

The systematics and zoogeography of Oriental¹⁾ and Australasian hornbills (Aves: Bucerotidae)

Alan C. Kemp

Abstract. A review of species limits and a cladistic analysis of relationships between species has been conducted on the avian family Bucerotidae. This paper covers the 30 species and 10 subspecies recognized for the Oriental region, as well as the single Australasian species. The species are grouped in the genera *Ocyceros* (3), *Anthracoceros* (5), *Buceros* (4), *Anorrhinus* (3), *Penelopides* (5) and *Aceros* (11). A zoogeographical analysis is presented and compared with the radiation of hornbills in the Afrotropical region. It is suggested that the complex topography and tectonics of the Oriental region, as well as the dispersal abilities of some clades, has facilitated speciation, much of it since the mid-Tertiary.

Key words. Bucerotidae, systematics, zoogeography, Oriental, Australasian.

Introduction

The avian family Bucerotidae has an Afrotropical and Oriental-Australasian distribution. A phylogenetic analysis of the family has been conducted and the systematics, taxonomy and zoogeography of the 23 species in the Afrotropical region has been reviewed (Kemp & Crowe 1985). The theoretical bases and methodology by which species limits were decided and the cladistic analysis performed are presented in that review. This paper reviews the systematics, taxonomy and zoogeography of the 30 species of hornbill recognized for the Oriental region and the one species for the Australasian region. Comparisons are drawn between the systematics and zoogeography of the Afrotropical and Oriental-Australasian clades of the family.

Cladistic analysis

The cladogram derived for the Bucerotidae (Kemp & Crowe 1985) is shown in Figure 1. Cladograms of the Oriental genera *Ocyceros*, *Anthracoceros*, *Buceros*, *Anorrhinus*, *Penelopides* and *Aceros* are shown in Figures 2 and 3. The distribution of the derived character states used to construct these cladograms has been tabled previously (Kemp & Crowe 1985). The few newly documented distributions of character states for Oriental species are presented in Table 1. An appendix offers a partial description and classification of the taxa recognized in this study. The derived characters used to determine each dichotomy of the cladogram are listed against each taxon in the appendix, so presenting a hierarchical sequence of characters that will distinguish each taxon.

¹⁾ After the printing of this paper, Clark et al. (Ibis 130: 447; 1988) proposed to use the term 'Indomalayan Region' instead of 'Oriental Region'.

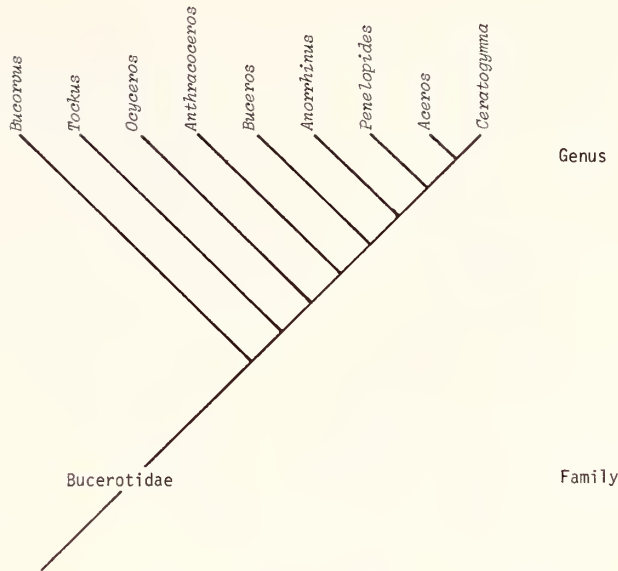


Fig. 1: Cladogram of the family Bucerotidae, showing the genera recognized in this study.

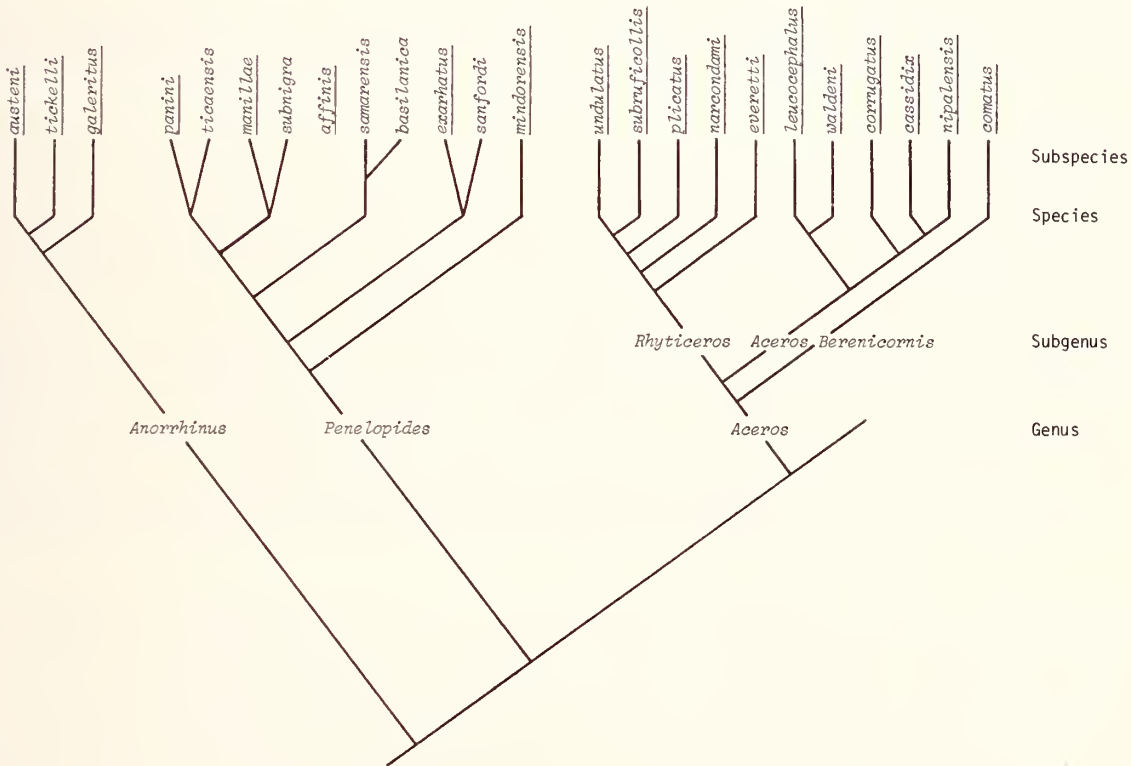


Fig. 2: Cladograms of the genera *Ocyceros*, *Anthracoceros* and *Bucerus*, showing the species (underlined), and subspecies recognized in this study.

Zoogeography of Oriental and Australasian hornbills

The geographical distribution and basic ecological requirements of Oriental-Australasian hornbills are well documented (Sanft 1960, Ali & Ripley 1970, Medway & Wells 1973, Kemp 1979). It might be noted that the historical distributions of taxa are used in this review, bearing as they do on the evolutionary history of the taxa, even though it is realised that the ranges of many taxa have been contracted recently through removal of forests. The distributions reveal a number of common patterns, common

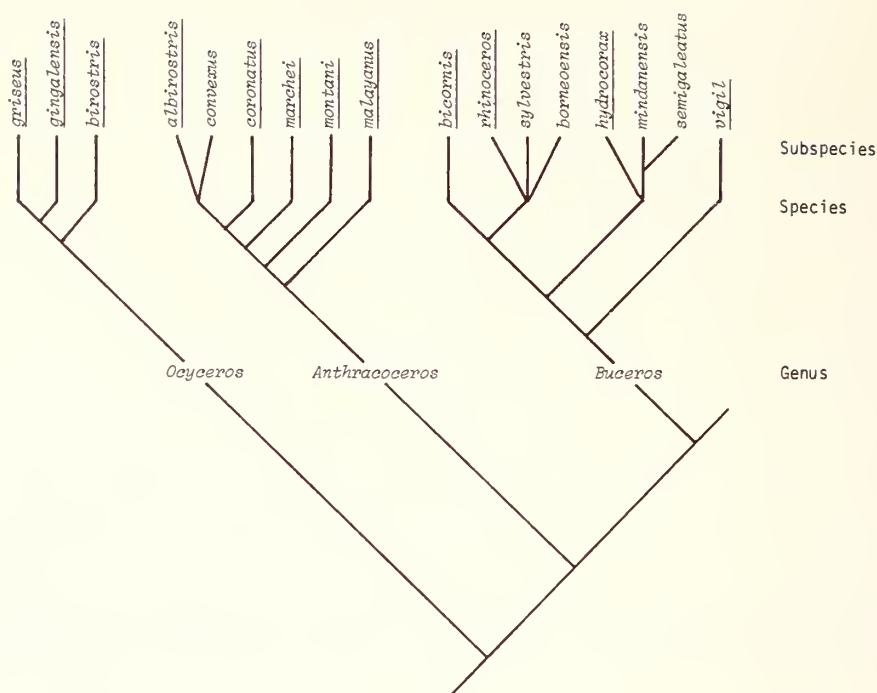


Fig. 3: Cladograms of the genera *Anorrhinus*, *Penelopides* and *Aceros*, showing the species (underlined), subspecies and subgenera recognized in this study. (Read *manilloe* instead of *manillae*).

boundaries and geographically isolated populations. The common features suggest the primary ecological determinants of hornbill ranges and indicate how and where populations might have become isolated in the past.

