

Re-description and phylogenetic assessment of the Late Miocene ducks *Aythya shihuibas* and *Anas* sp. (Aves: Anseriformes) from Lufeng, Yunnan, China

Thomas A. STIDHAM

(Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044 presbyornis@gmail.com)

Abstract In 1985, Hou Lianhai published a short paper on some of the bird specimens from the Miocene hominoid fossil locality of Lufeng in Yunnan, and in that paper, he named one species of duck (*Aythya shihuibas*) and described a second specimen as a member of *Anas*. Assessment of the phylogenetic characters preserved in those two anatid specimens, in combination with their currently known distribution, confirms that two different species (from different phylogenetic lineages) are present in the Lufeng avifauna, as originally published. The presence of the primitive state of a highly pneumatic cavity with bony struts in the ventral pneumotricipital fossa in *A. shihuibas* differs from nearly all living species in *Aythya* and helps to establish that it is a distinct extinct species likely outside the crown group of *Aythya*. The more fragmentary Lufeng anatid specimen, originally called *Anas* sp., cannot be as accurately constrained phylogenetically. It is likely a member of Anatinae and perhaps could be called *Anas*, although the species of that genus are not monophyletic. The Lufeng *Anas* specimen may be closely related to one of the unnamed species placed in *Anas* from the Mio-Pliocene of Mongolia because they share an uncommon combination of characters.

Key words Lufeng, Yunnan, Late Miocene, Aves, Duck, *Aythya*, *Anas*

1 Introduction

The fossil record of waterfowl is relatively poor in China, and that contrasts with the growing number of anseriform fossils being described from the Paleogene and Neogene of neighboring Mongolia (e.g., Zelenkov, 2011, 2012a, b; Zelenkov and Kurochkin, 2012; Kurochkin and Dyke, 2010). Currently, the oldest published anseriforms from China are Eocene stem anatids (cf. Romainvilliinae) and a purportedly anseriform tarsometatarsus (now lost) from the Xinjiang Uighur Autonomous Region (Chow et al., 1982; Stidham and Ni, 2014). The next oldest anseriform fossils in China are Neogene and come from the Middle Miocene Shanwang lacustrine deposits of Shandong (Yeh, 1980), the Late Miocene site of Lufeng in Yunnan Province (Hou, 1985), and multiple undescribed specimens (including what appears to be a goose) from the latest Miocene Shuitangba section (Zhaotong Region) in Yunnan (Zhang et al., 2013; Jablonski et al., 2014). At present, none of the Miocene

Chinese anatid specimens have been assessed in a phylogenetic context, and the original taxonomic allocations (of previously published specimens) have not been reexamined. As a result, comparison of the previously published Chinese Miocene ducks to temporally and geographically close new species from Mongolia, as well as other parts of the world cannot be adequately completed. Additionally, the changing hypotheses of anatid phylogeny necessitate a reassessment of previous taxonomic treatments of older published fossils. In this paper, I redescribe the Lufeng anatid specimens and discuss the characters of phylogenetic significance preserved in those specimens and their role in taxonomic diagnosis and identification. The aim is to provide a basis of comparison for any anatid remains from China and the region found in the future and to more accurately place the Lufeng specimens into an evolutionary context. The osteological terminology follows Baumel and Witmer (1993) with English equivalents of the Latin terms used.

Specimen background The Shihuiba/Lufeng site is best known for its diverse mammalian fauna, including the hominoid *Lufengpithecus* (Qiu and Qiu, 1995; Ni and Qiu, 2002; Dong and Qi, 2013). According to Jablonski et al. (2014), the Lufeng site is approximately the same age as the nearby Shuitangba section (~6–6.5 Ma) based on the shared small mammal fauna, and the absence of *Sinocastor* at Lufeng indicates that it is slightly older than Shuitangba. That age range is consistent with the reported paleomagnetic age of ~6.9–6.2 Ma for Lufeng (Dong and Qi, 2013). However, that very Late Miocene age interpretation is younger than the previous assessments of Lufeng based on the small mammal fauna as closer to ~7–8 Ma (Ni and Qiu, 2002; Qiu and Qiu, 1995). As with the younger Yunnan site, the Lufeng fauna preserves non-mammalian fossils, including six taxa of birds (Hou, 1985).

Among the avian remains from Lufeng, Hou (1985) discussed two fragmentary anatid bones. One of those described (and illustrated) specimens is a set of fragments of a right humerus that he allocated to the genus *Anas* (Hou, 1985), and that specimen includes shaft fragments, a portion of the cranial surface of the proximal humerus, and part of the distal humerus. Hou (1985) only obliquely discussed the proximal end (not illustrating it) and does not mention the shaft fragments. Only the distal humerus is mentioned in Li et al. (2008), while the fragment of the proximal end is illustrated (cranial view) along with a cranial view of the fragment of the distal end in He (2007:318) and Hou (2003).

The other anatid specimen (a proximal left humerus) was made the holotype of a new species *Aythya shihuibas* Hou, 1985. While it does not appear that the taxonomic allocation of the *Anas* specimen has since been discussed, that of *A. shihuibas* has, albeit briefly. Zelenkov (2012a) initially transferred *A. shihuibas* to the genus *Protomelanitta* based on the perceived ‘narrow’ humeral head in the photograph in Hou (2003) that appears to be taken in an oblique dorsocaudal view, not caudal view. Zelenkov’s (2012b: fig. 3) illustration of *Protomelanitta* shows a proximodistally narrower (rather than dorsoventrally short) humeral head. While this humeral head character state may be a bit narrower in *A. shihuibas*, it does not exhibit the same degree of narrowing as in *Protomelanitta* figured by Zelenkov (2012b). Furthermore, Zelenkov (2012a) states that the morphology of the dorsal tubercle in *A. shihuibas* does not occur in extant *Aythya*. However, I see no clear difference between that character state in *A. shihuibas* and the extant *A. ferina* (IVPP OV 1659; Fig. 1). In addition, the dorsal tubercle of

