Vol. 69, Number 3, Pp. 157–193

9 AUGUST 2000

HOMOLOGY AND PHYLOGENETIC IMPLICATIONS OF SOME ENIGMATIC CRANIAL FEATURES IN GALLIFORM AND ANSERIFORM BIRDS

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ABSTRACT

Two landmarks of the temporal region of the skull in most birds are the zygomatic process (processus zygomaticus) and the postorbital process (processus postorbitalis). The morphology and homology of these processes in gallinaceous birds (Galliformes) and waterfowl (Anseriformes), however, are not clear. Anseriformes usually are said to lack a processus zygomaticus. By contrast, the processus zygomaticus of many Galliformes often is described as connected to the tip of the processus postorbitalis, forming a temporal arch. Olson and Feduccia (1980*a*) cited these cranial differences as evidence opposing a hypothesis of sister relationship between the two orders, an hypothesis having a substantial history of advocacy (Seebohm, 1889; Shufeldt, 1901; Delacour, 1954; Johnsgard, 1965; Cracraft, 1981*a*, 1986; Schulin, 1987). Dzerzhinsky (1982, 1995) contradicted the proposal by Olson and Feduccia (1980*a*), interpreting the two processes as completely fused in Anseriformes, forming a unique "sphenotemporal process," which he averred to have been derived evolutionarily from the condition found in the Galliformes.

In the present study, we examined skulls and jaw muscles of juvenile and adult specimens of selected taxa from both orders to test these opposing hypotheses, and found that: (a) the processus zygomaticus is small or lacking in adult Galliformes, and absent in all Anseriformes; (b) the processus zygomaticus is connected to the tip of the processus postorbitalis by an ossified aponeurosis of m. adductor mandibulae externus (aponeurosis zygomatica) in adults of most galliforms, whereas the aponeurosis zygomatica of anseriforms has a linear origin along the os squamosum as far as the processus postorbitalis; the aponeurosis zygomatica is ossified in Anhimidae and unossified in Anatidae; (c) a laterally exposed fossa of the temporal region (fossa musculorum temporalium) is reduced in Galliformes and absent in Anseriformes; (d) pars superficialis and pars zygomatica of m. adductor mandibulae externus are shifted rostrad in Galliformes and Anseriformes, and (e) pars articularis of m. adductor mandibulae externus is much enlarged in both orders. Based on these observations, we conclude that the parts of musculus adductor mandibulae externus of Anseriformes have been misinterpreted in a number of previous studies, perhaps reflecting confusion about associated processes and fossae. These findings are interpreted with respect to the homology of the osteological features and their associated muscles. The distribution of the included states supports the growing consensus for a sister relationship between the Galliformes and Anseriformes.

KEY WORDS: Anseriformes, cranium, Galliformes, homology, myology, osteology, processus postorbitalis, processus zygomaticus

INTRODUCTION

Historical Background

A series of classic, nineteenth-century works-e.g., Blanchard (1859), Eyton (1867), Fürbringer (1888), Seebohm (1888, 1889, 1890, 1895), Gadow and Se-

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Two features of the avian skull-the processus postorbitalis and the processus zygomaticus (Fig. 1)-serve as landmarks for the structure and function of the jaws (Bühler, 1981) but have proven problematic for systematists concerned with the Anseriformes. In most birds, the processus postorbitalis provides the dorsal attachment for the ligamentum postorbito-mandibulare, a structure important in several aspects of cranial kinesis (Kripp, 1933; Zusi, 1962, 1967; Bock, 1964); the processus zygomaticus supports the origin of a major aponeurosis of the external adductor muscle of the mandibula. Absence of the processus postorbitalis is unusual and typically associated with a reduction or loss of the ligamentum postorbito-mandibulare. Absence of the processus zygomaticus, however, does not necessarily signify a change in the musculus adductor mandibulae externus. In the Anseriformes, the processus postorbitalis and adjacent fossae are uniquely modified among extant birds (Fig. 2), and the processus zygomaticus is essentially absent in Anseriformes (e.g., Gadow, 1892; Olson and Feduccia, 1980a). The processus postorbitalis has become an integral part of a reconstruction of the regio temporalis (Fig. 1) on the lateral surface of the neurocranium, that part of the skull enclosing the brain and sensory capsules (de Beer, 1937; ICVGAN, 1983; Baumel and Witmer, 1993). In Anseriformes, the stout, rostrally oriented processus postorbitalis also serves as origin for a part (pars zygomatica) of musculus adductor mandibulae externus that is independent of the processus postorbitalis in most avian taxa (Fig. 1). Thus the profound modification of these structures in waterfowl is of considerable functional and phylogenetic interest.

Conformation of the regio temporalis and mandibular rami reflects the structure of the primary, superficial adductor acting on the mandibula, m. adductor mandibulae externus (abbreviated hereafter as AME). This complex, multipennate muscle consists of two or more parts, each of which is more or less distinct and associated with one or more aponeuroses that provide extensive surface for the attachment of muscle fibers (Fig. 3). Despite several thorough anatomical surveys of the avian cranium (Lakjer, 1926; Hofer, 1950; Starck and Barnikol, 1954; Weber, 1993), delimitation of the parts of AME is somewhat arbitrary for many taxa because the fibers of one part may blend imperceptibly with those of another and some aponeuroses are shared by two or more parts. Disagreements about terminology and homology of the parts of AME in the Anseriformes are considerable (e.g., Lakjer, 1926; Starck and Barnikol, 1954; Dzerzhinsky, 1982; Weber, 1996).

These complexities notwithstanding, selected aspects of the AME and osteological features of the regio temporalis have figured prominently in studies of a orb





Fig. 1.—Diagrams of facies lateralis cranii of a hypothetical bird showing: (A) critical osteological features highlighted in the clear rectangle; and (B, C) critical myological features. See Methods for list of abbreviations used here and in the following figures.

diversity of avian orders (e.g., Möller, 1932; Hofer, 1945, 1950; Fiedler, 1951; Barnikol, 1952, 1953; Bas, 1954, 1955; Fisher and Goodman, 1955; Bams, 1956; Simonetta, 1960*a-b*, 1963, 1968; Zusi and Storer, 1969; Merz, 1963; Van der Klaauw, 1963; Yudin, 1965; Bock and McEvey, 1969; Richards and Bock, 1973; Burton, 1974*a-c*, 1984; Morioka, 1974; Bhattacharyya, 1980, 1989; Cracraft, 1982; Johnson, 1984; Zusi and Bentz, 1984; Van Gennip, 1986; Elzanowski, 1987; Zusi, 1993; Dzerzhinsky, 1999), including members of the Galliformes (Burggraaf, 1954; Burggraaf and Fuchs, 1954, 1955; Fuchs, 1954, 1955; Jollie, 1957; Fujioka, 1963; Dzerzhinsky and Belokurova, 1972; Dzerzhinsky, 1980; Weber, 1996) and Anseriformes (Davids, 1952; Starck and Barnikol, 1954; Good-



Fig. 2.—Facies lateralis cranii of: (A) an adult specimen of *Meleagris gallopavo* (USNM 556372), (Galliformes: Meleagrididae); (B) an adult specimen of *Sarkidiornis melanotos* (USNM 490276), (Anseriformes: Anatidae); and (C) an adult specimen of *Numida meleagris* (USNM 430657), Galliformes: Numididae). Features unlabelled or controversial in the literature are indicated by question marks. Scale bar = 1 cm.

man and Fisher, 1962; Zweers, 1974; Dzerzhinsky, 1982; Jäger, 1990). In addition to comparatively traditional studies, the complex has been examined with respect to structural details and functional roles of the constituent parts (e.g., Gans and Bock, 1965; Bock, 1964, 1968; Zweers, 1974; Dzerzhinsky, 1982).

The processus zygomaticus of Galliformes was described as well developed by Gadow (1892), Shufeldt (1909), and Baumel and Witmer (1993), but as absent or vestigial by Verheyen (1956). Starck and Barnikol (1954) found that the process zygomaticus was small in juvenile *Gallus*, and that the aponeurosis of AME, pars zygomatica, originating on the processus, ossified during maturation; they then referred to the combined process and ossified aponeurosis as the zygomatic process. Hofer (1950) considered the processus zygomaticus to be strong in *Meleagris* and *Tetrao*, taxa in which the aponeurosis zygomatica is ossified, but interpreted the processus to be lacking in *Numida*, in which the aponeurosis is not ossified (Fig. 2). Traditionally, the processus zygomaticus was said to be lacking in Anseriformes (e.g., Gadow, 1892; Olson and Feduccia, 1980*a*).



Fig. 3.—Diagrams of m. adductor mandibulae externus (AME) complex of a hypothetical bird: (A) AME superficialis; (B) AME coronoidea; (C) AME zygomatica; and (D) AME articularis. Aponeuroses shown in black.

Olson and Feduccia (1980*a*:4) argued against a close relationship between the Galliformes and Anseriformes, stating that "... the tip of the postorbital process fuses with that of the zygomatic process in Galliformes, leaving a foramen, whereas in the Anseriformes the zygomatic process is absent." This anatomical interpretation was part of a larger proposal in which the hypothetical "transitional shorebirds" (purportedly exemplified by the fossil *Presbyornis*) were considered ancestral to several modern orders (Livezey, 1997*a*), including waterfowl (Feduccia, 1977, 1978, 1980*a-b*, 1994, 1995, 1996; Olson and Feduccia, 1980*b*). By contrast, Dzerzhinsky (1995:327-328) concluded that "... in the Anseriformes, the [ossified muscular aponeurosis from the zygomatic process] fuses to the postorbital process over its entire caudoventral border to form a complete sphenotemporal process...." Dzerzhinsky (1995) considered the "sphenotemporal process" of the Anseriformes to be derived from the condition characteristic of the

Galliformes, bolstering his argument for a sister relationship between the two orders. Still other workers simply omitted these disputed features from consideration with respect to either order (Livezey, 1986; Cracraft, 1986, 1988; Ericson, 1996, 1997).

Objectives of Study

In this paper we interpret the homologies of osteological features unique to the Anseriformes through comparative study of skeletal and spirit (fluid-preserved) specimens of juvenile and adult examples of anseriform and galliform birds. Of primary concern are the nature of the processus zygomaticus, homologues of the aponeurosis zygomatica of AME, and the relationship of both with the processus postorbitalis in Anseriformes. This examination is associated with several new proposals regarding nomenclature for selected anatomical features. Finally, a comparison of the Anseriformes and Galliformes provides a perspective on the evolutionary derivation of the condition of these features in waterfowl.

MATERIALS AND METHODS

Specimens and Related Data

Criteria for Determination of Age.—Although none of the museum specimens studied herein was of known age in relation to hatching, we use the terms *chick*, *juvenile*, *immature* and *adult* as progressive stages of development based on size and degree of fusion of suturae cranii. Chicks are birds within a few days of hatching with fully evident suturae cranii. Juveniles are larger, even approaching full size, and their neurocranial suturae are variously unfused. Immatures are essentially full size with the suturae cranii fused except for those between the processes frontales of the ossa nasales and the neurocranium. In adults all neurocranial suturae are fused; only those between the processes nasales of the paired premaxillae may remain distinct. Adults often display a more robust skull than that of immatures.

Osteological Specimens.-Comparisons of adult skeletons of Galliformes and Anseriformes were based on the entire skeleton collection of USNM, as well as selected taxa from other museums (AMNH, BMNH, YPM). Taxa in which adult specimens were compared with one or more specimens of chicks, juveniles, or immatures are as follows: Galliformes: Megapodiidae-Megapodius freycinet, Leipoa ocellata; Cracidae—Ortalis vetula, Penelope jacuacu, P. superciliaris, P. purpurascens, Crax rubra, C. alector, C. fasciolata, Aburria pipile; Meleagrididae-Meleagris gallopavo; Tetraonidae-Lagopus lagopus, L. mutus, Tetrao tetrix, Bonasa bonasia, B. umbellatus, Centrocercus urophasianus; Phasianidae-Alectoris chukar, Francolinus adspersus, F. capensis, F. sephaena, F. pondicerianus, F. francolinus, Arborophila crudigularis, A. brunneopectus, Bambusicola thoracica, Ithaginia cruentatus, Lophura leucomelanos, Gallus domesticus, Crossoptilon crossoptilon, Catreus wallichii, Chrysolophus pictus, C. amherstiae, Pavo cristatus, P. muticus; Numididae-Numida meleagris; Odontophoridae-Callipepla squamata, Lophortyx californica, Colinus virginianus. Anseriformes: Anhimidae—Chauna torquata; Anatidae—Dendrocygna bicolor, Anser caerulescens, A. canagicus, Branta canadensis, B. bernicla, Cygnus atratus, C. bewickii, C. columbianus, Tachyeres pteneres, T. patachonichus, Tadorna radjah, T. tadorna, Casarca ferruginea, Chloephaga hybrida, C. picta, Heteronetta atricapillus, Oxyura jamaicensus, Anas platyrhynchos, Aythya americana, Somateria

mollisima, Histrionicus histrionicus, Melanitta perspicillata, M. fusca, Clangula hyemalis, Bucephala clangula, B. islandica, Mergus merganser, M. serrator.

Spirit Specimens.—Spirit specimens (adults unless specified) dissected for comparison of jaw muscles were as follows: Galliformes: Megapodiidae—Megapodius freycinet; Cracidae—Ortalis vetula; Meleagrididae—Meleagris gallopavo; Tetraonidae—Dendragopus canadensis; Phasianidae—Alectoris graeca, Gallus domesticus, Francolinus capensis; Numididae—Numida meleagris; Odontophoridae—Lophortyx gambelii. Anseriformes: Anhimidae—Chauna torquata; Anseranatidae—Anseranas semipalmata (chick); Anatidae—Dendrocygna bicolor (chick), D. autumnalis, Anser albifrons, Anas crecca, A. versicolor (chick), A. acuta (chick), Mergus merganser.

