

PHYLOGENY, BIOGEOGRAPHY, AND EVOLUTION OF THE BROADBILLS (EURYLAIMIDAE) AND ASITIES (PHILEPITTIDAE) BASED ON MORPHOLOGY

RICHARD O. PRUM

*Museum of Natural History and Department of Systematics and Ecology,
University of Kansas, Lawrence, Kansas 66045, USA*

ABSTRACT.—Phylogenetic analysis of syringeal morphology and two osteological characters indicates that the broadbills (Eurylaimidae) are not monophyletic, but consist of four clades with successively closer relationships to the Madagascan asities (Philepittidae). An analysis of these data combined with hindlimb myology characters described by Raikow (1987) yields the same result. The sister group to *Philepitta* and *Neodrepanis* is the African broadbill *Pseudocalyptomena*. The sister group to this clade includes all of the Asian broadbills, except the monophyletic genus *Calyptomena*. The African genus *Smithornis* is the sister group to all other broadbills and asities. A biogeographic analysis indicates that the Madagascan endemics share a most-recent biogeographic connection with the central African genus *Pseudocalyptomena*. Phylogenetic associations between transitions in bill morphology and diet indicate that bill morphologies have evolved both in association with evolution of frugivory and nectarivory, and in apparent response to intrinsic factors within the context of frugivorous and insectivorous diets. A phylogenetic classification of the broadbills and asities is proposed in which all broadbills and asities are placed in five subfamilies of the Eurylaimidae, and the separate family Philepittidae is abandoned. Received 27 January 1992, accepted 23 November 1992.

THE BROADBILLS (Eurylaimidae), asities (Philepittidae), and pittas (Pittidae) form a clade of Old World suboscine passerines (Sibley et al. 1982, Raikow 1987). They are broadly distributed in tropical Africa, Madagascar, Asia, and the Australo-Papuan region. Although they are much less diverse than the New World suboscines, the Old World suboscines include an ecologically diverse group of terrestrial and arboreal insectivores, frugivores, and nectarivores. As one of the major basal passerine clades, the broadbills, asities, and pittas are an interesting group with which to investigate the biogeographic history of the Old World tropical avifauna. In particular, the phylogenetic relationships of the asities may provide insight into the biogeographic history of Madagascar. In this paper, I present a phylogenetic analysis of the syringeal morphology of the broadbills (Eurylaimidae) and asities (Philepittidae), and use this phylogenetic hypothesis as a comparative framework in investigations of the biogeographic history and evolutionary ecology of the group.

The broadbills include 14 currently recognized biological species in eight genera (Peters 1951, Sibley and Monroe 1990). Six genera are restricted to southern Asia (*Corydon*, *Eurylaimus*,

Cymbirhynchus, *Serilophus*, *Psarisomus*, and *Calyptomena*) and two genera are found in Africa (*Smithornis* and *Pseudocalyptomena*). The asities include four species in two genera (*Philepitta* and *Neodrepanis*) that are restricted to Madagascar. The 23 to 31 species of pittas are usually placed in the single genus *Pitta* (Mayr 1979, Sibley and Monroe 1990). They range throughout the Old World tropics, but are most diverse in southern Asia.

The taxonomic history of the Old World suboscines and their position within the passerines has been thoroughly reviewed by Raikow (1987). Of particular interest here are the African and Madagascan genera that were originally classified as oscines and, subsequently, were recognized to be suboscines on the basis of syringeal morphology. *Smithornis* and *Pseudocalyptomena* were placed in the oscine flycatcher family Muscicapidae (Sharpe 1901, Rothschild 1909). Subsequent anatomical observations by Bates (1915) and Lowe (1924, 1931) demonstrated that they were not oscines, but rather African broadbills. In the 1800s, *Philepitta* was associated with the Sturnidae, Paradisaeidae, and Nectariniidae, but was confirmed by Forbes (1880b) to be a suboscine based on syringeal morphology. *Neodrepanis*, the Madagas-

can genus of sunbird-asities, was placed in the oscine family Nectariniidae until Amadon (1951) made syringeal observations demonstrating that it was suboscine, and placed it in the Philepittidae.

Although syringeal morphology was important in the initial recognition of the Old World suboscines (Forbes 1880a, b, Bates 1915, Lowe 1924, 1931, Köditz 1925, Amadon 1951), it has not been used explicitly to reconstruct the phylogenetic interrelationships of these birds. Ames (1971) described the syringes of a broad sample of Old World suboscines and recognized that the asities and some broadbills were quite similar in syringeal morphology. However, in the eclectic spirit of the day, he concluded that these similarities were primitive but still sufficient to support placement of the two families taxonomically near to one another.

Sibley et al. (1982) proposed that broadbills and pittas form a clade that is the sister group to the New World suboscines based on DNA-DNA hybridization. However, Sibley et al. (1982) lacked DNA samples of the asities, and no molecular hypothesis for their phylogenetic relationships has been published.

Most recently, Raikow (1987) performed a thorough phylogenetic analysis of the hindlimb myology of the Old World suboscines and produced a well-resolved hypothesis of phylogeny for the group using 23 hindlimb myological and 5 other morphological characters. Raikow concluded that: the Old World suboscines excluding the Acanthisittidae form a clade; the pitta, broadbill, and asity families are monophyletic; and the asities and broadbills are sister groups. He also presented the first phylogenetic hypothesis for the interrelationships of the broadbills, placing the African genus *Pseudocalyptomena* and the Asian *Calyptomena* as the first and second sister groups, respectively, to the rest of the genera in the family.

Here, I describe the syringeal morphology of the broadbills (Eurylaimidae) and asities (Philepittidae), and present a phylogenetic analysis of syringeal characters and two osteological characters. These data are analyzed in combination with hindlimb myology and other morphological characters described by Raikow (1987), and then this phylogenetic hypothesis is used as a historical framework for investigating the biogeography and evolutionary ecology of the broadbills and asities.

METHODS

I observed 46 syringeal specimens of 13 species of broadbills and asities. The sample included all but five species of broadbills and asities in 9 of 10 genera. An additional 23 specimens of 10 species of *Pitta* were examined for outgroup comparison. The sample included 28 specimens that were cleared and double stained for cartilage and bone (Dingerkus and Uhler 1977, Cannell 1988) by Wesley E. Lanyon. The remaining uncleared syringeal specimens were treated with reversible iodine stain (Bock and Shear 1972) for resolution of muscle fibers. Complete descriptions of the syringeal morphology of broadbills and asities, and list of the specimens examined are presented in the Appendix. The syringes of *Pitta*, *Smithornis*, *Calyptomena*, *Psarisomus*, and *Cymbirhynchus* are illustrated in Figure 1, and those of *Eurylaimus*, *Serilophus*, *Pseudocalyptomena*, *Philepitta*, and *Neodrepanis* are shown in Figure 2. I also examined suboscine skeletal specimens from the American Museum of Natural History and the Field Museum of Natural History. Syringes and skeletons were observed under a Wild M5A binocular dissecting microscope and illustrations were prepared with a camera lucida.

For the phylogenetic analysis, I accept the monophyly of the clade including broadbills and asities based on Raikow's (1987) observation of three shared derived myological characters (original character numbers from Raikow 1987): (13.1) attenuate *M. gastrocnemius pars medialis* with a concave cranial margin; (14.1) restricted insertion of *M. gastrocnemius*; and (18.1) plantar vinculum present, subsequently reversed in *Neodrepanis*. (These three characters are not included in the analysis to simplify the calculations.) For outgroup comparison, I accept the monophyly of the Old World suboscine clade—including the Philepittidae, Eurylaimidae, and Pittidae—with the New World suboscines (including Furnarioidea and Tyrannoidea) as their sister group (Feduccia 1974, 1975, 1976, Sibley et al. 1982, Raikow 1987, Sibley and Ahlquist 1990). The Acanthisittidae are grouped by some authors with the other Old World suboscines, but I accept Raikow's (1987) hypothesis that the Acanthisittidae are the sister group to the oscine passerines. Variations within the ingroup—the broadbills and asities—were polarized by outgroup comparison to the pittas, the New World suboscines, and the oscines (Wiley 1981, Maddison et al. 1984). The New World suboscines and the oscines were not included in the computer calculations because they were concluded to be primitive for all of the characters analyzed (see character descriptions).

Syringeal variation was coded as 19 characters. Complex multistate characters were coded as either ordered or unordered, depending upon whether the ingroup variation represented a coherent series of states. Complex characters were ordered if the derived states implied a hierarchical transition series

