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Relationships, adaptations, and habits of the extinct duck *'Euryanas' finschi*

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Abstract The relationships, adaptations, and habits of the extinct, endemic Finsch's duck (*Anas finschi* Van Beneden, 1875) from New Zealand were determined from skeletal comparisons. Finsch's duck, usually placed in the monotypic genus *Euryanas* Oliver (1930), was found to be most similar to the Australian wood duck (*Chenonetta jubata*). Because the differences are mainly those associated with loss of flight, *Euryanas* is synonymised with *Chenonetta*, and the species should now be known as *Chenonetta finschi*.

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INTRODUCTION

The original avifauna of New Zealand had an anatid component that was interesting not only for its diversity (18 species and 11 genera [Holdaway *et al.* 2001], higher than most groups in New Zealand), but also for the variety of morphologies displayed, and range of habitats occupied. This taxonomic diversity is almost never due to internal radiation, but to independent colonizations, almost always from Australia. The only exception within 'mainland' New Zealand is *Cnemiornis*, with two species. Insular speciation on the Chathams and subantarctic islands following colonization from the New Zealand mainland or Australia, account for at least five of the above 18 species. Nine species in eight genera are now extinct. An understanding of how these taxa coexisted and interacted in the original New Zealand environment is fundamental to an understanding of the ecology and behaviour of the surviving taxa. By determining their nearest relatives, we may hope to infer aspects of the ecology and behaviour of extinct taxa. For example, because all species of *Tadorna* are cavity nesters, this trait could be inferred for the extinct *Tadorna* on the Chathams. We might also infer that *Biziura delautouri* Forbes, 1892, preferred similar specialised habitats to *B. lobata* (Shaw, 1796) of Australia.

As *Euryanas finschi* is an endemic species and genus, little can be derived concerning its relationships, and knowledge of its true relationships are important to understanding its origins, divergence, and palaeoecology. For example, if its nearest relative is a grazer of largely terrestrial swards and did not much frequent lacustrine sites, we would expect the distribution of fossils to confirm or refute similar habitat choice in the fossil.

Euryanas finschi is one of the most common species in Late Quaternary fossil deposits of the eastern districts of both the South and North Islands of New Zealand. Hundreds of bones are found in some deposits, e.g., Castle Rocks (western Southland, South Island; Hamilton 1893, 1894; Worthy 1998a), Earnscleugh Cave (central Otago, South Island; Clark *et al.* 1996; Worthy 1998b), Waikari Cave (North Canterbury; South Island; Worthy & Holdaway 1996), Martinborough Number 1 (Wairarapa, lower North Island; Yaldwyn 1956). *Euryanas finschi* is one of a key group of species that signify the presence of grassland-shrubland mosaics in New Zealand palaeoenvironments (Worthy 1997a; Worthy & Holdaway 1993, 1994, 1995; Worthy & Mildenhall 1989). This species has also provided a rare example of the measured rate of evolutionary change towards flightlessness, with a 10% reduction in wing length between the late Pleistocene 10-12 kyr ago and the late Holocene, indicating a rapid and relatively recent loss of flight ability (Worthy 1988, 1997b). A trend towards

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flightlessness was common among non-passerine New Zealand birds, especially waterfowl. Both extinct species of *Cnemiornis* were flightless, as are the three species of the subantarctic teal (*Anas* spp.). Other extinct taxa, e.g. *Mergus* sp., *Pachyanas chathamica* Oliver, 1955, and *Tadorna* sp. in the Chathams, were weak fliers.

Finsch's duck *Euryanas finschi* was described as *Anas finschi* by Van Beneden (1875) after he and Dr Otto Finsch studied a series of bones from Earnscleugh Cave, Otago. Among living species, van Beneden found most similarities with *Dendrocygna eytoni* (Eyton, 1838), but among others he was struck by its resemblance to the Miocene *Anas blanchardi* Milne-Edwards, 1863 from Europe, now placed in the genus *Mionetta* (Livezey & Martin 1988). Van Beneden's original paper was published in an abridged form in the *Transactions and proceedings of the New Zealand Institute* for 1876 (Van Beneden 1877). Lydekker was the first to refer bones of *Euryanas finschi* to the wood or maned duck *Chenonetta jubata* (Latham, 1807) when he listed a skeleton (BM A.69) from Earnscleugh Cave and 4 crania (BM 46650-3) as *Bernicla jubata* (Lydekker 1891: 106) without mention of *Anas finschi.*

Oliver (1930) erected *Euryanas* to contain *Anas finschi.* Then, and thereafter (Oliver 1955: 403), he maintained that the species was closely related to *Chenonetta jubata.* Falla (1953) regarded *Euryanas finschi* as the New Zealand equivalent of *Chenonetta jubata,* and the close relationship of these taxa was accepted by Howard (1964).

Livezey (1989) studied the relationships of *Euryanas finschi* from a series of morphological characters of the skeleton and concluded that it was the sister group of Tadorninae + Anatinae, although the taxa examined in this study did not include *Chenonetta.* The Tadorninae and Anatinae were represented by *Tadorna* and *Anas,* respectively, which together with *Euryanas finschi* were the terminal taxa in a tree otherwise containing more primitive species. These three taxa, therefore, represented the majority of species in Anatidae. Later, when the typology of the family tree for species more derived than *Stictonetta* was assessed in detail (Livezey 1991, 1996), *Chenonetta jubata* was included, but *Euryanas finschi* was not. Significantly, as the data sets were improved, resolution of the relationships of some 'difficult' species changed. For example, *Plectropterus* was first considered by Livezey (1986, 1989) to constitute a distinct subfamily and the sister taxon of all other species more derived than *Stictonetta,* but later *Plectropterus* was brought into the Tadorninae as the sister taxon to *Sarkidiornis* (Livezey 1996). Also, Livezey (1996) found that new and improved computer programs allowed reanalysis of the 1986 data matrix to generate distinct topologies from those obtained by Livezey (1986): "*the majority of which* [topological differences] *were .... in the vicinity of the divergence of "tadornine" and "anatine" genera*" (Livezey 1996).

Livezey (1997) summarised the results of his studies in anatid systematics in a new phylogenetic classification of waterfowl. Shortly thereafter, more complete morphological datasets and genomic data have challenged some of Livezey's conclusions. *Cnemiornis* was found to be the sister taxon of *Cereopsis* within the Anserinae, rather than a distinctive basal family (Worthy *et al.* 1997). The moa-nalos of Hawaii, placed by Livezey (1997) with the true geese (Anserini), were reassigned to the Anatini by Sorenson *et al.* (1999). Also, the musk duck *Biziura lobata* has been found not to belong with the stifftail ducks (Oxyurini), its diving adaptations being convergent (McCraken *et al.* 1999).

Livezey (1996) placed *Chenonetta jubata* in his Nettapodeae, the sister group to his Cairineae, which together form the sister group to his Anateae. By not directly comparing *Euryanas finschi* with *Chenonetta jubata* in these cladistic analyses, Livezey failed to test the existing hypothesis of the relationships of *Euryanas* advanced by Oliver (1955).

In this paper, we describe the skeleton of *Euryanas finschi* (Van Beneden, 1875), and compare it with that of *Chenonetta jubata,* with which the species has long been allied (Lydekker 1891, Oliver 1930, 1955, Falla 1953), and other ducks formerly present in New Zealand and Australia. In these comparisons, we included *Nettapus,* which (Livezey 1991, 1997) made the sister group to *Chenonetta,* although contrary views are presented by Sraml *et al.* (1996) and Sorenson *et al.* (1999). *Cairina* is included as well, because Livezey's (1997) classification also placed this taxon near *Chenonetta.* Comparisons are also made with *Dendrocygna,* but in less detail, as this taxon is widely considered to be more primitive (Woolfenden 1961; Livezey 1986, 1989, 1997).

METHODS

The skeleton of *Euryanas finschi* was described with special reference to a near-complete skeleton collected by T. H. Worthy from Hodge's Creek Cave, northwest Nelson on 25 May 1995. This skeleton, presently in THW's collection, will be deposited in the Museum of New Zealand (MNZ). Numerous other bones in the MNZ, Canterbury Museum (CM) and Otago Museum (OM), of Holocene and Pleistocene age, were also examined during the course of this study, particularly those from Gabriele's Cave, Hawke's Bay (MNZ), Martinborough #1 Cave (MNZ), Honeycomb Hill Cave System (MNZ) and Takahe Tomo (MNZ) in northwest Nelson, Kings Cave in South Canterbury (MNZ, CM), Earnscleugh Cave in Otago (CM, OM) and Castle Rocks in Southland (MNZ). Anatomical terminology follows that advocated by Baumel & Witmer (1993), with English translations used preferentially after the first mention. Measurements were made with TESA® dial callipers to 0.01 mm and rounded to 0.1 mm.