Nomenclature and Classification of Galliformes and Anseriformes

For the Galliformes, we adopted the families recognized by Sibley and Monroe (1990), except that we elevated the three major groups included by them in Phasianidae (Tetraonidae, Meleagrididae, and Phasianidae sensu stricto) to family rank, as accorded them by Peters (1934) and Wetmore (1951), and used by del Hoyo et al. (1994).

For purposes of reference in comparative descriptions, tables, and figures, we adopted the higher-order, phylogenetic classification of waterfowl proposed by Livezey (1997*a*-*b*). The essentials of this framework are as follows:

Order Anseriformes (Wagler, 1831).---Waterfowl

Suborder Anhimae Wetmore & Miller, 1926

Family Anhimidae Stejneger, 1885.—Screamers

Genus Anhima Brisson, 1760.—Horned screamer

Genus Chauna Illiger, 1811.—Crested screamers

Suborder Anseres Wagler, 1831.-True waterfowl

Superfamily Anseranatoidea (Sclater, 1880)

Family Anseranatidae (Sclater, 1880)

Genus Anseranas Lesson, 1828.—Magpie goose

Superfamily Anatoidea (Leach, 1820).—Typical waterfowl

†Family Presbyornithidae Wetmore, 1926

Genus Presbyornis Wetmore, 1926

Family Anatidae Leach, 1820.—True ducks, geese and swans

Myological Technique

Dissection of jaw musculature was performed by RLZ on one specimen of each taxon. The specimens, of varying age and provenance, had been fixed in formalin and preserved in alcohol. Attention was focussed on m. adductor mandibulae externus, the muscle most often associated with the cranial features of concern in this paper. Although this muscle is largely superficial and readily accessible, an understanding of its complexity could be gained only through knowledge of its internal structure of aponeuroses and associated muscle fibers. After illustrating the superficial aspect of the muscle, all fibers were removed systematically, leaving intact the complex of interdigitating, aponeurotic origins and insertions. The identity of the major aponeuroses (coronoidea, superficialis, zygomatica, paracoronoidea externa and interna, and articularis—Fig. 3) could then be determined in most instances and the different taxa compared. Uncertainties were resolved by inspection of the opposite muscle, usually with only partial dissection.

Anatomical Nomenclature

General Nomenclatural References.—Osteological and arthrological nomenclature, respectively, followed Baumel and Witmer (1993) and Baumel and Raikow (1993), much of which remained unchanged from the first code proposed by the International Committee on Avian Anatomical Nomenclature (ICAAN); in the latter, osteology was treated by Baumel (1979*a*), arthrology by Baumel (1979*b*), and myology by Vanden Berge (1979). The two codes prepared by the ICAAN were paralleled by standards for veterinary anatomists (Komárek, 1979; Komárek et al. 1982), which in turn were intended to stabilize names used most frequently by avian anatomists in recent decades (e.g., Bellairs and Jenkin, 1960; Berger, 1960, 1966). Osteological features labeled using ICAAN nomenclature were figured in substantial detail elsewhere (Butendieck, 1980; Butendieck and Wissdorf, 1982).

Myological Nomenclature.—Weber (1996) recently compiled a synonymy of terms used in major myological studies of the cranium and mandibula. In this paper, myological nomenclature (listed below) for parts of AME mainly follows Weber (1996), with any synonyms from Vanden Berge and Zweers (1993) given in parentheses:

M. adductor mandibulae externus (AME)

pars coronoidea (rostralis; temporalis, or

rostralis temporalis)

caput temporale

caput mediale

pars superficialis (lateralis)

pars zygomatica (ventralis; medialis)

pars articularis (profunda; caudalis)

caput interna caput externa

M. pseudotemporalis superficialis

M. adductor mandibulae posterior (adductor mandibulae caudalis)

M. depressor mandibulae

The parts of AME will be abbreviated throughout the paper as AME coronoidea, AME superficialis, AME zygomaticus, and AME articularis, and the heads of the latter as AME articularis internis and AME articularis externis.

The name m. adductor mandibulae posterior was used traditionally until the compilation by Vanden Berge (1979), in which the term "posterior" was changed routinely to "caudal." Under this nomenclatural convention, the name for this muscle became M. adductor mandibulae caudalis. However, recognizing the possibility of confusion with AME articularis (also called AME caudalis; see above), Vanden Berge and Zweers (1993) proposed a new name—"M. adductor mandibulae ossis quadrati"—while retaining "adductor mandibulae caudalis" as an acceptable alternative. We retain the traditional name (m. adductor mandibulae posterior) in the present study because it is used universally in the pertinent literature on galliforms and anseriforms.

Each of the parts of m. adductor mandibulae externus (AME) is built around one or more major aponeuroses (as well as some smaller, unnamed aponeuroses), an architecture first emphasized for establishment of homologies by Barnikol (1952) and that is evolutionarily conservative despite many adaptive modifications ZUSI AND LIVEZEY-CRANIUM OF GALLIFORMES AND ANSERIFORMES

among avian taxa exhibited in the avian jaw mechanism (Starck and Barnikol, 1954; Zusi, 1962; Dzerzhinsky and Podanova, 1974; Dullemeijer, 1951, 1952; Weber, 1996). We use the following designations for the aponeuroses of the parts of the AME, largely after Weber (1996):

AME coronoidea.—aponeurosis coronoidea and aponeurosis temporalis;

AME superficialis.—aponeurosis superficialis; Weber (1996) included AME superficialis under AME zygomatica, but we provisionally recognize it

here pending a broader comparison of avian taxa;

AME zygomatica.—aponeurosis zygomatica;

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AME articularis.—aponeurosis paracoronoidea externa, aponeurosis paracoronoidea interna, and aponeurosis articularis.

Arthrological Nomenclature.--With respect to nomenclature of ligaments and joints, we mainly follow Baumel and Raikow (1993). However, in reference to the complex of ligamenta included by those authors under the name "ligamentum postorbitale," we distinguish three separate ligamenta for purposes of this study, thereby formalizing the substantial variations in attachments noted for this complex (e.g., Lebedinsky, 1921; Zusi and Storer, 1969; Elzanowski, 1987; Jäger, 1990): ligamentum postorbito-mandibulare (connecting processus postorbitalis with the mandibula), ligamentum postorbito-jugale (connecting processus postorbitalis with the arcus jugalis), and ligamentum postorbito-zygomaticum (connecting processus postorbitalis with the processus zygomaticus). The last of these three names is synonymous with the "ligamentum zygomaticum" provisionally recognized by Elzanowski (1987) and Weber (1996). Although this complex is extremely variable among taxa and the included ligaments vary in discernability within the fascia temporalis in which they are sometimes imbedded (Hofer, 1950; Barnikol, 1953; Bas, 1954; Zusi, 1975; Elzanowski, 1987; Weber, 1996), we concluded that separate, completely descriptive names for these important ligamenta were critical for the clarity of comparative descriptions.

Osteological Nomenclature.—A term of long-standing in osteological nomenclature of most tetrapods is "fossa temporalis" or "temporal fossa," traditionally associated with the origin of AME coronoidea. However, among birds, this sometimes prominent feature of the regio temporalis marks the origins of more than one muscle. For this study, it was critical to ascertain by dissection the relationships of specific muscles associated with specific osteological features of the neurocranium, and in this context a vague term encompassing a series of distinct, nonhomologous states was not only useless but also misleading. Accordingly, the "fossa temporalis" of birds has relevance for comparative study only as a broad, topographic area—a variably differentiated site of origin for one or more unspecified mandibular muscles. For this reason, we propose the explicitly descriptive "fossa musculorum temporalium" (new term), for "fossa for muscles of the temporal region," as a replacement for the misleading, traditional name.

The fossa musculorum temporalium of a given species could comprise the impressiones deriving from one or more of four muscles—AME coronoidea, m. pseudotemporalis superficialis, AME articularis externus, and even m. depressor mandibulae; the term "impressio temporalis" was proposed by van Gennip (1986) for the scar of a portion of m. depressor mandibulae in the Rock Dove (*Columba livia*). In addition, included muscles may occupy different portions of the fossa without osteological delimitation of the subdivisions. We recommend reference to the impression of the pertinent muscle whenever it is known (e.g., impressio m. AME coronoidea).

ANNALS OF CARNEGIE MUSEUM

A more obscure term in avian osteology is "fossa subtemporalis" or "subtemporal fossa." Typically occupied by AME articularis externus, this concavity also has been cited as the position of origo m. depressor mandibulae (Baumel and Witmer, 1993). Some authors (e.g., Vickers-Rich et al., 1995) regarded the confluence of impressiones AME coronoidea and articularis as the temporal fossa in *Megalapteryx* (Dinornithiformes), worsening the ambiguity of the term with respect to the homologies of the impressiones involved. Consequently, we abandon the term fossa subtemporalis and refer to this feature using a directly descriptive alternative—impressio AME articularis.

Abbreviations Used To Label Figures

Abbreviations of anatomical terms used in the accompanying figures are listed below in alphabetical order:

AME art.-musculus adductor mandibulae externus, pars articularis

AME art. ext.—musculus adductor mandibulae externus, pars articularis, caput externa

AME art. int.---musculus adductor mandibulae externus, pars articularis, caput interna

AME cor.—musculus adductor mandibulae externus, pars coronoidea

AME sup.-musculus adductor mandibulae externus, pars superficialis

AME zyg.---musculus adductor mandibulae externus, pars zygomatica

apon. art.—aponeurosis articularis

apon. par. ext.-aponeurosis paracoronoidea externa

apon. par. int.--aponeurosis paracoronoidea interna

apon. cor.-aponeurosis coronoidea

apon. sup.-aponeurosis superficialis

apon. temp.—aponeurosis temporalis

apon. zyg.—aponeurosis zygomatica

apon. zyg. oss.—aponeurosis zygomatica ossificans

arcus jug.-arcus jugalis

arcus suborb.-arcus suborbitalis

crist. AME art.--crista musculi adductoris mandibulae externus, pars articularis

crist. zyg.—crista zygomatica

fos. mus. temp.-fossa musculorum temporalium

impr. AME art.---impressio musculi adductoris mandibulae externus, pars articularis

impr. AME cor.---impressio musculi adductoris mandibulae externus, pars coronoidea

lam. parasph.—lamina parasphenoidalis

lig. lac.-mand.—ligamentum lacrimo-mandibulare

lig. post.-mand.-ligamentum postorbito-mandibulare

lig. post.-zyg.—ligamentum postorbito-zygomaticum

lig. suborb.—ligamentum suborbitale

m. add. mand. post.—musculus adductor mandibulae posterior mand.—mandibula

meat. acust. ext.--meatus acusticus externus

orb.—orbita

os front.---os frontale

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os lacr.—os lacrimale os lat.-sphen.—os laterosphenoidale os par.—os parietale os squam.—os squamosum pr. otic. quad.—processus oticus quadrati pr. postorb.—processus postorbitalis pr. zyg.—processus zygomaticus regio temp.—regio temporalis rost. parasph.—rostrum parasphenoidale sut. front.-squam.—sutura fronto-squamosa sut. lat.-squam.—sutura laterospheno-squamosa tuber.—tuberculum

Concepts and Diagnosis of Homology

General Principles and Terms.—The concept of the homologue, first defined by Owen (1843) as "... the same organ in different animals under a variety of form and function" (fide Panchen, 1994), originated and principally remains within the context of comparative anatomy (Boyden, 1943, 1947; Patterson, 1982; Van Valen, 1982; Young, 1993; Sluys, 1996). Despite the antiquity and generally narrow context of the concept, the issue of homology and its practical application remain the subject of substantial controversy (Rieppel, 1980, 1992, 1994; Roth, 1984, 1988, 1991; Sattler, 1984). Subsequently, however, the concept and criteria for the diagnosis of homology have been recognized as equally vital and challenging for phylogenetic interpretation of characters as diverse as DNA sequences (Patterson, 1988; Mindell, 1991; Hillis, 1994; Brower and Schawaroch, 1996), proteins (Fitch, 1970), metric abstractions (Bookstein, 1994; Fink and Zelditch, 1995; Zelditch et al., 1995, 1998; Adams and Rosenberg, 1998; Rohlf, 1998; Swiderski et al., 1998; Zelditch and Fink, 1998), and behavioral repertoires (Wenzel, 1992; Greene, 1994). In that Owen (1843) originally contrasted "analogues"-phylogenetically independent structures having common functions in different taxa-from "homologues," it is not surprising that an emphasis on function persists in the diagnosis of homology and the utility of characters for phylogenetic reconstruction (Bock, 1967, 1977, 1979, 1989; but see Cracraft, 1981b). In its most essential form, the definition of homologues is structures having a common evolutionary origin (Simpson, 1959; Bock, 1963a); an important implication of this definition is that homologues would share ontogenetic bases (Wagner, 1989a-b, 1994; Goodwin, 1994; Hall, 1994, 1995).

These theoretical essentials of homology, however instructive, provide little in the way of practical methodology for the recognition of homologues in a phylogenetic context. In this work, we essentially applied the three classical criteria of Remane (1952, 1956): (1) similarity of position; (2) quality of resemblance (see also Inglis, 1966); and (3) continuance of similarity through intermediate forms (Wiley, 1981). Problems of homology do not increase necessarily with the complexity of the characters in question; in fact, structural detail often provides the distinctions essential to diagnosis of homology, rendering many anatomical systems more amenable to such determinations than simple features such as sequence data (Wägele, 1995; McShea, 1996).

Specific Criteria Applied.—Use of published descriptions of jaw muscles is complicated by different terminologies and different judgments about homologies.