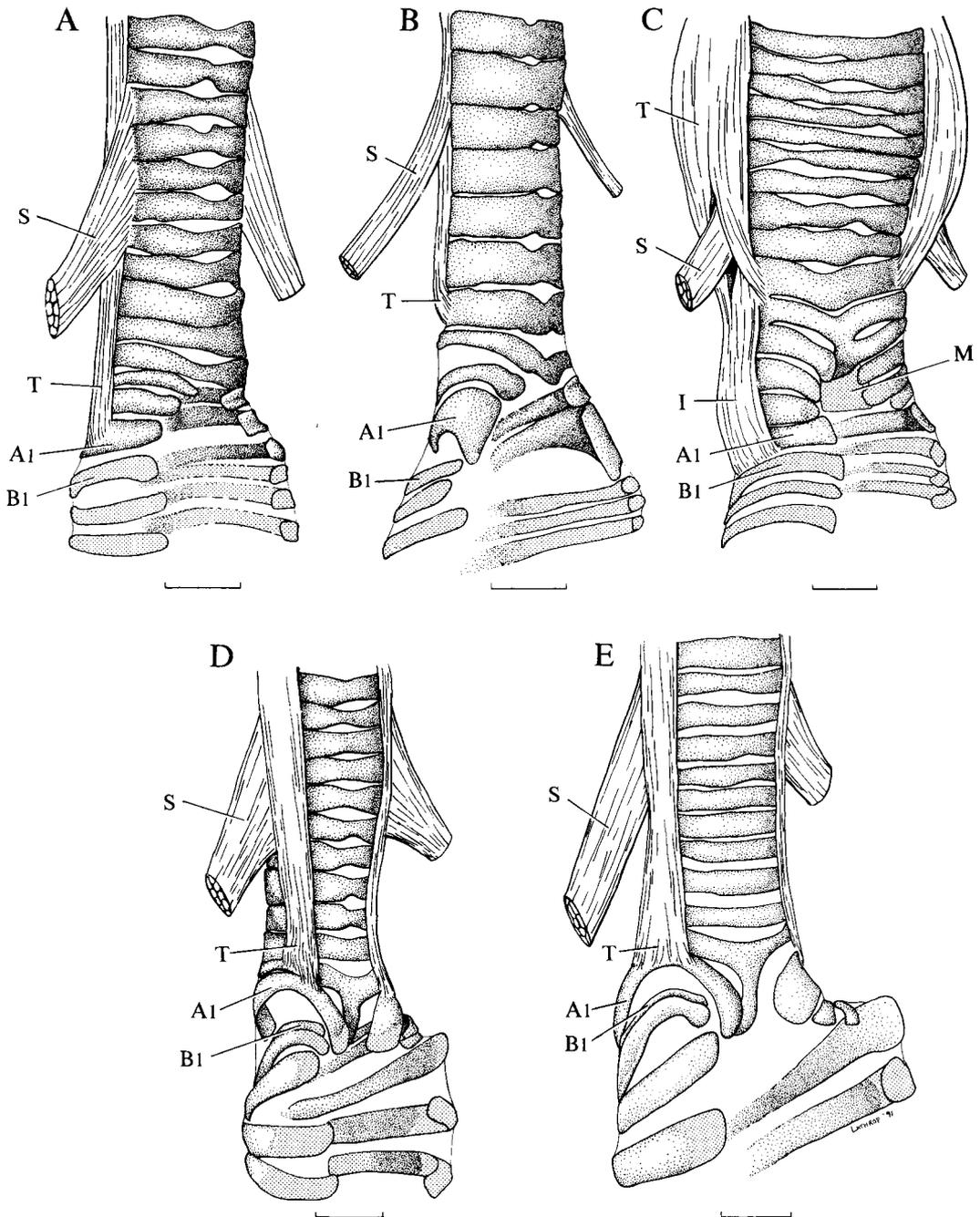


Fig. 1. Left dorsolateral view of syrinx of: (A) *Pitta versicolor* (AMNH 4378); (B) *Smithornis rufolateralis* (AMNH 2232); (C) *Calyptomena viridis* (AMNH 7999); (D) *Psarisomus dalhousiae* (AMNH 2998); and (E) *Cymbirhynchus macrorhynchus* (DMNH 61267). Scale bars equal 1 mm. Abbreviations: (A1) A1 syringeal supporting element. (A2) A2 syringeal supporting element. (B1) B1 syringeal supporting element. (I) intrinsic fibers of *M. tracheolateralis*. (M) medial cartilages. (S) *M. sternotrachealis*. (T) *M. tracheolateralis*.

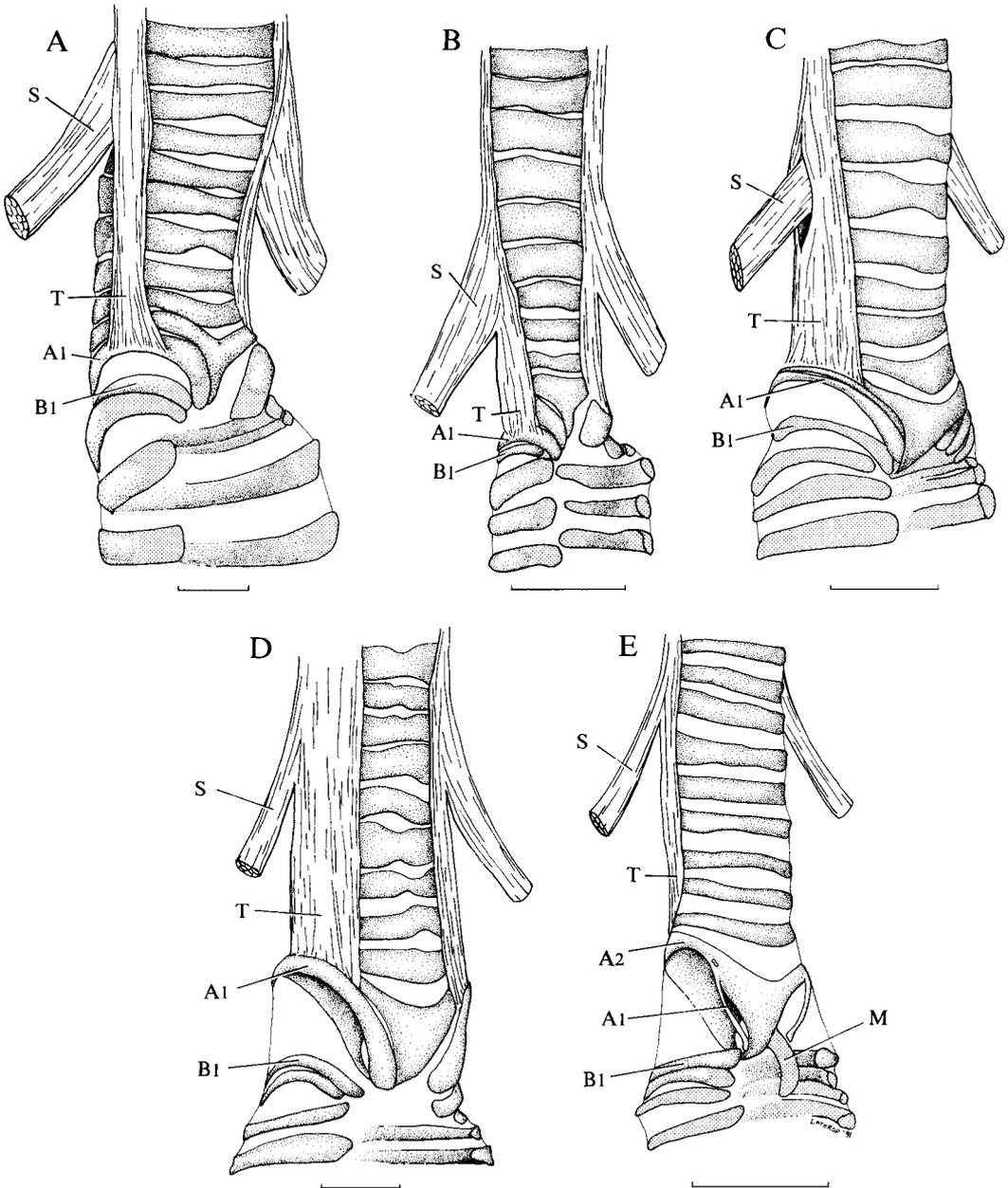


Fig. 2. Left dorsolateral view of syrinx of: (A) *Eurylaimus ochromalus* (USNM 223462); (B) *Serilophus lunatus* (USNM 509480); (C) *Pseudocalyptomena graueri* (BM 1930.10.19.2). (D) *Philepitta castanea* (BM 1968.30.46); and (E) *Neodrepanis coruscans* (BM 1968.30.112). Scale bars equal 1 mm. Abbreviations listed in Figure 1.

(i.e. one derived state has all the detail of another but some additional novel detail that appears to be secondarily derived). For convenience, ordered transition series were coded as a pair of additive binary characters (characters 15–16, 18–19), while unordered multistate characters were coded as alternative de-

rived states of a single multistate character (characters 1, 2, 7). In each character description, the hypothesized derived state and its distribution in the ingroup is described first, followed by the primitive state and its distribution in the ingroup and outgroups. In some cases, additional justifications of character polarity are

TABLE 1. Taxonomic distribution of derived morphological characters used in phylogenetic analyses of broadbills and asities. Characters 1–19 syringeal and 20–21 osteological. See text for descriptions. Characters 22–36 include informative morphological characters from Raikow (1987); his original numbers indicated. Codes: (0) primitive state; (1) derived state; (2) alternate derived state; (?) character state unknown.

Taxon	Character ^a															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Pitta</i> species	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Smithornis</i> species	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Calyptomena viridis</i>	0	0	0	0	0	0	2	1	0	0	0	0	1	0	0	0
<i>C. whiteheadi</i>	0	0	0	0	0	0	2	1	0	0	0	0	1	0	0	0
<i>Eurylaimus steeri</i>	2	2	0	0	0	0	1	0	1	1	1	1	0	0	0	0
<i>E. ochromalus</i>	2	2	0	0	0	0	1	0	1	1	1	1	0	0	0	0
<i>E. javanicus</i>	2	2	0	0	0	0	1	0	1	1	1	1	0	0	0	0
<i>Cymbirhynchus macrorhynchus</i>	2	2	0	0	0	0	1	0	1	1	1	1	0	0	0	0
<i>Serilophus lunatus</i>	2	2	0	0	0	0	1	0	1	1	1	1	0	0	0	0
<i>Psarisomus dalhousiae</i>	2	2	0	0	0	0	1	0	1	1	1	1	0	0	0	0
<i>Pseudocalyptomena graueri</i>	2	2	0	0	1	1	1	0	1	1	0	1	0	0	0	0
<i>Philepitta castanea</i>	2	2	0	1	1	0	1	0	1	1	0	1	0	1	1	0
<i>Philepitta schlegeli</i>	2	2	0	1	1	0	1	0	1	1	0	1	0	1	1	1
<i>Neodrepanis coruscans</i>	2	2	1	1	1	0	1	0	1	1	0	1	0	1	0	0

^a Characters 23–36 refer to Raikow's (1987) characters 2, 4–7, 11, 12, 15, 17–20, 24–26, respectively.

discussed. Each character has a reference number for use in figures and the text. The primitive (0), derived (1), and alternative derived (2) character states are referred to using a decimal following the character number.

The character data were analyzed using PAUP (Phylogenetic Analysis Using Parsimony, version 3.0s; Swofford 1991). The first analysis included the 19 syringeal and 2 osteological characters in Table 1. In the second analysis, these data were combined with 12 hindlimb myological characters and 3 other morphological characters from Raikow (1987) that were phylogenetically informative within the broadbills and asities (Table 1). In all analyses, I used the branch-and-bound of PAUP (which identifies the shortest phylogenetic trees) on the set with equally weighted characters and Acctran character optimization.

In the biogeographic analysis, an area cladogram was produced by substituting the range of each species for that species in the hypothesis of phylogeny (Nelson and Platnick 1981, Wiley 1981). This area cladogram was used as an initial hypothesis of the history of geographic fragmentation of a hypothetical, broadly distributed, undifferentiated ancestral taxon. Sympatry of any members of a clade indicates some secondary dispersal or expansion since allopatric speciation.

In the analysis of ecological evolution, the bill morphologies and diets of each taxon were superimposed on the phylogenetic hypothesis. The most-parsimonious historical scenario for evolutionary transitions in these traits were identified by coding them as unweighted characters in a PAUP analysis. Phylogenetic association between transitions in morphology and ecology were examined as evidence that changes may have been causally related.

CHARACTER ANALYSIS

The syringeal characters are described in the following order: A elements; pessulus; other accessory cartilages; B elements; and musculature. The two skeletal characters are presented last. The distribution of the states of these 19 characters and the 12 informative morphological characters from Raikow (1987) is presented in Table 1.