Abbreviations AM, Australian Museum, Sydney, Australia; ANSS, Australian National Wildlife Collection, CSIRO, Australia; CM, Canterbury Museum, Christchurch, New Zealand; MNZ, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; MVZ, Museum of Vertebrate Zoology, University of California, Berkley, California, United States of America; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Specimens used in comparison *Hymenolaimus malacorhynchos* (Gmelin, 1789); MNZ 12042, 23574, 24586; *Anas rhynchotis* Latham, 1801; MNZ 24588; *Anas superciliosa* Gmelin, 1789; 15030, 16476, 16584, 16586; *Anas platyrhynchos* Linnaeus, 1758; THW colln; MNZ 16199, 16474, 16502, 16503, 16504; *Anas chlorotis* Gray, 1845; MNZ 14978, 15628, 18898, 21544, 22086, 22802, 22806; THW colln; *Aythya novaeseelandiae* Gmelin, 1789; CM Av22382; MNZ 17002, 17003, 23144, 24225; *Chenonetta jubata* (Latham, 1807); MNZ 1487, 23188a, 25142, 25400, 25194a; USNM 430810; MVZ 133420, 155868; *Tadorna variegata* Gmelin, 1989; MNZ 15146, 16471, 16501, 25669; *Nettapus pulchellus* (Gould, 1842); AM O67002; *Dendrocygna eytoni* (Eyton, 1838); AM O64729; *Cairina moschata* (Linnaeus, 1758); MNZ 19842; *Stictonetta naevosa* Gould, 1841; MNZ 25141.

DESCRIPTION

Euryanas was a relatively large duck. Judging from the size of the pelvis, vertebral column, skull and sternum, it was slightly smaller than a mallard *Anas platyrhynchos*. We judge size this way because of the transformations apparent in the skeleton of *Euryanas* that are associated with flightlessness and a terrestrial lifestyle. Thus, it had large legs but reduced wings in comparison to volant anatids, so the application of allometric equations based on, for example, femora of volant species, would probably not be applicable because of the changes in body conformation. It was larger than *Chenonetta* (800 g), but was probably of similar weight to the mallard (1-2 kg).

Skull

The most striking feature of the skull (Fig. 1) of *Euryanas* is the short, truncated, premaxilla. Van Beneden (1875) thought this to be similar to *Dendrocygna*, but the premaxilla in *D. eytoni* is much longer relative to cranial length and the nares are short as in *Anas*, its only similarity to *Euryanas* being in the narrow tip compared with *Anas*. The premaxilla of *Nettapus* is short, as in *Euryanas*, but differs in having a more pointed tip, with the nares extending less than half way along it. In *Euryanas*, the tip of the premaxilla is rounded and the nares extend beyond midlength. This is quite unlike species of *Anas*, *Hymenolaimus*, *Cairina*, and *Aythya*, where the premaxilla is elongate and broad, and is most similar to *Chenonetta*. In *Euryanas*, the maxillary process of the *os nasale* is narrow and its posterior edge is angled forwards, and the posteromedial process on it does not extend caudally past the maxillonasal hinge. In *Dendrocygna*, *Nettapus*, *Anas*, *Hymenolaimus*, *Cairina*, and *Aythya*, the nasal bar is broad, its posterior margin is aligned vertically, and the posterior expansion is large and extends caudally of the maxillonasal hinge. In *Chenonetta*, the nasal bar is wider than in *Euryanas* but slopes forward and similarly lacks the posterior expansion.

The cranium of *Euryanas* has distinct supraorbital processes that protrude about 2 mm from the dorsal orbital margin. Similar development of the supraorbital is seen in *Nettapus*, *Anas chlorotis* and *A. rhynchotis*, but the processes are smaller in *Dendrocygna*, *Aythya*, *Hymenolaimus*, *Cairina*, and *Anas platyrhynchos*. In *Chenonetta*, the supraorbital processes are, compared to nasal width, relatively as broad as in *Euryanas*, but are not as excavated posteriorly. The lacrymal is a narrow descending process with little ventral expansion and is widely separated from the postorbital. In *Dendrocygna*, *Nettapus*, *Anas*, *Cairina*, and *Hymenolaimus*, the lacrymal is broad and in some species broadly expanded ventrally. In *Aythya*, it is narrow and pointed. In *Chenonetta*, it is very similar to that in *Euryanas*. The nasals are elongate and have a flat dorsal profile as in *Anas*, not like the foreshortened condition in *Dendrocygna*, *Nettapus*, and *Cairina*. In *Chenonetta*, the nasals are flat in dorsal profile but are not as elongate as *Euryanas*, which may be explained by the enlarged orbit having displaced the descending process of the lacrymal anteriorly.

The orbit of *Euryanas* is relatively large for ducks with a height from the postorbital process of ~14 mm (~32%) of occipital-maxillonasal hinge length, compared to 29% in *Anas platyrhynchos*, ~26% in *A. rhynchotis*, ~27% *A. chlorotis*, ~25 % in *Hymenolaimus*, ~34% in *Cairina*, and ~30% in *Aythya*. However the orbit of *Chenonetta* is, relatively, even larger at ~36% of occipital - maxillonasal hinge length and that of *Nettapus* larger still at ~39%. The orbits of *Euryanas*, *Cairina*, and *Chenonetta* are essentially circular, unlike *Dendrocygna*, *Nettapus*, and *Anas*, in which they are elongate. The naso-frontal area in *Euryanas* is planar, whereas because of the increased height of the orbit, in *Chenonetta* and *Cairina* it is convex.

Anatids vary markedly in the conformation of the tympanic cavity. In *Euryanas*, the tympanic cavity is slightly longer than high with a rounded postero-ventral margin. This conformation is most similar to that seen in *Chenonetta* and *Cairina*, in which the cavity is slightly longer than high with a convex ventral margin. In *Anas*, it is markedly longer than high, with a distinct ventrally directed posterior pocket. In *Hymenolaimus*, it is very compressed dorsoventrally with the 'pocket' directed more caudally than ventrally. In *Aythya*, it is markedly dorsoventrally compressed. In *Nettapus* and *Dendrocygna*, it is as high as long with no posterior pocket.

The *lamina parasphenoidalis* (basitemporal plate) has a flat centre with marked posteroventral processes (mamillar tuberosities). Laterad of the basitemporal plate are deep, somewhat parallel-sided depressions, bound laterally by the paroccipital processes. *Dendrocygna* has similarly developed mamillar tuberosities with associated deep depressions in the posterolateral region of the basitemporal plate; however, the plate is inflated with a definite medial keel. *Nettapus* has a prominent keel on the basitemporal plate and lacks mamillar tuberosities. In *Cairina*, the basitemporal plate has a very inflated keel and the mamillar tuberosities are well-developed, each comprising paired structures that face posteriorly. In *Anas* and *Aythya*, the basitemporal plate is markedly inflated centrally, the mamillar tuberosities are small, and the lateral depressions flare widely posteriorly. In *Hymenolaimus*, the basitemporal plate is inflated centrally but is also bound laterally by ventrally directed ridges along its whole length. The shape in *Chenonetta* is similar to that in *Euryanas* except that it has relatively smaller mamillar tuberosities, and the lateral depressions are not as excavated against the paroccipital processes.

The mandible in *Euryanas* is short to match the premaxilla, and the retroarticular processes taper in depth posteriorly, and rise to a point that is directed posterior to the cranium. The *os dentale* is deflected ventrally from the line of the *os prearticulare* so that the whole ventral profile is convex, rather than flat as in *Anas, Cairina, Aythya*, and *Hymenolaimus*. The mandibles of *Euryanas, Nettapus, Cairina*, and *Chenonetta* are very similar in overall shape, and differ mainly in that the *processus medialis mandibulae* is more robust and directed medially (in dorsal view) in *Euryanas* compared to posteriorly in *Chenonetta, Nettapus*, and *Cairina*, and the dentary is longer in *Cairina*. The dentary in *Euryanas* is narrower than it is in *Nettapus* and *Chenonetta*, which both have well-developed lamellae. Lamellae are not osseous so are not preserved on *Euryanas* mandibles. The structure of the retroarticular processes is very similar in *Anas, Aythya, Dendrocygna*, and *Hymenolaimus*, and differs markedly from *Euryanas, Chenonetta*, and *Nettapus* by being deep, and ending abruptly in a cranially directed point.