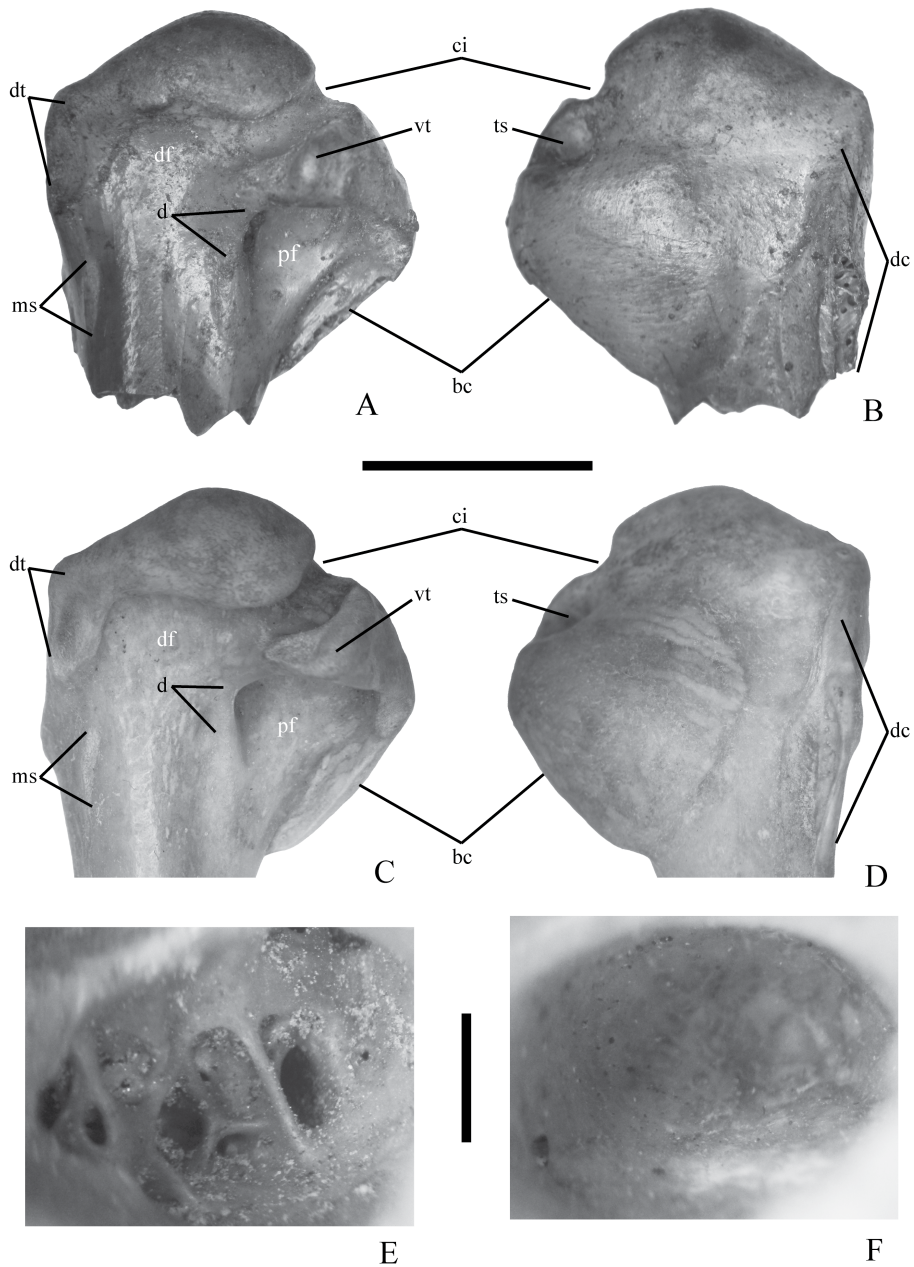


Fig. 1 Comparison of the holotype of *Aythya shihuibas* (IVPP V 7137) (A, B, and E) and the proximal humerus of *Aythya ferina* (IVPP OV 1659) (C, D, and F)

A, C. Proximal humerus in caudal view; B, D. Proximal humerus in cranial view; E, F. View dorsoproximally inside the ventral pneumotricipital fossa showing the pneumatic foramina and bony struts of the primitive state in E, and their absence (a bony wall) in F

Abbreviations: bc. bicipital crest; ci. capital incisure; d. depression along the crus; dc. deltopectoral crest; df. dorsal pneumotricipital fossa; dt. dorsal tubercle; ms. muscle scar of the *latissimus dorsi posterioris*; pf. ventral pneumotricipital fossa; ts. transverse ligamental sulcus; vt. ventral tubercle. Scale bar equals 1 cm for A-D and 2 mm for E-F

Protomelanitta differs from *A. shihuibas* in that it projects more dorsally, and the notch formed by the capital incisure is wider and more distinct than the narrower and shallower notch in *A. shihuibas*. Despite those initial suggestions, Zelenkov (2012b) quickly shifted the holotype's taxonomy back to *Aythya*. Even given his change of taxonomic opinion, phylogenetically relevant characters still have not been analyzed for this specimen, and its position relative to the extant species of *Aythya* is unclear. The holotype has been illustrated only in caudal view (Hou, 1985; Li et al., 2008: fig. 389; He, 2007:317), but see Fig. 1 for the cranial view.

Institutional abbreviations IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, California, USA; OV, extant bird skeleton in the IVPP collection; V, fossil vertebrate specimen in the IVPP collection.

2 Systematic paleontology

Aves Linnaeus, 1758

Anseriformes Wagler, 1831

Anatidae Leach, 1820

Aythya shihuibas Hou, 1985

Holotype IVPP V 7137 is a proximal left humerus.

Age and horizon The holotype is from Lufeng, Yunnan, and derives from the Late Miocene Shihuiba Formation (see above for a discussion of the age).