It is possible to allocate each species and subspecies to a zoogeographical area (Fig. 4, Table 2). By comparing the ranges of taxa with their position on the cladograms (Figs. 2 and 3), it is possible to suggest the interfaces between zoogeographical divisions at which taxa became isolated from one another. This does not imply necessarily the exact geographical position at which this isolation occurred.

Hornbills have broad ecological requirements, being widespread in forests in the Oriental-Australasian regions with only one species inhabiting savanna. Only major climatic events are likely, therefore, to have fragmented their habitats and so produce the isolated populations in which divergence could proceed. A succession of warm and cold episodes have been documented for the past 20 Myr (Brain 1981, 1983) and could produce such fragmentation. Sea levels appear to have ranged between about -70 and $+6$ m of present levels since the Cainozoic (Aharon et al. 1980, Brain 1983, Haile 1971, Miller & Fairbanks 1985). These variations in sea level can be compared to present submarine topography, with the caution that the Oriental area has experienced complex subduction, rifting, faulting and island arc collision during the Tertiary (Hamilton 1979, Lee & McCabe 1986).

It is assumed here that cool, dry periods would be associated with a fall in sea level, interconnection of land masses but fragmentation of forest: warm, wet periods would coincide with a rise in sea level, division of land masses and expansion of forest. It is possible to analyse further the zoogeography of Oriental-Australasian hornbills using these assumptions.

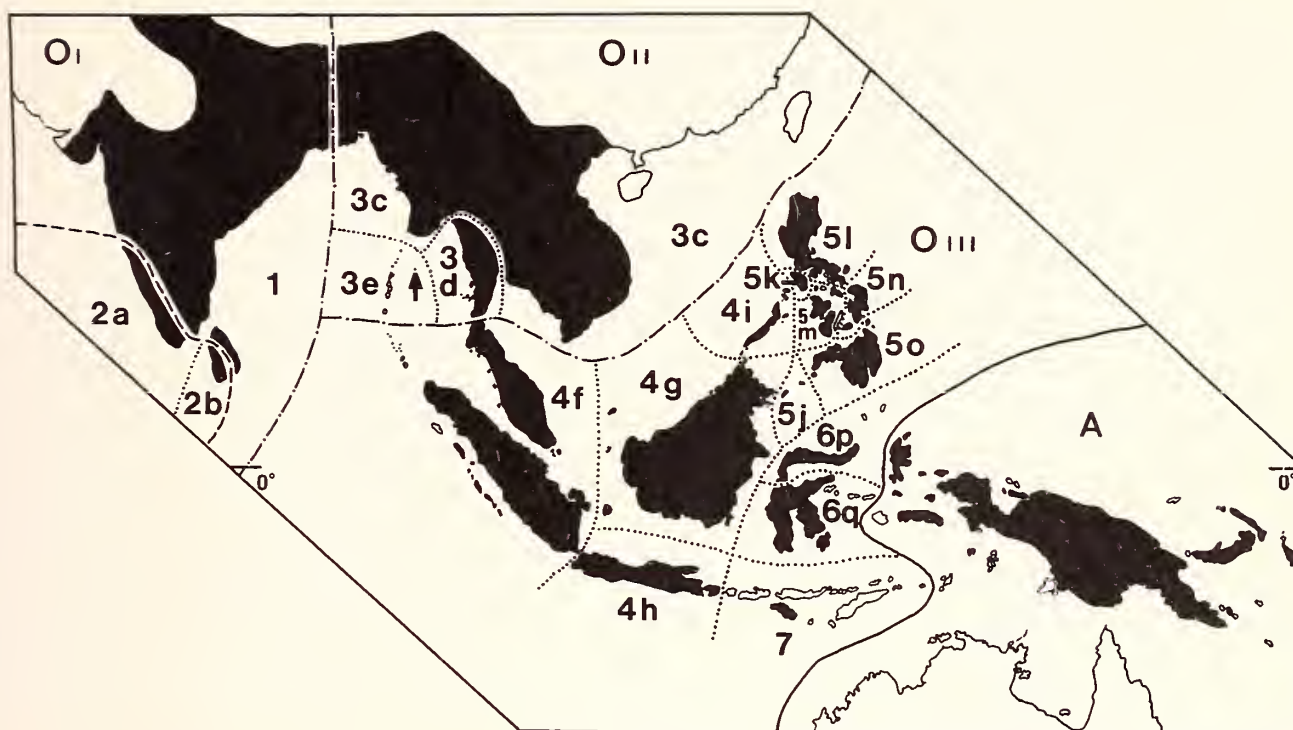


Fig. 4: Zoogeographical divisions of the Oriental and Australasian Regions based on hornbill distributions for comparison with Table 2 and divisions of the Afrotropical Region (Kemp & Crowe 1985). Areas occupied by hornbills are coloured black, Narcondam Island is arrowed but the extension of one species east of New Guinea onto the Solomon Islands is not shown. Regions: O — Oriental, A — Australasian. Subregions: I — Indian, II — Indo-Chinese, III — Indo-Malayan or Malayan. Provinces: (1) — Peninsular, (2) — South-western, (3) — Continental, (4) — Sundaic, (5) — Philippine, (6) — Sulawezian, (7) — Lesser Sundaic. Districts: (a) — Indian, (b) — Sri Lankan, (c) — Burmese-Thai, (d) — Tenasserimian, (e) — Andamanese, (f) — Malay-Sumatran, (g) — Bornean, (h) — Javan, (i) — Palawanese, (j) — Suluan, (k) — Mindoroan, (l) — Luzonian, (m) — Panay-Negrosian, (n) — Samaritan, (o) — Mindanaoan, (p) — Minahasan, (q) — Makassarian. The lines separating the Oriental from Australasian Regions, the Sundaic/Philippine from Sulawezian/Lesser Sundaic Provinces and the Sundaic from Philippine Provinces correspond to Weber's, Wallace's and Huxley's Modification of Wallace's Line respectively (Flenley 1979).

First, the cladogram can be superimposed on a succession of warm and cool periods, with branching points placed in conditions under which populations were thought to have been isolated based on their ecological requirements and geographical distribution (Fig. 5). Second, the zoogeographical divisions between or within which isolation is thought to have occurred can be added at each branching point (from Table 2). Third, the cladogram can be altered to accommodate knowledge of distributions. This permits more than just bifurcations to occur, where several populations could have become isolated simultaneously and given rise to more than one daughter species. Finally, isolation at the same zoogeographical divisions can be made synchronous, where the branching pattern allows. This produces an evolutionary tree (Fig. 6) showing the minimum sequence of isolation events necessary to produce the pattern of branching suggested by the hornbill cladogram and the distributions of extant species. This sequence, together with possible locations at which habitat fragmentation occurred, is shown in Table 3.

Table 3: Sequence in which habitats and/or geographical areas of the Oriental Region are thought to have been fragmented, on the basis of hornbill ecology and systematics, during alternating warm (wet) and cool (dry) climatic periods. This does not include speciation events which appear to have resulted from dispersion (Figs. 5 and 6).

Period	Isolation proposed for
1) Current warm	Islands of Sri Lanka, Sumatra, Borneo, Philippines.
2) First cool	a) Malay Peninsula from Tenasserim. b) Tenasserim from Asian mainland. c) Minahasa arc from southern Sulawesi.
3) First warm	a) Indian savanna. b) Islands of Borneo, Philippines.
4) Second cool	a) Indian from Indo-Chinese Subregion. b) Indo-Chinese Subregion from Sundaic Province.
5) Second warm	Islands of Palawan, Philippines, Sulawesi.
6) Third cool	No speciation to indicate isolation event.
7) Third warm	a) Islands of Sundaic, Sulawesi and Philippine Provinces. c) Indo-Chinese Subregion from Sundaic Province.
8) Fourth cool	Part of Malayan Province.
9) Fourth warm	a) Part of Sundaic Province. b) Part of Malayan Province.
All earlier isolation events must also have occurred within the Oriental Region but no finer resolution is possible	

Discussion

Delimitation of species and subspecies of Oriental-Australasian hornbills has been guided by the Recognition Concept of species and Allopatric Model of speciation, as for the review of Afrotropical species (Kemp & Crowe 1985). It has resulted in recognition of more species and fewer subspecies than previously (Sanft 1960). This includes recognition of the Sri Lankan *Ocyceros gingalensis* as distinct from *O. griseus* of the Indian mainland, and separation of *Annorrhinus austeni* and *A. tickelli*, based on differences in bill colour and sexual dimorphism. The separation of *Anthraceros coronatus* and *Aceros subruficollis* as distinct species, as suggested previously by Frith & Frith (1983) and Elbel (1969) respectively, is also supported.

The populations of Philippine hornbills, in particular, have been divided into several species, based on consistent differences in sexual dimorphism, ontogeny, plumage and/or softpart colours. *Aceros leucocephalus* and *A. waldeni* are considered separate species and it is suggested that further study may show nominate *Buceros hydrocorax* to be specifically distinct from the subspecies *B. h. semigaleatus* and *B. h. mindanensis*. The Philippine populations of *Penelopides* are considered to constitute at least four species, whereas they were considered one species (*P. panini*) previously. *P. affinis basilanica* may, with further study, prove to be a fifth species. Detailed information on softpart colours, calls and displays is lacking for many Oriental hornbill populations, especially those of the Philippines. Further documentation is essential for refinement of species and subspecies limits.