SYRINGEAL CHARACTERS

(1) *A1 elements oblique to sagittal plane.*—In *Smithornis*, A1–2 are moderately oblique to the midsagittal plane of the syrinx, creating a narrow lateral membrane between A1 and B1. In *Eurylaimus*, *Cymbirhynchus*, *Serilophus*, *Psarisomus*, *Pseudocalyptomena*, *Philepitta*, and *Neodrepanis*, the A1 elements are acutely oblique to the midsagittal plane, with the concave medial surface of the element oriented caudad. The oblique A1 elements create an extensive lateral tympaniform membrane between A1 and B1 in *Psarisomus*, *Pseudocalyptomena*, *Philepitta*, and *Neodrepanis*. In *Eurylaimus* and *Cymbirhynchus*, the lateral membrane is less extensive because the first two B elements are angled craniad. In *Serilophus*, B1 is expanded laterally, is arched, and lies adjacent to A1. All A and B elements are oriented transversely in *Calyptomena*, *Pitta*, and almost all New World suboscines. A similar orientation is found in the cotingid genera *Ampelion*, *Doliornis*, *Zaratornis*, and *Phytotoma*, but this morphology is an independently evolved synapomorphy of this cotingid group (Lanyon and Lanyon 1989). The oblique states of the A1 elements are hypothesized to be derived; the moderately (1.1) and acutely (1.2) oblique character states differ significantly in form, and are

TABLE 1. Extended.

Character																			
17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	2	1	1	0
0	1	1	1	1	1	1	1	0	1	0	0	0	0	1	0	2	1	0	0
0	1	0	1	1	1	1	1	0	1	0	0	0	0	1	0	2	1	0	0
0	0	0	1	1	0	0	1	0	0	1	1	2	0	1	0	2	1	1	0
0	0	0	1	1	0	0	1	0	0	1	1	2	0	1	0	2	1	1	0
0	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	0	0	1	1	0	0	1	0	0	1	1	2	0	1	0	2	1	1	0
0	0	0	1	1	0	0	1	0	0	1	1	2	0	1	0	2	1	1	0
0	0	0	1	1	0	0	1	0	0	1	1	2	0	1	0	2	1	1	0
0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	0	2	0	0	0
0	0	0	1	0	0	0	0	1	0	0	1	0	1	1	1	1	0	0	1
0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1

hypothesized to be alternative unordered derived states of a single character.

(2) *Dorsal ends of A1 widened.*—In *Smithornis*, the caudodorsal ends of A1 are widened into a prominent, asymmetrical hammer shape. In *Eurylaimus*, *Cymbirhynchus*, *Serilophus*, *Psarisomus*, *Pseudocalyptomena*, *Philepitta*, and *Neodrepanis*, the dorsal ends of A1 are widened, but into a symmetrical paddle shape. These shapes are not found in *Calyptomena*, *Pitta*, or most other passerines, and are hypothesized to be derived. There is no objective criterion for ordering these two derived states, so the hammer-shaped (2.1) and paddle-shaped (2.2) forms of dorsal widening are coded as alternative unordered derived states of a single character.

(3) *A1 fused laterally to A2.*—In *Neodrepanis*, the A1 elements are fused dorsolaterally to A2 to form a single element. The small forked ventral tip of this combined A1-2 element may be the ventral remnants of the A1s. This morphology is unique in Old World suboscines and is hypothesized to be derived.

(4) *Sides of A2 acutely oblique.*—In *Philepitta* and *Neodrepanis*, the lateral portions of the A2 element are acutely oblique to the midsagittal plane and fused ventrally into a prominent V-shape. In *Smithornis*, *Eurylaimus*, *Serilophus*, and *Psarisomus*, the lateral portions of A2 are weakly oblique. In *Cymbirhynchus* and *Pseudocalyptomena*, the caudoventral margin of A2 is widened caudad and obliquely oriented, but the cranial margin is nearly transverse. In other eurylamids, *Pitta*, and other suboscines, A2 and other single A elements are transversely oriented. The acutely oblique A2 element found in *Philepitta* and *Neodrepanis* is hypothesized to be derived.

(5) *A1 elements thin.*—In *Pseudocalyptomena*, *Philepitta*, and *Neodrepanis*, the A1 elements are thin and much narrower than the other A elements. In other

eurylamids and *Pitta*, the A1 elements are similar in width to other A elements. The thin A1 elements found in these three genera are hypothesized to be derived.

(6) *A2-3 fused ventrally.*—In *Pseudocalyptomena*, the A2-3 elements are ventrally fused. This morphology is unique in Old World suboscines and is hypothesized to be derived.

(7) *Pessulus present.*—In *Eurylaimus*, *Cymbirhynchus*, *Serilophus*, *Psarisomus*, *Pseudocalyptomena*, *Philepitta*, and *Neodrepanis*, an ossified pessulus is fused dorsally and ventrally to A2. In *Calyptomena*, an ossified pessulus is present and fused dorsally and ventrally to A4 or A5. In *Smithornis* and most *Pitta* species, there is no pessulus. A partial pessulus is present and fused ventrally to A3 in *Pitta sordida* and *P. brachyura*. A pessulus is absent in the furnarioids and uniformly present in the tyrannoids, acanthisittids, and oscines (secondarily lost in swallows, Hirundinidae; Ames 1971, Warner 1972). The homology of the pessulus at these highest levels within passerines has not been assessed. Any dorsoventrally oriented supporting element at the tracheobronchial junction has been called a pessulus; however, given the variation in shape, connection, and composition of these structures, there is little evidence to support their homology in all passerine lineages. It is equally parsimonious to hypothesize four independent origins for the pessulus in passerines or a single origin with three secondary losses or redevelopments. Here, the pessulus in eurylamids and philepittids is hypothesized to be derived independently from that in other passerines. Because of the dissimilarity in shape and relative position, the pessulus present in most eurylamids and philepittids (7.1) and the pessulus found in *Calyptomena* (7.2) are coded as alternative, unordered derived character states. These elements differ significantly in

position and shape, and may be evolutionarily independent.

(8) *Medial bronchial cartilage sheet*.—In *Calyptomena viridis* and *C. whiteheadi*, there is an accessory cartilaginous sheet at the craniomedial surface of the bronchi connecting the dorsal and ventral ends of the double A elements and the pessulus. In most specimens, the caudoventral margins of these cartilaginous sheets are connected by a transverse membrane. This structure is unique among Old World suboscines and is hypothesized to be derived. Similar, independently derived structures are known in a few piprid and cotingid genera (*Antilophia*, *Chiroxiphia*, *Neopelma*, *Tyrannetes*, *Lipaugus*, and *Tityra*; Prum 1990, 1992).

(9) *B elements ossified*.—In *Eurylaimus*, *Cymbirhynchus*, *Serilophus*, *Psarisomus*, *Pseudocalyptomena*, *Philepitta schlegeli*, and *Neodrepanis*, the two most-cranial B elements are completely ossified, and ossification is gradually reduced caudad. In *Neodrepanis*, only B1–2 are ossified. Ossification of B elements continues until B3–6 in *Eurylaimus* and *Psarisomus*, B7 in *Philepitta schlegeli*, and to B11–12 and beyond in *Pseudocalyptomena* and *Serilophus*. In *Philepitta castanea*, all B elements are entirely ossified. B elements in all other Old World suboscines and most New World suboscines are completely cartilaginous. The partially or completely ossified B elements are hypothesized to be derived.

(10) *B1–2 elements straightened*.—In *Eurylaimus*, *Cymbirhynchus*, *Serilophus*, *Psarisomus*, *Pseudocalyptomena*, *Philepitta*, and *Neodrepanis*, the medially incomplete B1–2 are not rounded and ringlike, but are straightened bars. In all other Old World suboscines, furnarioids, and most tyrannoids, B elements are rounded and ringlike. The straightened B elements in these genera are hypothesized to be derived.

(11) *B3 elements straightened, dorsally widened, and elongate*.—In *Eurylaimus*, *Cymbirhynchus*, *Serilophus*, and *Psarisomus*, the B3 elements are straightened, dorsally widened, and elongated, so that they extend beyond the dorsal ends of other B elements. This morphology is unique among Old World suboscines and is hypothesized to be derived.

(12) *A1, B1 and B2 fused ventrally by cartilage*.—In *Pseudocalyptomena*, *Philepitta schlegeli*, and *Neodrepanis*, the ventral ends of A1, B1 and B2 are fused together by a small block of cartilage. This fusion is reduced but present in *Philepitta castanea*. This morphology is unique in Old World suboscines and is hypothesized to be derived.

(13) *Ventral ends of B1–3 broadly fused*.—In *Calyptomena*, the ventral ends of B1–3 are broadly fused by an expanded cartilaginous lattice. This morphology is distinctly different from the ventral fusion of A1, B1–2 in *Pseudocalyptomena*, *Philepitta*, and *Neodrepanis* (12), and is unique in Old World suboscines. This morphology is hypothesized to be derived.

(14) *Insertion of M. tracheolateralis expanded ventrally*.—In *Neodrepanis*, *M. tracheolateralis* inserts on the lateral and ventral surfaces of the fused A1–2 element.

In *Philepitta*, *M. tracheolateralis* inserts on the entire length of A1, except for the extreme ventral ends. In eurylaimids, Old World suboscines, and primitively in New World suboscines, the insertion of *M. tracheolateralis* is restricted to the lateral and dorsolateral portions of A1. The ventral expansion of the insertion of *M. tracheolateralis* in *Neodrepanis* and *Philepitta* is here hypothesized to be independently derived.

(15–16) *M. tracheolateralis ventrally or dorsally united*.—In *Philepitta castanea*, *M. tracheolateralis* expands ventrally and dorsally from above A20 to cover the entire trachea except for a small gap on the dorsal surface. In *P. schlegeli*, *M. tracheolateralis* covers the entire surface of the trachea. In all other Old World suboscines and furnarioids, and primitively within tyrannoids, *M. tracheolateralis* is restricted to the lateral surfaces of the trachea and does not unite dorsally or ventrally into a single sheet of muscle. The ventral union (15) and the dorsal union (16) of *M. tracheolateralis* are hypothesized to be derived in an ordered transition series, and are coded as a set of additive binary characters.

(17) *M. tracheolateralis inserts on A3–5*. In *Smithornis*, *M. tracheolateralis* inserts on the lateral surface of A3, 4, or 5. In all other Old World suboscines, and primitively within New World suboscines, *M. tracheolateralis* inserts on the lateral surfaces of A1. In suboscines with intrinsic syringeal muscles, *M. tracheolateralis* inserts on some more cranial A elements often including A3–5, but *Smithornis* lacks intrinsic syringeal muscles. The unique state found in *Smithornis* is hypothesized to be derived.

(18–19) *M. tracheolateralis or intrinsic muscles insert on the lateral A1–B1 membrane*.—In *Calyptomena*, *M. tracheolateralis* inserts on the lateral surfaces of A5–7; intrinsic muscles originate just caudal to this insertion and continue caudad to insert themselves on the lateral membrane between A1–B1. In *C. whiteheadi*, *M. tracheolateralis* itself apparently inserts on the lateral A1–B1 membrane, and intrinsic fibers are lacking (Ames 1971). The insertion of *M. tracheolateralis* is absent in most other suboscines, but is present in the Neotropical cotingids and has been hypothesized to be a synapomorphy of the family (Prum 1990). I hypothesize that this insertion is independently derived in *Calyptomena* (18). Also, the presence of intrinsic muscles in *C. viridis* is unique among Old World suboscines and is hypothesized to be derived as well (19).