The quadrate and pterygoid of *Euryanas* are like those of *Chenonetta* and *Anas*. *Euryanas* had an ossified thyroid, a pair of arytenoid bones, and an ossified glossohyal. The males had a large ossified syringeal bulla, which is almost identical to, although larger than, that of *Chenonetta*. *Dendrocygna* lacks a syringeal bulla.

Vertebrae

Euryanas has 16 cervical and 5 thoracic vertebrae. Vertebra number 16 has small articulating ribs and a small ventral spine. Number 17, the first thoracic vertebra, has a well-developed *processus ventralis* (ventral spine) with prominent *alae cristae ventralis* (lateral projections). Vertebrae 18 and 19 have long ventral spines (18 with some lateral expansion); 20 and 21 have no ventral spine. Vertebrae 6-10 have prominent pneumatic foramina penetrating the *corpus vertebrae*. There are no foramina in 11 and 12, small foramina in 13-18, but none in 19- 21. There are neural spines on vertebrae 14-21 and no ossified tendons on any vertebrae.

Chenonetta also has 16 cervical and 5 thoracic vertebrae. Vertebrae 5-17 have prominent pneumatic foramina penetrating the corpus vertebrae; similar foramina are small in 18 and 19, and absent in 20 and 21. The fossae holding these foramina contain 2 or more foramina in vertebrae 5-12, but this reduces to 1 in vertebrae 13-17. There are ossified tendons on 17-20. *Cairina* has 16 cervical and 5 thoracic vertebrae. They differ from *Euryanas* in that vertebra 20 has a well-developed ventral spine, small pneumatic foramina are present only in vertebrae 15, 16, and 17, and vertebrae 16-21 have associated ossified tendons. Most species of *Anas* and *Hymenolaimus* also have 16 cervical and 5 thoracic vertebrae, while *Aythya* has 17 cervical and 5 thoracic for a total of 22 vertebrae (Woolfenden 1961). Shelducks, e.g., *Tadorna*, often have 17 cervical and 5 thoracic vertebrae and typical anserines have 19-20 cervical and 5 thoracic vertebrae (Woolfenden 1961). The Australasian anserines *Cnemiornis* and *Cereopsis* have 18 and 5 or 19 and 4 cervical and thoracic vertebrae, respectively (Worthy *et al.* 1997). *Dendrocygna* has 17-18 cervical and 5 thoracic vertebrae, and *Nettapus* has 16 cervical and 5 thoracic vertebrae (Woolfenden 1961).

Coracoid

The coracoid of *Euryanas* is relatively broad across its sternal end, has no pneumatic foramina in the *sulcus m. supracoracoidei*, and the ventral surface anterior to the sternal facet has no depression (Fig. 2). The *processus acrocoracoideus* overhangs the shaft medially (in dorsal view) as in *Dendrocygna*,

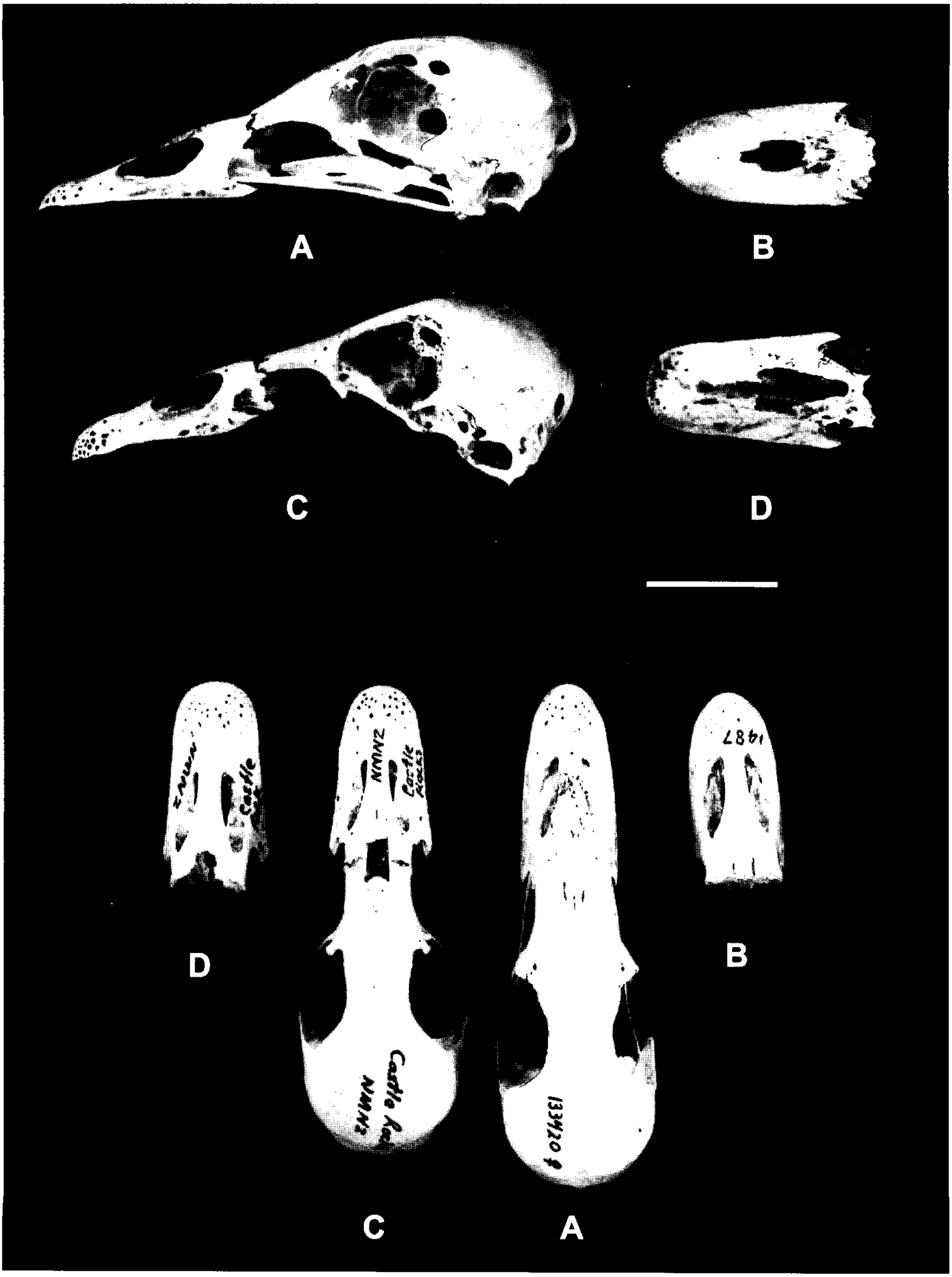

Fig. 1 Skulls (A,C) and rostra (B, D) of *Chenonetta jubata* MVZ 133420 (A) MNZ 1487 (B) and *Euryanas* (=*Chenonetta*) *finschi* MNZ S38931 (C,D) in lateral (above left), ventral (above right), and dorsal (lower) views. Scale bar = 20 mm.

Nettapus, Anas, Chenonetta, Cairina, and *Hymenolaimus,* but not in *Aythya* or *Tadorna,* in which its medial edge is in line with the shaft. The *sulcus m. supracoracoidei* is not deeply excavated under the ridge between the *facies articularis scapularis* and the acrocoracoid process, as it is to variable extents in *Anas, Aythya,* and especially *Tadorna,* in which the excavation is continuous under the *facies articularis clavicularis.* In *Euryanas, Nettapus, Chenonetta,* and *Anas,* the articular facet for the clavicle is rugose across its whole depth. In *Aythya,* and to a lesser extent in *Hymenolaimus,* the dorsal part of the articular facet for the clavicle closes off the *sulcus m. supracoracoidei* so that it does not proceed under the head. *Cairina* differs markedly in that the acrocoracoid has a deep highly pneumatic fossa under the head. *Nettapus* has a more globular acrocoracoid, and *Dendrocygna* has a concave ventral surface to the sternal end and a more abrupt medial angle.

Scapula

The scapula of *Euryanas* has no pneumatic fossae, is broadest at midlength as in most anatines (Woolfenden 1961), has a single elevated attachment scar on the neck, and the *tuberculum coracoideum* extends beyond a line drawn between the *facies articularis humeralis* (glenoid facet) and the acromion because of a reduced glenoid facet (Fig. 2). The acromion is similar in form to that of other anatines. *Cairina* has pneumatic foramina entering the acromion from the lateral surface. *Dendrocygna* lacks the prominent attachment scar on the neck.