We hypothesize homologies from similarity in external and internal structure of muscles, and location of muscles in relation to each other and to associated bony features. Within a phylogenetic context, inference of homology assumes an iterative nature, in which *a priori* assessments of homology can be questioned on the basis of the most parsimonious interpretation of the totality of evidence (Stevens, 1984; Bryant, 1989; de Pinna, 1991; Haszprunar, 1992, 1998; Lipscomb, 1992; Coddington, 1994; McKitrick, 1994; Brooks, 1996; Hawkins et al., 1997; but see Lauder, 1994). The confirmatory advantages of this process hinge on the validity of the delimitation of characters and composite states (Pogue and Mickevich, 1990; Barriel and Tassy, 1993). In this work, we emphasize the primary assessment of homology by comparative study, relegating most phylogenetic implications of this study to companion works (Livezey, 1997*a*, 1998).

Innervation is not included here because the muscles under discussion—parts of the AME—are supplied mainly by branches of nervus trigeminus mandibularis; this complex varies sufficiently within species (Barnikol, 1953, 1954) to suggest that data from single specimens could be misleading. Available information on the associated systema cardiovasculare (Baumel, 1993) also provided no critical, ancillary clues to homology of subdivisions of the AME (e.g., Richards, 1968).

Examination of crania of very young birds was critical for discernment of most or all suturae cranii. Therefore direct study of prepared skeletons and fluid-preserved specimens of juveniles was performed for as many relevant taxa as possible, supplemented by reference to the literature on the ontogeny of cranial elements and overlying musculature in a diversity of avian taxa (e.g., Edgeworth, 1907; Jollie, 1957; Hogg, 1978). Although all parts of the AME are derived from a single primordium (McClearn and Noden, 1988), the study of juveniles provided additional insight into the structure of AME in that parts of this complex were clearly separable even in early developmental stages.

Changes in aspects of osteological or myological features during development per se, however, were not used to infer directions of evolutionary change among taxa, but instead as a means for delimitation of homologous anatomical structures that are rendered less distinguishable in adults through variation in function and selection pressures (Hanken and Hall, 1993). The relevance of such information to the polarity of character states (i.e., the "ontogenetic criterion") remains controversial (Nelson, 1978; Alberch, 1985; de Queiroz, 1985; Kluge and Strauss, 1985; Kraus, 1987; Mabee, 1989, 1993; Wheeler, 1990; Williams et al., 1990; de Pinna, 1994; Meier, 1997). In the present paper, references to phylogenetic position and polarity were based on previous works in which outgroup comparisons were employed (Livezey, 1986, 1989, 1991, 1995*a*-*c*, 1996*a*-*c*, 1997*a*-*c*, 1998).

Pertinent Anatomical Issues

Processus Postorbitalis.—The processus postorbitalis usually arises from the caudolateral border of the orbita. With few exceptions, the processus postorbitalis is largely derived from the os laterosphenoidale, with variable contribution from the rostral portion of the os squamosum in most neognathous taxa. Typically the processus is oriented roughly perpendicularly to the long axis of the mandibula and it serves as origin for the ligamenta postorbito-mandibulare, postorbito-jugale, and ligamentum suborbitale, which extend ventrally to the mandibula and arcus jugalis and rostrally to the os lacrimale or os ectethmoidale, respectively. In some taxa, the complex of ligamenta arising from the processus postorbitalis includes,

in addition to the comparatively conspicuous ligamentum postorbito-mandibulare, a variably distinct component (ligamentum postorbito-zygomaticum) that attaches on the processus zygomaticus (Starck and Barnikol, 1954). The ligamenta arising from the processus postorbitalis may be slender or absent, and the processus postorbitalis correspondingly reduced.

Therefore the processus postorbitalis may support the complex comprising the ligamenta postorbitalia as well as the ligamentum suborbitale. These ligamenta ossify in some taxa such that, in adult birds, the processus postorbitalis may appear to be extended ventrally by dorsal ossification of the ligamentum postorbito-mandibulare, rostrally by partial or complete ossification of the ligamentum suborbitale, or caudally by ossification of the ligamentum postorbito-zygomaticum.

Processus Zygomaticus.—This processus of the os squamosum is located on the regio temporalis of the cranium between the processus postorbitalis and the meatus acusticus externus, in many taxa immediately rostral or dorsal to the meatus. Oriented rostroventrally, or sometimes extended laterally, it supports the aponeurosis zygomatica of AME zygomatica; in some taxa this aponeurosis becomes ossified at its base, effectively extending the processus. Although the AME zygomatica and aponeurosis zygomatica are usually present in birds, the processus zygomaticus may be absent or reduced to an indistinct crista in some taxa (e.g., Sulidae, Phalacrocoracidae, Ardeidae, Phoeniculidae).

Fossa Musculorum Temporalium.—Usually this impressio is occupied largely or wholly by the AME coronoidea in neognathous birds, but in paleognathous birds the area supports m. pseudotemporalis superficialis wholly or in part (Hofer, 1945; Webb, 1957; Elzanowski, 1987; Weber, 1996). Additional complexity of the muscles associated with this fossa were noted above.

Impressio AME Articularis.—This variably distinct depression, sometimes termed "fossa subtemporalis," lies caudal or ventral to the fossa musculorum temporalium in some taxa, and is partly delimited by the processus zygomaticus and the meatus acusticus externus. Occasionally it has been regarded as part of fossa musculorum temporalium. This impressio is occupied by AME articularis externus.

AME.—This complex muscle (Fig. 1, 3) arises variously from the fossa musculorum temporalium, processus zygomaticus, processus oticus quadrati, and impressio AME articularis in most birds. Pars coronoidea usually occupies part or all of the fossa musculorum temporalium and facies lateralis of aponeurosis temporalis and inserts on aponeurosis coronoidea of the mandibula. Pars zygomatica originates mainly from the medial surface of aponeurosis zygomatica and has a fleshy insertion on the lateral surface of the mandibula. Pars superficialis originates from the lateral surface of aponeurosis zygomatica and, in some taxa, from the fascia temporalis, ligamentum postorbito-mandibulare, and the ligamentum postorbito-zygomaticum. It inserts rostrally on aponeurosis superficialis and the adjacent mandibular surface. Caput interna of pars articularis originates from aponeurosis articularis and the processus oticus of os quadratum and inserts on aponeuroses paracoronoidea interna and externa and on the adjacent portion of the mandibula; some taxa have a caput externa of AME that originates from the impressio AME articularis and on part of the lateral surface of aponeurosis zygomatica, and inserts mainly on aponeurosis paracoronoidea externa and on the mandibula.

In the absence of the processus zygomaticus, we consider the point of attach-

ment of the aponeurosis zygomatica, which lies between the fossa musculorum temporalium and origo AME articularis, to be homologous among taxa. Although aponeurosis zygomatica is the major aponeurosis of AME zygomatica, it also receives fibers rostrolaterally from AME superficialis, dorsomedially from AME coronoidea, and ventrolaterally from AME articularis. Association with these three parts of the AME is characteristic of the aponeurosis zygomatica in various neognathous birds, whether the aponeurosis occurs as an extension of processus zygomaticus or originates from the cranium in the absence of the processus. Within a few orders (e.g. Pelecaniformes, Ciconiiformes, Coraciiformes, Passeriformes), the AME articularis externus and its impressio on the cranium are enlarged in some taxa, occupying a significant portion of the regio temporalis immediately caudal to fossa musculorum temporalium (Fiedler, 1951; Barnikol, 1952; Richards and Bock, 1973).

RESULTS

Processus Zygomaticus

Galliformes.—We found the processus zygomaticus to be present in most chicks and juveniles as an inconspicuous crista or tuberculum on the ventrolateral facies of os squamosum, between the processus postorbitalis and meatus acusticus externus (Fig. 4). The crista is typically oriented obliquely on a parasagittal plane along the ventral edge of os squamosum, and aponeurosis zygomatica arises from it as a flat band passing rostroventrally.

Anseriformes.---We found no clear evidence of a processus zygomaticus on the os squamosum in juveniles, immatures, or adults of many Anseriformes; in some taxa, however, a tuberculum on the crista of origin of the aponeurosis zygomatica at its caudal extremity may represent the processus (Fig. 5F). However, the conformation of the rostral portion of os squamosum resembles a processus in some juvenile anatids. Os squamosum borders the entire length of the processus postorbitalis at sutura laterospheno-squamosa in anhimids, and its basal (dorsal) onehalf in anatids. In most Anatidae, the processus postorbitalis is strongly angled rostroventrad, and sutura laterospheno-squamosa conforms to this orientation of the processus, as seen in immature specimens (Fig. 5). Furthermore, sutura frontosquamosa of anatids is located closer to the dorsal limit of the processus postorbitalis than in galliform birds, and in some anatids the sutura lies only slightly above the processus postorbitalis (Fig. 5). In the latter case, the dorsoventrally compressed, anterolateral facies of os squamosum, in combination with its sometimes pointed rostral extremity, offers a spurious resemblance to a processus zygomaticus in direct association with the processus postorbitalis.

Ossification of Aponeuroses

Galliformes.—Our survey of skeletal specimens of Galliformes of all age classes revealed that almost all chicks and juvenile specimens, and some immatures, lacked ossification of aponeurosis zygomatica as indicated by its absence from prepared skeletons. Occasional specimens of chicks and juveniles had tiny splints of ossified aponeurosis attached to the zygomatic process by syndesmosis or synostosis. By contrast, ossified portions of the aponeurosis were an integral part of most immature and all adult specimens of many galliform taxa (Fig. 4, 6).

During development, ossification of the aponeurosis begins basally and extends rostrad to the level of the processus postorbitalis or beyond, but never to the ZUSI AND LIVEZEY-CRANIUM OF GALLIFORMES AND ANSERIFORMES



Fig. 4.—Facies lateralis cranii of selected Galliformes: (A) *Leipoa ocellata* (USNM 346351), immature (Megapodidae); (B) *L. ocellata* (USNM 345086), adult (Megapodidae); (C) *Penelope jacquacu* (USNM 345564), immature (Cracidae); (D) *P. purpurascens* (USNM 613959), adult (Cracidae); (E) *Meleagris gallopavo* (USNM 611021), chick (Meleagrididae); (F) *M. gallopavo*, juvenile (USNM 501018); (G) *M. gallopavo* (USNM 556388), immature (Meleagrididae); and (H) *M. gallopavo* (USNM 556372), adult (Meleagrididae). Scale bar = 1 cm.

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Fig. 5.—Facies lateralis cranii of selected Anseriformes: (A) *Chauna torquata* (BMNH 1954-5-3), juvenile (Anhimidae); (B) Anatinae sp. (AMNH 8737), chick (Anatidae); (C) *Anas platyrhynchos* (BMNH 1986-48-1), juvenile (Anatidae); (D) *Clangula hyemalis* (AMNH 6046), juvenile (Anatidae); (E) *Dendrocygna bicolor* (USNM 501992), juvenile (Anatidae); and (F) *D. javanica* (USNM 343514), adult (Anatidae). Scale bar = 1 cm.

rostral extremity of the aponeurosis. The juncture of aponeurosis zygomatica ossificans with processus zygomaticus is usually synostotic, but occasionally the juncture is syndesmotic even in adults, indicating the limited extent of the processus. Typically, the aponeurosis zygomatica ossificans is markedly flattened lateromedially or in a ventrolateral-dorsomedial plane, but instead it may be irregular, with longitudinal plicae (e. g., *Aepypodius, Chauna*; Fig. 7). In the latter case, the delimitation of the processus from a stout, ossified aponeurosis in adults



Fig. 6.—Diagrams of the typical arrangement of the aponeurosis zygomatica of: (A) a generalized neornithine bird; (B) a galliform; (C) an anhimid; and (D) a member of the Anseres. Membranous portion is cross-hatched, ossified portion is shown in black.

is more difficult, but the longitudinal patterning of robust and complicated aponeuroses is continuous with their ossified portion (Zusi, personal observation). Although no juvenile of *Aepypodius* was examined, we compared adults of *Alectura lathami* with the illustration of a juvenile (Weber, 1996:fig. 3). The aponeurosis zygomatica ossificans of adult *A. lathami* resembles that of *Aepypodius*, but the processus zygomaticus of the juvenile is a robust tuberculum as in other megopodes. Aponeurosis zygomatica, whether or not ossified, may have no connection with the processus postorbitalis (Megapodiidae). However, in most taxa this aponeurosis is anchored to the processus by a connection with ligamentum postorbito-zygomaticum, which is ossified in adults of most galliforms (Phasianidae, Tetraonidae, Meleagrididae, Odontophoridae, and some Cracidae).

Anseriformes.—In the anhimid Chauna, the aponeurosis zygomatica has a linear attachment along lamina lateralis cranii from a point rostral to meatus acusticus externus to, or nearly to, the processus postorbitalis, where the aponeurosis passes medial or ventromedial to the terminus of the processus (Fig. 7). Rostral to the processus postorbitalis, the aponeurosis is free from the cranium (Fig. 6). In adults the aponeurosis is ossified to a point level with, or more often, rostral



Fig. 7.—Facies rostrolateralis cranii (A) and facies lateralis cranii (B-E) of adult specimens of: (A, B) *Chauna torquata* (USNM 614547), (Anseriformes: Anhimidae); (C) *Anseranas semipalmata* (USNM 347638), (Anseriformes: Anseranatidae); (D) *Sarkidiornis melanotos* (USNM 490276), (Anseriformes: Anatidae); and (E) *Aepypodius arfakensis* (YPM 7594), (Galliformes: Megapodiidae). Scale bar = 1 cm.

to the processus postorbitalis, but as in galliform birds, the rostral-most portion of the aponeurosis does not ossify.

Anatids show little or no ossification of aponeurosis zygomatica (Fig. 6). The caudal-most portion of the aponeurosis arises on the cranium from the rostral limit of impressio AME articularis or sometimes within the impressio, and continues rostrad along a linea or weak crista as far as the apex of the processus postorbitalis; beyond the processus the aponeurosis extends rostroventrad toward the mandibula, independent of the cranium. Ossification, if any, produces a low, irregular crista (crista zygomatica) where the aponeurosis meets the cranium (Fig. 6).