SKELETAL CHARACTERS

(20) *Spina externa unforked*.—In *Philepitta* and all broadbills except *Smithornis*, the spina externa of the sternum is pointed and bladelike (Olson 1971, pers. observ.); in *Neodrepanis*, it is weakly bifid and lacks any lateral arms. In *Smithornis* and almost all other passerine birds, it is strongly forked with extensive lateral arms (Olson 1971). The pointed, unforked or weakly bifid condition present in all broadbills and asities except *Smithornis* is hypothesized to be derived.

The unforked condition found in some species of *Procnias* (Cotingidae) is independently derived.

(21) *Two free cervical ribs.*—*Neodrepanis* and all broadbills except *Smithornis* have two free cervical ribs, resulting in 15 cervical vertebrae. In these taxa, the first pair of cervical ribs are small, and lack the uncinete process and ventral segment. The second pair of cervical ribs have uncinete processes and, in some species, a ventral segment, but none articulates with the sternum. In *Neodrepanis*, both pairs of cervical ribs lack uncinete processes and ventral segments. In *Smithornis*, *Philepitta castanea*, and most other passerines known, there are only a single pair of free ribs and, correspondingly, only 14 cervical vertebrae (Olson 1971; pers. observ.). The second ribs have ventral segments that articulate with the sternum. The condition in *P. schlegeli* is unknown. The loss of the sternal connection of the second pair of ribs and the consequent increase in the number of cervical vertebrae is hypothesized to be derived.

RESULTS

Phylogeny.—A phylogenetic analysis of the 19 syringeal characters and the two osteological characters described above yields a single, most-parsimonious tree of length 25 and a consistency index of 0.96 with zero-branch-lengths collapsed (Fig. 3). A phylogenetic analysis of these data combined with 15 informative morphological characters from Raikow (1987) yields the same phylogenetic tree with a length of 50 and consistency index of 0.82 with zero-branch-lengths collapsed. (An additional tree of the same length placed *Eurylaimus javanicus* outside of the clade including other *Eurylaimus* species because myological data were missing for *javanicus*.) Optimizations for the evolution of the syringeal and myological characters on this phylogeny are shown in Figure 4.

Raikow's (1987) hypothesis for the phylogeny of the broadbills and asities, in which they are monophyletic sister groups, requires a length of 59 and a consistency index of 0.69 to explain the distribution of the characters in both the syringeal and myological data sets. The revised hypothesis of phylogeny (Fig. 3) better explains all the evidence than the previous hypothesis of the group in which the broadbills and asities are monophyletic sister groups (Raikow 1987). The broadbills as currently recognized (Peters 1951, Raikow 1987, Sibley and Monroe 1990) are not monophyletic. The broadbills apparently consist of four clades with successively closer phylogenetic relationships to the monophyletic asities. The three species in the mono-

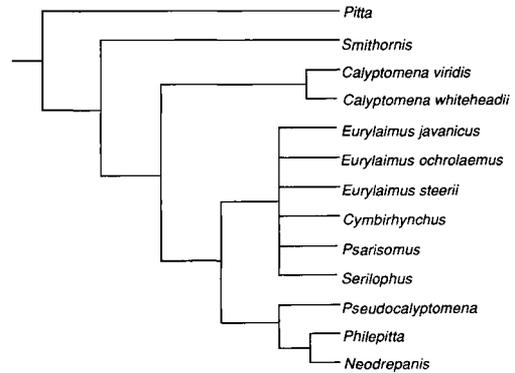


Fig. 3. Single most-parsimonious phylogenetic hypothesis for broadbills and asities. Phylogenetic analysis of 21 characters yielded this hypothesis with length of 25 and consistency index of 0.96. Phylogenetic analysis of these data combined with 15 additional morphological characters from Raikow (1987) yielded the same phylogenetic hypothesis with length of 50 and consistency index of 0.82. *Pitta* was the outgroup. Tree does not include *Corydon sumatranus*, which was unavailable for analysis.

phyletic African genus *Smithornis* are the sister group to the rest of the broadbills and asities. The next clade consists of the three species of *Calyptomena*. The sister group to *Calyptomena* includes the other Asian broadbills, *Pseudocalyptomena*, and the asities. These Asian genera—*Eurylaimus*, *Cymbirhynchus*, *Serilophus*, and *Psarisomus*—form a clade that is the sister group to *Pseudocalyptomena* and the asities. The asities are monophyletic, as are both *Philepitta* and *Neodrepanis*.

Among the six species in *Eurylaimus*, *Cymbirhynchus*, *Serilophus*, and *Psarisomus*, there are five diagnosable syringeal morphologies. Each species is distinct except for the generally similar *Eurylaimus ochromalus* and *E. javanicus*. It was not possible to polarize variations among these species confidently, so their interrelationships could not be resolved by this analysis. Furthermore, the monophyly of *Eurylaimus* remains unsupported by any characters, including obvious clearly derived plumage traits.

Four species of broadbills and asities could not be examined in this study because no specimens were available (Wood et al. 1982). Three of these species—*Smithornis sharpei*, *Calyptomena hosei*, and *Neodrepanis hypoxantha*—are hypothesized to belong to their respective monophyletic genera. Following Raikow (1987), I hypothesize that *Corydon sumatranus* is a member

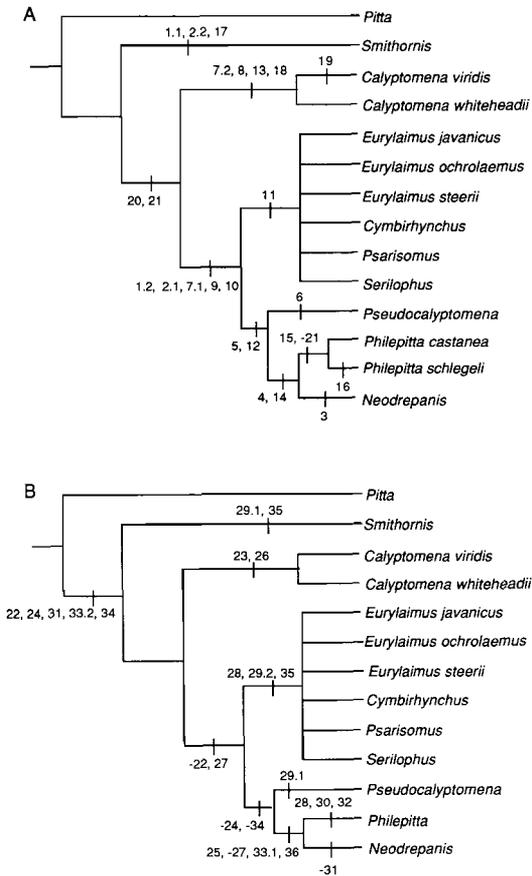


Fig. 4. Parsimonious optimizations for evolution of morphological characters within the proposed phylogenetic hypothesis for broadbills and asities: (A) 21 syringeal and skeletal characters used; (B) 15 informative characters from hindlimb myology and external morphology described by Raikow (1987). Characters 22 and 27 each presented as a gain and a loss, but two gains are equally parsimonious.

of the Asian broadbill clade including *Eurylaimus*, *Cymbirhynchus*, *Serilophus*, and *Psarisomus*.

Biogeography.—An area cladogram based on this hypothesis of phylogeny was produced by replacing each terminal taxon with its extant range (Fig. 5). The biogeographic history of the broadbills and asities has been complex, including expansion or dispersal into secondary sympatry a number of times. An informative hypothesis of historical area interrelationships is supported by the clade including all broadbills and asities excluding *Smithornis* and *Calyptomena* (Fig. 5). This branch of the area cladogram provides evidence that a broadly distributed ancestral lineage was secondarily

isolated into Asian and African/Madagascan lineages subsequent to the diversification of *Smithornis* and *Calyptomena*. The African and Madagascan lineages were later isolated from each other and became *Pseudocalyptomena* and the asities. The former clade diversified within Asia to become *Eurylaimus*, *Cymbirhynchus*, *Psarisomus*, *Serilophus*, and probably *Corydon*.

The close phylogenetic relationship of the asities to a restricted endemic from montane Central Africa, *Pseudocalyptomena*, implies that the Madagascan avifauna had a most recent geographic contiguity with Africa and not with Asia. The earlier branches of the area cladogram are not strictly informative because of secondary sympatry between the African genera and among the six Asian genera. However, the position of the widespread African genus *Smithornis* as the sister group to the rest of the broadbills and asities implies that there may have been an earlier, initial geographic isolation of African and Asian lineages that resulted in the differentiation of *Smithornis* from the ancestor of all other genera, and was subsequently obscured by secondary dispersal into Africa. This biogeographic pattern is similar to those supported by phylogenies of the barbets and toucans (Prum 1988), and the hornbills (Kemp and Crowe 1985). All of these groups have paraphyletic or polyphyletic African assemblages that include the initial lineage of a diverse multicontinental radiation.

Evolution of bill shape, diet, and nest architecture.—The revised hypothesis of phylogeny proposed here provides an historical framework for analysis of the ecological and behavioral diversification of the broadbills and asities. By parsimoniously superimposing transitions in bill morphology and diet on the hypothesis of phylogeny, it is possible to identify phylogenetic correlations or dislinkages among these traits and to investigate hypotheses of morphological and ecological adaptation.

Raikow (1987) coded the broad bill as a derived character state present in *Smithornis* and all Asian genera, excluding *Calyptomena* (character 25, Table 1), but the variation in bill size also includes a potentially independent factor, the wide gape present in *Calyptomena*, *Pseudocalyptomena*, and *Philepitta*. The highly decurved bill in *Neodrepanis* differs strikingly from all other genera in the family.