Furcula

The furcula of *Euryanas* is broadly U-shaped, but the rami are comparatively less robust than in similar-sized, strongly flying anatids, e.g., *Anas* or *Chenonetta* (Fig. 2). There are no pneumatic fossae, coracoidal tuberosities are present, the rami are somewhat flattened, and there is no furcula process. The synostosis is more pointed in *Dendrocygna* and *Nettapus,* not broadly U-shaped.

Sternum

The sternum of *Euryanas* is broad with a low carina with no forward projection (Fig. 3). The depth of the carina has been reduced markedly in depth through the Holocene (Worthy 1988). There is a single circular pneumatic foramen on the dorsal surface. The *spina externa* (ventral manubrial spine) is short and variable in form: usually it is small and pointed, but it is occasionally bifid. Except for the carina, these features of the sternum of *Euryanas* are similar to *Anas, Chenonetta, Tadorna,* and *Hymenolaimus.* In *Nettapus,* the ventral manubrial spine is large. *Cairina* and *Dendrocygna* lack a ventral manubrial spine (Woolfenden 1961). The dorsal manubrial area is marked by a wide, shallow notch with a small central prominence as in *Chenonetta,* but unlike *Anas, Nettapus, Aythya, Tadorna, Cairina,* and *Hymenolaimus,* in which there is no central prominence. *Dendrocygna* lacks a distinctive notch in this area. *Cairina* differs further in that the dorsal surface has several pneumatic foramina on the mid-line and others sited more laterally beneath the *processus craniolateralis.*

The *trabecula lateralis* (posterior lateral processes) extend to a point level with the post-pectoral line. The costal margin comprises about 1 / 3 of the basin length. The intermuscular line extends posteriorly to the medial side of the sternal notch, as in *Anas, Cairina, Tadorna,* and *Chenonetta,* and does not extend to the carinal base.

Humerus

The humerus is considered one of the more useful bones in determining phylogenetic relationships in anatids (Woolfenden 1961; Livezey 1986, 1991). The humerus of *Euryanas* has a large pneumatic *fossa pneumotricipitalis,* the *crista deltopectoralis* is concave on its caudal surface, and the *tuberculum dorsale* is raised off the shaft (Fig. 2). The *incisura capitis* is not excavated under the *caput humeri.* The shaft on its caudal surface is compressed into a ridge adjacent to the distal half of the deltoid crest. This could be interpreted as the capital shaft ridge *sensu* Woolfenden (1961), but it is neither directed towards the head nor the dorsal tubercle, as described for various volant species by Woolfenden (1961). Rather, it ends distal to the dorsal tubercle, and a flat surface separates it from the head and the dorsal tubercle. Similar ridges are seen in humeri of flightless teal, e.g. *Anas marecula* Olson & Jouventin, 1996, and *Anas aucklandica* Gray, 1844. A parallel is also seen in the difference between humeri of the volant *Porphryio melanotus* Temminck versus the flightless *P. hochstetteri* (Meyer) – humeri of the latter having a compressed caudal face to the shaft adjacent to the bicipital crest. It, therefore, seems that this feature is a consequence of flightlessness. We prefer to term this ridge a pseudo-capital shaft ridge to acknowledge the lack of homology in the structure seen in *Euryanas* compared to other species, e.g., *Tadorna.*

The humerus of *Euryanas* differs from that of *Anas.* In *Anas,* humeri lack a capital shaft ridge, the dorsal tubercle is flush with the shaft, and the deltoid crest is convex caudally. In *Cairina,* a capital shaft ridge is present and directed towards the dorsal tubercle, the dorsal tubercle is not elevated, the capital groove is excavated under the head, and the deltoid crest is concave caudally. In *Hymenolaimus,* there is a capital shaft ridge, the dorsal tubercle is raised off the shaft, the deltoid crest is concave

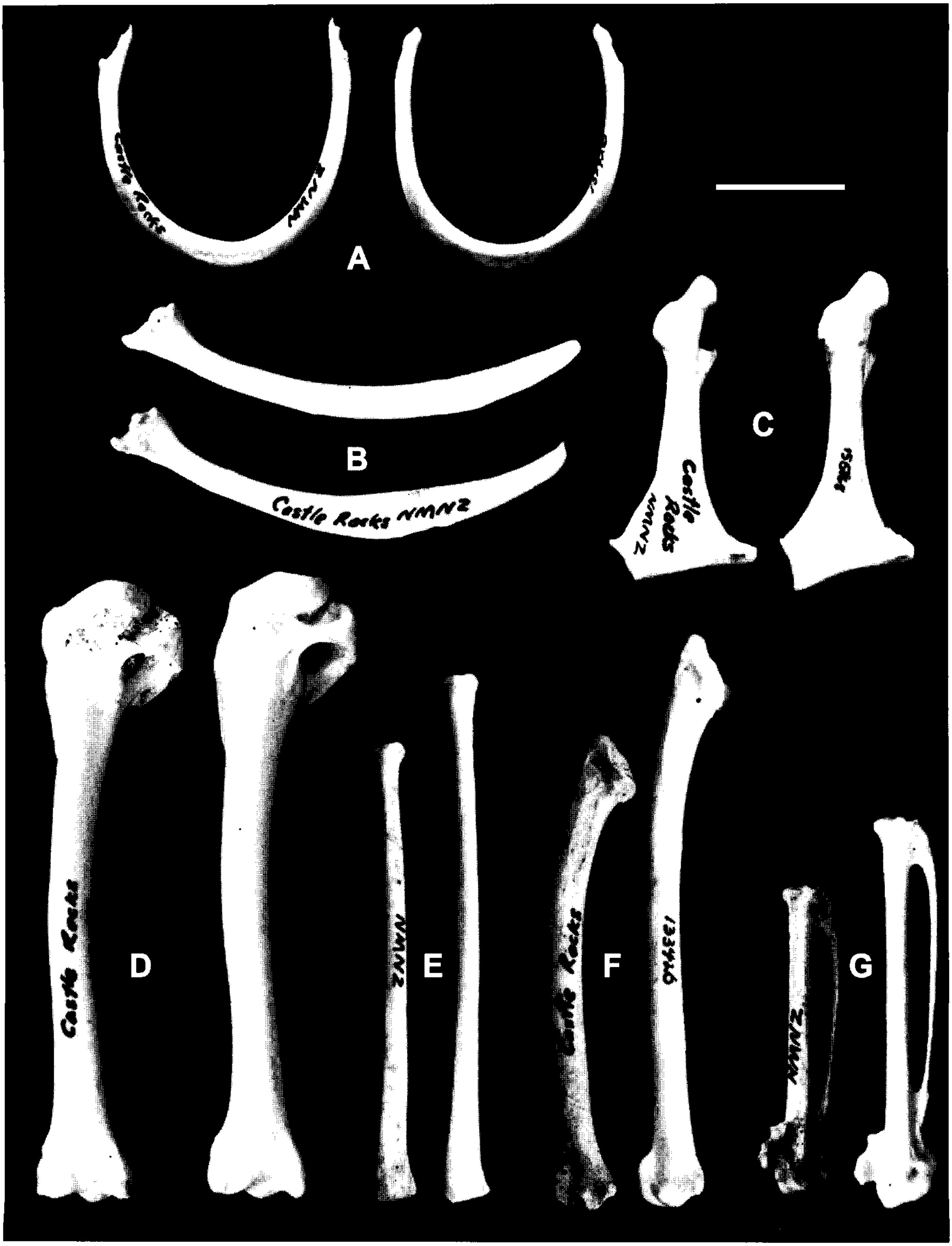

Fig. 2 Pectoral girdle and wing elements of *Euryanas* (=*Chenonetta*) *finschi* MNZ S38931 (A, B, C, D, F, G) and MNZ S38932 (E), on left in each pair, bottom for scapulae, and *Chenonetta jubata* MVZ 133420 or MVZ 155868, on right in each pair: A, furculae in anterior view; B, scapulae in lateral view; C, coracoids in ventral view; D, humeri in caudal view; E, radii in dorsal view; F, ulnae in ventral view; G, carpometacarpi in ventral view. Scale bar = 20 mm.