Processus Postorbitalis and Processus "Sphenotemporalis"

Galliformes.—The processus postorbitalis of Galliformes is well developed, straight, and oriented approximately ventrad or somewhat rostrad, and continuous with the margo (rima) caudalis of the orbita. The processus arises largely from the os laterosphenoidale, and meets os squamosum only at its dorsal limit. The ligamentum postorbitale-mandibulare is strong and unossified except at its extreme dorsal limit in some Tetraonidae.

Anseriformes.—In the Anhimidae, the processus postorbitalis is not well defined as a process in lateral view, but in rostral perspective it constitutes a ventrally directed hook of os laterosphenoidale (Fig. 7). Caudal to the apex of the processus postorbitalis, the lamina lateralis cranii is undercut ventrally, forming an overhanging crest that extends caudodorsally from the processus postorbitalis. Dorsal to this crista AME articularis (new term), the regio temporalis forms a wedgeshaped area defining an angle of 60–70° and delimited by the caudal contour of the orbita and by crista AME articularis (Fig. 7). Dzerzhinsky (1982) termed this wedge the "sphenotemporal process." Aponeurosis zygomatica lies adjacent and medial to crista AME articularis, arising along the facies medialis of the crista as far as the apex of the processus postorbitalis, to which it passes ventromediad.

The skull of a large anhimid chick (*Chauna*) exhibits a sutura laterosphenosquamosa that borders the processus postorbitalis for almost its full length. By contrast, in chicks and immatures of the Anatidae, os squamosum borders only the base of the processus postorbitalis (Fig. 5). A processus zygomaticus is not visible in any anseriform, and the aponeurosis zygomatica takes its caudalmost point of origin well caudal to the processus postorbitalis (Fig. 6). These facts suggest that the "sphenotemporal" process was formed (in an evolutionary sense) not by fusion of processes, but more likely by medial retreat of impressio AME coronoidea and rostral extension of origo aponeurosis zygomatica to the processus postorbitalis.

Anseres differ from anhimids in several respects. First, the processus postorbitalis of os laterosphenoidale extends well beyond os squamosum (Fig. 5). Second, the processus postorbitalis usually extends rostrad to form the caudoventral margin of the orbita, and the sutura laterospheno-squamosa often is angled correspondingly. Third, the homologue of the crista AME articularis of anhimids is not a well-defined crest in Anseres (except *Anseranas*), but rather a faint linea or crest extending caudad from margo caudoventralis of the processus postorbitalis roughly parallel to crista zygomatica and continuous with the margo dorsalis of impressio AME articularis. Aponeurosis zygomatica attaches just medial or ven-

ANNALS OF CARNEGIE MUSEUM



Fig. 8.—Detailed illustrations of the AME complex (left lateral views) of: (A) Ortalis vetula (USNM 344381), adult (Galliformes: Cracidae); (B) Alectoris graeca (USNM 540255), adult (Galliformes: Phasianidae); (C) Chauna torquata (USNM 508682), adult (Anseriformes: Anhimidae); (D) Anseranas

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tromedial to crista AME articularis (Fig. 6, 7). Fourth, the aponeurosis zygomatica is unossified or forms only a roughened crista along its origin on os squamosum.

M. Adductor Mandibulae Externus

Our findings on the structure of AME in terms of muscle fibers and aponeuroses agree essentially with those of Weber (1996) for the Megapodiidae, Dzerzhinsky (1980) for the Cracidae, and Dzerzhinsky and Belokurova (1972) for the Tetraonidae. Also, our inferences concur in large part with those by Davids (1952) and Zweers (1974) for the Anatidae, and with those by Dzerzhinsky (1982) for the Anhimidae. However, our interpretations of homology of muscle parts differ from the conclusions of those authors to varying degrees.

We applied the following anatomical generalizations derived from the literature on avian jaw musculature to the interpretation of structure in Galliformes and Anseriformes: (a) muscle fibers from all four parts of AME originate on aponeurosis zygomatica in the Galliformes, Anseriformes, and other avian orders (Fig. 3); (b) by contrast, fibers to aponeurosis superficialis represent largely AME superficialis, those to aponeurosis coronoidea represent mainly AME coronoidea, and those to aponeuroses paracoronoidea externa and interna represent primarily AME articularis; (c) some fibers of AME superficialis are inseparable from some fibers of AME coronoidea and AME zygomatica; and, (d) similarly, fibers of AME zygomatica blend with those of AME articularis. Based on the above conventions, we conclude that AME articularis is much enlarged in galliform and anseriform birds, and that AME zygomatica and AME superficialis are thereby displaced rostrally (Fig. 8). Although our interpretations differ radically from those of Lakjer (1926) and his followers (see below and Table 1), they agree substantially with those of Dzerzhinsky (1982) and Weber (1996).

In anseriforms, AME superficialis and AME zygomatica are distinct and typical in form except that both arise from aponeurosis zygomatica rostral to its attachment on the processus postorbitalis, and from an additional, short aponeurosis arising on that processus. Unique to adult specimens of *Dendrocygna* is an ossified ligamentum suborbitale, a structure fused with the tip of the processus postorbitale and os lacrimale, and forming an arcus suborbitalis (Shufeldt, 1914; Schiøler, 1926; Livezey, 1995b). In adults, some fibers of AME superficialis arise from the arcus rostral to the processus postorbitalis (Fig. 8).

The interpretation of homologies within galliformes is clouded by certain specializations. AME superficialis and AME zygomatica are variously developed or merged within Galliformes, but, except for the Megapodiidae, their origins from aponeurosis zygomatica are supported by the processus postorbitalis, as they are in the anseriforms. These combined muscle parts blend also with AME articularis externus in phasianid galliforms. Commensurate with the blending of muscle parts are modifications of aponeuroses superficialis and paracoronoidea externa, which form a continuous sheet that inserts along the facies lateralis of the mandibula

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semipalmata (USNM, uncataloged), chick (Anseriformes: Anseranatidae); (E) *Dendrocygna bicolor* (CM 2117), chick (Anseriformes: Anatidae); (F) *D. autumnalis* (CM 5247), adult (Anseriformes: Anatidae); (G) *Anas versicolor* (USNM 345162), chick (Anseriformes: Anatidae); and (H) *Anas acuta* (USNM 225218), chick (Anseriformes: Anatidae), with AME superficialis, zygomatica, and articularis externa removed. Scale bar = 5 mm.

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Non-an	seriform birds	Anseri	form birds
Lakjer (1926) ^a	Present study ^b	Lakjer (1926) ^c	Present study ^d
III profundus ^e I superficialis	AME coronoidea AME superficialis	[absent] I superficialis a	AME articularis externus
III profundus ^f II medialis	AME articularis AME zygomatica	I superficialis b I superficialis c III profundus II medialis	AME zygomatica AME superficialis AME articularis internus AME coronoidea
Starck and Barnikol (1954) ^g	Present study ^b	Starck and Barnikol (1954) ^h	Present study ^d
Aponeurosis 1 portion	AME coronoidea	Aponeurosis 1 portion (right) Aponeurosis 1 portion (middle)	AME articularis externus (part) AME zygomatica
		Aponeurosis 1 portion (left)	AME superficialis et coronoidea
Aponeurosis 2 portion	AME zygomatica et superficialis	Aponeurosis 2 portion	AME articularis externus (part)
Aponeurosis 3 portion	AME articularis internus et externus	Aponeurosis 3 portion	AME articularis internus

Table 1.—Anatomical nomenclatures applied to the m. adductor mandibularis externus complex(AME) of selected non-anseriform and anseriform birds by Lakjer (1926), Starck and Barnikol (1954),
and the present study.

^a Cepphus grylle.

^b Cepphus grylle.

^c Melanitta nigra.

^d Anseranas semipalmata, Dendrocygna bicolor, D. autumnalis, Anser albifrons, Anas versicolor, and A. acuta.

^e Labelled "rostr" in some figures.

f Labelled "kaud" in some figures.

^g Various non-passeriform taxa.

^h Anas platyrhynchos.

and merges with aponeurosis paracoronoidea interna in at least some members of all galliform families.

Impressio AME Coronoidea

Galliformes.—The impressio AME coronoidea is variable in size but always limited in extent among galliform birds, and it occupies the lamina lateralis cranii between the processus postorbitalis and processus zygomaticus. In many taxa, but most prominently in the Megapodiidae, the fossa is barely perceptible in lateral view and the impressio is rotated mediad, occupying portions of ossae squamosum and laterosphenoidale (Fig. 4, 7, 9). In those taxa characterized by an ossified ligamentum postorbito-zygomaticum, the fossa is partially enclosed laterally (Fig. 4).

Anseriformes.—Most waterfowl lack a laterally exposed impressio AME coronoidea. Instead, the impressio occupies a comparatively medial position, and is largely or completely overhung by crista AME articularis (Anhimidae, Anseranatidae) or crista zygomatica (most Anatidae). From a ventrolateral perspective, impressio AME coronoidea is visible at the junctura of the os squamosum and 2000



Fig. 9.—Facies lateralis cranii (A, B) and facies ventrolateralis cranii (C, D) of: (A, B) *Mergus merganser* (USNM 555255), adult, (Anseriformes: Anatidae), showing fossa musculares temporalis and (B) origins of AME coronoidea (horizontal hatching) and AME articularis (vertical hatching), inferred through dissection of USNM 505780; (C) *Meleagris gallopavo* (USNM 501018), juvenile (Galliformes: Meleagrididae); and (D) *Anas platyrhynchos* (BMNH 1986·48·1), juvenile (Anseriformes: Anatidae). Scale bar = 1 cm.

os laterosphenoidale, between the tip of the processus postorbitalis and impressio AME articularis (Fig. 9).

In most members of Anatidae, impressio AME coronoidea extends to the tip of processus postorbitalis as a ventrolaterally directed planum. Processus postorbitalis is variably reduced in size and more ventrally directed within Mergini, and exhibits a corresponding reduction in its involvement with impressio AME coronoidea. Only in *Lophodytes*, *Mergellus*, and *Mergus* (Mergini) is impressio AME coronoidea largely free from the processus postorbitalis and fully exposed in lateral view, where it merges imperceptibly with impressio AME articularis (Fig. 9). A less extreme but similar condition occurs in *Biziura* (Oxyurini). In these birds, crista zygomatica is much reduced in prominence. However, it is likely that AME coronoidea is obstructed largely or completely in lateral view by AME articularis in all Anseriformes.

Impressio AME Articularis

Galliformes.—Usually, this impressio is small or absent in gallinaceous birds (Fig. 9). The AME articularis originates extensively from the portions of aponeurosis zygomatica that lie both caudal and somewhat rostral to the processus postorbitalis, whether or not the aponeurosis is ossified (Fig. 8). Although AME articularis is enlarged, it does not expand dorsally on the regio temporalis as mentioned above for some other avian taxa.

Anseriformes.—The impressio AME articularis is small and located medially in Anhimidae and Anseranatidae, but the AME articularis expands rostrally along aponeurosis zygomatica as in Galliformes. Most Anatidae have a small- to medium-sized impressio AME articularis (Fig. 5, 7). When small, the fossa occupies the cranium between the caudal attachment of aponeurosis zygomatica and the meatus acusticus externus as in some Galliformes. Anseres resemble galliforms and anhimids in their relatively large AME articularis, which attaches rostrad along the caudal section of aponeurosis zygomatica to the processus postorbitalis. In addition, crista AME articularis gives rise to a superficial aponeurosis that extends rostrad, roughly parallel and dorsal to the linear origin of aponeurosis zygomatica. The narrow area between the lines of origin of these aponeuroses constitutes a rostral expansion of impressio AME articularis.

In some anatids (e.g., *Mergus merganser*), the impressio also expands dorsally and crista zygomatica is much reduced; thus, the fossa includes impressio AME coronoidea rostrally and impressio AME articularis caudally (Fig. 9). As there is no linea separating these adjacent muscle scars in *Mergus*, the single fossa is best referred to as fossa musculorum temporalium in this genus. Also, we could not confirm the finding of Goodman and Fisher (1962) that AME coronoidea (their AME medialis) occupies the entire fossa.

DISCUSSION

Homology of Processus Zygomaticus

Among the Galliformes, the processus zygomaticus is represented by an indistinct boss or crista. The processus is separated from the processus postorbitalis, and in many taxa the aponeurosis zygomatica is supported by the processus postorbitalis through ligamentum postorbito-zygomaticum (ossified or unossified). Anseriformes are characterized by the absence of a distinct processus zygomaticus, but the homologous locus may be marked by a tuberculum. However, waterfowl also are characterized by the extended origin of aponeurosis zygomatica along a linea or crista extending from impressio AME articularis rostrad toward or to the processus postorbitalis. Thus, in both the Galliformes and Anseriformes, processus zygomaticus (or its homologous locus) lies caudal to the processus postorbitalis.

This interpretation is contrary to the description by Dzerzhinsky (1982, 1995) of a processus "sphenotemporalis" in Anseriformes and its evolutionary derivation by fusion of the processus zygomaticus (or ossified aponeurosis zygomatica). with the processus postorbitalis. Our interpretation is influenced by the following facts pertaining to Anseriformes: (a) much of processus postorbitalis is formed exclusively from the os laterosphenoidale, a composition typical of many avian orders; (b) there is no indication of a processus zygomaticus (much less a long one) or an ossified aponeurosis zygomatica in skulls of juvenile, immature, or adult Anseres; and, (c) an ossified aponeurosis zygomatica in anhimids fuses with 2000

os squamosum mainly caudal to processus postorbitalis, and in some specimens passes medial or ventromedial to the apex of that processus. These distinctions, although subtle, permit a more precise definition of homologous characters.