There are two alternative hypotheses for the evolution of bill shape in the broadbills and

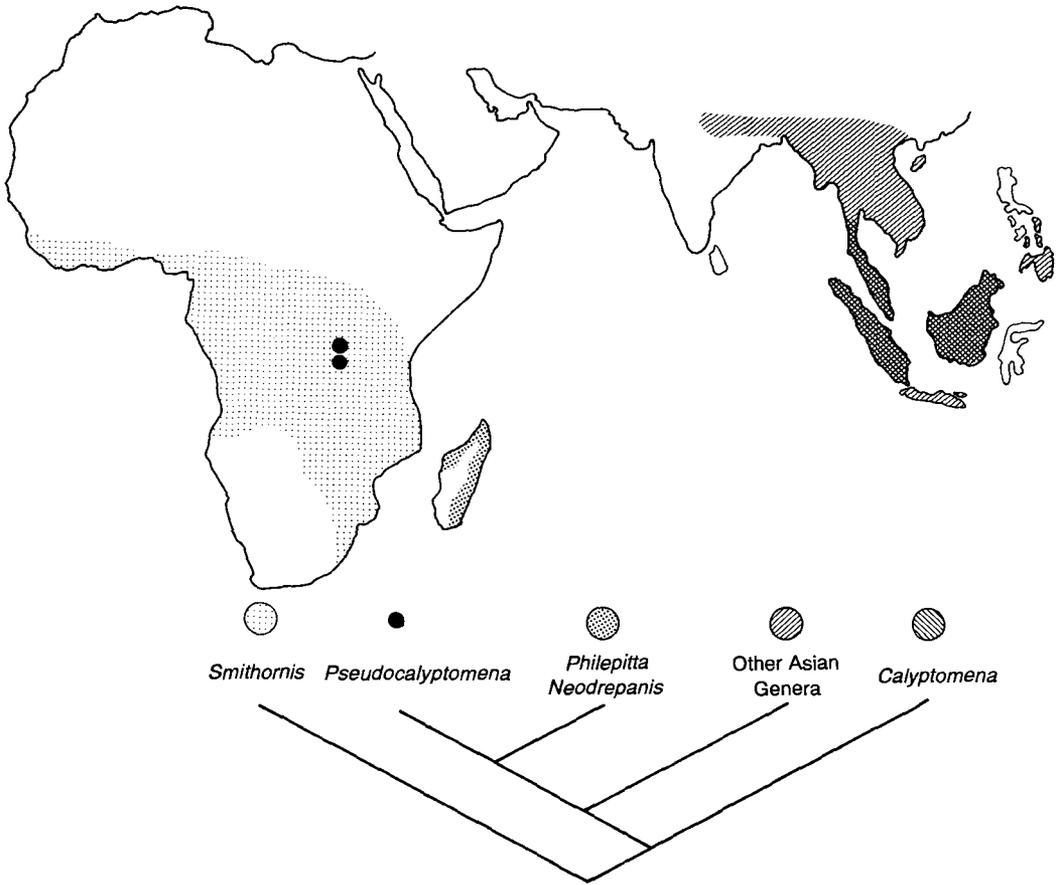


Fig. 5. Range map and area cladogram based on higher level interrelationships among broadbills and asities. Range of each taxon is shaded with pattern displayed above its name. "Other asian genera" includes *Eurylaimus*, *Cymbirhynchus*, *Serilophus*, and *Psarisomus*. Central clade yields informative hypothesis of area history.

asities. (Bill shape has diversified into a variety of forms in *Eurylaimus*, *Cymbirhynchus*, *Psarisomus*, *Serilophus*, and *Corydon*, but these will not be analyzed here.) In the first, the wide bill and gape are hypothesized to have evolved in the common ancestor of all broadbills and asities, with subsequent reductions in bill size in *Calyptomena* and the *Pseudocalyptomena*-asity clade (Fig. 6A). Subsequently, the wide gape is lost and an elongate decurved bill has evolved in the genus *Neodrepanis*. The alternative hypothesis differs in that the wide gape evolves in the common ancestor of the group, with subsequent evolution of the wide or swollen bill morphology twice independently in *Smithornis* and the large clade of Asian broadbills (Fig. 6B).

Although the second hypothesis is numerically more parsimonious (five character-state

changes instead of six), the first appears more likely. The wide bill and wide gape were coded as separate characters in this analysis to permit the possibility of the independent, convergent origin of the broad bill. However, it is unlikely that these two characters are entirely independent, and it is improbable that the wide bill and wide gape would have had independent origins from one another if they evolved in a single lineage (Fig. 6A). Rather, the origin of the two traits in the first hypothesis is more realistically considered to be a single correlated change in bill morphology, making the two hypotheses numerically equivalent. Furthermore, there are detailed similarities in bill morphology between *Smithornis* and the broad-billed Asian genera that strongly support the homology of these bill morphologies, as proposed by Raikow

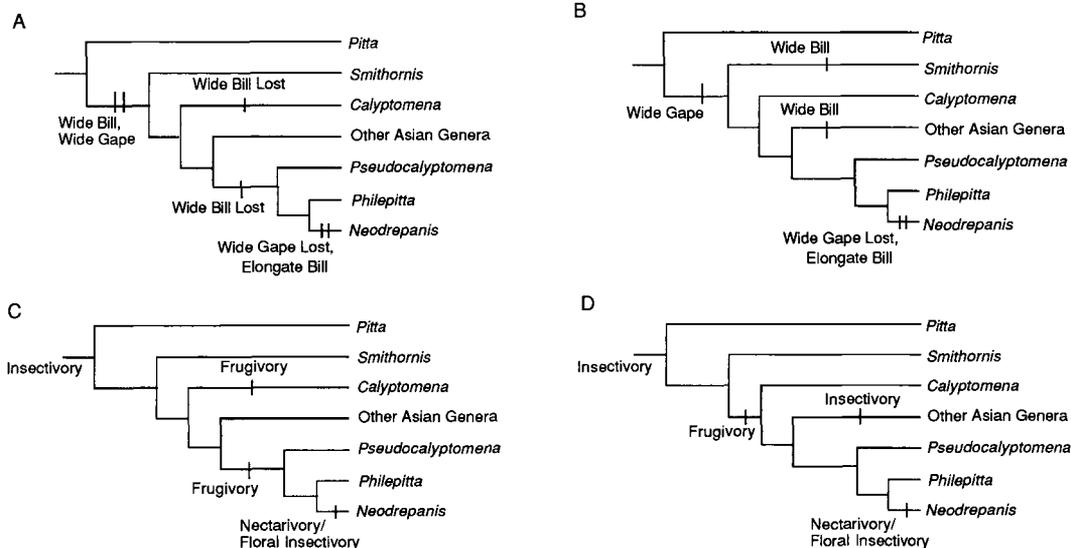


Fig. 6. Alternative hypotheses for evolution of (A, B) bill morphology and (C, D) diet in broadbills and asities. (A) Single, correlated origin of wide bill and wide gape with two subsequent losses of wide bill. (B) Single origin of wide gape and two subsequent origins of wide bill. In both hypotheses, wide gape lost and elongate bill evolved in *Neodrepanis*. (C) Two independent origins of frugivory. (D) One origin for frugivory, with secondary reversal to insectivory.

(1987). Overall, the first hypothesis is best supported by the data.

The diet of most broadbills apparently consists largely of insects, spiders, land snails, and small lizards (Delacour 1947, Chapin 1953, Smythies 1960, Ali and Ripley 1970, Friedmann and Williams 1970). In contrast, *Calyptomena*, *Pseudocalyptomena*, and *Philepitta* are largely frugivorous, although all are known to take insects occasionally (Rockefeller and Murphy 1933, Rand 1936, Delacour 1947, Chapin 1953, Smythies 1960, Friedmann 1970, Wong 1986, Langrand 1990, S. M. Goodman pers. comm.). *Neodrepanis* feeds on insects attracted to flowers (Langrand 1990), or insects and nectar (Rand 1936, Collar and Stuart 1985, S. M. Goodman pers. comm.). By outgroup comparison to *Pitta*, which is insectivorous and carnivorous (Delacour 1947, Chapin 1953, Smythies 1960, Ali and Ripley 1970, Friedmann and Williams 1970), the insectivorous/carnivorous diet of most broadbills is parsimoniously hypothesized to be the primitive condition within the broadbills and asities.

Although the data on the diets of broadbills and asities are limited, the evolutionary transition in diet from mainly insectivory to frugivory probably occurred in one of two differ-

ent, equally parsimonious ways: (i) twice, independently in the genus *Calyptomena* and in the *Pseudocalyptomena*-asity clade (Fig. 6C); or (ii) as a single transition to frugivory in the common ancestor to all genera except *Smithornis* followed by a reversal to insectivory in the large clade of Asian broadbills excluding *Calyptomena* (Fig. 6D). Both hypotheses require two evolutionary changes, but the former hypothesis of two convergent origins for frugivory is more likely for several reasons. The two alternatives give us an opportunity to accept or reject a hypothesis of ecological homology between two frugivorous clades. Although the frugivorous diets of *Calyptomena* and the *Pseudocalyptomena*-asity clade are both derived from insectivory, no details about these diets have been documented to support this hypothesis of ecological homology with additional detail or special similarity. In the absence of such evidence, it is better to reject the hypothesis of dietary homology and accept these frugivorous diets as historically independent. In addition, frugivory is often accompanied by digestive specializations that may be more likely to evolve twice than to reverse evolutionarily. In either optimization, the nectarivory/floral insectivory of *Neodrepanis* evolved in that genus from frugi-

vory and not from insectivory, demonstrating that frugivory is not evolutionarily completely constrained.

The best-supported optimizations for the evolution of diet and bill morphology can be used to test the hypothesis that bill shape has adapted to major transitions in the type of diet. The current hypothesis documents two transitions in diet from insectivory to frugivory and a single transition from frugivory to floral foraging. Both evolutionary reductions in bill size are exactly correlated with the two transitions from insectivory to frugivory. Furthermore, the unique derivations of floral insectivory and the elongate bill are also exactly correlated. These correlations between potential natural selection pressures in the form of novel diets and derived bill morphologies provide comparative support for the hypothesis of the adaptive origin of these morphological novelties.

All of the broadbills and asities build hanging, globular nests with side entrances that are made of interwoven sticks and vegetation (Rand 1936, Chapin 1953, Smythies 1960, Collar and Stuart 1985, Langrand 1990). Pittas make domed nests that usually are placed on the ground or horizontal branches near the ground. Elsewhere in suboscine passerines, woven hanging nests are found in various lineages, including the flatbilled tyrannids and the tyrannoid genus *Pachyramphus*, but these nests have been hypothesized to be independently evolved synapomorphies of these two groups (Lanyon 1988, Prum and Lanyon 1989). The hanging or globular nest architecture of the broadbills and asities is derived, and constitutes an additional, behavioral synapomorphy of the group. Interestingly, the oscine sunbirds (Nectariniidae) also build woven, hanging nests (e.g. Rand 1936, Bannerman 1953). The strong convergent similarity between the nests of the sunbirds and the sunbird-asity (*Neodrepanis*) may have contributed to the confidence of its original placement in that family.

DISCUSSION

Alternative phylogenies of the broadbills and asities.—The syringeal morphology of many of the broadbills and asities has been previously described (Forbes 1880a, b, Bates 1915, Lowe 1924, 1931, Köditz 1925, Amadon 1951, Ames 1971), but it has not been analyzed phylogenetically. When Lowe (1931:454) described the

syrinx of *Pseudocalyptomena*, he recognized "strangely enough" that it was even more similar to *Philepitta* than to other broadbills; he was perplexed because he was convinced that "there is no reason to regard *Philepitta* as a member of the Eurylaemid [sic] group of Passeres."

Ames (1971) concluded that the syringeal morphology of the asities and some broadbills was very similar but that these similarities were probably primitive. Using a phylogenetic analysis to polarize many of the syringeal features described by Lowe, Ames, and others has yielded a highly consistent, novel hypothesis of phylogeny for the group.