Original and other published diagnoses There is no English language diagnosis in the original paper (Hou, 1985), only a list of characters is provided in English (that may have been meant as a diagnosis, but those characters are in fact not diagnostic to the species level). In addition, there is no description of the specimen in Chinese or English. Those diagnostic characters are made in comparison to *Aythya* (mentioned in the Chinese, but not English text) and include (paraphrasing the Chinese and English text) a smaller humeral head, a larger “capital” crest (Hou, 1985:125), the attachment of the *m. latissimus dorsi posterioris* is a vertical groove, the dorsal tubercle is not obvious, the deltopectoral crest does not expand dorsally, the transverse ligament groove is deep, and the bicipital surface is small.

The English language diagnosis given by Hou (2003) is “Humer head small, capital ridge big, attachment of latissimus dorsi posterioris is a vertical groove. External tuberosity of humerus unclear proximally. Deltoid crest not extended. Ligamental furrow deep, attachment of bicipital surface small.” (2003:142). It parallels the English character list provided in the original paper (Hou, 1985) with some different word choices. He (2007:317) republished that diagnosis (including the misspelled “humer”), and that diagnosis differs little from the original one in Hou (1985) except for the absence of numbered characters. However, if the reader does not read the original Chinese text (Hou, 1985), the point/taxon of comparison for the ‘diagnosis’ would be unknown (i.e. *Aythya*).

The main problem is that none of those characters separate the holotype from any species of *Aythya* (or really any species of anatid). The statement that the deltopectoral crest is not extended is curious since its distal end is not preserved and much of the crest is missing in the specimen. It is true that the ligamental furrow is deep, but it is also very short dorsoventrally. What Hou (1985) termed the ‘capital’ crest (or ridge in later publications) is unclear. It might refer to a capital shaft ridge, but that feature is not present in the holotype specimen and is absent in other species of *Aythya*. The size of the humeral head does not appear significantly different from that in other species of *Aythya* (Fig. 1), and the bicipital crest is broken not allowing for detailed comparisons.

Revised and emended diagnosis The holotype lacks a distinct capital shaft ridge differentiating it from many anatids (such as *Bucephala* and *Nettapus*). It differs from all extant members of *Aythya* (except some specimens of *A. australis*) and the fossil taxon *A. molesta* in the presence of a proximally deep ventral pneumotricipital fossa lined dorsally with small pneumatic foramina and bony struts (rather than derived a bony wall with only occasional foramina in the extant species). It is smaller than *A. ferina* (IVPP OV 1659) and *A. australis* (MVZ 143330), and similar in size to *A. molesta* (Zelenkov, personal communication; contra Zelenkov, 2012b). See below for a further discussion of the phylogenetic distribution of characters in the specimen.

Description The specimen is a proximal left humerus that is broken just distal to the distal end of the bicipital crest. It is a light tan to dark brown color. The edges of the bicipital crest and the deltopectoral crest are both damaged. Otherwise the specimen is complete. The maximum proximodistal length of the specimen is 18.1 mm, and the dorsoventral depth of the specimen is 16.2 mm (from the dorsal tubercle to the ventral edge of the broken bicipital crest). Those measurements differ slightly from those (18 and 17 mm, respectively) given in Hou (1985), and could be the result of damage to the specimen since its initial publication.

The distal end of the humeral head (caudal view) has a distinct lip adjacent to the dorsal pneumotricipital fossa, and that concavity/overhang is more pronounced adjacent to the capital incisure. The distal tip of the dorsal tubercle extends somewhat distal to the proximodistal level of the ventral tubercle. The *m. latissimus dorsi posterioris* scar is present distal to the dorsal tubercle and ends proximal to the distal end of the fragment. There is a proximodistally elongate but shallow depression just dorsal and slightly distal to the dorsal crus of the ventral pneumotricipital fossa (also present but more distinct in *Aythya ferina* IVPP OV 1659). The depression’s distal end is proximal to the level of the junction of the bicipital crest and the humeral shaft, and its proximal end is near the proximodistal level of the distal tip of the ventral tubercle. The area inside the capital incisure (dorsal side of the ventral tubercle) is concave. The transverse ligamental sulcus is dorsoventrally short and limited to an area just cranial to the ventral tubercle.

Phylogenetically important characters There is no capital shaft ridge present on the specimen, but the area where one is located in other taxa is somewhat convex, not forming

a ridge (Worthy and Lee, 2008: character 51 - state 1). However, the area is not any more convex or ridge-like than that of *A. ferina* (IVPP OV 1659). The dorsal pneumotricipital fossa is wide and nearly flat to very shallowly concave (Worthy and Lee, 2008: character 53 - state 2). However, the dorsal pneumotricipital fossa appears to be less dorsoventrally wide than the state in *A. ferina* (IVPP OV 1659). The preserved proximal end of the deltopectoral crest is relatively flat caudally (anconally; Worthy and Lee, 2008: character 54 - state 1). Worthy and Lee's (2008) character about the relative length of the deltopectoral crest versus the junction of the bicipital crest with the humeral shaft cannot be fully determined. The distal end of the deltopectoral crest is broken, but the distal tip of the bicipital crest is preserved (its junction with the shaft). Given that the bicipital crest-humeral shaft junction is ventral to the enlarged muscle scar on the deltopectoral crest, the character state is likely character state 1 or 2 (i.e. less than 40% of the deltopectoral crest extended distal to the proximodistal level of the junction). The dorsal tubercle is essentially an indentation at the same level as the shaft (Worthy and Lee, 2008: character 56 - state 1), but its distal tip is slightly raised up compared to the adjacent area of the shaft. That slightly raised tip produces a slightly concave area just distal to the distal tip of the dorsal tubercle (that also is present in the left and right humeri of *A. ferina* IVPP OV 1659, and other individuals of *Aythya*). This character state is likely something similar to what Hou (1985) was referring to when he said that the tubercle was not clear. The ventral tubercle is not directed proximally, but its distal margin is at near right angles to the fossorial plane (Worthy and Lee, 2008: character 57 - state 1). The ventral pneumotricipital fossa is a highly pneumatic fossa that extends into the shaft dorsally with multiple smaller and bony struts lining its dorsal extreme (Worthy and Lee, 2008: character 58 - state 0; Fig. 1). The ventral pneumotricipital fossa does not seem to extend under the humeral head (i.e. as in the derived state 1). The proximal profile of the humerus exhibits a very distinct notch from the capital incisure in cranial/caudal view (Worthy and Lee, 2008: character 59 - state 2). The width of the pneumatic foramen of the ventral pneumotricipital fossa from its dorsal edge to its ventral end is nearly equal to that of its length from the ventral tubercle distally to the junction of the bicipital crest and the humeral shaft (Worthy and Lee, 2008: character 60 - state 1; Fig. 1). The attachment scar of *m. latissimus dorsi anterioris* is not preserved on the specimen (even at the distal edge of the specimen), only the *m. latissimus dorsi posterioris* is present. Thus character states relating to that muscle cannot be determined.