Evolution of Unique Anseriform Morphology

We found little evidence favoring any single ontogenetic or evolutionary mechanism that would best explain the probable transformation to anseriform morphology from that of a common ancestor with galliforms. However, two such hypotheses could be modelled after morphological states represented among the galliform taxa we examined: (a) reduction and medial rotation of impressio AME coronoidea and development of an overhanging crista (Megapodiidae); (b) reconfiguration of the position or shape of the processus zygomaticus or ossified aponeurosis zygomatica (and/or processus postorbitalis) to constrict the impressio AME coronoidea (*Coturnix*). A third hypothesis—ossification of the aponeurotic surface of AME coronoidea, thereby closing the fossa musculorum temporalium—was not reflected in the morphology of any galliform examined.

Interpretation of Adductor Mandibulae Externus

Here we compare our interpretation of muscle homologies with those of authors who have studied not only Galliformes and Anseriformes, but also a variety of other orders. Terminology applied by each author to jaw muscles in taxa whose structure is non-controversial provided the key to understanding their concepts of muscle homologies in the more problematic Galliformes and Anseriformes.

In order to facilitate comparisons with the published works that disagree most markedly with our interpretation of the myology of anseriforms, we present a synonymy for the nomenclature applied to the AME by Lakjer (1926) and Starck and Barnikol (1954), based on taxa for which their interpretations of the muscles agree with those presented here (Table 1). We also show the interpretations of both authors concerning the AME in the Anatidae, using both their terminology and ours to highlight the differences in interpretation (Table 1). Lakjer (1926) did not distinguish between AME articularis externus and internus. In essence, Lakjer grouped our AME articularis externus, zygomaticus, and superficialis into AME superficialis, and he considered AME coronoidea to be absent. Starck and Barnikol (1954) synonymized our AME superficialis as part of AME zygomatica. They combined our AME articularis externus (rostral portion), AME zygomaticus, AME superficialis, and AME coronoidea into AME coronoidea. Their AME zygomaticus is our AME articularis externus (caudal portion). These studies postulate an expansion and diversification of AME superficialis (Lakjer, 1926) or AME coronoidea (Starck and Barnikol, 1954), whereas we hypothesize an expansion of AME articularis externus and a rostral displacement of AME zygomaticus and superficialis.

Dzerzhinsky (1982, 1995) identified muscle fibers that interconnect aponeuroses zygomatica and paracoronoidea externa as AME superficialis rather than AME articularis, and Weber (1996) regarded these same fibers as AME zygomatica (which subsumes AME superficialis). Since these fibers are already incorporated within a well-defined block of muscle tissue associated with aponeurosis paracoronoidea externa in chicks of several Anseres (Fig. 8), we think it more likely that the fibers in question represent AME articularis externus. Starck and Barnikol (1954:12) included comparable fibers with AME articularis (their Ap. 3 portion)

Taxon	Processus zygomaticus	Crista zygomatica ^a	Fossa musculi temporales ^b	Impressio AME articularis ^c
Galliformes				
Megapodiidae	Small or absent	Absent	Partly medial and lateral (latter small)	Small or absent
Cracidae	Small or absent	Absent	Lateral (moderate)	Small or absent
Phasianidae	Small or absent	Absent	Lateral (moderate)	Small or absent
Anseriformes				
Anhimidae	Absent	Present	Entirely medial	Small, medial
Anseranatidae	Absent	Present	Entirely medial	Small, lateral
Anatidae	Absent	Present	Typically medial	Small, lateral

Table 2.—Distribution of states of osteological characters associated with the AME complex in selected taxa of Galliformes and Anseriformes, based on the present study.

^a From processus postorbitalis.

^b Broadly equivalent to the "fossa temporalis" as traditionally defined (see text).

^c Broadly equivalent to the "fossa subtemporalis" of some authors (see text).

in *Buteo buteo* (Accipitridae). Under our interpretation it follows that, in Galliformes and Anseriformes, the origins of AME superficialis and AME zygomatica are displaced to the portion of aponeurosis zygomatica rostral to the processus postorbitalis, and their insertions typically are restricted to the mandibula rostral to aponeurosis paracoronoidea externa.

Burton (1984) made comparisons between the AME of the Phoeniculidae (Coraciiformes) and Anseriformes with special reference to portions originating on the processus postorbitalis. He referred to these portions in both orders as the "postorbital lobe" and suggested that the lobes were homologous and plesiomorphous in the two orders. His "postorbital lobe" in Anseriformes equates to our AME superficialis and AME zygomatica. However, we found that AME zygomatica lies caudal to the "postorbital lobe" in *Phoeniculus*. Caput mediale of AME coronoidea has not been discussed previously in this paper because it is not present in the Galliformes and Anseriformes, but it occurs in Coraciiformes and other avian orders (Richards and Bock, 1973; Burton, 1984). The "postorbital lobe" of *Phoeniculus* may include elaborations of AME coronoidea medialis and AME superficialis.

Interpretations of Characters and Phylogenetic Implications

Alternative Views of Characters, States, and Ordering.—Although a phylogenetic analysis incorporating the anatomical information described herein is beyond the scope of this paper, the comparisons provide a framework for partitioning the Galliformes and Anseriformes into several broad taxonomic groups (Tables 2-3). Although most characters differ in the specific groupings suggested, most are hierarchically consistent with each other; i.e., one character suggests a nested subdivision of groups implied by another character (Table 3). Also, some characters are redundant; e.g., complementarity of fossa musculorum temporalium (Table 2) vs. origo AME coronoidea (Table 3).

Livezey (1997*a*) included one multistate, composite character (Appendix 1: character 8) that was intended to summarize the anatomical changes described herein (Table 3), one that emphasized the pattern of apparent changes in the cranial skeleton (notably orientation of processus postorbitalis and prominence of

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Table 3.—Distrib	ution of states of n	nyological an taxa	d arthrological chu of Galliformes an	aracters associ d Anseriforme.	ated with the . s, based on th	AME (m. adı e present stı	ductor mandı ıdy.	bulae externus)	complex in selected
Order	Family	Ligamentum postorbito- mandibulare	Ligamentum postorbito- zygomaticum	Ossification aponeurosis zygomatica	Aponeurosis articularis	Origo AME superficialis	Origo AME zygomatica	Origo AME coronoidea	Origo AME articularis
Galliformes	Megapodiidae	Vertical	Absent	Variable	Strong	Rostral ^a	Rostral ^a	Lateral and medial	Rostrad to pro- cessus postor- bitalis ^b
	Cracidae	Vertical	Present, ossi- fied or unos- sified	Ossified	Strong	Rostral ^a	Rostral ^a	Lateral	Rostrad to pro- cessus postor- bitalis ^b
	Phasianidae	Vertical	Present, ossi- fied	Ossified	Strong	Rostral ^a	Rostral ^a	Lateral	Rostrad to pro- cessus postor- bitalis ^b
Anseriformes	Anhimidae	Vertical	Absent	Ossified	Moderate	Rostral ^a	Rostral ^a	Medial	Rostrad to pro- cessus postor- bitalis ^b
	Anseranatidae	Angled caudad	Absent	Unossified	Weak	Rostral ^a	Rostral ^a	Medial	Rostrad to pro- cessus postor- bitalis ^b
	Anatidae	Angled caudad	Absent	Unossified	Weak	Rostral ^a	Rostral ^a	Medial	Rostrad to pro- cessus postor- bitalis ^b

^a I.e., origin at point parallel or rostral to apex of processus postorbitalis, a condition rare in other taxonomic groups of Aves. ^b Rostral extension of origo AME articularis unknown in other taxonomic groups of Aves. processus zygomaticus). Nomenclatural differences between this earlier character description and the present study aside, and in spite of the fact that the earlier character description was based primarily on assessments of prepared skulls, the four states delimited are consistent with the broad groupings substantiated by the present study (Tables 2-3). Furthermore, it should be noted that ordering of the previous coding scheme was not analytically influential, and the character had a consistency index of 1.0 whether or not the four states were treated *a priori* as ordered (Livezey, 1997*a*:420). Also, in the final phylogenetic hypotheses, the ordering implied by the sequence of states was preserved (Table 3), an ordering that confirmed the general primitive-derived sequence implied by the summary classification (Galliformes, Anhimidae, Anseranatidae, and Anatidae).

A majority of recent phylogenetic studies indicate that the basal polarities (primitive states) of these anatomical characters for the Galliformes and Anseriformes (Tables 2-3) are sought most reliably among the paleognathous birds (Cracraft, 1988; Livezey, 1997a; Groth and Barrowclough, 1999). Although detailed anatomical descriptions of these features among paleognaths are beyond the scope of the present study, several published works (Bock, 1963b; Elzanowski, 1987; Weber, 1996) provide a basis for some preliminary comparative comments. Presence of a strong processus zygomaticus in close proximity to the os quadratum is diagnostic for paleognaths, suggesting that the reduction of the processus and its disassociation from the os quadratum represent a synapomorphy of neognathous birds (including Galliformes and Anseriformes). Similarly, the well-defined AME articularis found in most neognaths is probably apomorphic relative to its absence or minimal development in paleognaths. The distinctive pattern of development of AME articularis described in this paper apparently is derived relative to its usual form in other neognaths; the pattern includes enlargement of AME articularis by expansion rostrally along aponeurosis zygomatica and along the mandibula, and rostral displacement of AME zygomatica and AME superficialis.

Given these provisional inferences of polarity, the details of interpretation of the anatomical states described (Table 3) have little or no impact on coding schemes. All of the alternative interpretations of the plausible evolutionary events that underlie these anatomical patterns considered here are consistent with the four-state coding scheme used by Livezey (1997*a*), and most would permit any of several alternative coding schemes (e.g., separate, binary characters treating changes in three to five of the osteological or myological features involved). Moreover, even the evolutionary interpretation proposed by Dzerzhinsky (1982)—including the disputed hypothesis of the "sphenotemporal process"—would be consistent with most or all of these alternative coding schemes, necessitating only a revision of the accompanying descriptions of character states. This "transparency" of evolutionary interpretation in the coding of this character complex is substantiated by the fact that an earlier draft of the description for this character by Livezey (1997*a*) was based in large part on the interpretation by Dzerzhinsky (1982), wherein the allocation of states among taxa was conserved.

Implications for Interordinal Relationships.—Data presented herein regarding the skeleton and musculature associated with the AME complex (Table 3) and provisional inferences of polarity based on the literature (Elzanowski, 1987; Dzerzhinsky, 1999) support (i.e., confirm without homoplasy) a sister relationship between the orders Galliformes and Anseriformes, as proposed in earlier anatomical assessments by Dzerzhinsky (1982, 1995) and Livezey (1997*a*). This proposal has been favored by a number of authorities for decades (e.g., Delacour, 1954; 2000

Johnsgard, 1965), and is gaining support from recent morphological (Cracraft, 1988; Livezey, 1997*a*; Müller and Weber, 1998) and molecular analyses (Cracraft, 1981*a*; Cracraft and Mindell, 1989; Caspers et al., 1997; Groth and Barrowclough, 1999). Further insights into this interordinal group, and the morphological transformations which support this complex, may be gained through the continued study of several fossil taxa recently inferred to be allied with the Anseriformes—the Diatrymidae (Andors, 1992) and Dromornithidae (Murray and Megirian, 1998).

At least two cranial characters—absence of the ligamentum postorbito-zygomaticum, and medial displacement of impressio AME coronoidea—suggest that megapodes possess a morphotype intermediate to the condition typical of most Galliformes and that observed in modern Anseriformes. An "intermediate" condition of this complex in the Megapodiidae relative to other Galliformes is consistent with the majority view regarding it as the likely sister group of other Galliformes (review by Crowe, 1988). These conclusions can be tested by broader comparative studies within Aves (e.g., Livezey, 1997*a*), especially those emphasizing detailed comparisons of new character complexes and intensive sampling of Galliformes and Anseriformes.

ACKNOWLEDGMENTS

This research was supported by National Science Foundation (NSF) grant BSR-9396249 to Livezey, NSF grant DEB-9815248 to Livezey and Zusi, and National Museum of Natural History grant RI85337000 to Zusi. We thank the curators of the following museums for permitting study of their collections or for lending specimens: U.S. National Museum of Natural History (USNM), American Museum of Natural History (AMNH), The (British) Natural History Museum (BNMH), Carnegie Museum of Natural History (CM), and Yale Peabody Museum (YPM). W. Boles donated a chick of *Anseranas* from The Australian Museum (Sydney) to USNM in support of this work. Original illustrations in Figures 2, 4, 5, 7, and 9 were executed by Susan Escher; others were drawn by Zusi. Personnel of the Office of Imaging, Printing, and Photographic Services of the USNM assisted with the digitizing of plates for labelling and reproduction. Finally, we are grateful for the helpful comments provided by three anonymous reviewers of this paper.

LITERATURE CITED

- ADAMS, D. C., AND M. S. ROSENBERG. 1998. Partial warps, phylogeny, and ontogeny: a comment on Fink and Zelditch (1995). Systematic Biology, 47:168–173.
- ALBERCH, P. 1985. Problems with the interpretation of developmental sequences. Systematic Zoology, 34:46–58.
- ANDORS, A. V. 1992. Reappraisal of the Eocene groundbird *Diatryma* (Aves: Anserimorphae). Pp. 109–125, *in* Papers in Avian Paleontology Honoring Pierce Brodkorb (K. E. Campbell, Jr., ed.). Contributions in Science No. 330. Natural History Museum of Los Angeles County, Los Angeles, California.
- BAMS, R. A. 1956. On the relation between the attachment of jaw muscles and the surface of the skull in *Podiceps cristatus* L., with some notes on the mechanical properties of this part of the head. Parts I–IV. Verhandlingen der Koninklijke Nederlandse Akademie van Wetenschappen (Series C), 59:82–101, 248–262.
- BARNIKOL, H. A. 1952. Korrelationen in der Ausgestaltung der Schädelform bei Vögeln. Gegenbaurs Morphologisches Jahrbuch 92:373–414.