caudally, but there is a marked excavation under the head. In *Dendrocygna,* there is a prominent capital shaft ridge directed towards the head, the dorsal tubercle is raised off the shaft, the ventral tubercle is relatively small and pointed, the deltoid crest is concave caudally, the pneumatic fossa is closed by a pneumatic wall internally, and there is a distinct *processus supracondylaris dorsalis* unlike in other ducks. *Aythya,* like other diving anatids, has a medially closed pneumatic fossa. In *Nettapus,* humeri have no capital shaft ridge, the dorsal tubercle is level with the shaft, and the deltoid crest is not concave caudally. Humeri of *Tadorna variegata* have similar features to that of *Euryanas,* and differ mainly in that the capital shaft ridge extends to the ventral side of the dorsal tubercle. The general shape of the humerus of *Chenonetta* is very similar to that of *Euryanas,* with a deltoid crest that is concave caudally, a dorsal tubercle raised off the shaft, and no marked excavation under the head. Livezey (1986) found that *Chenonetta* was 'problematic' in the determination of the state for the character of presence or absence of the capital shaft ridge. In this study, we found that *Chenonetta* had a slightly dorsoventrally compressed shaft where the pseudocapital shaft ridge is found, and lacks both the highly inflated condition seen in *Anas* and a well-developed capital shaft ridge as in *Tadorna.*

Ulna

The ulna of *Euryanas* is ~84% of humerus length (Fig. 2). This is similar to other anatids: *Anas platyrhynchos* ~86%, *A. rhynchotis* ~86%, *Cairina* ~86%, *Nettapus* ~86%, *Hymenolaimus malacorhynchus* ~85%, *Aythya novaeseelandiae* ~85%, greater than the weak flier *A. chlorotis* ~80%, but less than the strongly volant *Chenonetta* ~93% and *Dendrocygna* ~102%.

Radius

The radius of *Euryanas* is unremarkable among ducks: distally it is of average width, neither narrow as in *Aythya,* nor wide as in *Hymenolaimus* (Fig. 2).

Carpometacarpus

The carpometacarpus of *Euryanas* is shorter and stouter than that of other similar-sized anatids (Fig. 2). It has no rugose knob on metacarpal 1. The internal rim of the carpal trochlea in ventral view diverges at about 20° from the shaft, as in *Anas, Dendrocygna, Cairina,* and *Aythya,* but unlike *Hymenolaimus* and *Nettapus,* in which it is parallel to the shaft. In *Euryanas,* the external rim has a distinct notch in its ventral surface, the proximal dorsal surface of metacarpal 2 is rounded and the distal extent of the attachment points for the major and the minor digit are approximately equal, and is thus similar to *Anas, Tadorna, Cairina, Aythya,* and *Chenonetta* in these features. *Dendrocygna* lacks a distinct notch on the ventral surface of the external rim of the carpal trochlea. *Euryanas* differs from *Dendrocygna, Nettapus, Cairina, Anas,* and *Tadorna* in that the synostosis of the major and minor metacarpal is only slightly distad of the alula process rather than markedly distad of it, and the distal synostosis of the metacarpals is relatively shorter than in these taxa, except *Nettapus.*

Legs and pelvis

Euryanas had large, robust leg bones compared to aquatic anatids such as *Anas, Aythya,* and *Hymenolaimus.* Anatids that spend a significant amount of time on dry land, such as *Tadorna, Chenonetta* and geese, have leg bones that approach *Euryanas* in stoutness, so this feature in *Euryanas* was probably related to its terrestrial habit.

Pelvis

As expected from the robust leg bones, the pelvis in *Euryanas* is proportionally broad and robust (Fig. 4). It is, however, typically anatid-like in general shape. There are 4 rows of *foramina intertransversaria,* of which the pair closest to the midline are the biggest, and all enlarge posteriorly. This is as in *Aythya, Cairina,* and *Chenonetta,* and in some species of *Anas,* but differs from *Nettapus, Hymenolaimus* and *Tadorna,* in which the medial foramina are mostly closed and those in the lateral row are largest. Some species of *Anas,* e.g., *A. platyrhynchos,* have the medial row open and the lateral row closed.

The *foramen ilioischiadicum* is moderately large, extending more than half way to the posterior edge of the ischium. This is similar to *Tadorna* and *Nettapus,* but differs from *Anas, Cairina, Chenonetta, Dendrocygna, Aythya* and *Hymenolaimus,* in which this foramen extends less than halfway to the posterior edge of the ischium.

The *foramen obturatum* is open posteriorly as in *Nettapus, Chenonetta* and *Anas,* but unlike *Dendrocygna, Tadorna, Cairina, Hymenolaimus,* and *Aythya,* in which it is closed posteriorly.

Femur

The femoral shaft is straight, the popliteal fossa shallow and the dorsal surfaces of the distal condyles essentially parallel (Fig. 5). The depth of the trochanter is substantially greater than the depth of the head. In the foregoing features, femora of *Euryanas* are similar to those of *Anas, Dendrocygna, Tadorna, Cairina,* and *Chenonetta* but differ from divers such as *Aythya,* in which the shaft is curved, the popliteal fossa deep and the trochanter shallow, and *Hymenolaimus,* in which the popliteal fossa is deep. In *Euryanas,* the *linea intermuscular caudalis*

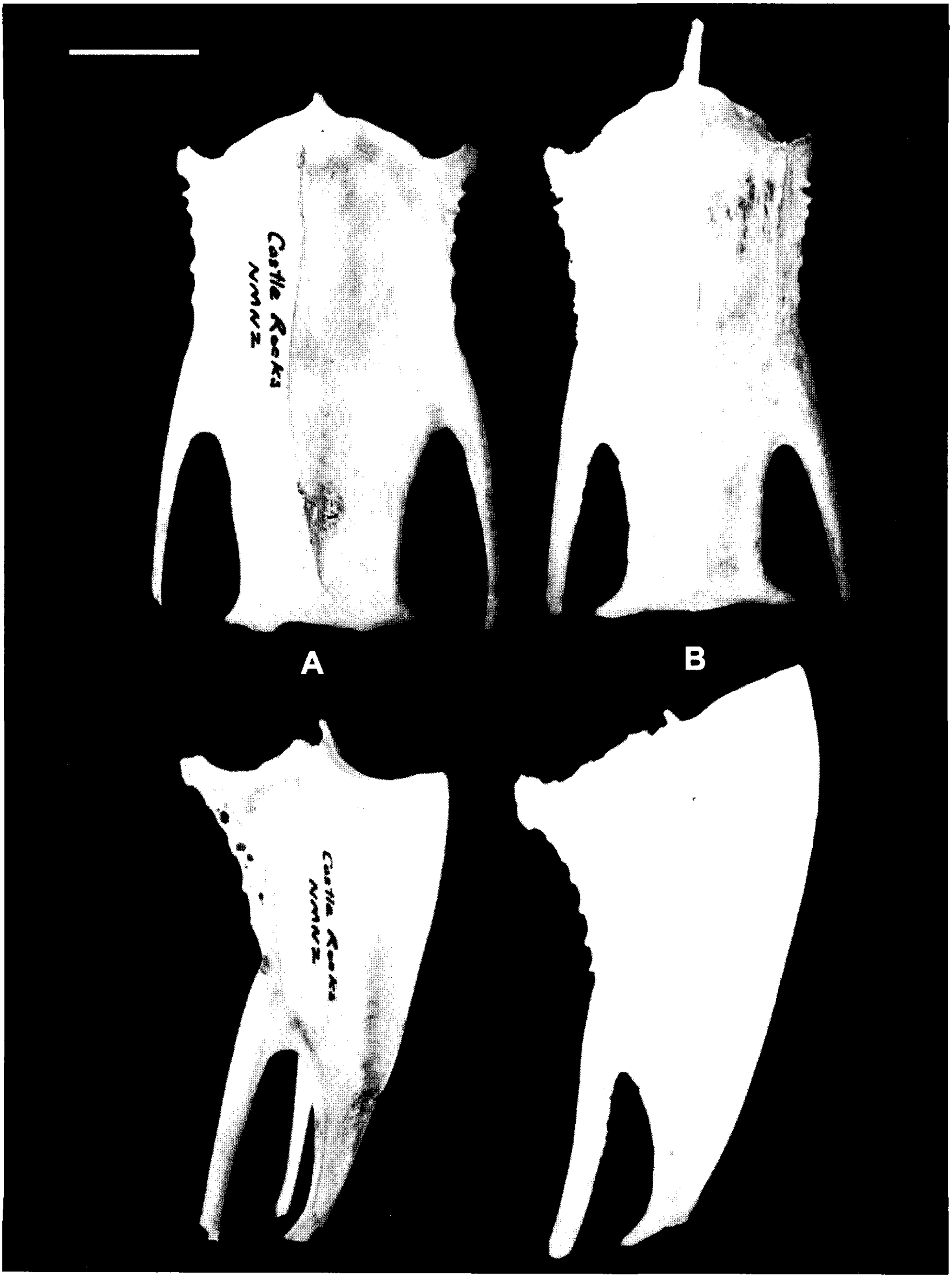

Fig. 3 Sterna of *Euryanas* (=*Chenonetta*) *finschi* MNZ S38931 (A) and *Chenonetta jubata* MVZ 133420 (B) in ventral view (above) and lateral view (below). Scale bar = 20 mm.

passes distal of the nutrient foramen (which is at the midpoint of the shaft) and ends about midway between it and the *tuberculum m. gastrocnemialis lateralis* or at a point 60% of the bone length. The minute femora of *Nettapus* have a shallow trochanter and convergent condyles in dorsal view. In *Anas,* the *linea intermuscular caudalis* ends at the nutrient foramen at midlength, whereas in *Tadorna, Cairina,* and *Chenonetta* it extends well distally of the midlength point. The main difference between femora of *Euryanas* and those of *Dendrocygna, Chenonetta, Cairina,* and *Tadorna* other than size, is that the medial condyle is proportionally shorter and higher in the former, creating a markedly deeper rotular groove.