The cladistic analysis offered poor resolution of relationships between major clades but was more robust in defining relationships within clades (Kemp & Crowe

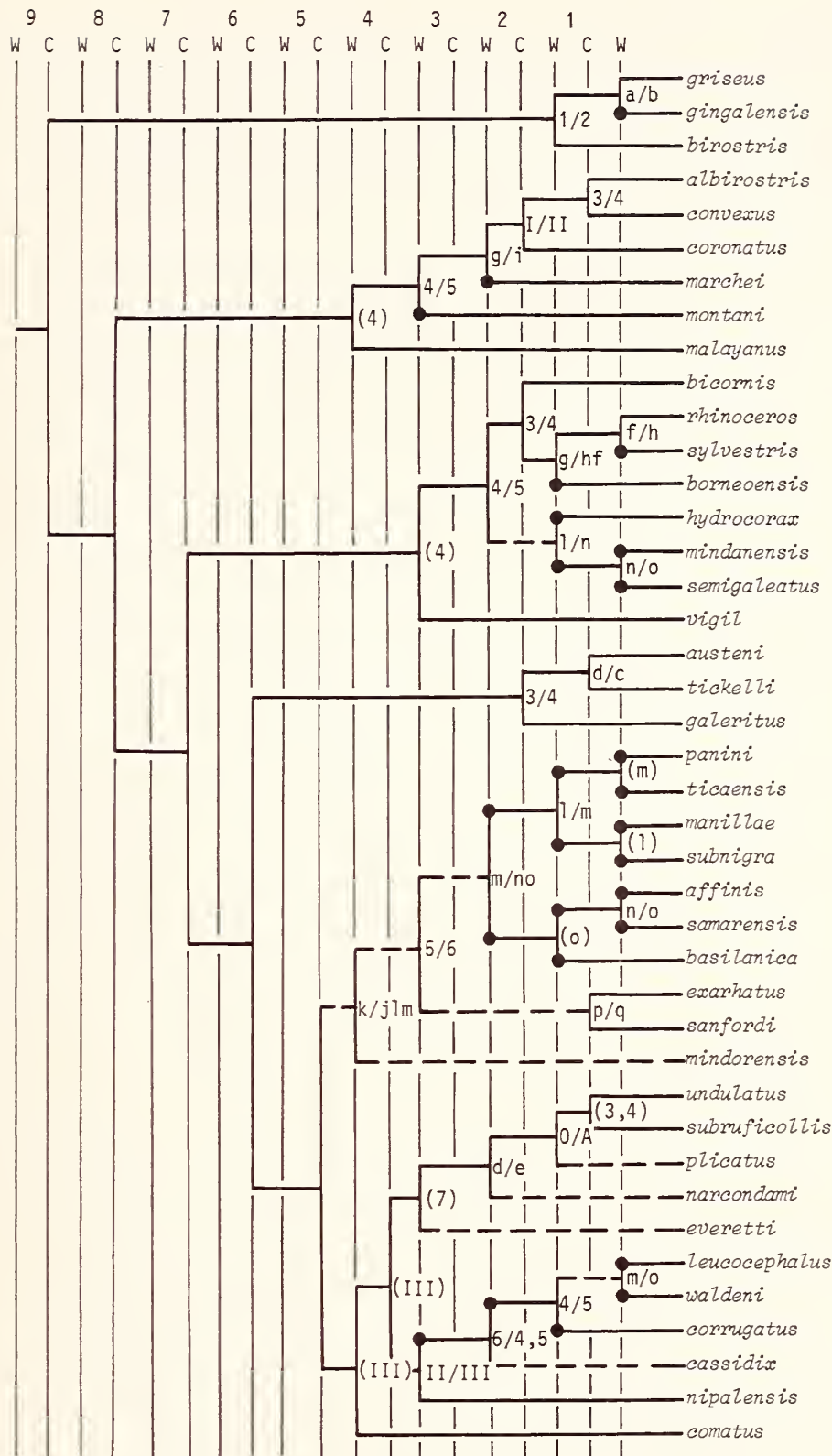


Fig. 5: Cladogram of Oriental and Australasian hornbill species and subspecies (from Figs. 1–3) superimposed on alternating periods of warm, wet (W) and cool, dry (C) climate. Branching points are positioned on climatic periods during which the ecology of the clade suggests that its habitat or range would have been fragmented and its populations isolated. Dashed lines indicate where the clade or species must have originated by dispersal from one island to another. Large dots indicate where clades or species could have been isolated by rising sea level. Zoogeographical divisions (from Fig. 4, Table 2) that became isolated from one another (eg. c/d) or within which isolation occurred (eg. g) are suggested for each branching point. (Read *manilloe* instead of *manillae*).

1985). The primary clades have been recognized as genera, to cause minimum disruption to existing nomenclature until the higher taxonomy of hornbills is better resolved. It is notable, however, that four species placed previously in monotypic genera, (*Rhinoplax vigil*, *Ptilolaemus tickelli/austeni*, *Berenicornis comatus* and *Aceros nipalensis*), have been grouped with their nearest relatives in *Buceros*, *Anorrhinus*, *Aceros* and *Aceros* respectively.

It is unlikely that future studies will support the independent branching of each Oriental genus (Fig. 1). It appears, subjectively, that some members of the genera *Ocyrceros*, *Anthracoceros* and *Buceros* (Fig. 2) have derived characters in common, such as tarsi coloured other than black, sexual dimorphism slight in casque form but marked in eye and casque colour and central rectrix pair elongated. *Ocyrceros* was previously joined with Afrotropical *Tockus* species and, although they are quite distinct (Kemp 1979), it is notable that the call of *O. griseus* most resembles that of the primitive *T. albocristatus* (Kemp & Crowe 1985). Furthermore, the scattered distribution of some derived characters in *Anthracoceros* suggests that this genus is artificially constituted and some species are closely allied to *Buceros*. It is retained at present only because allocation of species to other genera is equivocal.

The genera *Anorrhinus*, *Penelopides* and *Aceros* (Fig. 3) also share some derived characters between their species, notably unique plumage of adult females and elaboration of bare facial skin. *Anorrhinus* species exhibit the least derived condition but their apomorphies suggest early separation from the other genera. These rough generic groupings may prove to be the two primary clades of Oriental-Australasian hornbills when further characters for comparison become available.

The zoogeography of the 31 hornbills species of the Oriental-Australasian region appears more complex than that of the 23 Afrotropical species. Vicariance events in the Afrotropical region are explicable solely from the effect of climatic fluctuations on distribution of vegetation types (Kemp & Crowe 1985). Furthermore, the radiation of Afrotropical hornbills can be explained without invoking dispersion between "islands" of habitat (although this does not prove that dispersion did not occur).

Vicariance events in the Oriental region appear to have occurred through climatic changes effecting either connections between land masses (through changes in sea level), changes in vegetation distribution or both combined. It is even possible, based on tectonic interpretations, that some Oriental taxa originated from populations rifted off on fragments of land (eg. Palawan and Sulawesi Islands, Lee & McCabe 1986). This would produce vicariance without changes in sea level or vegetation distribution. Dispersion from one area to another, resulting in an isolated daughter population, also appears to have been involved frequently in the radiation of Oriental-Australasian hornbills. If the tectonic history, submarine topography and hornbill distribution in the region is compared with the relationships proposed between hornbill species, dispersion must have occurred at least ten times (dashed lines in Figs. 5 and 6) during their radiation.

It is notable that dispersion must be invoked most frequently in the related genera *Penelopides* and *Aceros*, but for one instance in *Buceros*. Other branches in the radiation of these genera might also have resulted from dispersion but can be equally well explained by vicariance through the effects of changes in sea level. The clear differences between adjacent species and subspecies of *Penelopides* in the Philippines,