—. 1953. Vergleichend anatomische und taxonomisch phylogenetische Studien am Kopf der Opisthocomiformes, Musophagidae, Galli, Columbae und Cuculi. Ein Beitrag zum *Opisthocomus*-Problem. Zoologische Jahrbücher Systematische, 81:487–526.

— 1954. Zur Morphologie des Nervus trigeminus der Vögel unter besonderer Berücksichtigung der Acciptres, Cathartidae, Striges und Anseriformes. Zeitschrift für Wissenschaftliche Zoologie, 157:285–332.

BARRIEL, V., AND P. TASSY. 1993. Characters, observations and steps: comment on Lipscomb's "Parsimony, homology and the analysis of multistate characters." Cladistics, 9:223–232. BAS, C. 1954. On the relation between the masticatory muscles and the surface of the skull in Ardea cinerea L. Part I. Verhandlingen der Koninklijke Nederlandse Akademie van Wetenschappen (Series C), 57:678–685.

———. 1955. On the relation between the masticatory muscles and the surface of the skull in Ardea cinerea L. Parts II–III. Verhandlingen der Koninklijke Nederlandse Akademie van Wetenschappen (Series C), 58:101–108, 109–113.

- BAUMEL, J. J. 1979. Osteologia. Pp. 53–121, *in* Nomina Anatomica Avium (J. J. Baumel, A. S. King, A. M. Lucas, J. E. Breazile, and H. E. Evans, eds.). Academic Press, London, United Kingdom.
 ——. 1979. Arthrologia. Pp. 123–174, *in* Nomina Anatomica Avium (J. J. Baumel, A. S. King,
- A. M. Lucas, J. E. Breazile, and H. E. Evans, eds.). Academic Press, London, United Kingdom.
 ——. 1993. Systema cardiovasculare. Pp. 407–475, *in* Handbook of Avian Anatomy: Nomina Anatomica Avium, Second edition (J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge, eds.). Nuttall Ornithological Club, Cambridge, Massachusetts.
- BAUMEL, J. J., AND R. J. RAIKOW. 1993. Arthrologia. Pp. 133–188, *in* Handbook of Avian Anatomy: Nomina Anatomica Avium, Second edition (J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge, eds.). Nuttall Ornithological Club, Cambridge, Massachusetts.
- BAUMEL, J. J., AND L. M. WITMER. 1993. Osteologia. Pp. 45–132, in Handbook of Avian Anatomy: Nomina Anatomica Avium, Second edition (J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge, eds.). Nuttall Ornithological Club, Cambridge, Massachusetts.
- BEDDARD, F. E. 1898. The Structure and Classification of Birds. Longmans, Green, and Company, London, England.
- BELLAIRS, A. D'A., AND C. R. JENKIN. 1960. The skeleton of birds. Pp. 241–300, *in* Biology and Comparative Physiology of Birds, Volume 1 (A. J. Marshall, ed.). Academic Press, New York, New York.
- BERGER, A. J. 1960. The musculature. Pp. 301–349, *in* Biology and Comparative Physiology of Birds, Volume 1 (A. J. Marshall, ed.). Academic Press, New York, New York.

------. 1966. The musculature. Pp. 224–473, *in* Avian Myology (J. C. George and A. J. Berger, eds.). Academic Press, New York, New York.

BHATTACHARYYA, B. N. 1980. The morphology of the jaw and tongue musculature of the common pigeon, *Columba livia*, in relation to its feeding habit. Proceedings of the Zoological Society (Calcutta), 31:95–126.

——. 1989. Functional morphology of the jaw muscles of two species of imperial pigeons, *Ducula aenea nicobarica* and *Ducula badia insignis*. Gegenbaurs Morphologisches Jahrbuch, 135:573–618.

BLANCHARD, C. É. 1859. Recherches sur les caractères ostéologiques des oiseaux, appliquées à la classification naturelle de ces animeaux. Annales des Sciences Naturelles (Série 4), 11:1–141.

BOCK, W. J. 1963a. Evolution and phylogeny in morphologically uniform groups. American Naturalist, 92:265–285.

—. 1963b. The cranial evidence for ratite affinities. Pp. 39–54, *in* Proceedings XIII International Ornithological Congress, Volume 1 (C. G. Sibley, ed.). American Ornithologists' Union, Washington, D.C.

—. 1964. Kinetics of the avian skull. Journal of Morphology, 114:1–42.

—. 1967. The use of adaptive characters in avian classification. Pp. 61–74, *in* Proceedings XIV International Ornithological Congress (D. W. Snow, ed.). Blackwell Scientific Publications, Oxford, United Kingdom.

. 1968. Mechanics of one- and two-joint muscles. American Museum Novitates, 2319:1–45.
 . 1977. Adaptation and the comparative method. Pp. 57–82, *in* Major Patterns in Vertebrate

Evolution (M. K. Hecht, P. Goody, and B. Hecht, eds.). Plenum Press, New York, New York.

—. 1979. The synthetic explanation of macroevolutionary change—a reductionist approach. Pp. 20–69, *in* Models and Methodologies in Evolutionary Theory (J. H. Schwartz and H. B. Rollins, eds.). Carnegie Museum of Natural History Bulletin Number 13. Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

——. 1989. The homology concept: its philosophical foundation and practical methodology. Zoologische Beiträge (Neue Folge), 32:327–353.

- BOCK, W. J., AND A. MCEVEY. 1969. Osteology of *Pedionomus torquatus* (Aves: Pedionomidae). Proceedings of the Royal Society of Victoria (New Series), 82:187–232.
- BOOKSTEIN, F. L. 1994. Can biometrical shape be a homologous character? Pp. 197–227, *in* The Hierarchical Basis of Comparative Biology (B. K. Hall, ed.). Academic Press, New York, New York.
- BOYDEN, A. 1943. Homology and analogy: a century after the definition of "homologue" and "analogue" of Richard Owen. Quarterly Review of Biology, 18:228–241.

2000

———. 1947. Homology and analogy: a critical review of the meanings and implications of these concepts in biology. American Midland Naturalist, 37:548–669.

- BROOKS, D. R. 1996. Explanations of homoplasy at different levels of biological organization. Pp. 3– 36, in Homoplasy: The Recurrence of Similarity in Evolution (M. J. Sanderson and L. Hufford, eds.). Academic Press, San Diego, California.
- BROWER, A. V. Z., AND V. SCHAWAROCH. 1996. Three steps of homology assessment. Cladistics, 12: 265–272.
- BRYANT, H. N. 1989. An evaluation of cladistic and character analyses as hypothetico-deductive procedures, and the consequences for character weighting. Systematic Zoology, 38:214–227.
- BÜHLER, P. 1981. Functional anatomy of the avian jaw apparatus. Pp. 439–468, *in* Form and Function in Birds, Volume 2 (A. S. King and J. McLelland, eds.). Academic Press, London, United Kingdom.
- BURGGRAAF, P. D. 1954. On the correlation between the skull structure and the muscles in the male *Phasianus colchicus* L. II. The attachment of the musculus adductor mandibulae externus. Verhandlingen der Koninklijke Nederlandse Akademie van Wetenschappen (Series C), 57:292–303.
- BURGGRAAF, P. D., AND A. FUCHS. 1954. On the correlation between the skull structure and the muscles in the male *Phasianus colchicus* L. I. General introduction. Verhandlingen der Koninklijke Nederlandse Akademie van Wetenschappen (Series C), 57:286–303.
- ------. 1955. On the correlation between the skull structure and the muscles in the male *Phasianus* colchicus L. VII. General considerations. Verhandlingen der Koninklijke Nederlandse Akademie van Wetenschappen (Series C), 58:98–100.
- BURTON, P. J. K. 1974a. Jaw and tongue features in Psittaciformes and other orders with special reference to the anatomy of the Tooth-billed Pigeon (*Didunculus strigirostris*). Journal of Zoology (London), 174:255–276.
- . 1974b. Anatomy of head and neck in the Huia (*Heteralocha acutirostris*) with comparative notes on other Callaeidae. Bulletin of the British Museum (Natural History), 27 (Zoology):1–48.
- . 1974*c*. Feeding and the Feeding Apparatus in Waders: A Study of Anatomy and Adaptations in the Charadrii. British Museum (Natural History), London, United Kingdom.
- ------. 1984. Anatomy and evolution of the feeding apparatus in the avian orders Coraciiformes and Piciformes. Bulletin of the British Museum (Natural History), 47 (Zoology):331–443.
- BUTENDIECK, E. 1980. Die Benennung des Skeletts beim Truthuhn (*Meleagris gallopavo*) unter Berücksischtigung der Nomina Anatomica Avium (1979). Ph.D. Dissert., Tierärztiliche Hochschule Hannover, Hannover, Germany.
- BUTENDIECK, E., AND H. WISSDORF. 1982. Beitrag zur Benennung der Knochen des Kopfes beim Truthuhn (*Meleagris gallopavo*) unter Berücksichtigung der Nomina Anatomica Avium (1979). Zoologische Jahrbücher (Abteilung für Anatomie), 107:153–184.
- CASPERS, G.-J., D. U. DE WEERD, J. WATTEL, AND W. W. DE JONG. 1997. α-crystallin sequences support a galliform/anseriform clade. Molecular Phylogeny and Evolution, 7:185–188.
- CODDINGTON, J. A. 1994. The roles of homology and convergence in studies of adaptation. Pp. 53– 78 *in* Phylogenetics and Ecology (P. Eggleton and R. I. Vane-Wright, eds.). Academic Press, London, United Kingdom.
- CRACRAFT, J. 1968. The lacrimal-ectethmoid bone complex in birds: a single character analysis. American Midland Naturalist, 80:316–359.
 - ——. 1981*a*. Toward a phylogenetic classification of the Recent birds of the world (Class Aves). Auk, 98:681–714.
 - ——. 1981*b*. The use of functional and adaptive criteria in phylogenetic systematics. American Zoologist, 21:21–36.
- . 1982. Phylogenetic relationships and monophyly of loons, grebes, and hesperornithiform birds, with comments on the early history of birds. Systematic Zoology, 31:35–56.
 - —. 1986. The origin and early diversification of birds. Paleobiology, 12:383–399.
- ———. 1988. The major clades of birds. Pp. 339–361, in The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds (M. J. Benton, ed.). Clarendon Press, Oxford, United Kingdom.
- CRACRAFT, J., AND D. P. MINDELL. 1989. The early history of modern birds: a comparison of molecular and morphological evidence. Pp. 389–403, *in* The Hierarchy of Life (B. Fernholm, K. Bremer, and J. Jornvall, eds.). Exerptica Medica, Amsterdam, The Netherlands.
- CROWE, T. M. 1988. Molecules vs morphology in phylogenetics: a non-controversy. Transactions of the Royal Society of South Africa, 46:317–334.
- DAVIDS, J. A. G. 1952. Étude sur les attaches au crâne des muscles de la tête et du cou chez *Anas platyrhyncha platyrhyncha* L. Parts I–III. Verhandlingen der Koninklijke Nederlandse Akademie van Wetenschappen (Series C), 55:81–94, 525–533, 534–540.

DE BEER, G. 1937. The Development of the Vertebrate Skull. Clarendon Press, Oxford, United Kingdom.

DELACOUR, J. 1954. Waterfowl of the World, Volume 1. Country Life, London, United Kingdom.

DEPINNA, M. C. C. 1991. Concepts and tests of homology in the cladistic paradigm. Cladistics, 7: 367–394.

. 1994. Ontogeny, rooting, and polarity. Pp. 157–172, in Models in Phylogeny Reconstruction (R. W. Scotland, D. J. Siebert, and D. M. Williams, eds.). Clarendon Press, Oxford, United Kingdom.

DE QUEIROZ, K. 1985. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. Systematic Zoology, 34:280–299.

- DOYLE, J. J. 1996. Homoplasy connections and disconnections: genes and species, molecules and morphology. Pp. 37–66, *in* Homoplasy: The Recurrence of Similarity in Evolution (M. J. Sanderson and L. Hufford, eds.). Academic Press, San Diego, California.
- DULLEMEIJER, P. 1951. The correlation between muscle system and skull structure in *Phalacrocorax* carbo sinensis (Shaw & Nodder): I–III. Proceedings of Koninklijke Nederlandse Akademie van Wetenschappen (Series C), 54:247–259; 400–404; 533–536.
- ——. 1952. The correlation between muscle system and skull structure in *Phalacrocorax carbo sinensis* (Shaw & Nodder): IV. Proceedings of Koninklijke Nederlandse Akademie van Wetenschappen (Series C), 55:95–102.
- DZERZHINSKY, R. YA. 1980. [Adaptive transformation of the maxillary apparatus in the evolution of gallinaceous birds.] Pp. 148–158, *in* Morphological Aspects of Evolution (V. E. Sokolov and N. S. Lebedkina, eds.). Moscow State University, Moscow, USSR. [In Russian.]
 - —. 1982. Adaptive features in the structure of maxillary system in some Anseriformes and probable ways of evolution of the order. Zoologichesky Zhurnal, 56:1030–1041. [Russian with English summary.]
 - —. 1995. Evidence for the common ancestry of Galliformes and Anseriformes. Courier Forschungsinstitut Senckenberg, 181:325–336.
 - —. 1999. Implications of the cranial morphology of paleognaths for avian evolution. Pp. 267–274, *in* Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, D. C., 4–7 June 1996 (S. L. Olson, ed.). Smithsonian Contributions to Paleobiology, 89:1–344.
- DZERZHINSKY, R. YA., AND I. N. BELOKUROVA. 1972. [On the comparative anatomy of the maxillary musculature of birds. Jaw muscles of the Capercaillie (*Tetrao urogallus*).] Zoologichesky Zhurnal, 51:555–564. [Russian with English summary.]
- DZERZHINSKY, R. YA., AND E. G. POTANOVA. 1974. [The system of tendinous formations as an object of comparative myology of the maxillary apparatus of birds.] Zoologichesky Zhurnal, 53:1341–1351. [Russian with English summary.]
- EDGEWORTH, F. H. 1907. The development of the head-muscles in *Gallus domesticus*, and the morphology of head-muscles in the Sauropsida. Quarterly Journal of Microscopical Science (Series 2), 51:511–556.
- ELZANOWSKI, A. 1987. Cranial and eyelid muscles and ligaments of the tinamous (Aves: Tinamiformes). Zoologische Jahrbücher (Abteilung für Anatomie), 116:63–118.
- ERICSON, P. G. P. 1996. The skeletal evidence for a sister–group relationship of anseriform and galliform birds—a critical evaluation. Journal of Avian Biology, 27:195–202.