Discussion and comparisons Livezey (1996) conducted a phylogenetic analysis of pochards (Aythyini). In that analysis, he concluded that the extant species of *Aythya* (his Subtribe Aythyeae) form a clade with other genera (i.e. *Marmaronetta*, *Rhodonessa*, and *Metopiana* in his usage) placed in Aythyini as outgroups to the species of *Aythya* (Livezey, 1996). Those results are consistent with some molecular analyses that conclude similar results with a monophyletic clade composed of the species of *Aythya* with the other genera (including species currently placed within *Netta*) as sister groups and outgroups to that clade (e.g., Gonzalez et al., 2009). However, the molecular analysis of Fulton and coauthors (2012)

placed *Netta peposaca* within the clade formed by the species of *Aythya*, and Gonzalez et al. (2009) supported a position of *Netta* (*N. rufina* and *N. peposaca*) outside of *Aythya* (Fig. 2). Furthermore, their molecular clock analysis indicates an origin of the crown of *Aythya* + *Netta* in the Pliocene (Fulton et al., 2012), younger than this and other Miocene fossils attributed to *Aythya*. Worthy and Lee's (2008) and Worthy's (2009) work on extinct waterfowl demonstrated the effect of convergence in diving related morphologies on the phylogenetic reconstruction of waterfowl. When diving related characters are included in their analysis (and the tree search is not constrained), the species of *Aythya* form a paraphyletic assemblage leading to more derived diving taxa including *Oxyura* and *Mergus* (Worthy and Lee, 2008: fig. 8), in contrast to the non-monophyly of diving ducks supported by molecular analyses. Monophyly of *Aythya* is restored if those characters are excluded and a constraint tree is used (Worthy and Lee, 2008: fig. 10).

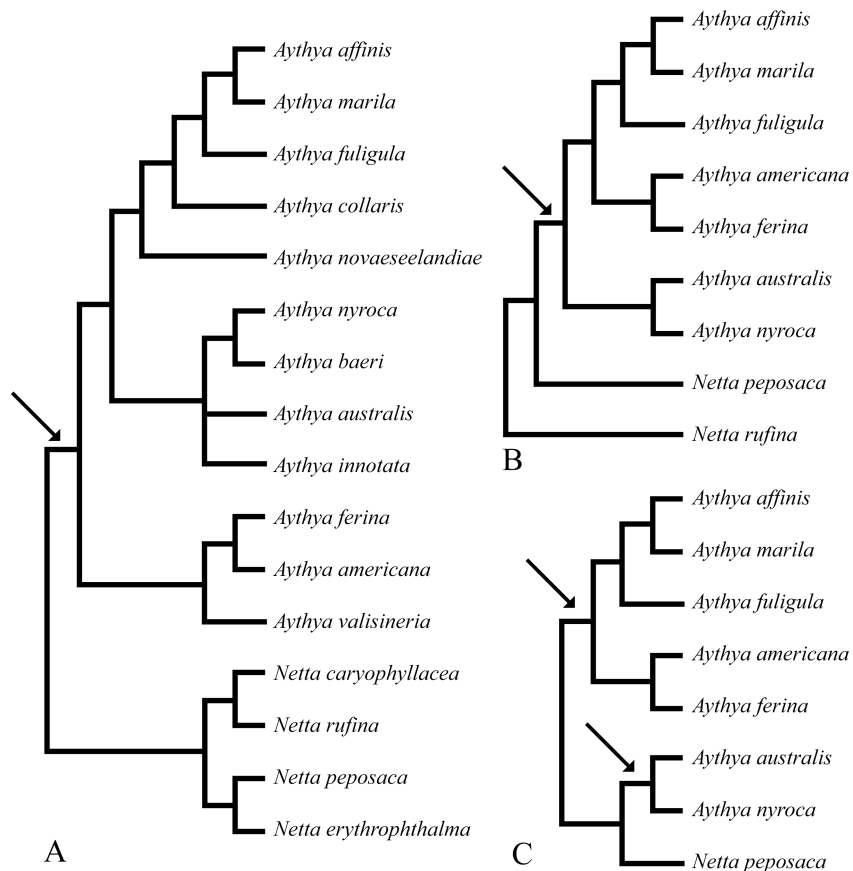


Fig. 2 The phylogenetic placement of *Aythya shihuibas*

A. Morphological cladogram from Livezey (1996); B. Molecular cladogram from Gonzalez et al. (2009); C. Molecular cladogram from Fulton et al. (2012). Arrows indicate the parsimonious positions of *A. shihuibas* within each tree