Olson (1971) concluded that variation within broadbills and other passerines in two osteological characters—(20) unforked spina externa, and (21) an additional free, cranial rib and cervical vertebra—did not justify the taxonomic placement of broadbills as a separate suborder of passerines. However, he did not go on to identify the more exclusive group of genera that share these derived osteological features. With a single reversal, both these skeletal novelties identify *Smithornis* as the earliest, differentiated lineage within the broadbills and asities, and are congruent with syringeal characters in supporting the paraphyly of the broadbills.

A previous, explicit hypothesis of phylogeny for the broadbills and asities was proposed by Raikow (1987). Raikow identified three synapomorphies of the broadbills and asities, including the presence of the plantar vinculum. Raikow (1987) commented on the surprising weakness of the myological support for the monophyly of broadbills, but he concluded that two characters with two derived states provided synapomorphies of the family (original character numbers 29 and 33 from Raikow 1987). Although Raikow (1987:9) stated that analyses of his ordered and unordered data gave the same results, neither of these characters provides an unambiguous synapomorphy of the broadbills in Raikow's hypothesis of phylogeny if they are treated as unordered.

Thus, within Raikow's (1987) data set, there is less support for the monophyly of the broadbills than he supposed. Furthermore, Raikow expressed some skeptical concern about non-myological characters that supported two other major broadbill clades within his hypothesis of phylogeny: (34.1) well developed syndactyly; and (35.1) bill enlarged.

My analysis indicates that the available char-

acters from all morphological systems are most parsimoniously explained by the revised phylogenetic hypothesis proposed here. This result is related to the extensive internal congruence between the syringeal data set and Raikow's (1987) myological characters. The phylogenetic hypothesis proposed here is identical to the network of interrelationships among broadbills and asities proposed by Raikow (1987), but rooted with *Smithornis* as the sister group to the other broadbills and asities.

Within this revised phylogenetic hypothesis, the monophyly of *Smithornis*, of *Calyptomena*, of the clade including all other genera, and of the asities is well supported by several derived morphological characters. The clade including *Eurylaimus*, *Cymbirhynchus*, *Psarisomus*, and *Serilophus* is supported by a single syringeal synapomorphy and a number of myological novelties. The *Pseudocalyptomena*-asity clade is supported by two detailed syringeal characters, but may be considered less-well supported than those above. The monophyly of the broadbills and asities excluding *Smithornis* is supported by two osteological synapomorphies, and may require further corroboration by other data.

Although this phylogenetic hypothesis is only partially resolved, the optimizations are not affected by this lack of resolution because all of the taxa in the unresolved clade are identical for all the characters analyzed. Additional ordering of the unordered syringeal characters (1, 2, 7) will yield the same hypothesis of relationships if dorsally, hammer-shaped A elements are primitive to paddle-shaped ones, but the relationships of *Smithornis* and *Calyptomena* to the clade including all other genera are equivocal if the opposite order is hypothesized. However, there is no objective basis for applying additional ordering to these traits, and one of the unordered characters would provide additional strength to the current hypothesis if it were ordered (7).

Syringeal evolution.—I examined 13 of the 17 species of broadbills and asities, and described 11 different, diagnosable syringeal morphologies. In this respect, the broadbills and asities resemble the syringeally diverse New World suboscines, and differ strikingly from the oscines, which are relatively homogeneous in syringeal morphology. By comparison, only a few families of the true oscines are known to have distinct, diagnosable syringeal morphologies, even though this clade includes thousands of

species (Ames 1971, 1975, 1987, Warner 1972, Cutler in Baptista and Trail 1988).

Although the syringes of most broadbills and asities have been described previously, I made a number of novel observations. Intrinsic syringeal muscles have not been described previously in any Old World suboscine, however, completely intrinsic muscles were observed in the syrinx of male and female *Calyptomena viridis*. These muscles have independent origins immediately caudal to the insertion of *M. tracheolateralis* fibers and, like the intrinsic syringeal muscles in other passerines, they are clearly the derived caudal ends of *M. tracheolateralis*. Intrinsic muscles have originated at least five times in manakins (Pipridae; Prum 1992), at least once in the oscines, and probably several more times in flycatchers (Tyrannidae) and cotingas (Cotingidae; Prum and Lanyon 1989, Prum 1990). These numerous convergent developments of syringeal muscular complexity provide many evolutionarily independent examples for comparative analysis of the role of these muscles in syringeal function and in vocal evolution. Medial syringeal cartilages, or internal cartilages, were observed in *Neodrepanis*. These structures are similar to those of the tyrannids but are evolutionarily independent (Prum 1990).

Another interesting variation in the syringes of the Old World suboscines is the presence or absence of a pessulus, which divides the left and right medial tympaniform membranes into potentially separate sound sources. Greenewalt (1968) hypothesized that laterally independent musculature, innervation, and vibratile membranes are necessary for control of two simultaneous syringeal sound sources. Greenewalt's "two-voice" model predicts that *Smithornis* and most *Pitta* should lack the independent two-voice vocal ability because they lack a pessulus dividing the medial tympaniform membranes, whereas all of the other broadbills and asities that have the structural potential should have the two-voice ability.

Biogeography of Old World tropics and Madagascar.—Phylogenetic analyses of the biogeographic history of Old World tropical birds are just beginning (Kemp and Crowe 1985, Cracraft 1986, 1988, Prum 1988, Cristidis et al. 1991). There are few corroborated hypotheses of phylogeny for the numerous radiations of African and Asian tropical birds. In addition, there are no corroborated phylogenetic hypotheses for the relationships of the other Madagascan en-

dem radiations to other Old World tropical birds (e.g. Mesornithidae, Leptostomatidae, Brachypteraciidae, Hyposittidae, Vangidae).

This investigation supports a closest biogeographic relationship between the avifauna of Madagascar and Africa. The asities are most closely related to *Pseudocalyptomena graueri*, which is restricted in range to two small highland regions in eastern Zaire and southwestern Uganda (Rockefeller and Murphy 1933, Friedmann 1970, Collar and Stuart 1985). Although Madagascar and Africa are relatively close geographically, the two land masses apparently began separating between 165 and 130 million years ago during the Middle Jurassic (Coffin and Rabinowitz 1987). The Somali Basin that separates the two land masses was likely the earliest rift among the extant Gondwanan continental elements, and had reached near-modern dimensions by the Jurassic-Cretaceous boundary (Coffin and Rabinowitz 1987). Although fossil passerines from distinctive modern oscine genera have been found in late Oligocene-Miocene deposits in Australia (Boles 1991), the age of the separation of Africa and Madagascar makes a vicariant origin for this biogeographic pattern extremely unlikely. However, there are few objective criteria for ageing these taxa, and this hypothesis cannot be ruled out entirely. If the asity lineage originally dispersed to Madagascar, the phylogenetic evidence indicates that it was from Africa by their common ancestor with *Pseudocalyptomena*. Additional phylogenetic studies of other Madagascan endemic birds should be conducted to further aid in the reconstruction of the biogeographic history of the region.

Neither the African nor Asian broadbills are monophyletic, and the phylogenetic hypothesis supported here indicates that their biogeographic history has been complex. A simple overall scenario for their diversification is: (i) a primary division between undifferentiated Asian and African broadbills giving rise to *Smithornis* in Africa and the common ancestor of all other genera in Asia; (ii) diversification of *Calyptomena* from other populations within Asia; (iii) subsequent dispersal or expansion into Africa and Madagascar of the undifferentiated Asian lineage followed by isolation of these Asian and Afro-Madagascan lineages; (iv) isolation of Madagascan lineage from African proto-*Pseudocalyptomena* and subsequent diversification of asities in Madagascar; and (v) complex

diversification of the remaining genera in Asia. Although this hypothesis is not strictly testable, it is parsimonious, given that secondary expansion or dispersal is necessary to explain their phylogenetic interrelationship and current distributions. The lack of phylogenetic resolution among most Asian broadbills and their secondary sympatry also limits further analysis of their biogeographic history.

Evolution of ecology and behavior.—The broadbills and asities exhibit a wide variety of bill morphologies and diets. A phylogenetic hypothesis for the group provides an historical perspective on the process of this diversification.

Within the broadbills and asities, phylogenetic correlation between novel diets and derived bill shapes supports the hypothesis that bill shape has adapted to ecological natural selection (Fig. 6A, C). There are two independent phylogenetic associations between the transition from insectivory to frugivory and the reduction in bill size: in *Calyptomena*; and in the *Pseudocalyptomena*-asity clade. In both cases, the primitive wide gape was retained through the transition to frugivory. The reduced bill size in these genera apparently constitutes an adaptation to frugivory, but the wide gape itself cannot be an adaptation to frugivory in broadbills because it originated earlier in a lineage with the primitive insectivorous diet.

In traditional classifications (Peters 1951, Amadon 1979), the closest relatives to the asities were insectivores, implying that the morphology of *Philepitta* was itself a derived adaptation to frugivory. However, this revised phylogeny of the group supports the origin of frugivory prior to the differentiation of the asities. The bill morphology of *Philepitta* has evolved in apparent response to detailed aspects of frugivory on Madagascar (e.g. a depauperate flora), rather than as an adaptation to frugivory itself. Likewise, the diversification of bill morphology in the insectivorous/carnivorous Asian broadbill genera occurred within the context of a primitive insectivorous/omnivorous diet.

The evolution of the elongate, decurved bill in *Neodrepanis* is phylogenetically correlated with the evolution of nectarivory or floral insectivory found in the genus, and constitutes a putative adaptation to that diet. The history of the bill of *Neodrepanis* is apparently a continuity of successive reductions in the primitive bill morphology of the group. The striking and fre-

quently cited convergence in bill shape and ecology among *Neodrepanis*, the oscine sunbirds, and the Hawaiian honeycreepers (Salomonsen 1934, 1965, Amadon 1951, Langrand 1990) is even more remarkable given that the sunbird-asities are essentially broadbills.

PROPOSED CLASSIFICATION

I propose an explicit phylogenetic classification of the broadbills and asities. Wiley (1981) and Raikow (1985) have discussed the advantages of phylogenetic classifications in detail. In order to reflect the best supported hypothesis of the evolutionary history of these birds, I propose placing all genera of broadbills and asities in a single, monophyletic family. The name Eurylaimidae Lesson, 1831 has priority over Philepittidae Sharpe, 1870 (W. Bock pers. comm.). Continued recognition of the Eurylaimidae as separate from the Philepittidae would require acceptance of an ahistorical, paraphyletic group—the broadbills—that can only be characterized arbitrarily by the absence of the derived features that diagnose the monophyletic asities.

Within the Eurylaimidae, I place all of the broadbills and asities in five subfamilies. These subfamilies are arranged by a sequencing convention so that each subfamily is the sister group to the remaining subfamilies in the sequence (Raikow 1985). For example, Eurylaiminae is the sister group to the Pseudocalyptomeninae and Philepittinae. Among the many options for recognizing intrafamilial taxa for the broadbills and asities, I have chosen the present level of subfamily designations to preserve previously recognized subfamilies (Calyptomeninae, Eurylaiminae, and Philepittinae) and limit the number of new taxonomic names.