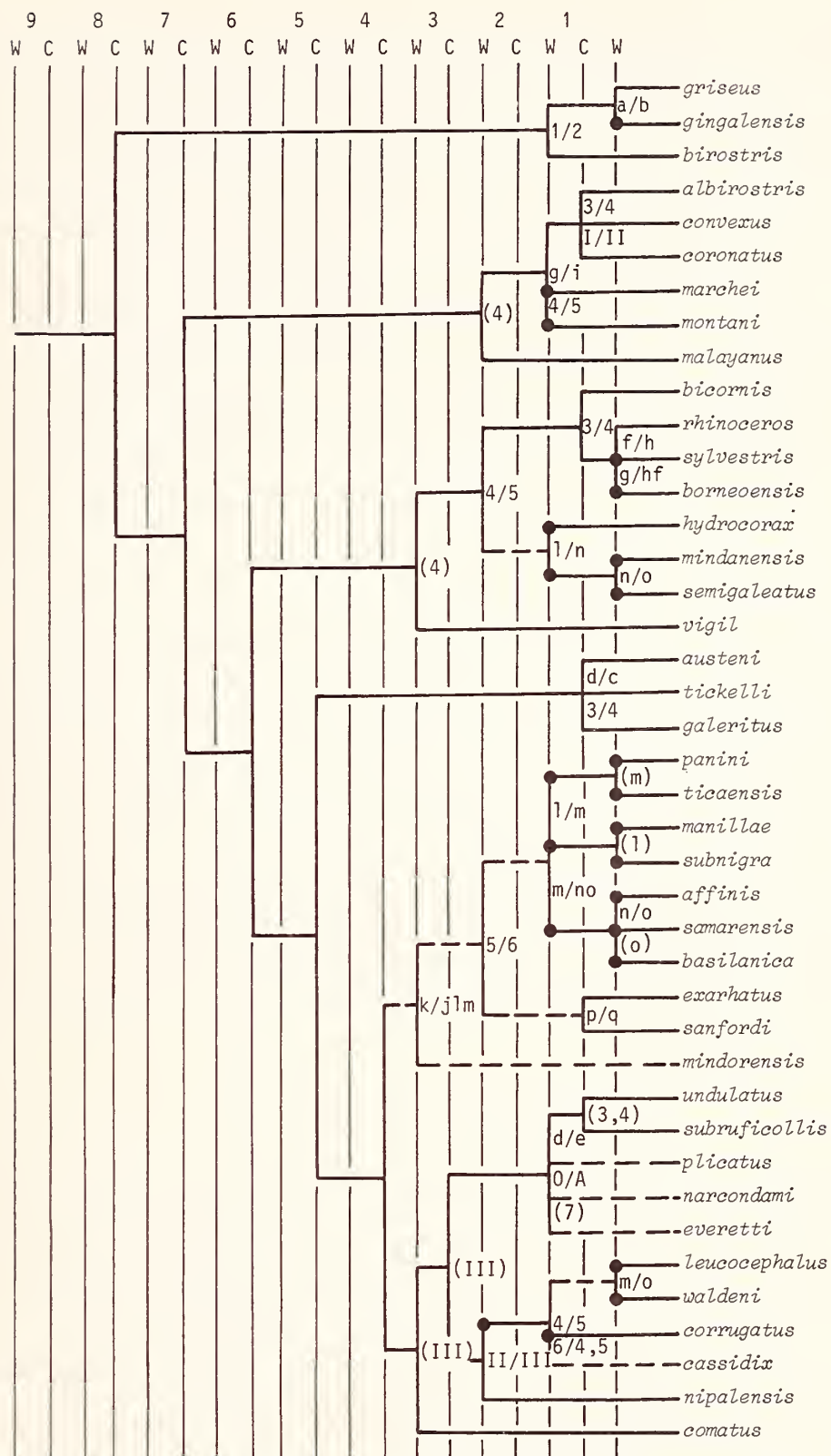


Fig. 6: Evolutionary tree of Oriental and Australasian hornbill species and subspecies superimposed on alternating periods of warm, wet (W) and cool, dry (C) climate. Branching points are positioned on climatic periods during which the ecology of the clade suggests that its habitat or range would have been fragmented and its populations isolated. Dashed lines indicate where the clade or species must have originated by dispersal from one island to another. Large dots indicate where clades or species could have been isolated by rising sea level. Zoogeographical divisions (from Fig. 4, Table 2) that became isolated from one another (eg. c/d) or within which isolation occurred (eg. g) are suggested for each branching point. The tree differs from the cladogram (Fig. 5) in that the same isolation events are made synchronous where this is compatible with the branching sequence and geographical/ecological distribution of the taxa. Furthermore, cladogenesis is not confined to bifurcations if zoogeographical data permit multiple furcations. (Read *manilloe* instead of *manillae*).

despite quite short distances separating several islands, suggest that dispersion is less important than vicariance in subsequent radiation within this genus. Even where dispersion must be invoked, the distances crossed by *Penelopides* species are generally short (Sunda Shelf to Mindoro Island, Mindoro Island to the rest of the Philippines, the colonization of Sulawesi from either the Sunda shelf or the Philippines).

No subspecies are recognized in the genus *Aceros* and at least four species must have arisen through dispersion. It is notable that this is the most geographically extensive and speciose of Oriental-Australasian clades, one species extending far into the Australasian region and others incorporating such outlying islands as Narcondam and Sumba. The extensive movements of many *Aceros* today, especially in the subgenus *Rhyticeros* which regularly visit offshore islands (Kemp 1979), suggests that mobility is an exaptation (*sensu* Gould & Vrba 1982) important in the radiation of this clade and its lack of subspeciation. The habit of several species of travelling and roosting in flocks would also aid dispersion, through providing a founder population with a better chance of viability.

The more varied opportunities for speciation in the Oriental region can explain, alone, its more extensive radiation of hornbills compared with the Afrotropical region. The combination of varied topography, allowing fragmentation of habitats by changes in sea level as well as in distribution of vegetation types, together with the inherent dispersal potential of some hornbill clades, would have provided many opportunities for small populations to become isolated. This explanation is more parsimonious than ones based on ecological considerations, such as the relative diversity of niches between regions. The broad habitat requirements of most hornbill species, but the discontinuous and erratic distribution of plants (with little congruence between faunal and floral zoogeography in the Oriental region (Flenley 1979), support this contention.

Radiation of Oriental-Australasian hornbills has been confined almost entirely to forest, with 30 species in this habitat compared to 12 in the Afrotropical region. In contrast, only *Ocyrceros birostris* occupies savanna in the Oriental region compared to 11 species in the Afrotropical region. These differences can be explained, once again, by the relative opportunities for isolation of populations in forest and savanna within each region. Africa, as one land mass covered with extensive savanna and forest habitats which expanded, contracted and fragmented one another, can be predicted to generate a quite different pattern of isolated populations from the fragmented land masses of the Oriental region, most of which have supported forest throughout the Tertiary (Flenley 1979).

A minimum of four cool-warm climatic cycles are necessary to generate the proposed branching patterns of Oriental-Australasian hornbill genera (Fig. 6, Table 3). This is one cycle less than is needed for radiation of Afrotropical genera (Kemp & Crowe 1985), despite the fewer species generated in the latter region, and is further evidence of differences in speciation opportunities between the regions. Much of the speciation within the Oriental region, especially in the Philippine and Sulawesi Provinces (Wallacea), must have taken place since the middle or late Tertiary, based on the tectonic history of the area (Hamilton 1979, Whitmore 1981, Lee & McCabe 1986). It is encouraging that three primary episodes of global cooling are recognized since the mid-Tertiary, at about 15, 10 and 5.5 Myr, followed by lesser episodes at

about 2,4 and 0,9 Myr (Brain 1981, 1983; Miller & Fairbanks 1985). Such major episodes may provide the primary impetus to speciation in groups with broad habitat requirements, such as hornbills, whereas more restricted or specialized species may also respond to lesser fluctuations.

It is not possible to set such time limits to the radiation of Afrotropical hornbills nor to discover other possible sources of vicariance. However, it is feasible for the five major episodes of global cooling since the mid-Tertiary to have also produced the radiation proposed for the African clades. Further precision in Afrotropical zoogeography will only be possible if dated fossils become available or spatial and temporal distributions of vegetation types can be reconstructed. Cladistic analyses of speciose clades with more specialized habitat requirements than hornbills, such as francolins or some passerine families, may assist in this resolution.

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Zusammenfassung

Nach der vorliegenden Untersuchung sind die Bucerotidae in der Orientalis mit 30 Arten und 10 Unterarten und in der Australasiatischen Region mit 1 Art vertreten. *Ocyrceros* umfaßt 3 Arten, die bisher zu den Afrotropischen *Tockus* gestellt wurden. Die Arten, die bisher die monotypischen Gattungen *Rhinoplax*, *Ptilolaemus*, *Aceros* und *Berenicornis* bildeten, werden jeweils mit den ihnen nächstverwandten Arten zusammengefaßt, wobei allerdings *Aceros* als Gattungs- und *Berenicornis* als Untergattungsname erhalten bleiben. *O. gingalensis*, *Anthracosceros coronatus*, *Anorrhinus austeni*, *Penelopides manilloe*, *P. affinis*, *P. mindorensis*, *Aceros subruficollis* und *A. waldeni* werden als eigenständige Arten aufgefaßt. Eine zoogeographische Analyse legt nahe, daß die Möglichkeiten zur Artbildung in Waldgebieten, nicht jedoch in Savannen, für Bucerotidae in der Orientalis größer waren als in der Afrotropis. Die vielgestaltige Topographie des Meeresbodens und die Tektonik in der orientalischen Region haben gemeinsam mit der Mobilität einiger Hornvogel-Arten diese Radiation ermöglicht. Einige Hornvogel-Gruppen in der Orientalis müssen sich seit dem Mittleren Tertiär aufgespalten haben, wenn man die Tektonik in dieser Region zugrundelegt. Die anschließende Radiation fällt zeitlich mit den 3–5 großen Phasen weltweiter Abkühlung zusammen.

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Dr Alan C. Kemp, Department of Birds, Transvaal Museum, P. O. Box 413, Pretoria, 0001 Republic of South Africa.