——. 1997. Systematic relationships of the palaeogene family Presbyornithidae (Aves: Anseriformes). Zoological Journal of the Linnean Society, 121:429–483.

EYTON, T. C. 1867. Osteologia Avium; Or, a Sketch of the Osteology of Birds. R. Hobson, Salop, England.

FEDUCCIA, A. 1977. Hypothetical stages in the evolution of modern ducks and flamingos. Journal of Theoretical Biology, 67:715–721.

——. 1978. *Presbyornis* and the evolution of ducks and flamingos. American Scientist, 66:298–304.

—. 1980*a*. Evolution von Enten und Flamingos. Pp. 1243–1248, *in* Acta XVII Congressus Internationalis Ornithologici, Volume 2 (R. Nöhring, ed.). Deutschen Ornithologen-Gesellschaft, Berlin, Germany.

——. 1980b. The Age of Birds. Harvard University Press, Cambridge, Massachusetts.

———. 1994. Tertiary bird history: notes and comments. Pp. 178–189, in Major Features of Vertebrate Evolution (D. R. Prothero and R. M. Schoch, eds.). Paleontological Society, Knoxville, Tennessee.

-. 1995. Explosive evolution in Tertiary birds and mammals. Science, 267:637–638.

--. 1996. The Origin and Evolution of Birds. Yale University Press, New Haven, Connecticut.

FIEDLER, W. 1951. Beiträge zur Morphologie der Kiefermuskulatur der Oscines. Zoologische Jahrbücher (Abteilung für Anatomie und Ontogenie Tiere), 71:235–288.

FINK, W. L., AND M. L. ZELDITCH. 1995. Phylogenetic analysis of ontogenetic shape transformations: a reassessment of the piranha genus *Pygocentrus* (Teleostei). Systematic Biology, 44:343–360.

FISHER, H. I., AND D. C. GOODMAN. 1955. The Myology of the Whooping Crane, *Grus americana*. University of Illinois Press, Urbana, Illinois.

FITCH, W. M. 1970. Distinguishing homologous from analogous proteins. Systematic Zoology, 19: 99–113.

FUCHS, A. 1954. On the correlation between the skull structure and the muscles in the male *Phasianus* colchicus L. IIIA. The attachment of the musculus adductor mandibulae posterior and the musculus adductor mandibulae internus. Verhandlingen der Koninklijke Nederlandse Akademie van Wetenschappen (Series C), 57:454–470.

. 1955. On the correlation between the skull structure and the muscles in the male *Phasianus* colchicus L. VI. Some remarks on a number of ligaments and other connective tissue connections.
 Verhandlingen der Koninklijke Nederlandse Akademie van Wetenschappen (Series C), 58:114–120.

FUJIOKA, T. 1963. On the origins and insertions of the muscles of the head and neck in fowl. Part I. Muscles of the head. Japanese Journal of Veterinary Science, 25:207–226.

FÜRBRINGER, M. 1888. Untersuchungen zur Morphologie und Systematik der Vögel, zugleich ein Beitrag zur Anatomie der Stütz- und Bewegungsorgane, 2 Volumes. T. J. Van Holkema, Amsterdam, Holland.

GADOW, H. 1892. On the classification of birds. Proceedings of the Zoological Society of London, 1892:229–256.

-----. 1893. Vögel. II. Systematischer Theil. *In* Klassen und Ordnungen des Their-Reichs (H. G. Bronn, ed.). C. F. Winter, Leipzig, Germany.

GADOW, H., AND E. SELENKA. 1891. Vögel. I. Anatomischer Theil. In Klassen und Ordnungen des Their-Reichs (H. G. Bronn, ed.). C. F. Winter, Leipzig, Germany.

GANS, C., AND W. J. BOCK. 1965. The functional significance of muscle architecture—a theoretical analysis. Review of Anatomy, Embryology, and Cell Biology, 38:115–142.

GOODMAN, D. C., AND H. I. FISHER. 1962. Functional Anatomy of the Feeding Apparatus in Waterfowl. Southern Illinois University Press, Carbondale, Illinois.

GOODWIN, B. 1994. Homology, development, and heredity. Pp. 229–247, *in* Homology: The Hierarchical Basis of Comparative Biology (B. K. Hall, ed.). Academic Press, San Diego, California.

GREENE, H. W. 1994. Homology and behavioral repertoires. Pp. 369-391, in Homology: The Hierarchical Basis of Comparative Biology (B. K. Hall, ed.). Academic Press, New York, New York.

GROTH, J. G., AND G. F. BARROWCLOUGH. 1999. Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. Molecular Phylogenetics and Evolution, 12:115–123.

HALL, B. K. 1994. Introduction. Pp. 1–19, in Homology: The Hierarchical Basis of Comparative Biology (B. K. Hall, ed.). Academic Press, New York, New York.

-----. 1995. Homology and embryonic development. Pp. 1–37, *in* Evolutionary Biology, Volume 28 (M. K. Hecht, R. J. MacIntyre, and M. T. Clegg, eds.). Plenum Press, New York, New York.

HANKEN, J., AND B. K. HALL. 1993. Mechanisms of skull diversity and evolution. Pp. 1–36, *in* The Skull, Volume 3: Functional and Evolutionary Mechanisms (J. Hanken and B. K. Hall, eds.). University of Chicago Press, Chicago, Illinois.

HASZPRUNAR, G. 1992. The types of homology and their significance for evolutionary biology and phylogenetics. Journal of Evolutionary Biology, 5:13–24.

. 1998. Parsimony analysis as a specific kind of homology estimation and the implication for character weighting. Molecular Phylogenetics and Evolution, 9:333–339.

HAWKINS, J. A., C. E. HUGHES, AND R. W. SCOTLAND. 1997. Primary homology assessment, characters and character states. Cladistics, 13:275–283.

HENNIG, W. 1966. Phylogenetic Systematics. University of Illinois Press, Urbana, Illinois.

HILLIS, D. M. 1994. Homology in molecular biology. Pp. 339–368, *in* Homology: The Hierarchical Basis of Comparative Biology (B. K. Hall, ed.). Academic Press, New York, New York.

HOFER, H. 1945. Untersuchungen über den Bau des Vogelschädels, besonders über den der Spechte und Steißhühner. Zoologische Jahrbücher (Abteilung für Anatomie), 69:1–158.

—. 1950. Zur Morphologie der Kiefermuskulatur der Vögel. Zoologische Jahrbücher (Abteilung für Anatomie), 70:427–556.

——. 1955. Neuere Untersuchungen zur Kopfmorphologie der Vögel. Pp. 104–137, *in* Acta XI Congressus Internationalis Ornithologici (A. Portmann and E. Sutter, eds.). Birkhäuser Verlag, Basel, Switzerland.

- Hogg, D. A. 1978. The articulations of the neurocranium in the postnatal skeleton of the domestic fowl (*Gallus gallus domesticus*). Journal of Anatomy (London), 127:53–63.
- DEL HOYO, J., A. ELLIOTT, AND J. SARGATAL. 1994. Handbook of the Birds of the World, Volume 2. Lynx Edicions, Barcelona, Spain.
- ICVGAN (INTERNATIONAL COMMITTEE ON VETERINARY GROSS ANATOMICAL NOMENCLATURE). 1983. Nomina Anatomica Veterinaria, Third edition. Ithaca, New York.

INGLIS, W. G. 1966. The observational basis of homology. Systematic Zoology, 15:219–228.

JÄGER, O. 1990. Die Kopfligamente der Anseriformes (Wolters, 1982). Ein Beitrag zum Grundplan der Entenvögel. Acta Biologica Benrodis (Düsseldorf), 2:209–223.

JOHNSGARD, P. J. 1965. Handbook of Waterfowl Behavior. Constable, London, United Kingdom.

- JOHNSON, R. 1984. The cranial and cervical osteology of the European Oystercatcher *Haematopus* ostralegus L. Journal of Morphology, 182:227–244.
- JOLLIE, M. T. 1957. The head skeleton of the chicken and remarks on the anatomy of this region in other birds. Journal of Morphology, 100:389–436.
- KLUGE, A. G., AND R. E. STRAUSS. 1985. Ontogeny and systematics. Annual Review of Ecology and Systematics, 16:247–268.

KOMÁREK, V. 1979. Anatomia Avium Domesticarum, Volume 1. Priroda, Bratislava, Czecholslovakia.

- KOMÁREK, V., L. MALINOVSKY, AND L. LEMEZ. 1982. Anatomia Avium Domesticarum, Volumes 2 and 3. Priroda, Bratislava, Czecholslovakia.
- KRAUS, F. 1987. An empirical evaluation of the use of the ontogeny polarization criterion in phylogenetic inference. Systematic Zoology, 37:106–141.
- KRIPP, D. VON. 1933. Der Oberschnabelmechanismus der Vögel. (Nach den Methoden der graphischen Statik bearbeitet). Gegenbaurs Morphologisches Jahrbuch, 71:469–544.
- LAKJER, T. 1926. Studien über die Trigeminus-versorgte Kaumuskulatur der Sauropsiden. C. A. Reitzel, Kopenhagen, Denmark.
- LAUDER, G. V. 1994. Homology, form, and function. Pp. 151–196, *in* Homology: The Hierarchical Basis of Comparative Biology (B. K. Hall, ed.). Academic Press, New York, New York.

LEBEDINSKY, N. G. 1921. Zur Syndesmologie der Vögel. Anatomischer Anzeiger, 54:8–15.

LIPSCOMB, D. L. 1992. Parsimony, homology and the analysis of multistate characters. Cladistics, 8: 45–65.

LIVEZEY, B. C. 1986. A phylogenetic analysis of Recent anseriform genera using morphological characters. Auk, 103:737–754.

—. 1989. Phylogenetic relationships of several subfossil Anseriformes of New Zealand. University of Kansas Museum of Natural History, Occasional Paper, 128:1–25.

——. 1991. A phylogenetic analysis and classification of Recent dabbling ducks (Tribe Anatini) based on comparative morphology. Auk, 108:471–508.

———. 1995a. Phylogeny and evolutionary ecology of modern seaducks (Anatidae: Mergini). Condor, 97:233–255.

——. 1995b. A phylogenetic analysis of the whistling and White-backed ducks (Anatidae: Dendrocygninae) using morphological characters. Annals of Carnegie Museum, 64:65–97.

——. 1995*c*. Phylogeny and comparative ecology of stiff-tailed ducks (Anatidae: Oxyurini). Wilson Bulletin, 107:214–234.

. 1996a. A phylogenetic analysis of modern pochards (Anatidae: Aythyini). Auk, 113:74–93.
 . 1996b. A phylogenetic reassessment of the tadornine-anatine divergence (Aves: Anserifor-

mes: Anatidae). Annals of Carnegie Museum, 65:27-88.

——. 1996c. A phylogenetic analysis of the geese and swans (Anseriformes: Anserinae), including selected fossil species. Systematic Biology, 45:415–450.

- ——. 1997a. A phylogenetic analysis of basal Anseriformes, the fossil *Presbyornis*, and the interordinal relationships of waterfowl. Zoological Journal of the Linnean Society, 121:361–428.
- ——. 1997b. An annotated phylogenetic classification of waterfowl (Aves: Anseriformes), including selected fossil species. Annals of Carnegie Museum, 67:457–496.

. 1997c. A phylogenetic analysis of modern shelducks and sheldgeese (Anatidae, Tadornini). Ibis, 139:51–66.

———. 1998. Erratum. Zoological Journal of the Linnean Society, 124:397–398.

MABEE, P. M. 1989. An empirical rejection of the ontogenetic polarity criterion. Cladistics, 5:409–416.

—. 1993. Phylogenetic interpretation of ontogenetic change: sorting out the actual and artefactual in an empirical case study of cetrarchid fishes. Zoological Journal of the Linnean Society, 107: 175–291.

MCKITRICK, M. C. 1994. On homology and the ontological relationship of parts. Systematic Biology, 43:1–10.

McCLEARN, D., AND D. M. NODEN. 1988. Ontogeny of architectural complexity in embryonic quail visceral arch muscles. American Journal of Anatomy, 183:277–293.

McShea, D. W. 1996. Complexity and homoplasy. Pp. 207–225, in Homoplasy: The Recurrence of Similarity in Evolution (M. J. Sanderson and L. Hufford, eds.). Academic Press, San Diego, California.

MEIER, R. 1997. A test and review of the empirical performance of the ontogenetic criterion. Systematic Biology, 46:699-721.

MERZ, R. L. 1963. Jaw musculature of the Mourning and White-winged doves. Publication of University of Kansas Museum of Natural History, 12:521–551.

MINDELL, D. P. 1991. Similarity and congruence as criteria for molecular homology. Molecular Biology and Evolution, 8:897–900.

Möller, W. 1932. Biologisch-anatomische Studien am Schädel von Ara macao. Gegenbaurs Morphologisches Jahrbuch, 70:305–342.

MORIOKA, H. 1974. Jaw musculature of the swifts (Aves, Apodidae). Bulletin of the National Museum of Japan (Series A), 17:1–16.