Family Eurylaimidae

Subfamily Smithornithinae, **new**, type genus = *Smithornis*.

Genus *Smithornis*

Subfamily Calyptomeninae

Genus *Calyptomena*

Subfamily Eurylaiminae

Genus *Cymbirhynchus*, *sedis mutabilis*

Genus *Psarismus*, *sedis mutabilis*

Genus *Serilophus*, *sedis mutabilis*

Genus *Eurylaimus*, *sedis mutabilis*

Genus *Corydon*, *incertae sedis*

Subfamily Pseudocalyptomeninae, **new**, type genus = *Pseudocalyptomena*

Genus *Pseudocalyptomena*

Subfamily Philepittinae

Genus *Philepitta*

Genus *Neodrepanis*

The classification includes two new subfamilies: Smithornithinae and Pseudocalyptomeninae. I chose not to recognize the available subfamily group name Neodrepaninae Amadon, 1979 to include *Neodrepanis* alone, because placement of the genus itself within the monophyletic Philepittinae communicates efficiently both its monophyly and its phylogenetic relationships.

No spirit specimens of the genus *Corydon* were available (Wood et al. 1982), so *Corydon* is included in the Eurylaiminae *incertae sedis* as a preliminary hypothesis requiring further investigation. The other genera in the Eurylaiminae are labeled *sedis mutabilis* to indicate that their interrelationships to one another are not resolved (Wiley 1981, Raikow 1985).

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APPENDIX

SYRINGEAL MORPHOLOGY OF THE OLD WORLD SUBOSCINES

The syringeal terminology used follows Ames (1971) and Prum (1992). Homology among syringeal supporting elements was based on special similarities in shape, relative position to other elements and muscle insertions, and composition (in decreasing importance). An alternative, functional terminology based on relative position to the tracheobronchial junction (King 1989) is completely inappropriate for comparative or systematic studies, since evolutionary changes in the relative position of the tracheobronchial junction to the supporting elements will produce mistakes in homology assignments among elements.

The syrinx of the Old World suboscines is tracheobronchial, incorporating specialized tracheal and bronchial elements. The ringlike supporting syringeal elements are divided into two classes or series: A elements, which are the more cranial series including tracheal and some bronchial elements; and B elements, which are the caudal, entirely bronchial series. Each series is numbered beginning with the first element in each series near and proceeding away from the tracheobronchial junction either cranially (A series) or caudally (B series). These ringlike elements can be described as: complete or incomplete; single or double; ossified, partially ossified, or cartilaginous; and fused or unfused to other elements. In contrast, Ames (1971) described double, medially incomplete elements as "divided," and double, complete elements as "double."

In addition, there are accessory syringeal supporting elements that are not ringlike. These include the pessulus (a transverse bar at the tracheobronchial junction that separates the medial tympaniform mem-

branes) and various novel cartilaginous structures in this area. A pessulus is present in all asities and most broadbills, but is absent in *Smithornis* and most *Pitta*. Other accessory cartilages are found in *Calyptomena* and *Neodrepanis*, and are described below.

The syringeal musculature of the Old World suboscines includes two paired muscles that are found in all passerine birds: *M. tracheolateralis*, which originates on the cranial end of the trachea and the cricoid cartilages and usually inserts on A1; *M. sternotrachealis*, which originates on medial surface of cranio-lateral process of the sternum and inserts on lateral surfaces of trachea. Both muscles are classified here as extrinsic. In these Old World suboscine genera, intrinsic syringeal muscles are found only in *Calyptomena viridis*, and are referred to here simply as lateral intrinsic muscles. Specialized structures associated with the medial tympaniform membranes are present in some species and these are described below.

Specimens examined were from the collections of the American Museum of Natural History, AMNH; Delaware Museum of Natural History, DMNH; British Museum (Natural History), BM; Field Museum of Natural History, FMNH; U.S. National Museum of Natural History, USNM; and University of Michigan Museum of Zoology, UMMZ. Specimens followed by an asterisk (*) were cleared and double stained.

Pitta species (Fig. 1A)

Supporting elements.—All A elements ossified. From A1-2 to A1-4 double and medially incomplete. Subsequent A elements single and complete. In some species, dorsal ends of double A elements tipped with cartilage. A5 dorsally cartilaginous in some species, whereas in a few other species, A4-5 dorsally fused. No A elements obliquely angled. In most species, a pessulus absent. In *P. sordida* and *P. brachyura*, ossified pessulus fused ventrally to A3 and dorsally unfused. All B elements double, medially incomplete, and cartilaginous, and none fused, straight, or ossified.

Musculature.—*M. tracheolateralis* restricted to lateral surfaces of trachea, and inserts on lateral surface of A1. *M. sternotrachealis* inserts on lateral surface of trachea between A8 and A11.

Membranes.—No specialized membranous structures observed.

Specimens examined.—*angolensis*, AMNH 8262*, 8940, 9680; *baudi*, DMNH 61995, 61998; *brachyura*, AMNH 2237*, *caerulea*, BM 1970.27.1*; *erythrogaster*, AMNH 2236*, 4373, uncat. TG-15, uncat. TL-163; *granatina*, BM 1906.3.16.11; *guajana*, AMNH 4034*; *iris*, AMNH 4530; *oatesi*, AMNH 2234*, 2235*; *sordida*, AMNH 4033*, 8259*; *soror*, BM 1928.6.26.1832*; *superba*, AMNH 2239*; *versicolor*, AMNH 4374, 4376*, 4378*.

Smithornis rufolateralis and *S. capensis* (Fig. 1B)

Supporting elements.—All A elements ossified. A1-2 double and medially incomplete. A1-2 angled oblique

to midsagittal plane at about 45°. A1 robust, and its dorsal end widened caudally in hammer shape and caudally tipped with cartilage. A1 larger in *capensis* than *rufolateralis*. A2 and subsequent elements narrower. A3 and above single, complete, and unfused. Large membrane gap on ventral surface of trachea between oblique A2 elements and normally oriented A3. No pessulus. All B elements cartilaginous, double, medially incomplete, and rounded. Small lateral membrane gap between B1 and A1. Medial tympaniform membrane continuous between two bronchi and connected to dorsal and ventral end of B elements, A1-2, and dorsocaudal section of A3.

Musculature.—*M. tracheolateralis* restricted to lateral surface of trachea and inserts on A4 (in 1 *capensis* specimen), on A3 on left side and A4 on right (in 2 *rufolateralis* specimens), or on A5 (in 1 *rufolateralis* specimen). *M. sternotrachealis* thin and inserts directly on *M. tracheolateralis* at A5-7, immediately cranial to insertion of *M. tracheolateralis*.

Membranes.—No specialized membranous structures observed.

Specimens observed.—*S. rufolateralis*, AMNH 2232*, 2232A*, uncat. *S. capensis*, UMMZ RBP4023.

Smithornis sharpei

None available for examination (Wood et al. 1982). Previous description by Bates (1915) consistent with these observations of other species of *Smithornis*.

Calyptomena viridis (Fig. 1C)

Supporting elements.—All A elements ossified and all B elements cartilaginous. A1-4 double, medially incomplete, rounded, and normal in orientation. A1 straighter and longer dorsally than other double A elements, and it juts out dorsally beyond other supporting elements. A1-2 ventrally tipped with cartilage. A5 and subsequent elements single, complete and unfused. (In one specimen, one anomalous half ring (A4L) on left side fused dorsally and ventrally to A5.) Series of single A elements increase in diameter cranial (from A8 to 11) and then decrease in diameter (from A11 to 16), producing prominent bulge in trachea. Trachea widens from approximately 2.5-2.8 mm in diameter to 3.8-4.2 mm. (More accurate measurements not possible because of presence of *M. tracheolateralis*.) Flat ossified pessulus fused dorsally to A5 and ventrally to A4 or A5. All B elements double, medially incomplete, and rounded. B1-3 broadly fused at ventral ends. Dorsomedial surface of each bronchus composed of sheet of cartilage fused to dorsal and ventral ends of A3-4 and to pessulus. This accessory cartilage sheet forms dorsal margin of medial tympaniform membrane. Lateral membrane between A1 and B1 narrow and not tympaniform.

Accessory cartilages and membranes.—A large sheet of cartilage forms cranial margin of lateral tympaniform membrane and fused to pessulus and to dorsal and

caudal ends of double, medially incomplete A elements (A1-4).

Musculature.—M. tracheolateralis well developed and restricted to lateral surfaces of trachea. Muscle forms prominent belly at tracheal expansion between A8-15. A few fibers originate on lateral surface of trachea at cranial margin of drum and join deep fibers of muscle. M. tracheolateralis splits into dorsal and ventral bundles at insertion of M. sternotrachealis at A8-9, and these separate bellies insert on dorso- and ventrolateral surfaces of trachea at A6-7. An independent, intrinsic group of lateral fibers originate on lateral surface of A5-7 in complex interdigitating pattern with inserting fibers of M. tracheolateralis. These intrinsic fibers continue caudad to insert on lateral surface of lateral membrane between A1 and B1. M. sternotrachealis also robust, and inserts through gap in M. tracheolateralis onto lateral surface of A7-8 at caudal margin of tracheal expansion.

Membranes.—Caudoventral margin of accessory cartilage sheet connected by narrow transverse membrane in most specimens.

Specimens observed.—AMNH 7999*; DMNH 60813, 60971, 61648, 61849, 61997.

Calyptomena whiteheadi

Syrinx of this species not examined, but previously described by Ames (1971). Syrinx apparently generally similar to *C. viridis*. Accessory cartilages present on medial surface of bronchi. However, Ames (1971) did not mention any expansion in diameter of trachea. He did not describe any intrinsic belly in M. tracheolateralis. Completely extrinsic M. tracheolateralis apparently inserts on lateral A1-B1 membrane as in *C. viridis*.

Calyptomena hosei

No previous descriptions. No specimens available for examination (Wood et al. 1982).

Eurylaimus ochromalus, *E. javanicus*, and *E. steerii* (Fig. 2A)

Supporting elements.—Generally, as in *Cymbirhynchus* except as follows. A1 elements less oblique and do not meet extensively at ventral ends. A2 also less expanded ventrally. B1-2 elements less steeply angled than in *Cymbirhynchus* since A1-2 not as long ventrally. B elements ossified only to B3-6. In *ochromalus*, B1 elements thin and B2 more robust, as in *Cymbirhynchus*, but in *steerii* both B1-2 relatively thin. In *javanicus*, both B1-2 relatively robust. Syrinx of *steerii* also generally smaller in diameter than *Cymbirhynchus* and other *Eurylaimus*.

Musculature.—Generally as in *Cymbirhynchus*. M. sternotrachealis inserts on trachea between A7-11.

Membranes.—No specialized membranous structures.

Specimens observed.—*ochromalus*, USNM 223462*, 540477, 540478; *steerii*, USNM 432343, 510278; *javanicus*, USNM 509475, 509476.