Appendix

Classification and description of taxa

The taxa of hornbills recognized in this study are described below in a classification and sequence derived from the cladogram (Figs. 1–3, Kemp & Crowe 1985). The numbers in brackets after each taxon indicate the derived characters by which the taxon is recognized (Table 1, Kemp & Crowe 1985). Where a number is preceded by a minus sign, this indicates homoplasy and assumes secondary development of the primitive character state. In some instances, details of the characters are included in brackets after the number. Descriptions of supraspecific taxa are not presented, as these can be constructed from the derived characters which they exhibit and those shared with higher taxa.

Details of specific and subspecific plumages have been documented by Sanft (1960) and a detailed review of the genus *Anthracoceros* has been presented by Frith & Frith (1983). Only those plumage, casque and softpart details by which subspecies and similar species differ from one another are mentioned here. Most attention is given to describing characters assumed to be used in communication. Casque form and softpart colours, with special reference to sex and age differences, are detailed. That females are smaller than males, and that juveniles have only a rudimentary casque structure, is not repeated for each species. Sonagrams and descriptions of the loudest calls are presented where available. These calls are assumed to be used in long-distance communication, and to be homologous in comparisons between species and subspecies. Any movements made or postures adopted while calling are described. Further study of softpart colours, calls and displays is required, so where information is lacking or conflicting this is indicated. Where subspecies have been described by Sanft (1960) and subsequent workers, but are not recognized here, they are mentioned in a brief account of the geographical or ecophenotypic variation they are assumed to represent.

Family: Bucerotidae Gray, 1841. (characters supporting monophyly in Kemp and Crowe 1985.)

Genus: *Bucorvus* Lesson, 1830. (11, 13, 14, 17, 19a [primaries all white], 25 b, 26, 36.) (Species: *abyssinicus*, *cafer*.) Afrotropical genus.

Genus: *Tockus* Lesson, 1830. (1–6, 15, 16.) (Species: *albocristatus*, *hartlaubi*, *camurus*, *monteiri*, *erythrorhynchus*, *leucomelas*, *flavirostris*, *deckeni*, *hemprichii*, *fasciatus*, *bradfieldi*, *alboterminatus*, *pallidirostris*, *nasutus*.) Afrotropical genus.

Genus: *Ocyceros* Hume, 1873. (7–9.)

Species: *O. birostris* (Scopoli, 1786) (30, 38.)

Casque form: adult male, discrete ridge along the top of the bill terminating in a point midway down the bill; adult female, low ridge at base of upper mandible. Bill colour: adult male and adult female, dark brown with pale yellow on tip of casque, bill and underside of lower mandible; juvenile, yellow (Ali & Ripley 1970). Bare skin: smooth, circumorbital only: adult male, adult female and juvenile, undescribed. Eye colour: adult male, red-brown; adult female, brown; juvenile, undescribed. Leg colour: adult male, grey-brown; adult female and juvenile, undescribed. Loudest call (no recording available): shrill monotonous squeal, various loud cackling and squealing notes (Ali & Ripley 1970). Display: tail depressed under perch while calling and swung slowly back and forth (Ali & Ripley 1970).

Species: *O. gingalensis* (Shaw, 1811). (19d, 35?, 37 [bill], round nostril.)

Casque form: adult male, slight ridge along top of bill merging into tip; adult female, like male but merging midway into bill. Bill colour: adult male, cream with black base to upper

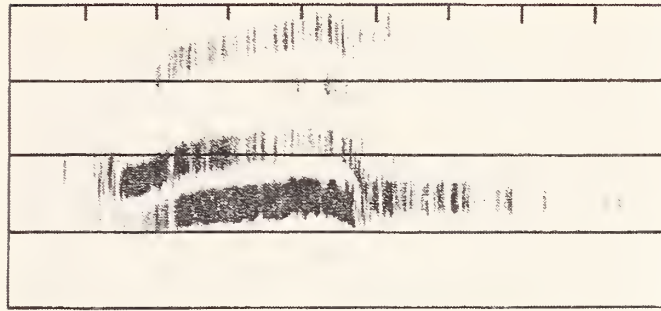


Fig. 7: Sonagram of the loudest call of *Ocyrceros griseus*.

Sonagram prepared on a Voice Identification Series 700 audiospectograph set for wide band (300 Hz) analysis. Vertical divisions — frequency at 1000 Hz intervals from baseline of zero, horizontal divisions — time in 100 msec intervals. See appendix for source and verbal description of call (shown in Figs. 7–12).

mandible and patch on underside of lower mandible; adult female, black with cream stripe along side of upper mandible; juvenile, pale greenish. Bare skin: smooth, circumorbital and small gular patches: adult male, adult female and juvenile, undescribed. Eye colour: adult male, red; adult female, brown (Ali & Ripley 1970); juvenile, dark blue-grey. Leg colour: adult male, adult female and juvenile, undescribed. Loudest call (no recording available): loud k a a . . . k a a . . . k a k a k a k a or k u k . . . k u k . . . k u k - k u k - k u k k o k o k o k o k o (Henry 1971) Display: none recorded.

Species: *O. griseus* (Latham, 1790). (19e [eyestripe], 37 [bill], oval nostril.)

Casque form: adult male, slight ridge along top of bill merging into tip; adult female, like male but merging midway into bill. Bill colour: adult male, yellow becoming more orange at base; adult female, pale yellow with black casque and patch at base of lower mandible; juvenile, horn coloured with greenish tinge on lower mandible, developing black lines along sides of upper mandible to resemble adult female (Abdulali 1951). Bare skin: smooth, circumorbital and small gular patches: adult male and adult female, black; juvenile, undescribed. Eye colour: adult male and adult female, red-brown (Ali and Ripley 1970); juvenile, grey (Abdulali 1951). Leg colour: adult male and adult female, dark grey-green (Ali 1936); juvenile, undescribed. Loudest call (Fig. 7, India, Ben King): various loud harsh croaks (Fig. 7), chuckles, mock laughter and raucous cackling (Ali & Ripley 1970). Display: Tail somewhat fanned while calling, to display white tip (pers. obs.).

Genus: *Anthracoceros* Reichenbach, 1849. (7–10.)

Species: *A. malayanus* (Raffles, 1822) (30, 39b, 40.)

Casque form: adult male, large cylinder rising above forehead and becoming projecting blade over end of bill; adult female, smaller cylinder over base of bill tapering to point midway along bill. Bill colour: adult male, light yellow with narrow black base to bill and casque; adult female, black; juvenile, pale greenish-yellow (Dunselman 1937, Frith & Douglas 1978, pers. obs.). Bare skin: smooth, circumorbital and two separate gular patches: adult male, circumorbital and gular dark blue-black, often with yellow patch below eye; adult female, circumorbital flesh-coloured, gular yellowish-buff; juvenile, dull yellow with orange surround to eye smudged black (Frith & Douglas 1978). Eye colour: adult male, dark red; adult female, dark brown; juvenile, dark brown. Leg colour: adult male and adult female, black; juvenile, grey (Dunselman 1937). Loudest call (Fig. 8A, Sarawak, Alan Kemp): harsh prolonged cawing notes (Bartels & Bartels 1937), rising and falling in pitch and volume before ending abruptly with brief second note. Display: none recorded.

Species: *A. montani* (Oustalet, 1880). (19d, 37 [facial skin], 39a.)

Casque form: adult male and adult female, high blade originating above forehead and ending abruptly two-thirds of way along bill. Bill colour: adult male and adult female, black; juvenile, undescribed. Bare skin: smooth, extensive circumorbital and gular patches at base of bill just meeting under throat: adult male and adult female, black; juvenile, undescribed. Eye colour: adult male, cream; adult female, dark brown; juvenile undescribed. Leg colour: adult male, black; adult female and juvenile undescribed. Loudest call (no recording available): undescribed. Display: none recorded.

Species: *A. marchei* Oustalet, 1885. (19d.)

Casque form: adult male, low cylinder originating above forehead and ending as pointed projection above bill tip; adult female, low cylinder above bill ending in point midway along bill. Bill colour: adult male and adult female, pale yellow with black base to lower mandible; juvenile, cream with grey base. Bare skin: smooth, circumorbital and extensive, barely separated gular patches: adult male and adult female, white with bluish tinge and black ring round eye; juvenile, white with bluish tinge and lacking black ring round eye. Eye colour: adult male, red-brown; adult female, brown; juvenile, grey. Leg colour: adult male, black; adult female and juvenile, undescribed. Loudest call (no recording available): soft kiew notes repeated, similar to *A. albirostris* (Frith & Douglas 1978). Display: none recorded.

Species: *A. coronatus* Boddaert, 1783). (30, 37 [facial skin].)

Casque form: adult male, large axe-like structure ridged along sides, originating above forehead and ending as projecting blade near end of bill; adult female, like adult male. Bill colour: adult male, yellow with black base to casque and bill and extensive black patch over end of casque (extent of black variable and increases with age); adult female, similar to adult male without black back to casque and with smaller black patch on casque; juvenile, undescribed. Bare skin: smooth, circumorbital and extensive, barely separated gular patches: adult male, circumorbital blue-black, gular flesh-coloured; adult female, circumorbital white with pink tinge, gular flesh-coloured; juvenile, like adult of same sex (Ali & Ripley 1970). Eye colour: adult male, red to orange-red; adult female, brown to blue-brown; juvenile, undescribed. Leg colour: adult male, dark greenish-grey; adult female and juvenile, undescribed. Loudest call (Fig. 8B, Sri Lanka, Ben King): similar to *A. albirostris*, but deeper in tone and less modulated. Display: none recorded.