Tibiotarsus

On the tibiotarsus of *Euryanas* (Fig. 5) the *crista cnemialis cranialis* (procnemial crest) forms as a weakly defined crest down the medial side, not a well-developed crest as in divers, e.g. *Aythya* or *Mergus,* or the highly aquatic *Nettapus.* The shaft is more rounded between the *crista fibularis* (fibular crest) and the ridge extending from the procnemial crest than in other ducks, which in order of increasing flatness are *Dendrocygna, Hymenolaimus, Nettapus, Cairina, Chenonetta, Tadorna, Anas,* and *Aythya.* The *impressio lig. collat. med.* is weakly defined, as in *Chenonetta, Cairina, Hymenolaimus, Anas,* and *Aythya,* but unlike *Tadorna* and *Dendrocygna,* in which it is prominent. The most distinctive feature of the tibiotarsus of *Euryanas* is that the *crista cnemialis lateralis* (ectocnemial crest) extends as a thin buttress to the shaft to a point level with the anterior extreme of the fibular crest. In *Dendrocygna, Tadorna, Cairina, Chenonetta, Anas* and *Aythya,* the ectocnemial crest is more hooked, more robustly buttressed, and joins the shaft well anterior of the fibular crest. Only *Hymenolaimus* among the taxa compared is similar to *Euryanas* in this feature.

Tarsometatarsus

The tarsometatarsus in *Euryanas* is characterised by the marked lateral expansion of trochlea 4 (Fig. 5). A slight lateral deviation is seen in *Tadorna* and *Chenonetta,* but most anatids have none: this feature is associated with a terrestrial habit. Another character of *Euryanas* is the medial expansion of trochlea 2. Specifically, in anterior aspect, the trochlea is initially directed medially from the shaft, then is directed distally so that the distal face of the trochlea is nearly at right angles to the shaft. This differs markedly from most anatids, e.g., *Dendrocygna, Anas, Cairina, Aythya,* and *Hymenolaimus,* in which trochlea 2 has a single distal-medial alignment such that the distal face (tarsometatarsus viewed anteriorly) is directed at 45° to the shaft. This difference is further illustrated in Fig. 5E, where the trochleae are shown in distal view. In *Euryanas,* the medial face of trochlea 3 and the anterior face of trochlea 2 form a right angle. In *Dendrocygna, Nettapus, Anas* spp., *Cairina, Aythya,* and *Hymenolaimus* these form a wide angle of about 130°. The shape of both these features in *Chenonetta* and *Tadorna* are similar to *Euryanas.*

In *Euryanas,* the distal extremity of trochlea 2 is distad of the intertrochlear groove between trochleae 3 and 4. It is proximad of it in *Anas, Aythya, Nettapus,* and *Hymenolaimus,* reaches it in *Dendrocygna* and *Tadorna,* but is distad of it in *Chenonetta* and *Cairina,* which are thus similar to *Euryanas.* Trochlea 2 is grooved distally in *Euryanas* as are all other anatids compared here except *Dendrocygna,* which lacks the groove.

In *Euryanas,* there are 4 *crista hypotarsi* (hypotarsal ridges) that define 4 *sulci hypotarsi* (hypotarsal canals). There are 2 canals between the *crista medialis hypotarsi* (ridge 1) and the adjacent ridge 2, with the floor of the more posterior one enclosing the other. In medial profile the hypotarsal ridge 1 slopes steeply to the shaft distally without a distally directed hook. This is as in *Tadorna,* and similar to *Chenonetta.* In *Cairina, Dendrocygna,* and *Nettapus* the hypotarsal ridge 1 ends abruptly distally, and in *Anas, Aythya,* and *Hymenolaimus,* it usually ends in a distally directed hook.

DISCUSSION

Similarities between *Euryanas* and *Chenonetta*

The following combination of characters are uniquely shared by *Euryanas* and *Chenonetta*: Skull with a very short premaxilla effected by prenarial shortening; a similar shaped maxillary process of the *os nasale;* a narrow descending lacrymal; large orbits; a deep (dorsoventrally) tympanic cavity without a ventrally directed posterior pocket; and a similar basisphenoid platform. The syringeal bulla of males is very similar. The vertebral column has 16 cervical and 5 thoracic vertebrae. The coracoid is not pneumatic, the acrocoracoid overhangs the shaft medially, the supracoracoidal sulcus is not deeply excavated and is not pneumatic, and the ventral surface of the sternal end has no depression. The humerus has a concave deltoid crest, an elevated dorsal tubercle, a large pneumatic tricipital fossa, and a capital groove that is not excavated under the head. The pelvis has the *foramen obturatum* open posteriorly and a similar arrangement to the *foramina intertransversaria.* The tarsometatarsus has a similar trochlear conformation, particularly the lateral and medial expansion of trochlea 4 and trochlea 2, respectively. The hypotarsus slopes steeply to the shaft without a distally-directed hook.

These similarities and the fact that this combination of characters is not shared between *Euryanas*