In Livezey's analysis (1996), he scored one humeral character relevant to the study of this fossil, the presence or absence of a pneumatic foramen in the ventral pneumotricipital fossa (his skeletal character 4). Livezey (1996) reported the absence of that foramen (that coincides with the presence of a deep pneumatic fossa that extends under the humeral head) as occurring in all extant species of *Aythya*, and thus it would appear to be a 'local' synapomorphy of that anatid clade (the extant species of *Aythya*). The absence or loss of pneumaticity of the ventral pneumotricipital fossa occurs convergently multiple times among different species of waterfowl (Worthy and Lee, 2008). Thus, the presence of a pneumatized ventral pneumotricipital fossa (i.e. a primitive character state) in the holotype of *Aythya shihuibas* seems to indicate that this extinct taxon is not a member of the crown clade of Subtribe Aythyinae (i.e. the clade composed of the extant species of *Aythya*), although the presence of pneumaticity in *A. shihuibas* could be a character reversal. However, Worthy and Lee (2008) scored *A. australis* as having a pneumatic cavity with bony struts that contrasts with Livezey's (1996) treatment of that (similarly circumscribed) character in the same species. A specimen of *A. australis* (Field Museum of Natural History skeleton 339068) exhibits the derived condition in line with the original scoring of Livezey (1996). In contrast, all *A. australis* specimens in the MVZ (specimens 141918, 143330, 143331, and 154312) are from osteologically adult individuals of both sexes and exhibit the primitive pneumatic state. However, one specimen (MVZ 143330, a female) approaches the derived state with a partial wall in the fossa. This character clearly is variable within that species of *Aythya*, and that variability does not (at present) appear related to ontogenetic age or gender.

Depending on the phylogenetic hypothesis of anatids examined, the derived absence of the capital shaft ridge likely has occurred more than once among anatids (e.g., species of *Nettapus*, *Mergus*, *Anas*, *Aix*, and *Aythya*) (data matrix from Worthy and Lee, 2008). However, the reduction and loss of the capital shaft ridge is not easily reconstructed given variation in its morphology across specimens. At a minimum, the absence of the ridge would mean this fossil is likely not part of *Dendrocygna* or Anserinae. The ridge is reportedly present in *Netta rufina* (data matrix from Worthy and Lee 2008), present, but indistinct proximally, in *Netta peposaca* (MVZ 135151), and would suggest that the absence of the ridge in *Aythya* could be a loss within Aythyinae (given Livezey's 1996 topology). The presence of the ridge in *Bucephala* and *Melanitta* (along with *N. rufina* and *N. peposaca*) given Worthy and Lee's constrained tree (2008: fig. 10) would support the loss of the capital shaft ridge as a potential 'local' synapomorphy of the species of *Aythya*, but the character's homoplasy might reflect convergence in function rather than providing a strong phylogenetic signal. While the derived loss or reduction of the capital shaft ridge among the species of *Aythya* may be a synapomorphy of a clade composed of *Aythya* (and possibly its close relatives), further documentation of the phylogenetic distribution and inter and intraspecific variability of this character is needed to determine how homoplastic the character is and what its phylogenetic utility may be at lower taxonomic levels.

The relative widths of the dorsal and ventral pneumotricipital fossae (Worthy and Lee, 2008: character 53) being roughly equal in the fossil is similar to the character state present among species in multiple anatid clades, such as *Aythya*, *Mionetta*, and *Chloephaga* (data matrix from Worthy and Lee, 2008). That state is present in *Aythya*, *Netta*, *Bucephala*, and *Melanitta* meaning that the subequal width likely is a plesiomorphy of Aythyini (data matrix from Worthy and Lee, 2008).

The caudally (anconally) flat deltopectoral crest in *Aythya shihuibas* (Worthy and Lee, 2008: character 54) is similar to many other groups including *Aythya*, *Oxyura*, *Mergus*, and *Anas*, but contrasts with the concave state in the anserines, *Dendrocygna*, and *Tadorna*. Therefore, the character does not appear to allow for a finer level of phylogenetic inference within or among members of Aythyini since it is plesiomorphic for the Aythyini. The dorsal tubercle being nearly coplanar with the shaft (Worthy and Lee, 2008: character 56) is likely also plesiomorphic for Aythyini, but again the intra and interspecific variability of this character state should be examined further to demonstrate its phylogenetic usefulness at low taxonomic levels. Additionally, the capital incisure making a distinct notch in the proximal outline of the humerus in cranial or caudal view (Worthy and Lee, 2008: character 59 - state 2) appears to be plesiomorphic for Aythyini.

Character 57 of Worthy and Lee (2008) where the ventral tubercle is directed craniocaudally and either overhangs the ventral pneumotricipital fossa or is at a right angle to the fossorial plane occurs across much of Anatinae and likely is primitive for Aythyini, but the character state is absent in *Netta rufina* (data matrix from Worthy and Lee, 2008), while being present in *N. peposaca* (MVZ 135151). That absence could further suggest that *Aythya shihuibas* is not closer to *N. rufina* than it is to the extant species of *Aythya*, depending on the cladogram used (see Fig. 2). Worthy and Lee's character (2008: character 60 - state 1) about the relative length and width of the bicipital crest being subequal is also absent (i.e. state 0) in *N. rufina* and *N. peposaca*, but present in *Aythya* (and the fossil). It is another character supporting that this fossil is not closely related to *Netta* (to the exclusion of species of *Aythya*).

Based on published phylogenetic analyses and the currently known distribution of osteological features, it would appear (parsimoniously) that *Aythya shihuibas* lies outside of the crown clade of Aythyae (the crown clade composed of the extant species of *Aythya*), but that it is also more derived than *Netta* (e.g., in the absence of the capital shaft ridge). However it is also possible that *A. shihuibas* is within the crown of *Aythya* (a less parsimonious reconstruction), and either convergently expresses the pneumatic ventral pneumotricipital fossa or it may be related to *A. australis* given the intraspecific variability in its character states (Fig. 2). Given the intra and interspecific variability of some of the characters (discussed above), it also is possible that *A. shihuibas* even could lie outside of the *Aythya* + *Netta* clade along its stem, or possibly allied to *Netta*. Given currently published data, the parsimonious reconstruction of the character distributions would seem to be consistent with the hypothesis that *A. shihuibas* is an extinct sister taxon to Aythyae as a non-crown *Aythya* Aythyini anatid

and placing a minimum (Late Miocene) age on the stem group of Aythya (Fig. 2). However, if *Netta* (and by extension *Aythya*) is not monophyletic, then it is possible that *A. shihuibas* fits in two locations in the molecular cladogram with one position close to *A. australis* and one outside of a grouping formed by other species of *Aythya* (Fig. 2C). If there is greater homoplasy than currently recognized among the characters used by Worthy and Lee (2008), then confidence in the phylogenetic placement of *A. shihuibas* would be lowered.

