011) and several previous fossil calibrations have been shown to be inappropriate by later revisions (Mayr 2005; Ksepka 2009; Wijnker and Olson 2009; Smith 2011). Thus, new phylogenetically and stratigraphically vetted fossil calibration points for birds are desirable.

Thiornis sociata provides a fossil calibration point for the basal divergence amongst dabchicks (the split of *Limnodytes dominicus* from *Tachybaptus* and *Polioccephalus*). Parham *et al.* (2012) outlined five key guidelines for justifying fossil calibration points: (1) basing each calibration on an individual specimen, (2) referencing an apomorphy-based diagnosis or phylogenetic analysis including this specimen, (3) resolving any conflict between morphological and molecular data sets that affect the reliability of the fossil calibration, (4) providing the explicit stratigraphical context of the fossil and (5) translating stratigraphical placement to a numerical date via connection to radiometric dates and/or the geological timescale. We follow these best practices here by designating MNHN 1930–1 (the holotype of *Thiornis sociata*) as the calibrating specimen and referencing the phylogenetic analysis presented in this paper as phylogenetic justification for the position of the calibration point. At present, there is no molecular phylogeny available for grebes, so comparisons between morphological and molecular signal cannot be made. The holotype of *Thiornis sociata* was collected from the Libros Gypsum of Teruel, Spain. The Libros Gypsum is considered Vallesian (Late Miocene) in age (Anadón *et al.* 1989; Ortí *et al.* 2010). Because the Vallesian is a European mammal age defined by the appearance of mammal taxa (which may appear asynchronously at different localities), tying it to precise absolute dates remains difficult. Within Spain, the Vallesian is estimated to span 8.7–11.1 Ma (Garcés *et al.* 1996). As the minimum possible age of the relevant fossil including associated dating uncertainty should be taken as the starting point for calibrations (e.g. van Tuinen *et al.* 2004; Donoghue and Benton 2007; Benton and Donoghue 2007; Benton *et al.* 2009; Ho and Phillips 2009), we specify 8.7 Ma as the minimum age for the basal split in dabchicks. This age is based on the best available estimate of the Vallesian/Turolian (MN 10/11)

boundary, which is correlated to the base of Chron C4r.2r (Steininger 1999).

CONCLUSIONS

Lake Truckee provides an interesting window into a Miocene avifauna, particularly given that deposits from this large shallow alkaline lake preserve both taxa presumed to have inhabited the waters of the lake itself (Podicipediformes, Phalacrocoracidae) and taxa representing the surrounding terrestrial environment (Passeriformes). Additional components of this avifauna will be formally described in future contributions. Discovery of these fossils has added to our understanding of grebe evolution, particularly by motivating a new phylogenetic analysis of Podicipediformes. Clearly, however, more molecular data and taxonomic sampling (particularly for recently extinct species) are needed to firmly resolve the relationships of the living and extinct Podicipediformes. Although many species of fossil Podicipediformes have been described, few fossils preserve sufficient phylogenetically informative features to offer much insight into early patterns of grebe evolution. *Thiornis sociata* at least provides evidence that two major clades of living grebes had diverged by the Miocene.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Morphological character descriptions.

Appendix S2. Morphological character matrix.

Appendix S3. Specimens examined for morphological character coding.

Appendix S4. Nexus file (v1.0).

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