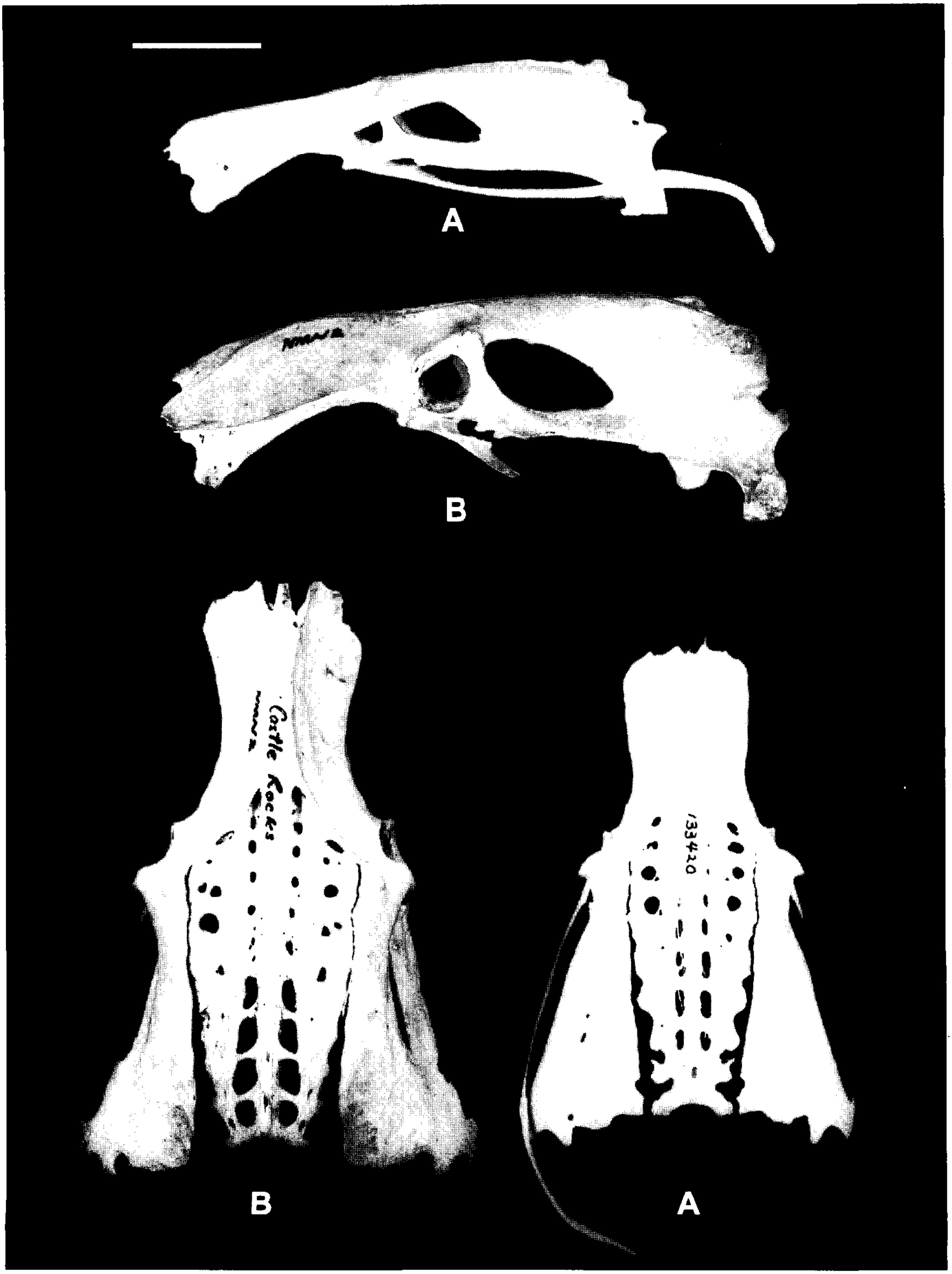

Fig. 4 Pelves of *Chenonetta jubata* MVZ 133420 (A) and *Euryanas* (=*Chenonetta*) *finschi* MNZ S38931 (B) in lateral (above) and dorsal (below) views. Scale bar = 20 mm.

and any other taxon support the conclusions of Oliver (1930, 1955) that *Euryanas* was most similar to *Chenonetta*.

Differences between *Euryanas* and *Chenonetta*

Regardless of whether characters may be inferred as primitive or derived, most are the same for *Euryanas* and *Chenonetta*. All differences between the two taxa can be related to functional differences or those associated with loss of flight ability in *Euryanas* but not in *Chenonetta*.

Adaptations to a more terrestrial lifestyle and associated loss of flight ability

A markedly heavier form of the elements of the pelvic girdle and reduced elements of the pectoral girdle are common manifestations of flightlessness in birds. Associated with this in *Euryanas* is the reduced height of the sternal carina, a narrower acromion on the scapula, narrowing of the humeral shaft and development of a pseudo-capital shaft ridge, and a reduction in the pneumaticity of the vertebrae and the loss of ossified tendons compared with *Chenonetta*. The increased musculature associated with walking in a relatively larger bird has also led to differences in the pelvis in *Euryanas*. Rather than having a straight dorsal profile as in most ducks (e.g., *Anas* and *Chenonetta*), the pelvis of *Euryanas* has a prominent rounded hump to the preacetabular region and the post-acetabular region is broader and deeper; both features provide an increase in the available area for the leg muscles, which is related to the larger size of the legs. In *Dendrocygna*, which also has relatively large legs compared to aquatic taxa, there is a slight dorsal elevation of the anterior ilia.

Adaptations related to different functional requirements

Apart from differences related to relative flight ability, *Euryanas* differs from *Chenonetta* in seemingly major, yet phylogenetically superficial, changes associated with different functional requirements of the senses and feeding adaptations. For example, *Chenonetta* is partly nocturnal and flies at night, and has large eyes to facilitate this. *Euryanas* has smaller eyes, which seem to have been compensated for by a greater olfactory ability as shown by a swollen premaxilla to accommodate enlarged nares. The nares in *Euryanas* are proportionally higher than they are in *Chenonetta*, creating a larger internal narial opening and a more extensive anterior furrow leading from it. Together these features result in a completely different anterior profile of the skull between the taxa.

Although both taxa have very reduced bills, which are unusual among anatines, the comparatively large nares in both taxa indicate this is the result of prenarial shortening from the typical anatid condition. They differ in that the bill tip in *Euryanas* is wider and more rounded or truncated than in *Chenonetta*, in which it is somewhat tapered and more pointed. These differences in the shape of the tip can easily be explained as adaptations to different feeding niches. The short bill of *Nettapus*, which Livezey (1996) made the sister taxon of *Chenonetta*, is the result of overall size reduction rather than prenarial shortening as seen in *Chenonetta*.

In conclusion, the major differences between *Chenonetta* and *Euryanas* are explained as being due to modifications arising from loss of flight ability and adoption of a more terrestrial lifestyle, or a change in emphasis from vision dominated senses to one where olfactory ability was more significant.

Classification of *Euryanas*

In his preliminary study where the relationships of *Euryanas* were assessed in the absence of *Chenonetta*, Livezey (1989) concluded that:

> "*Euryanas* is plesiomorphic with respect to the Anatinae in a number of characters, notably in the rounded, anconally concave deltoid crest (25a) and prominent, buttressed external tuberosity (32a) of its humerus.
>
> These characters indicate that *Euryanas* diverged from modern anatid lineages after the basal anatid grade of *Dendrocygna*, *Thalassornis*, and the Anserinae, but before the Tadorninae..." (Livezey 1989).

In his most recent classification of the Anatidae, Livezey (1997) has accepted a large subfamily Tadorninae, comprised of four tribes. *Euryanas* is placed in the tribe Euryanatini before Tadornini, which includes the true shelducks and sheldgeese. *Chenonetta* is included in the Anatinae, within the tribe Anatini, subtribe Nettapodina, immediately before Anatina and all species of *Anas*. *Hymenolaimus* was placed in Merganettini within Tadorninae, before *Euryanas*.

As seen above, we doubt that the pseudo-capital shaft ridge seen in *Euryanas* is homologous with the capital shaft ridge of taxa such as *Tadorna* and *Dendrocygna*, but instead results from reduction of the humerus following facultative flightlessness. Other characters of apparent phylogenetic significance, for example, the presence of an elevated dorsal tubercle (=external tuberosity) and concave anconal deltoid crest to the humerus, support the suggestion that *Euryanas* is primitive with respect to *Anas*. However, other observations suggest that *Euryanas* is derived with respect to *Tadorna* and *Hymenolaimus* in several ways, notably, the open obturator foramen and form of the dorsal foramina on the pelvis, the vertebral count, and features of the coracoid, yet is similar to anatines including *Chenonetta* (sensu Livezey 1996). Cranial features