Cymbirhynchus macrorhynchus (Fig. 1E)

Supporting elements.—All A elements ossified and complete. A1 double, medially incomplete, and acutely oblique to sagittal plane. A1 generally broad, rounded dorsally, and elongate at ventral end. Cranial margins of these oblique ventral ends meet extensively on ventral midline. A2 single, complete, and fused dorsally and ventrally to ossified pessulus. Dorsal and ventral surfaces of A2 triangular and expanded caudad and closely nested to A1. A3 and above single, complete, unfused rings. All B elements double, medially incomplete, and at least partially ossified. B1-2 completely ossified, weakly curved, and slightly oblique to sagittal plane. B1 thin and B2 more robust. B1-2 closely nested next to one another and dorsal and ventral ends close to those of A1; also angled craniocaudally from their dorsal to their ventral ends, producing narrow lateral tympaniform membranes between A1-B1 and between B2-B3. Ventral ends of A1, B1-2 fused with cartilage. B3 transversely oriented, almost completely straight, and extends dorsally beyond ends of A1 and other B elements. B3 ossified for dorsal half, and ossification of subsequent B elements gradually reduces to lateral third by B7. B4 and subsequent B elements transversely oriented, and successively more rounded.

Musculature.—M. tracheolateralis restricted to lateral surface of trachea. Inserts on lateral and dorso-lateral surface of A1. M. sternotrachealis robust muscle, and inserts on lateral surface of trachea between A8-A12. Caudodorsal fibers continuous with M. tracheolateralis, but cranioventral fibers insert directly on A elements at ventral margin of M. tracheolateralis. M. sternotrachealis constitutes large portion of mass of M. tracheolateralis cranial to its insertion at A8, and, consequently, M. tracheolateralis much less massive caudal to A8.

Membranes.—All but one specimen has prominent, oval fibrous mass in center of medial tympaniform membrane medial to B1 and B2.

Specimens observed.—DMNH 60941, 61226, 61267, 61300.

Serilophus lunatus (Fig. 2B)

Supporting elements.—Generally as in *Cymbirhynchus*, except as follows. A1 and A2 not elongated ventrally. B1 broad laterally, arched, not dorsoventrally angled, and lies close to A1, eliminating any lateral tympaniform membrane. B2 thinner and lies close to B1 and B3. Caudal margin of B3 distinctively tapered at its ventral end. Ossification of B elements continues caudad until at least B11.

Musculature.—M. tracheolateralis restricted to lateral surfaces of trachea. Inserts by broad sheet of con-

nective tissue on A1 element and A1-B1 lateral membrane. M. sternotrachealis robust and inserts on lateral surface of A6-9. *Serilophus* lack fibrous mass on internal tympaniform membrane.

Membranes.—Small patch of fibrous tissue forms knobby structure on medial tympaniform membrane. Caudal end of this structure continuous with broad strip of connective tissue that extends to interclavicular air sac.

Specimens observed.—USNM 505628, 509479, 509480*, 534659.

Psarisomus dalhousiae (Fig. 1D)

Supporting elements.—All A elements completely ossified. A1 double, medially incomplete, and acutely oblique to mid-sagittal plane. Dorsal ends of A1 widened, rounded and tipped with cartilage, but element also broad laterally and ventrally. A2 single, complete, and fused dorsally and ventrally to wide ossified pessulus. Left and right halves of A2 weakly angled obliquely. A3 and subsequent elements single, complete, and unfused. All B elements double and medially incomplete. B1-2 thin, straight, closely nested to one another, and ossified except for dorsal ends. Ventral ends nearly meet ventral ends of A1-2, producing extensive lateral tympaniform membrane between B1 and oblique A1. B3 slightly curved, wider than B1-2, and ossified except for dorsal eighth and ventral tip. B4 and subsequent elements broad, rounded, unfused and ring-like in shape. Ventrolateral halves and quarters of B5 and B6 ossified, respectively. Subsequent B elements cartilaginous.

Musculature.—M. tracheolateralis restricted to lateral surfaces of trachea. Caudal to A8, it gradually expands dorsad to insert on lateral surface of A2 and dorsolateral surface of A1. M. sternotrachealis well developed and inserts on ventrolateral surface of A8-10, ventral to M. tracheolateralis. Lateral fibers of both muscles continuous at insertion.

Membranes.—No specialized membranous structures.

Specimens observed.—AMNH 7998*; USNM 509482-509484.

Corydon sumatranus

No specimens available for examination (Wood et al. 1982). Previous description by Müller (1847, 1878) refers only to absence of intrinsic syringeal muscles (Ames 1971).

Pseudocalyptomena graueri (Fig. 2C)

Supporting elements.—All A elements ossified. A1 double and narrow, and each side acutely oblique to mid-sagittal plane of syrinx. Dorsal ends of A1 widened and fused to pessulus by small cartilaginous extensions. A2-3 single and dorsally unfused. Ventrally, A2-3 completely fused, and combined element

expanded caudally to occupy area between narrow, acutely oblique ventral ends of A1 elements. Cranial margins of A2-3 element transversely oriented. A4 and above single and unfused. A wide ossified pessulus fused dorsally and ventrally to A2. All B elements double, medially incomplete, and partially ossified. B1 elements narrow, almost straight, oblique, and ossified except for dorsal tips. B1s situated in center of an extensive lateral tympaniform membrane. B2 elements almost straight, slightly oblique, and ossified for their ventrolateral third. Ventral ends of A1 and B1-2 fused with cartilage. All subsequent B elements rounded, ringlike, transverse, and partially ossified. B3 ossified for about 2/3 of element, and ossification reduced gradually to lateral quarter of element at B12.

Musculature.—M. tracheolateralis restricted to lateral surface of trachea. Muscle splits into dorsolateral and ventrolateral portions at A7-5, where M. sternotrachealis inserts directly on lateral surface of trachea. Muscle reunites at A4-5 into continuous sheet, and inserts on ventrolateral and lateral surfaces of A1 and dorsolateral surface of A2. M. sternotrachealis inserts directly on lateral surface of A5-8, passing through gap in fibers of M. tracheolateralis.

Specimens observed.—AMNH 2233, BM 1930.10.19.2*.

Philepitta castanea (Fig. 2D)

Supporting elements.—All A and B elements completely ossified. A1 double, medially incomplete, and each side acutely oblique to mid-sagittal plane. Dorsal ends of A1 widened but A1 thin laterally and narrow and pointed at ventral ends. A2 single and complete. Lateral portions thin, nested closely to A1 elements, and acutely oblique. Dorsal portion of A2 widened in triangular shape, but ventrally two thin, oblique sections of A2 fuse in an acute V-shape. A2 continuous dorsally and ventrally with narrow, curved pessulus. A3 and above single, complete and unfused. All B elements double, medially incomplete, and completely ossified. B1-2 thin and only slightly curved. B1 narrow and bladelike in shape, and acutely oblique. Its dorsal and ventral ends nearly touch ends of A1, but its lateral portion greatly separated from A1 forming large lateral tympaniform membrane. B2 slightly more rounded than B1, but lies close next to that element. Ventral ends of A1 and B1-2 weakly fused by cartilage. B3 and subsequent elements double, unfused, transverse, medially incomplete rings. A second, smaller lateral tympaniform membrane present between straightened B2 and round B3.

Musculature.—M. tracheolateralis forms well developed sheet around trachea from above A20 with only small gap at dorsal midline. Muscle divides on ventral midline at A8 and inserts on dorsal margin of A1 and possibly A2. Insertion extends from oblique ventral to dorsolateral portions of A1 (illustrated in Fig. 2D). In some male specimens, insertion extends

dorsally to extreme widened dorsal ends of A1 element. In some specimens, fibers on dorsal and ventral midlines insert on surface of A2. M. sternotrachealis inserts on lateral midline of trachea on A8–10, and fibers partially continuous with M. tracheolateralis fibers after insertion.

Membranes.—Large, tear-drop-shaped piece of fibrous tissue present on medial tympaniform membrane between B3 and B5. Dorsal margin broadly rounded and caudal end narrow and free from membrane. Thin thread of connective tissue extends from caudal tip of structure and to surface of interclavicular air sac just lateral to midline of trachea.

Specimens observed.—AMNH 2213, 2228*, 2229, 2230*; BM 1968.30.46; FMNH 345696, 345697, 345708–345710.

Philepitta schlegeli

Supporting elements.—As in *P. castanea* (Fig. 2D) except as follows. Ventral fusion of A1 and B1–2 more extensive. B1–3 completely ossified as in *castanea*, but ossification of subsequent B elements reduced. B4 ossified for its ventrolateral third, and B5 ossified for ventrolateral quarter. Subsequent B elements completely cartilaginous.

Musculature.—Apparently as in *P. castanea* (Fig. 2D), except as follows. M. tracheolateralis surrounds dorsal surface of trachea caudal to A10. Ventrally, it divides on midline into left and right sides at A5 and inserts as in *castanea*. Dorsally, it remains in continuous sheet and inserts on dorsal ends of A1 and possibly on dorsal surface of A2.

Membranes.—Fibrous structure on medial tympaniform membrane smaller than in *P. castanea*. Caudal end continuous with thin thread of connective tissue that may connect with interclavicular air sac.

Specimens observed.—BM 1968.30.44*.

Neodrepanis coruscans (Fig. 2E)

Supporting elements.—All A elements completely ossified. A1 double, thin, slightly widened at dorsal

ends, and completely fused to A2 at dorsolateral corner of that element. A2 single, complete, and broad and triangular dorsally. Combined A1–2 element acutely angled oblique along its lateral portions, and fused ventrally in an acute V-shape. Extreme caudoventral end of combined A1–2 element a finely split fork, which may be ventral ends of fused A1s. A3 and above single, complete and unfused. Thin, ossified pessulus fused dorsally to A2 and ventrally to combined A1–2 element. A pair of broad, curved, horn-shaped medial cartilages connected to dorsal ends of A1–2 and pessulus, and they extend medioventrally into medial tympaniform membrane. All B elements double, transversely oriented and medially incomplete. B1–3 nearly straight, closely nested to one another, producing an extensive lateral tympaniform membrane between A1 and B1. B1 completely ossified, and its ventral end dorsally widened. B2 ossified except for dorsal and ventral eighths. B1–3 fused ventrally to A1–2-pessulus complex by square of cartilage. B3 and subsequent elements cartilaginous. B4 and below double, medially incomplete, rounded, ringlike, and unfused.

Musculature.—Cranially, M. tracheolateralis restricted to lateral surface of trachea. At A8, it begins to expand ventrally and inserts on lateral and ventrolateral surfaces of combined A1–2 element. M. sternotrachealis narrow and inserts on ventrolateral surface of A11–12, at ventral margin of M. tracheolateralis. Fibers of M. sternotrachealis continuous with M. tracheolateralis cranial to their insertion.

Membranes.—No specialized membranous structures.

Specimens observed.—AMNH 2231*, BM 1968.30.112*, FMNH 345711.

Neodrepanis hypoxantha

No previous descriptions. No specimens available for examination (Wood et al. 1982).