Given the parsimonious reconstruction of *A. shihuibas* outside of the crown of *Aythya*, it would be tempting to change its taxonomic ('genus') name to reflect that hypothesis. However, I suggest no change to its taxonomy at present considering the relatively few characters that support its phylogenetic position. Both *Aythya* and Aythya (taxonomic names with currently equal membership) have not been defined phylogenetically, and with the exception of Zelenkov (2012a and his later reversal in 2012b, see above) no one has discussed any changes to the taxonomy of *A. shihuibas*. Therefore, a potential close relative (i.e. the extinct sister to the crown clade) could easily be included into a monophyletic (though expanded beyond its crown clade) *Aythya* and/or Aythya. Clearly, if *Aythya shihuibas* is actually a member of the crown clade, then its species' taxonomy needs no modification.

Anatinae Leach, 1820

cf. *Anas* sp.

Specimen IVPP V 7132 (published as *Anas* sp. by Hou in 1985) is a distal right humerus associated with shaft fragments and the cranial surface of the proximal end.

Age and horizon The specimen is from Lufeng, Yunnan, and derives from the Late Miocene Shihuiba Formation (see above for a discussion of the age).

Previously published information In the English summary of Hou (1985), he provides no diagnostic or descriptive characters of this specimen. However, he provides some diagnosis and some description in the Chinese part of the paper's text (Hou, 1985). The diagnosis appears to be a broad one of the position of *Anas* (not necessarily just this specimen) within Anatidae. He lists a relatively small bicipital surface, a constricted distal end, the absence of an obvious *m. brachialis anticus* scar/fossa, and a small ventral supracondylar prominence as diagnostic for *Anas* within Anatidae (Hou, 1985). The diagnosis of the specimen is given as "Bicipital surface small. Posterior shaft humerus not expanded. Impression of brachialis anticus unclear. Small ectepicondylar prominence." in Hou (2003:139). That diagnosis (including the misspelled "humerus") was republished by He (2007:318).

Hou's (1985) description paraphrased from the Chinese text is: the width of the distal humerus proximal to the ventral supracondylar tuber is 7.5 mm; the junction of the bicipital surface and the humeral body is curved; the deltopectoral crest and the body of the humerus form an obtuse angle; and the ventral condyle is large and inclined ventrally, the distal part of the body is constricted, and the *m. brachialis anticus* is obscure and small.

New description The distal fragment is 20.5 mm in length, and the proximodistal length

of the proximal fragment is 15.9 mm. The specimen is smaller than the equivalent element in *Anas penelope* (IVPP OV 1749). The bone fragments are dark brown to tan in color. The dorsal epicondylar/supracondylar ridge has a proximodistally elongate muscle scar at its proximal tip with a wider/larger scar that is a little more distal and on the dorsal aspect of the ridge. The dorsal rim of the scapulotriceps fossa extends around the distal end and onto the cranial aspect as a ridge adjacent to the dorsal condyle. The ridge's proximal end on the cranial face is approximately half of the proximodistal length of the dorsal condyle (Fig. 3). The *m. brachialis* scar is hard to see, but present as a flat oval shaped outline with its long axis oblique to the long axis of the humeral shaft (Fig. 3). The area proximal to the dorsal condyle on the cranial face is concave. There are five additional fragments of what appears to be the shaft of the humerus. All are 1–2 cm in length. There is a single fragment from the cranial face of the proximal end of the humerus that is from a region distal to the level of the ventral tubercle. The cranial fragment preserves part of the deltopectoral crest (with a nearly complete muscle scar on its surface) and the area ventral to the crest almost to the bicipital crest.

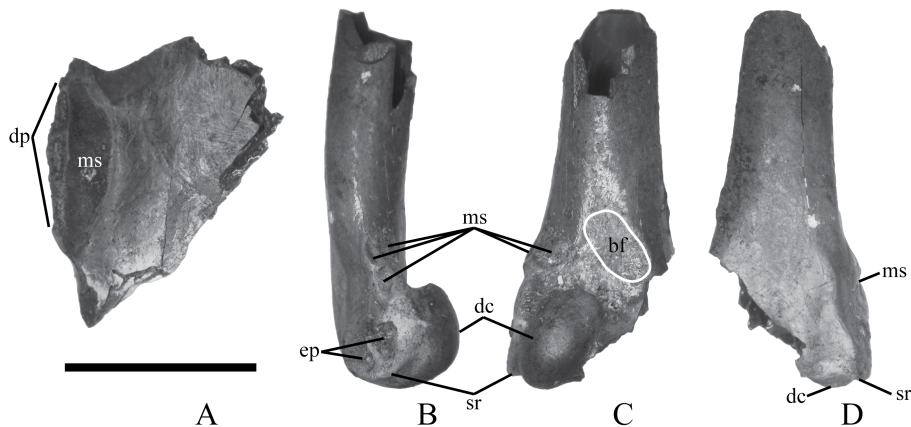


Fig. 3 The cf. *Anas* sp. specimen (IVPP V 7132) from Lufeng

A. Proximal end of humerus in cranial view with the proximal anatomical direction as 'up' and dorsal to the left; B. Distal end of the humerus in dorsal view; C. Distal end of the humerus in cranial view; D. Distal end of the humerus in caudal view. The extent of the flattened *m. brachialis* scar is outlined in white in C. Abbreviations: bf. brachial fossa/scar; dc. dorsal condyle; dp. deltopectoral crest; ep. epicondylar pair of pits; ms. muscle scar; sr. dorsal scapulotriceps ridge. Scale bar equals 1 cm

Phylogenetically relevant characters The preserved caudal surface of the proximal fragment appears to indicate that the humeral shaft was pneumatized through the ventral pneumotricipital fossa and the bases of the internal bony struts are preserved (Worthy and Lee, 2008: character 58 - state 0). The distal end of the dorsal supracondylar tubercle (in cranial view) is a short proximally directed ridge that is not distinct from the dorsal epicondyle (Worthy and Lee, 2008: character 64 - state 1). The scapulotricipitalis sulcus is present, it continues distally around the dorsal epicondyle, and it extends as distal notch in caudal view (Worthy and Lee, 2008: character 66 - state 2). At first glance, it would appear that the brachial fossa and

scar are missing on the specimen. However, the scar is present, but it is incredibly flat and not recessed at all (i.e. no brachial ‘fossa’) (Worthy and Lee, 2008: character 68 - state 1).