MÜLLER, W., AND E. WEBER. 1998. /Re-discovery of a supposedly lost muscle in palaeognathous birds and its phylogenetic implications. Mitteilungen aus dem Museum für Naturkunde in Berlin (Zoologische Reihe), 74:11–18.

MURRAY, P. R., AND D. MEGIRIAN. 1998. The skull of dromornithid birds: anatomical evidence for their relationship to Anseriformes. Records of the South Australian Museum, 31:51–97.

NELSON, G. 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. Systematic Zoology, 27:324–345.

——. 1994. Homology and systematics. Pp. 101–149, in Homology: The Hierarchical Basis of Comparative Biology (B. K. Hall, ed.). Academic Press, New York, New York.

OLSON, S. L., AND A. FEDUCCIA. 1980a. *Presbyornis* and the origin of the Anseriformes (Aves: Charadriomorphae). Smithsonian Contributions to Zoology, 323:1–24.

------. 1980b. Relationships and evolution of flamingos (Aves: Phoenicopteridae). Smithsonian Contributions to Zoology, 316:1–73.

OWEN, R. 1843. Lectures on Comparative Anatomy and Physiology of the Invertebrate Animals, Delivered at the Royal College of Surgeons in 1843. Longman, Brown, Green, and Longman, London, England.

PANCHEN, A. L. 1994. Richard Owen and the concept of homology. Pp. 21–62, *in* Homology: The Hierarchical Basis of Comparative Biology (B. K. Hall, ed.). Academic Press, New York, New York.

PATTERSON, C. 1982. Morphological characters and homology. Pp. 21–74, *in* Problems of Phylogenetic Reconstruction (K. A. Joysey and A. E. Friday, eds.). Academic Press, New York, New York.
 ———. 1988. Homology in classical and molecular biology. Molecular Biology and Evolution, 5: 603–625.

PETERS, J. L. 1934. Checklist of Birds of the World, Volume 2. Harvard University Press, Cambridge, Massachusetts.

POGUE, M. G., AND M. F. MICKEVICH. 1990. Character definitions and character state delineations: the *bête noire* of phylogenetic inference. Cladistics, 6:319–361.

REMANE, A. 1952. Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik. Geest and Portig, Leipzig, Germany.

------. 1956. Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik, Second edition. Akademische Verlagsgesellschaft, Leipzig, Germany.

RICHARDS, L. P., AND W. J. BOCK. 1973. Functional anatomy and adaptive evolution of the feeding apparatus in the Hawaiian honeycreeper genus *Loxops* (Drepanididae). Ornithological Monograph 15. American Ornithologists' Union, Washington, D. C.

RICHARDS, S. A. 1968. Anatomy of the veins of the head in the domestic fowl. Journal of Zoology (London), 154:223–234.

RIEPPEL, O. 1980. Homology, a deductive concept? Zeitschrift für Zoologische Systematiks und Evolutionforschung, 18:315–319.

—. 1992. Homology and logical fallacy. Journal of Evolutionary Biology, 5:701–715.

——. 1994. Homology, topology, and typology: the history of modern debates. Pp. 63–100, *in* Homology: The Hierarchical Basis of Comparative Biology (B. K. Hall, ed.). Academic Press, New York, New York.

ROHLF, F. J. 1998. On applications of geometric morphometrics to studies of ontogeny and phylogeny. Systematic Biology, 47:147–158.

ROTH, V. L. 1984. On homology. Biological Journal of the Linnean Society, 22:13-29.

—. 1988. The biological basis of homology. Pp. 1–26, *in* Ontogeny and Systematics (C. J. Humphries, ed.). Columbia University Press, New York, New York.

——. 1991. Homology and hierarchies: problems solved and unresolved. Journal of Evolutionary Biology, 4:167–194.

SANDERSON, M. J., AND L. HUFFORD. 1996. Homoplasy and the evolutionary process: an afterword. Pp. 327–330, *in* Homoplasy: The Recurrence of Similarity in Evolution (M. J. Sanderson and L. Hufford, eds.). Academic Press, San Diego, California.

SATTLER, R. 1984. Homology-a continuing challenge. Systematic Botany, 9:382-394.

SCHIØLER, E. L. 1926. Danmarks Fugle, Volume 2. Nordisk Forlag, Kobenhavn, Denmark.

- SCHULIN, R. 1987. Hind limb myology and phylogenetic relationships of the Australian Magpie Goose *Anseranas semipalmata* (Latham). Zoologische Jahrbücher (Abteilung für Anatomie und Ontogenie der Tiere), 116:217–243.
- SEEBOHM, H. 1888. An attempt to diagnose the suborders of the great Gallino–Gralline group of birds, by the aid of osteological characters alone. Ibis, 30:415–435.

——. 1889. An attempt to diagnose the suborders of the ancient Ardeino-Anserine assemblage of birds by the aid of osteological characters alone. Ibis, 31:92–104.

- ——. 1890. The Classification of Birds: An Attempt to Classify the Subclasses, Orders, Suborders, and Some of the Families of Existing Birds. R. H. Porter, London, England.
- ——. 1895. The Classification of Birds: An Attempt to Classify the Subclasses, Orders, Suborders, and Some of the Families of Existing Birds. Supplement. R. H. Porter, London, England.
- SHUFELDT, R. W. 1901. On the osteology and phylogenetic position of the screamers (Palamedea: *Chauna*). American Naturalist, 35:455–461.

-. 1909. Osteology of birds. New York State Museum Bulletin, 130:1-381.

———. 1914. Contributions to the study of the "tree-ducks" of the genus *Dendrocygna*. Zoologische Jahrbücher (Systematik, Geographie und Biologie Tiere), 38:1–70.

SIBLEY, C. G., AND B. L. MONROE, JR. 1990. Distribution and Taxonomy of Birds of the World. Yale University Press, New Haven, Connecticut.

SIMPSON, G. G. 1959. Anatomy and morphology: classification and evolution, 1859 and 1959. Proceedings of the American Philosophical Society, 103:286–306.

SIMONETTA, A. M. 1960a. On the mechanical implications of the avian skull and their bearing on the evolution and classification of birds. Quarterly Review of Biology, 35:206–220.

——. 1960b. Observazioni sull meccanica del cranio degli uccelli e sulla sua influenza sull'evoluzione e classificazione degli uccelli (nota preliminare). Monitore Zoologico Italiano, 68: 1–14.

—. 1963. Cinesi e morfologia del cranio negli uccelli non passeriformi. Studio su varie tendenze evolutive. Parte Ia. Archivio Zoologico Italiano (Torino), 48:53–135.

- ———. 1968. Cinesi e morfologia del cranio negli uccelli non passeriformi. Studio su varie tendenze evolutive. Parte II. Striges, Caprimulgiformes ed Apodiformes. Archivio Zoologico Italiano (Torino), 52:1–36.
- SLUYS, R. 1996. The notion of homology in current comparative biology. Journal of Zoological Systematics and Evolutionary Research, 34:145–152.
- STARCK, D., AND A. BARNIKOL. 1954. Beiträge zur Morphologie der Trigeminus-muskulatur der Vögel (besonders der Acciptres, Cathartidae, Striges und Anseres). Gegenbaurs Morphologisches Jahrbuch, 94:1–64.
- STEVENS, P. F. 1984. Homology and phylogeny: morphology and systematics. Systematic Botany, 9: 395–409.
- SWIDERSKI, D. L., M. L. ZELDITCH, AND W. L. FINK. 1998. Why morphometrics is not special: coding quantitative data for phylogenetic analysis. Systematic Biology, 47:508–519.
- VANDEN BERGE, J. C. 1979. Myologia. Pp. 175–219, in Nomina Anatomica Avium (J. J. Baumel, A. S. King, A. M. Lucas, J. E. Breazile, and H. E. Evans, eds.). Academic Press, London, United Kingdom.
- VANDEN BERGE, J. C., AND G. A. ZWEERS. 1993. Myologia. Pp. 189–250, *in* Handbook of Avian Anatomy: Nomina Anatomica Avium, Second edition (J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge, eds.). Nuttall Ornithological Club, Cambridge, Massachusetts.
- VAN DER KLAAUW, C. J. 1963. Projections, deepenings and undulations of the surface of the skull in relation to the attachment of muscles. Verhandlingen der Koninklijke Nederlandse Akademie van Wetenschappen (Series 2), 55:1–247.
- VAN GENNIP, E. M. S. J. 1986. The osteology, arthrology and myology of the jaw apparatus of the pigeon (*Columba livia* L.). Netherlands Journal of Zoology, 36:1–46.

VAN VALEN, L. 1982. Homology and causes. Journal of Morphology, 173:305–312.

VERHEYEN, R. 1956. Contribution à l'anatomie et à la systématique des Galliformes. Bulletin de Institut Royal des Sciences Naturelles de Belgique, 32(42):1–24.

VICKERS-RICH, P., P. TRUSLER, M. J. ROWLEY, A. COOPER, G. K. CHAMBERS, W. J. BOCK, P. R. MILLENER,

ZUSI AND LIVEZEY—CRANIUM OF GALLIFORMES AND ANSERIFORMES

T. H. WORTHY, AND J. C. YALDWYN. 1995. Morphology, myology, collagen and DNA of a mummified upland moa, *Megalapteryx didinus* (Aves: Dinornithiformes) from New Zealand. Tuhinga: Records of the Museum of New Zealand Te Papa Tongarewa, 4:1–26.

WÄGELE, J.-W. 1995. On the information content of characters in comparative morphology and molecular systematics. Journal of Zoological Systematics and Evolutionary Research, 33:42–47.

WAGNER, G. P. 1989a. The origin of morphological characters and the biological basis of homology. Evolution, 43:1157–1171.

. 1989b. The biological homology concept. Annual Review of Ecology and Systematics, 20: 51–69.

—. 1994. Homology and the mechanisms of development. Pp. 273–299, *in* Homology: The Hierarchical Basis of Comparative Biology (B. K. Hall, ed.). Academic Press, San Diego, California.

WEBB, M. 1957. The ontogeny of the cranial bones, cranial peripheral and cranial parasympathetic nerves, together with a study of the visceral muscles of *Struthio*. Acta Zoologica, 38:81–203.

WEBER, E. 1993. Zur Evolution basicranialer Gelenke bei Vögeln, insbesondere bei Hühner- und Entenvögeln (Galloanseres). Zeitschrift für Zoologische Systematiks und Evolutionforschung, 31: 300–317.

——. 1996. Das Skelet-Muskel-System des Kieferapparates von *Aepypodius arfakianus* (Salvadori, 1877) (Aves, Megapodiidae). Courier Forschungsinstitut Senckenberg, 189:1–132.

WENZEL, J. W. 1992. Behavioral homology and phylogeny. Annual Review of Ecology and Systematics, 23:361–381.

WETMORE, A. 1951. A revised classification for the birds of the world. Smithsonian Miscellaneous Collections, 117:1–22.

WHEELER, Q. D. 1990. Ontogeny and character phylogeny. Cladistics, 6:225–268.

WILEY, E. O. 1981. Phylogenetics: The Theory and Practice of Phylogenetic Systematics. John Wiley and Sons, New York, New York.

WILLIAMS, D. M., R. W. SCOTLAND, AND S. BLACKMORE. 1990. Is there a direct ontogenetic criterion in systematics? Biological Journal of the Linnean Society, 39:99–108.

YOUNG, B. A. 1993. On the necessity of an archetypal concept in morphology: with special reference to the concepts of "structure" and "homology." Biology and Philosophy, 8:225–248.

YUDIN, K. A. 1961. On the mechanism of the jaw in Charadriiformes, Procellariiformes, and some other birds. Trudy Zoologichesky Institut (Leningrad), 29:257–302.

———. 1965. [The phylogeny and classification of the Charadriiformes.] Fauna of the USSR: Birds— Volume II (1), Part 1. Zoological Institute (New Series), No. 91. Academy of Science, Leningrad, USSR.

ZELDITCH, M. L., AND W. L. FINK. 1998. Partial warps, phylogeny and ontogeny: a reply to Adams and Rosenberg. Systematic Biology, 47:345–348.

ZELDITCH, M. L., W. L. FINK, AND D. L. SWIDERSKI. 1995. Morphometrics, homology, and phylogenetics: quantified characters as synapomorphies. Systematic Biology, 44:179–189.

ZELDITCH, M. L., W. L. FINK, D. L. SWIDERSKI, AND B. L. LUNDRIGAN. 1998. On applications of geometric morphometrics to studies of ontogeny and phylogeny: a reply to Rohlf. Systematic Biology, 47:159–167.

ZUSI, R. L. 1962. Structural adaptations of the head and neck in the Black Skimmer, *Rynchops nigra*, L. Publication of the Nuttall Ornithological Club, 3:1–101.

. 1967. The role of the depressor mandibulae muscle in kinesis of the avian skull. Proceedings of the United States National Museum, 123:1–28.

. 1975. An interpretation of skull structure in penguins. Pp. 59–84, *in* The Biology of Penguins (B. Stonehouse, ed.). Macmillan Press, London, United Kingdom.

ZUSI, R. L., AND G. D. BENTZ. 1984. Myology of the Purple-throated Carib (*Eulampis jugularis*) and other hummingbirds (Aves: Trochilidae). Smithsonian Contributions to Zoology, 385:1–70.

ZUSI, R. L., AND R. W. STORER. 1969. Osteology and myology of the head and neck of the piedbilled grebes (*Podilymbus*). Miscellaneous Publications of the University of Michigan Museum of Zoology, 139:1–49.

ZWEERS, G. A. 1974. Structure, movement, and myography of the feeding apparatus of the Mallard (Anas platyrhynchos L.): a study in functional anatomy. Netherlands Journal of Science, 24:323– 467.



Zusi, Richard L. and Livezey, Bradley C. 2000. "Homology and phylogenetic implications of some enigmatic cranial features in galliform and anseriform birds." *Annals of the Carnegie Museum* 69(3), 157–193. https://doi.org/10.5962/p.330539.

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