Species: *A. albirostris* (Shaw & Nodder, 1807). (30, 37 [facial skin].)

Subspecies: *A. a. albirostris* (Shaw & Nodder, 1807). (30, 37 [facial skin].) Casque form: adult male, cylinder above base of upper mandible tapering to blade midway down bill; adult female, similar to adult male but less convex and tip not projecting. Bill colour: adult male, yellow with black base to and patch on side of casque extending onto bill; adult female, yellow with distal half of casque and bill black and dark brown patch at sides and base of lower mandible; juvenile, pale yellow (Hutchins 1976); extent of black variable and increases with age (Frith & Frith 1983). Bare skin: smooth, circumorbital and two separate extensive gular patches: adult male and adult female, circumorbital white with black spot in front of eye, gular white with bluish tinge; juvenile, circumorbital white tinged pink, gular flesh blue-white. Eye colour: adult male, dark red; adult female, brown to grey-brown; juvenile, dark brown. Leg colour: adult male and adult female, dull greenish-grey; juvenile, undescribed. Loudest call (Fig. 8C1, Thailand, Pilai Poonswad): variety of loud shrill squeals and raucous cackles (Ali & Ripley 1970), loud cackling kleng-keng, kek-kek-kek-kek-kek (Medway & Wells 1976), rising and falling in pitch and volume. Display: none recorded.

Subspecies: *A. a. convexus* (Temminck, 1832). (37 [bill, facial skin].) Plumage same as *A. a. albirostris* but for flecks of black in white areas of tail of many specimens, smaller than

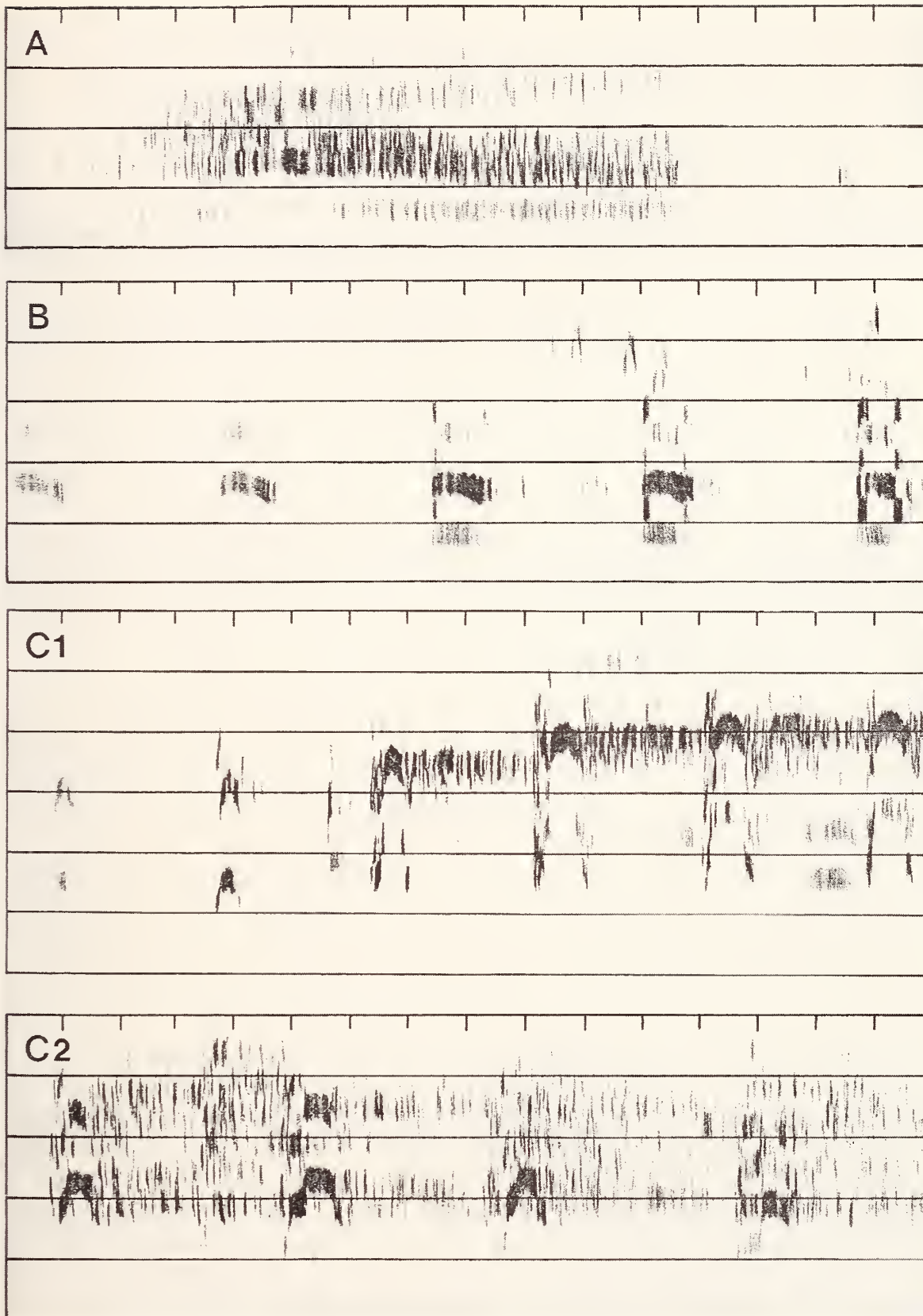


Fig. 8: Sonagrams of the loudest calls of *Anthracoceros* hornbill species. A — *A. malayanus*; B — *A. coronatus*; C1 — *A. a. albirostris*; C2 — *A. a. convexus*.

nominate northern subspecies, as part of cline from north to south of range. Casque form and bill colour like *A. a. albirostris*, but less black on bill of adult female despite considerable local and geographical variation. Circumorbital skin of adults apparently lacks black spot before eye. Eye colour of adults of both sexes described as light brown (Bartels & Bartels 1937),

juvenile grey-brown. Leg colour: adult male, adult female and juvenile, dull greyish-green. Loudest call (Fig. 8C2, Indonesia, Ben King): described as similar to nominate subspecies (Bartels & Bartels 1937). Display: none recorded.

Genus: *Buceros* Linnaeus, 1758. (7–9, 11, 17, 18, 25 b, 27 a, 28 a, 37 [cosmetic colouration], 40.)

Species: *B. vigil* (Gloger, 1841). (30, 36, 40.)

Casque form: adult male and adult female, high broad ridge with ridge along side arising above forehead and terminating in solid plate midway along bill. Bill colour: adult male, red but for yellow front of casque and distal half of bill; adult female, similar to adult male but yellow tip speckled with black; juvenile, yellowish-green. Bare skin: smooth, circumorbital as well as whole of neck and throat: adult male, blood red; adult female, lilac with blue and cream under throat veined with pale blue; juvenile, similar to adult of relevant sex. Eye colour: adult male, dark red or red-brown; adult female, red-brown; juvenile, pale red-brown. Leg colour: adult male and adult female, red-brown; juvenile, undescribed. Loudest call (Fig. 9A1–4, Sarawak, Alan Kemp): a series of prolonged H ou notes (Fig. 9A1) rising and quickening (into double notes, Haimhoff 1987) until the crisis is an unbroken series of shrill chuckles — Hee-Hee-Hee (Fig. 9A2) . . . dying away to mocking Ha notes (Fig. 9A3) (Banks 1935, see especially Haimhoff 1987 for a detailed analysis of this call sequence). Also a braying flight call repeated (Fig. 9A4, pers. obs.). Display: last phase of the loud call is uttered with bill pointing upwards and mouth wide open (Haimhoff 1987).

Species: *B. hydrocorax* Linnaeus, 1766. (19d, 35?, 38 [juvenile plumage].)

Subspecies: *B. h. hydrocorax* Linnaeus, 1766. (27 a [juvenile], 37 [facial skin]). Casque form: adult male and adult female, flat block extending from forehead to point overhanging middle of bill. Bill colour: adult male, crimson with black base; adult female, all crimson; juvenile, black. Bare skin: smooth, circumorbital only: adult male, yellow; adult female, black; juvenile, undescribed. Eye colour: adult male, red; adult female, white; juvenile, undescribed. Leg colour: adult male, red-brown; adult female and juvenile, undescribed. Loudest call (Fig. 9B, locality assumed to be Luzon, Ben King): described as similar to *B. h. mindanensis*, a clear resonant honk repeated, with female at higher pitch (middle call Fig. 9B). Display: none recorded.

Subspecies: *B. h. mindanensis* Tweeddale, 1877. (30b, 39c.). Plumage of juvenile differs from *B. h. hydrocorax* in basal half of tail black (not just black band across centre). Casque form: adult male and adult female, high, flat block extending from over forehead to point almost overhanging bill tip. Bill colour: adult male, crimson with black base and distal half yellow; adult female, crimson with distal half yellow; juvenile, black. Bare skin: smooth, circumorbital and small gular patches: adult male, circumorbital black with yellow patch below eye, gular yellow; adult female and juvenile, undescribed. Eye colour: adult male, pale yellow or green; adult female, white, pale blue or cream; juvenile male, pale yellow; juvenile female pale blue or brown. Leg colour: adult male and adult female, light coral red; juvenile, black. Loudest call (no recording available): clear resonant honk, repeated (Stott 1947). Display: none recorded.