Comparison and discussion That particular character state (character 68 - state 1) with a flat brachialis scar/fossa is a relatively rare character state among anatids (data matrix from Worthy and Lee, 2008). Worthy and Lee (2008) only scored that state as present in *Stictonetta*, *Nettapus pulchellus*, *Tadorna ferruginea*, *Somateria*, *Lophodytes cucullatus* (scored as variable), *Melanitta fusca*, and *Clangula*. There does not appear to be a broad phylogenetic pattern to its occurrence. Meanwhile, none of the species of *Anas* scored by Worthy and Lee (2008) have that character state. Many anatines and the fossil have the same codings for Worthy and Lee’s (2008) characters 64 and 66, and those states are absent in *Dendrocygna* and the anserines. One of the Mio-Pliocene dabbling ducks from Mongolia (designated *Anas* sp. 1 by Zelenkov, 2012b) also has the flat brachialis scar, in addition to the elongate scapulotriceps dorsal ridge extending to the cranial face of the specimen. Perhaps the Yunnan specimen and Zelenkov’s (2012b) *Anas* sp. 1 are conspecific or closely related since they are of similar age (Late Miocene and Early Pliocene) and both from eastern Asia. However, additional material would be needed to determine the phylogenetic relationship of those specimens/species. Given the variability of characters within Anatinae and the species called *Anas*, it is not entirely accurate to call this fossil as *Anas* (as in the original publication). IVPP V 7132 maybe part of that non-monophyletic grouping of species (i.e. the ‘genus’ *Anas*), but the limited phylogenetic data in the specimen does not place this Lufeng fossil accurately within Anatinae. So a taxonomic designation of Anatinae sp. or perhaps cf. *Anas* sp. (above) should be used for this specimen at this time.

The flat ovoid *m. brachialis* scar is present among species of *Anas* (and in other clades) and absent among other anatid taxa including *Aythya* (concave brachial fossa). Given that morphological difference (in addition to the others mentioned above), the anatine distal humerus comes from a second anatid taxon/species and is from a different lineage/clade than that of diving duck *Aythya shihuibas*.

3 Discussion

Zelenkov (2012b) discusses three species of Late Miocene and Early Pliocene *Aythya* from western Mongolia, and each is based on a different set of skeletal elements. There is one proximal humerus that he identifies as *A. molesta* (Zelenkov, 2012b), and it differs from *A. shihuibas* in lacking the primitive state of pneumatic foramina and bony struts within the ventral pneumotricipital fossa (erroneously described as the ‘dorsal’ pneumotricipital fossa). Given that derived character state, *A. molesta* may belong to the crown clade of *Aythya*. The other two Mongolian species of *Aythya* are not known from proximal humeri and cannot be compared to *A. shihuibas* (Zelenkov, 2012b).

No *Aythya*-type duck has been described from neighboring Thailand in the Miocene

(Cheneval et al., 1991; Zelenkov, 2011, 2012a, b). However, a possible member of Anatinae was described by Cheneval et al. (1991) from the Miocene of Thailand, and their specimen is a scapula and not directly comparable to the partial humerus from Lufeng. In addition, it is from a site older than the Lufeng locality because it is Middle (rather than very Late) Miocene (Cheneval et al., 1991). However, one of the specimens that Zelenkov (2012b) allocates to *Anas* exhibits a flattened ovoid brachialis scar and an elongate dorsal rim of the scapulotriceps groove like that of the Lufeng anatine. Given the rarity of those characters (in combination) across Anatidae, it could mean that the Lufeng specimen and Zelenkov's (2012b) *Anas* sp. 1 are conspecific or from closely related extinct species since they are similar in age and both from eastern Asia.

There are two species of anatids represented by the fossils from Lufeng. One should be referred to as Anatinae sp. or perhaps cf. *Anas* sp., and the other is a member of the *Aythya* clade, although likely outside of the crown clade of that group of species. It appears that *Aythya shihuibas* is distinct from other Miocene Asian anatids, and that the cf. *Anas* fossil could be the same species as one from Mongolia. The presence of two different anatid phylogenetic lineages (one from a diving duck and one from a possible dabbling duck) along with the occurrence of beavers (*Stenofiber* sp.) in the Lufeng site may indicate that there was a variety of aquatic habitat types (Dong and Qi, 2013).

Acknowledgements I am supported by the Chinese National Natural Science Foundation (41472025) and the Strategic Priority Research Program of the Chinese Academy of Sciences (CAS, XDB03020501). I thank Hu Han for her helpful translation of Hou's original descriptions and for the Chinese version of the abstract below; Ni Xijun for assistance with references and general discussion about the Lufeng site; Nikita Zelenkov provided information and photos on Neogene ducks from Mongolia housed at the Paleontological Institute of the Russian Academy of Sciences; N. Adam Smith supplied the information about the *Aythya australis* specimen housed in the Field Museum of Natural History, USA; Carla Cicero and Rauri Bowie provided access to avian skeletons in the MVZ; Trevor Worthy and Nikita Zelenkov provided helpful comments on an earlier draft of the manuscript.