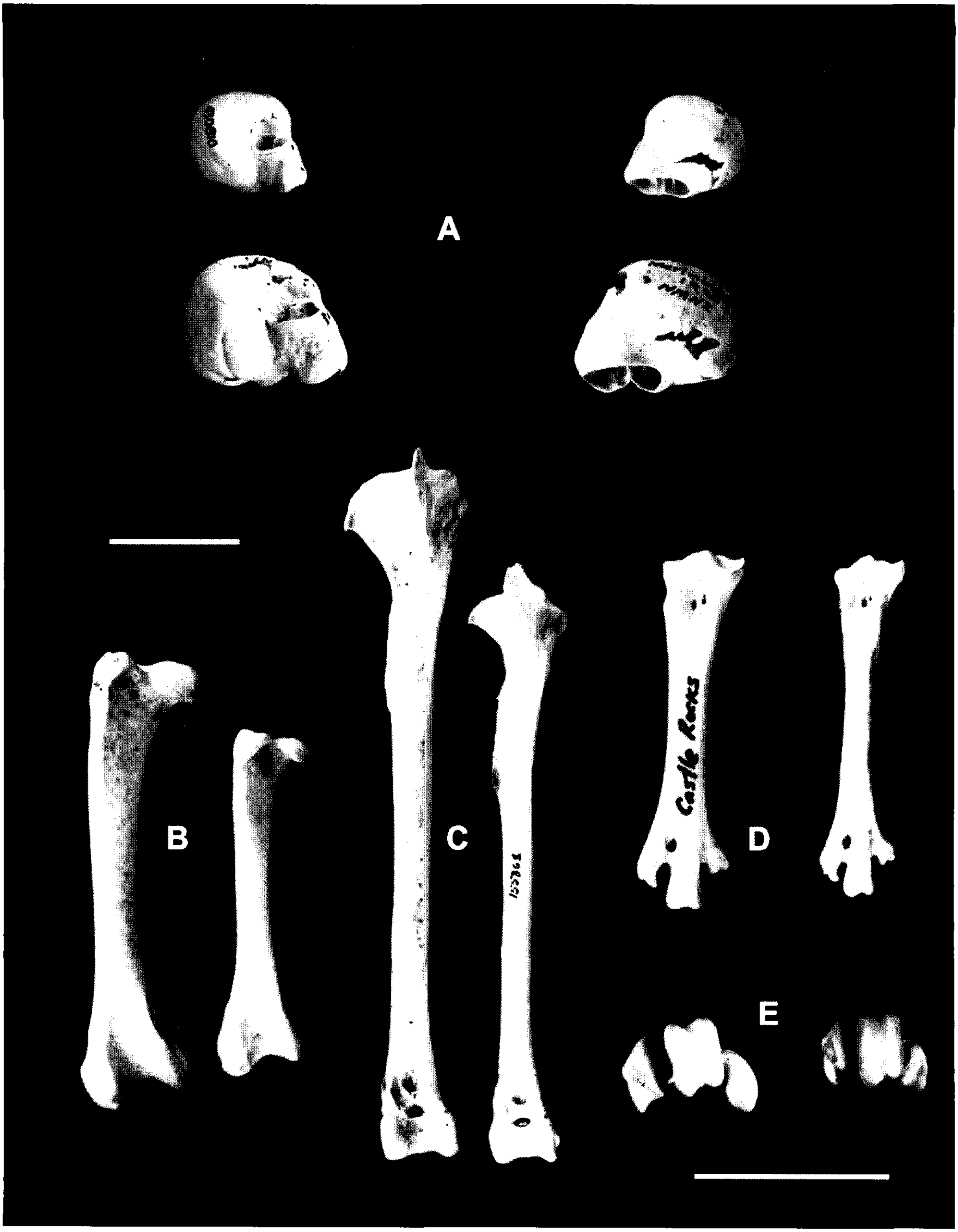

Fig. 5 Syringeal bullae (A) of *Chenonetta jubata* USNM 430810 (above) and *Euryanas* (=*Chenonetta*) *finschi* MNZ S38932 (below) in dorsal (left) and ventral (right) views; and hindlimb elements of *Euryanas* (=*Chenonetta*) *finschi* MNZ S38931 (B, C, D) and Hodge Creek indiv., THW colln (E), on left in each pair, and *Chenonetta jubata* MVZ 155868 (B, C, D) and MNZ 25400 (E), (on right in each pair): B, femora; C, tibiotarsi in cranial view; D, tarsometatarsi in dorsal view; E, tarsometatarsi in distal view. Scale bars = 20 mm.

Table 1 Humerus/femur and wing/femur ratios for known-aged samples of *Euryanas finschi* (after Worthy 1997b) compared with those of individual *E. finschi* from Cape Wanbrow and Hodge's Creek, and 2 from Hawke's Bay, and individuals of *Chenonetta jubata*.

Site	Status	Age	Humerus/Femur	Wing/Femur
Hawke's Bay S35886	Indiv.	Late Holocene (<1850 yrs)	1.28	3.02
Hawke's Bay S35885	Indiv.	Late Holocene (<1850 yrs)	1.26	2.95
Martinborough	Sample	Late Holocene (1-5 kyr BP)	1.27	2.96
Castle Rock	Sample	Late Holocene (1-5 kyr BP)	1.27	3.01
Kings Cave	Sample	Holocene (1-5 kyr BP)	1.32	3.09
Takahe Tomo	Sample	Late Pleistocene (12 kyr BP)	1.36	3.25
Hodge's Ck (THW colln)	Indiv.	Presumed Late Pleistocene	1.37	3.29
Graveyard L2	Sample	Pleistocene (11-14.5 kyr BP)	1.39	3.34
Wanbrow J41/f8226	Indiv.	Pleistocene (c.100 kyr BP)	1.46	3.57
Chenonetta jubata	Indiv.	Modern (MNZ 25400)	1.82	4.66
Chenonetta jubata	Indiv	Modern (MNZ 25142)	1.74	4.39

that are not directly related to functional changes such as occurred in the orbits and nares, e.g., the form of the tympanic cavity or basitemporal plate, are very similar in *Chenonetta* and *Euryanas*, yet differ from most other taxa. Also, the syringeal bulla is essentially identical in the two taxa, although this feature may show great variation among anatids (e.g., Livezey 1991), and is absent in members of the Anserinae and *Dendrocygna*.

Proposed classification of *Anas finschi* Van Beneden

The comparisons above reveal that there are no phylogenetically significant differences between *Euryanas* and *Chenonetta* worthy of generic rank. Accordingly, we recommend that *Euryanas* Oliver be placed in the synonymy of *Chenonetta* Brandt, and the following classification be adopted.

Family Anatidae
  Subfamily Anatinae
    Genus *Chenonetta* Brandt, 1836
      C. jubata (Latham, 1807) – maned duck or Australian wood duck
      C. finschi (Van Beneden, 1875) – Finsch's duck

We have not attempted to assess the relationships of *Chenonetta* within the anatines. For present purposes, it makes little difference what the relationships of *Chenonetta* may be within the Anatidae, as *Euryanas* would go with *Chenonetta* wherever it is placed. Skeletal morphology alone probably lacks the resolution to determine the generic relationships. Molecular data sets have suggested relationships at considerable variance to those suggested by Livezey's (1997) classification; for example, Sraml *et al.*'s (1996) study of Australasian waterfowl found no support for a close relationship between *Nettapus* and *Chenonetta*. Similarly, Sorenson *et al.*'s (1999) study suggests a markedly different classification from Livezey (1997). We leave the resolution of this problem to larger data sets that include both morphological and genomic information.

Palaeoecology of *Chenonetta finschi* (Finsch's duck)

Chenonetta jubata is highly vagile, adapted to exploit seasonal and unpredictable abundances in food supply. Its dispersal ability has doubtless contributed to its occasional appearance in mainland New Zealand and in the Snares Islands south of New Zealand (Oliver 1955; Turbott 1990).

Chenonetta finschi probably evolved from a population of *C. jubata* that colonised New Zealand from Australia. We predict that this ancestor probably arrived in New Zealand during 1 of the glacial periods of the Pleistocene when widespread 'new' habitats of open grasslands and shrublands had become available enabling a successful colonisation. That the New Zealand population is known still to have been in the process of evolving flightlessness during the Holocene (Worthy 1988, 1997b) suggests a relatively recent arrival in New Zealand. An indication of just how recent this was is provided by a fossil deposit of last Interglacial age in the Hillgrove Formation at Oamaru. The fossils include the associated bones (AU4159 and AU11251) of an individual of *Chenonetta finschi* that displays a stage in flight regression 1 step before that known in bones <20,000 years old (Table 1, Fig. 6). In this last interglacial-aged fossil (~100 kyr), the leg as measured by the femur is relatively smaller compared to geologically more recent specimens. But, even at 100kyr

Fig. 6 Humeri in caudal view (top row), femora in caudal view (middle row), and tarsometatarsi in dorsal view (bottom row) of *Chenonetta jubata* MNZ 25400 (A), *Euryanas* (=*Chenonetta*) *finschi* AU4159, c. 100 kyr old (B), and *Euryanas* (=*Chenonetta*) *finschi* Hodge's Creek individual, *c.* 10-12 kyr old (C). Scale bar = 20 mm.

BP, the legs were relatively larger than *C. jubata*, implying a presence in New Zealand for some time. If so, it seems likely that its ancestor arrived in the ante-penultimate glaciation.

Because *Chenonetta finschi* is the sister taxon of *C. jubata*, the 2 species may have had similar ecological requirements. In Australia, *C. jubata* is a very common bird that is primarily a terrestrial grazer in grassland, pasture, open or dense woodland (small, well-spaced trees, with well-developed undergrowth), but not dense forest. It feeds only sparingly in very shallow water, takes insects when available, and nests in tree holes (Marchant & Higgins 1990). Most fossils of *C. finschi* are found in areas with mainly less than 1200 mm rainfall where grassland-shrubland mosaics predominated, in places well removed from water (Worthy 1997a, 1997b, 1998a, 1998b; Worthy & Holdaway 1994, 1995). This suggests that the New Zealand bird also was primarily a terrestrial grazer. From the behaviour of *C. jubata*, we may predict that *C. finschi* would have fed on insects at times, and nested in holes, probably in fallen tree trunks or under rocks, as *Tadorna* does. As have most birds in the relatively predator-free environment of New Zealand (Holdaway 1999), *C. finschi* probably changed its breeding strategy from the *r*-selection strategy of the Australian bird (*C. jubata* lays on average 10 eggs [Marchant & Higgins 1990]) to the K-selection strategy of few eggs. The combination of weak or poor flying ability and a K-selected breeding strategy meant that when *C. finschi* was again brought into contact with ground-based predators, such as rats and humans, beginning about 2000 yrs BP (Holdaway 1999), it rapidly became extinct.

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