Subspecies: *B. h. semigaleatus* Tweeddale, 1878. (39c.) Plumage of juvenile like *B. h. mindanensis*. Casque form: adult male and adult female, flat wedge merging into middle of bill. Bill colour like *B. h. mindanensis*. Bare skin: circumorbital and small gular patches: adult male, circumorbital black, gular yellow; adult female, all greenish-yellow; juvenile, yellowish-green. Eye colour: adult male, pale yellow or green; adult female, pale blue or white; juvenile, brown. Leg colour like *B. h. mindanensis*. Loudest call (no recording available): described as similar to *B. h. mindanensis*. Display: none recorded.

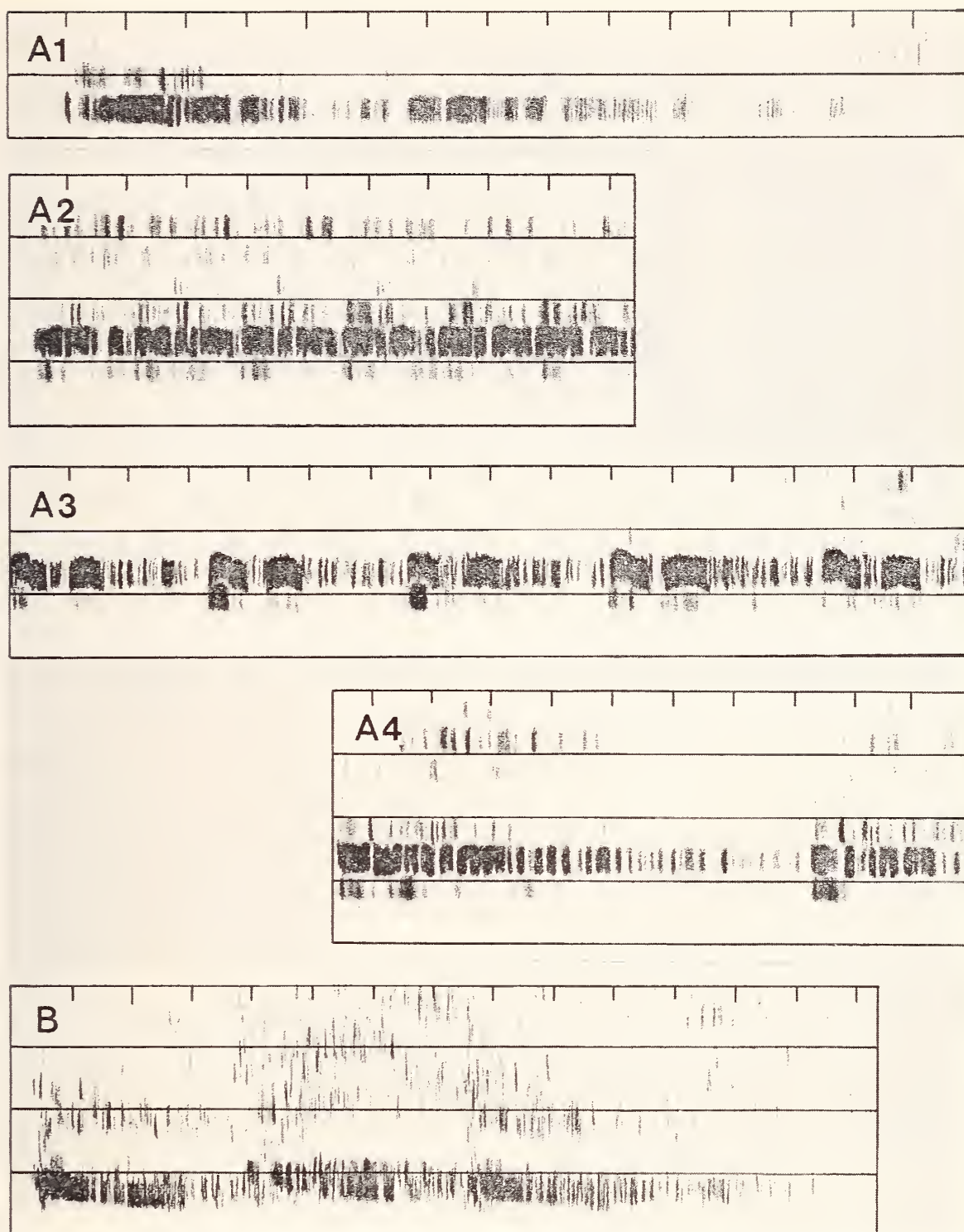


Fig. 9: Sonograms of the loudest calls of some *Buceros* hornbill species. A1–4 — *B. vigil*; B — *B. hydrocorax*.

The difference in softpart colours, extent of gular skin and juvenile plumage between *B. h. hydrocorax* and the other two subspecies *B. h. mindanensis* and *B. h. semigaleatus* suggests that two species may be involved. Field study and documentation of softpart differences are required.

Species: *B. rhinoceros* Linnaeus, 1758. (28a, 39ac.)

Subspecies: *B. r. rhinoceros* Linnaeus, 1758. (27a, 28a.) Casque form: adult male and adult female, large cylinder arising above forehead and with tip curving up and back to varying degree about midway along bill. Bill colour: adult male, yellow with orange preen oil applied over basal half, black rear to casque, base of mandibles and line along side of casque; adult

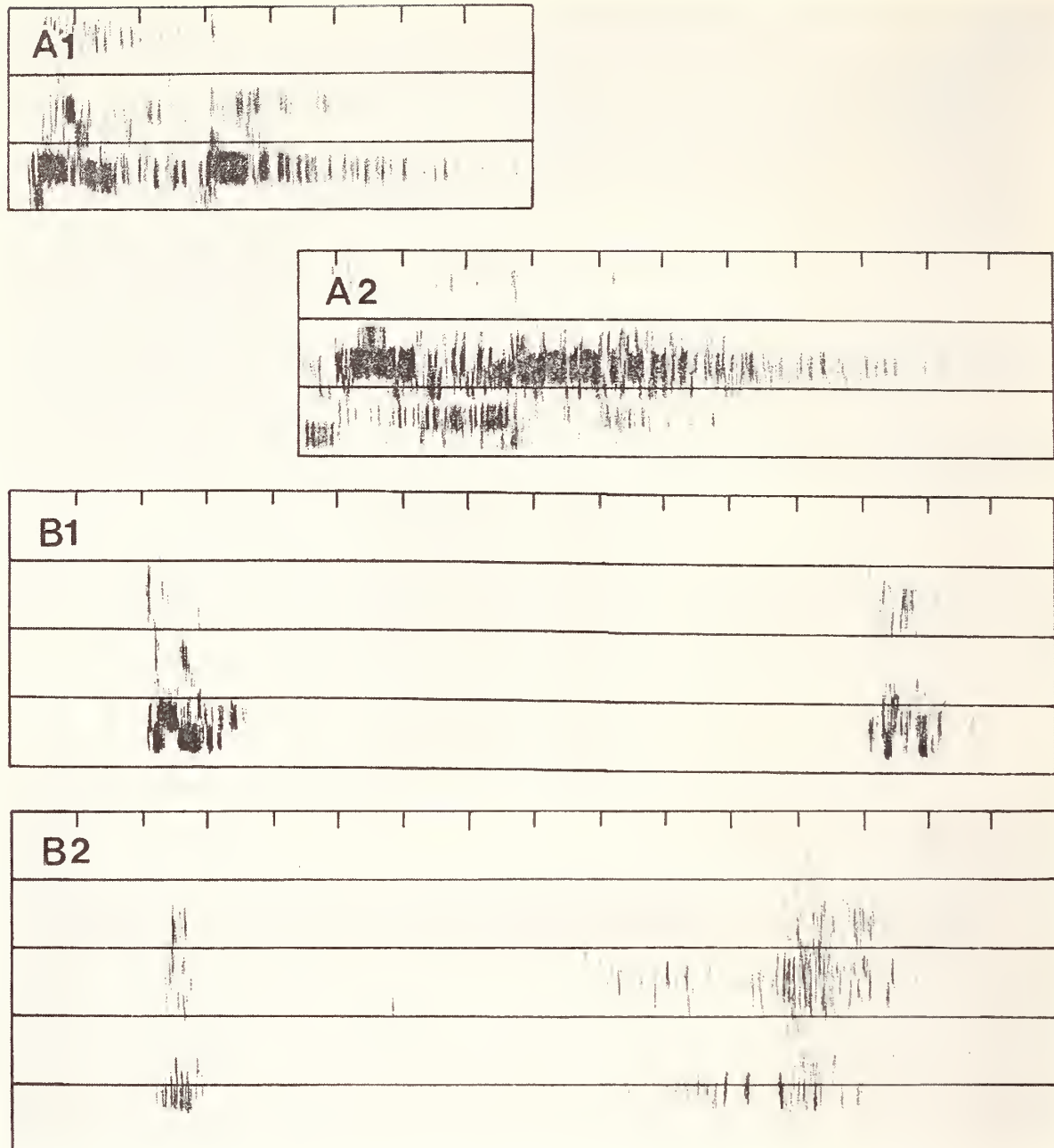


Fig. 10: Sonagrams of the loudest calls of some *Buceros* hornbill species. A1–2 — *B. rhinoceros*; B1–2 — *B. bicornis*.

female, yellow with orange preen oil applied over basal half; juvenile, yellow with orange base (Frith & Douglas 1978). Bare skin: smooth, circumorbital only: adult male, black; adult female, red with black eyelids forming ring round eye (Lint 1972, Riley 1938); juvenile, grey. Eye colour: adult male, red; adult female, white; juvenile, grey (Frith & Douglas 1978). Leg colour: adult male and adult female, olive-green (Riley 1938); juvenile, undescribed. Loudest call (no recording available): harsh croak, more wheezy in females (Banks 1935), sharp kak note when perched with loud goose-like honking, usually uttered antiphonally by pair, in flight (Medway & Wells 1976). Display: jerks head upwards with each note, raising bill skywards (Frith & Douglas 1978).