云南禄丰晚中新世鸭类标本的再研究与系统发育分析

Thomas A. STIDHAM

(中国科学院脊椎动物演化与人类起源重点实验室, 中国科学院古脊椎动物与古人类研究所 北京 100044)

摘要: 1985年侯连海初步报告了发现于云南禄丰中新世古猿地点的部分鸟类化石, 建立了一新种石灰坝潜鸭(*Aythya shihuibas*), 并将另一件标本定为河鸭属未定种(*Anas* sp.)。针对

这两件鸭类标本保存的特征进行系统发育分析,并结合二者目前已知的分布情况,可以确定禄丰鸟类至少存在两个不同种(不同的系统发育支系),这和之前的结论相似。石灰坝潜鸭的肱骨腹侧气窝中具有骨质支柱,异于现生潜鸭类,代表了气窝演化的较原始形态,依此认为其很可能为一潜鸭类冠群以外的绝灭支系。另一件原命名为*Anas* sp.的鸭类标本保存非常破碎,无法对其进行较精确的系统发育分析。它很可能为鸭科成员,或许可以称为河鸭类,尽管此属(*Anas*)为非单系类群。这件禄丰河鸭类标本可能与发现于蒙古中新世-上新世的另一河鸭属未定种关系较近,二者具有相似的特殊特征组合。

关键词: 云南禄丰,晚中新世,鸟类,鸭科,潜鸭,河鸭

中图法分类号: Q915.865 **文献标识码:** A **文章编号:** 1000-3118(2015)04-0335-15

References

- Baumel J J, Witmer L, 1993. Osteologica. In Baumel J J, King A S, Breazile J E et al. eds. Handbook of Avian Anatomy: Nomina Anatomica Avium, 2nd ed. Cambridge, Massachusetts: Publications of the Nuttall Ornithological Club 23. 45–132
- Cheneval J, Ginsburg L, Mourer-Chauviré C et al., 1991. The Miocene avifauna of the Li Mae Long locality, Thailand: systematics and paleoecology. *J Southeast Asian Earth Sci*, 6: 117–126
- Chow M C, Rich P V, Qi T, 1982. A Late Eocene-Early Oligocene bird and mammal from Usu (Wusu) Xinjiang (Sinkiang), northwestern China. *Mem Beijing Mus Nat Hist*, 16: 1–11
- Dong W, Qi G Q, 2013. Hominoid-producing localities and biostratigraphy in Yunnan. In: Wang X M, Flynn L J, Fortelius M eds. Fossil Mammals of Asia – Neogene Biostratigraphy and Chronology. New York: Columbia University Press. 293–313
- Fulton T L, Letts B, Shapiro B, 2012. Multiple losses of flight and recent speciation in steamer ducks. *Proc R Soc B*, 279: 2339–2346
- Gonzalez J, Düttman H, Wink M, 2009. Phylogenetic relationships based on two mitochondrial genes and hybridization patterns in Anatidae. *J Zool*, 279: 310–318
- He Z, 2007. The Fossils of China. Beijing: China University of Geosciences Press. 1–500
- Hou L H, 1985. Upper Miocene birds from Lufeng, Yunnan. *Acta Anthropol Sin*, 4: 118–126
- Hou L H, 2003. Fossil Birds of China. Kunming: Yunnan Science and Technology Press. 1–234
- Jablonski N G, Su D F, Flynn L J et al., 2014. The site of Shuitangba (Yunnan, China) preserves a unique, terminal Miocene fauna. *J Vert Paleont*, 34: 1251–1257
- Kurochkin E N, Dyke G J, 2010. A large collection of *Presbyornis* (Aves: Neornithes) from the Late Paleocene and Early Eocene of Mongolia. *Geol J*, 45: 375–387
- Li J L, Wu X C, Zhang F C, 2008. The Chinese Fossil Reptiles and Their Kin. Beijing: Science Press. 1–473
- Livezey B C, 1996. A phylogenetic analysis of modern pochards (Anatidae: Aythyini). *The Auk*, 113: 74–93
- Ni X J, Qiu Z D, 2002. The micromammalian fauna from the Leilao, Yuanmou hominoid locality: implications for biochronology and paleoecology. *J Human Evol*, 42: 535–546
- Qiu Z X, Qiu Z D, 1995. Chronological sequence and subdivision of Chinese Neogene mammalian faunas. *Palaeogeogr, Palaeoclimat, Palaeoecol*, 116: 41–70
- Stidham T A, Ni X J, 2014. Large anseriform (Aves: Anseriformes: Romainvilliinae?) fossils from the Late Eocene of

- Xinjiang, China. Vert PalAsiat, 52: 98–111
- Worthy T H, 2009. Descriptions and phylogenetic relationships of two new genera and four new species of Oligo-Miocene waterfowl (Aves: Anatidae) from Australia. Zool J Linn Soc, 156: 411–454
- Worthy T H, Lee M S Y, 2008. Affinities of Miocene waterfowl (Anatidae: *Manuherikia*, *Dunstanetta*, and *Miotadorna*) from the St Bathans fauna, New Zealand. Palaeontology, 51: 677–708
- Yeh H K, 1980. Fossil birds from Linqu, Shandong. Vert PalAsiat, 18: 116–125
- Zelenkov N V, 2011. Diving ducks from the Middle Miocene of western Mongolia. Paleontol J, 45: 191–199
- Zelenkov N V, 2012a. A new duck from the Middle Miocene of Mongolia, with comments on Miocene evolution of ducks. Paleontol J, 46: 520–530
- Zelenkov N V, 2012b. Neogene geese and ducks (Aves: Anatidae) from localities of the Great Lakes Depression, western Mongolia. Paleontol J, 46: 607–619
- Zelenkov N V, Kurochkin E N, 2012. Dabbling ducks (Aves: Anatidae) from the Middle Miocene of Mongolia. Paleontol J, 46: 421–429
- Zhang Y G, Ji X P, Jablonski N G et al., 2013. Stratigraphic significance of the avian fauna from the Late Miocene of Zhaotong Region, Yunnan Province. Acta Palaeontol Sin, 52: 281–287