Subspecies: *B. r. borneoensis* Schlegel & Müller, 1840. (28a.) Smaller than *B. r. rhinoceros* with casque shorter, broader and tip more recurved. Form and softpart colours like *B. r. rhinoceros*. Loudest call (Fig. 10A1–2, Sarawak, Alan Kemp): loud, deep grunts (Fig. 10A1) and braying flight call (Fig. 10A2), female following male antiphonally at slightly higher pitch in each case. Display: like *B. r. rhinoceros* (pers. obs.).

Subspecies: *B. r. silvestris* Vieillot, 1816. (27 a.) Plumage differs in broader black band across rectrices. Casque only raised at tip without any recurvature. Form and softpart colours like *B. r. rhinoceros*. Loudest call (no recording available): similar to nominate subspecies (H. Bartels pers. comm.). Display: none described.

Species: *B. bicornis* Linnaeus, 1758. (28 a, 39 c.)

Casque form: adult male and adult female, broad concave block arising over forehead and dividing into two points on either side of middle of bill. Bill colour: adult male, yellow becoming orange at tip and centre, black base to casque, mandibles and beneath overhang of casque; adult female, yellow with black base to mandibles and red-brown base to casque; juvenile, undescribed. Bare skin: smooth, circumorbital only: adult male, black; adult female, flesh-coloured with black eyelids forming ring round eye; juvenile, fleshy-pink (Frith & Douglas 1978). Eye colour: adult male, red; adult female, white; juvenile, blue-grey (Frith & Douglas 1978) or white (Choy 1980). Leg colour: adult male and adult female, olive-green; juvenile, greenish-yellow (Deignan 1945, Choy 1980). Loudest call (Fig. 10B1, Thailand, Pilai Poonswad, 10B2, Hawaii Zoo, W. & J. Ward): very loud reverberating kok repeated at slow regular intervals (Ali & Ripley 1970, Fig. 10B1), coarse guttural whaa (Frith & Douglas 1978) or double who-whaa uttered at takeoff and in flight (Fig. 10B2). Display: neck stretched vertically up and bill pointing skywards with each kok call (Ali & Ripley 1970).

The populations of continental Asia are larger than the nominate form on Peninsular Malaya and Sumatra and are described as *B. b. homrai* Hodgson, 1832. This conforms with a cline of decreasing size from north to south (Deignan 1945).

Genus: *Anorrhinus* Reichenbach, 1849. (7, 8, 10, 21 b, 29 b.)

Species: *A. galeritus* (Temminck, 1831). (35, 36.)

Casque form: adult male and adult female, low ridge terminating midway along bill. Bill colour: adult male, black; adult female, black with broad yellow stripe along upper mandible and tip of lower mandible; juvenile, pale greeny-horn (Dunselman 1937, Madge 1969). Bare skin: smooth, circumorbital and extensive gular: adult male and adult female, blue with white area behind eye and on angles of jaw (Riley 1938) and black eyelids forming ring round eye (Frith & Douglas 1978); juvenile, dull pale yellow with pink ring round eye. Eye colour: adult male and adult female, red; juvenile, blue-grey. Leg colour: adult male, dark brown; adult female, blue-grey (Sharpe 1890); juvenile, undescribed. Loudest call (Fig. 11A, Sarawak, Alan Kemp): quiet wah wah wo hawha rising and falling in volume, or alternating with wild strident squarking (Madge 1969), in which the notes are repeated rapidly (Fig. 11A). Display: none recorded.

Species: *A. tickelli* (Blyth, 1855). (21 a.)

Casque form: adult male, low ridge terminating midway along bill; adult female, similar to adult male. Bill colour: adult male, yellowish-white (Poonswad et al. 1983); adult female, black; juvenile, ivory yellow with greenish wash at base especially on lower mandible (Frith & Douglas 1978). Bare skin: smooth, circumorbital with small gular patches just connecting under throat: adult male, blue; adult female and juvenile, pale pink with yellow wash below eye. Eye colour: adult male and adult female, brown (Tickell 1864); juvenile, grey. Leg colour: adult male, adult female and juvenile, black. Loudest call: (Fig. 11B, Thailand, Pilai Poonswad): loud plaintive scream whey-wheyo repeated (Tickell 1864). Display: none recorded.

Species: *A. austeni* Jerdon, 1872. (35.)

Casque form: adult male, low ridge terminating midway along bill; adult female, similar to adult male. Bill colour: adult male, adult female and juvenile, pale yellow. Bare skin: smooth, circumorbital with small gular patches just connecting under throat: adult male and adult

female, light blue; juvenile, yellowish. Eye colour: adult male and adult female, brown (Ali & Ripley 1970, Deignan 1945); juvenile, grey-brown. Leg colour: adult male and adult female, dull greenish-brown (Tickell 1890); juvenile, brown. Loudest call (no recording available): loud croaks, chuckles and squeaks (similar to *Anthracoseros albirostris* (Ali & Ripley 1970)). Display: none recorded.

This species is separated from *A. tickelli* primarily on the difference in bill colour of adult females, black in the latter but yellow, like the male in *A. austeni*. *A. austeni* also lacks white tips to the secondaries and tertials, the face and throat are white (not red-brown) and the breast and upperparts are lighter, less reddish, brown. There may also be differences in calls and softpart colours but these remain to be clarified.

Genus: *Penelopides* Reichenbach, 1849. (7–10, 20 a, 36.)

The Philippine populations of *Penelopides* have usually been lumped into one species *P. panini*. However the marked differences in characters of plumage, sexual dimorphism, juvenile plumage, bill form and softpart colours, correlated with their fragmented insular distributions, suggest that several species are involved. Careful documentation of these differences in the field and their role in mate recognition are necessary to test the specific divisions suggested below.

Species: *P. mindorensis* Steere, 1890. (37 [facial skin].)

Differs from other *Penelopides* species in that there is no sexual dimorphism in plumage and juveniles resemble adults. Casque form: adult male and adult female, low ridge terminating midway along bill. Bill colour: adult male and adult female, black with yellow tip and yellow stripes across upper mandible; juvenile, undescribed. Bare skin: smooth, circumorbital and separate gular patches: adult male, white; adult female, dark blue; juvenile, undescribed. Eye colour: adult male, red-brown; adult female, light brown; juvenile, undescribed. Leg colour: adult male, dark brown; adult female and juvenile, undescribed. Loudest call (no recording available): undescribed. Display: none recorded.

Species: *P. exarhatus* (Temminck, 1823). (20 a [grooved]), 21 b, 27 b.)

Subspecies: *P. e. exarhatus* (Temminck, 1823). 37 [bill].) Casque form: adult male, low ridge grooved along length and terminating abruptly almost at tip of bill; adult female, ridge merges into distal half of bill. Bill colour: adult male, pale yellow with dark brown casque and black patch at base of lower mandible; adult female, black patch at base of lower mandible less developed; juvenile, undescribed. Bare skin: smooth, circumorbital and small gular patches just connecting under throat: adult male, flesh-coloured; adult female, black with yellow stripe below eye; juvenile, pale yellow. Eye colour: adult male and adult female, red; juvenile, dark brown. Leg colour: adult male, black, adult female and juvenile, undescribed. Loudest call (Fig. 11C, Sulawesi, Derek Holmes): harsh quacking note, repeated rapidly. Display: none recorded.

Subspecies: *P. e. sanfordi* (Stresemann, 1932). (37 [bill].) Like *P. e. exarhatus* except that in adult males the black area at the base of the lower mandible is barred with yellow and the casque is a redder brown. Loudest call (no recording available): undescribed. Display: none recorded.

Species: *P. affinis* Tweeddale, 1877. (21 b.)

Subspecies: *P. a. affinis* Tweeddale, 1877. (37 [bill].) Resembles *P. panini* in plumage and in juvenile females resembling adult males, but differs in bill form and softpart colours. Casque form: adult male and adult female, low ridge terminating midway along bill. Bill colour: adult male and adult female, horn-coloured with base of upper mandible black, casque and ridges across base of lower mandible dark brown; juvenile, grey-brown with greenish base to lower mandible. Bare skin: smooth, circumorbital and separate gular patches: adult male,

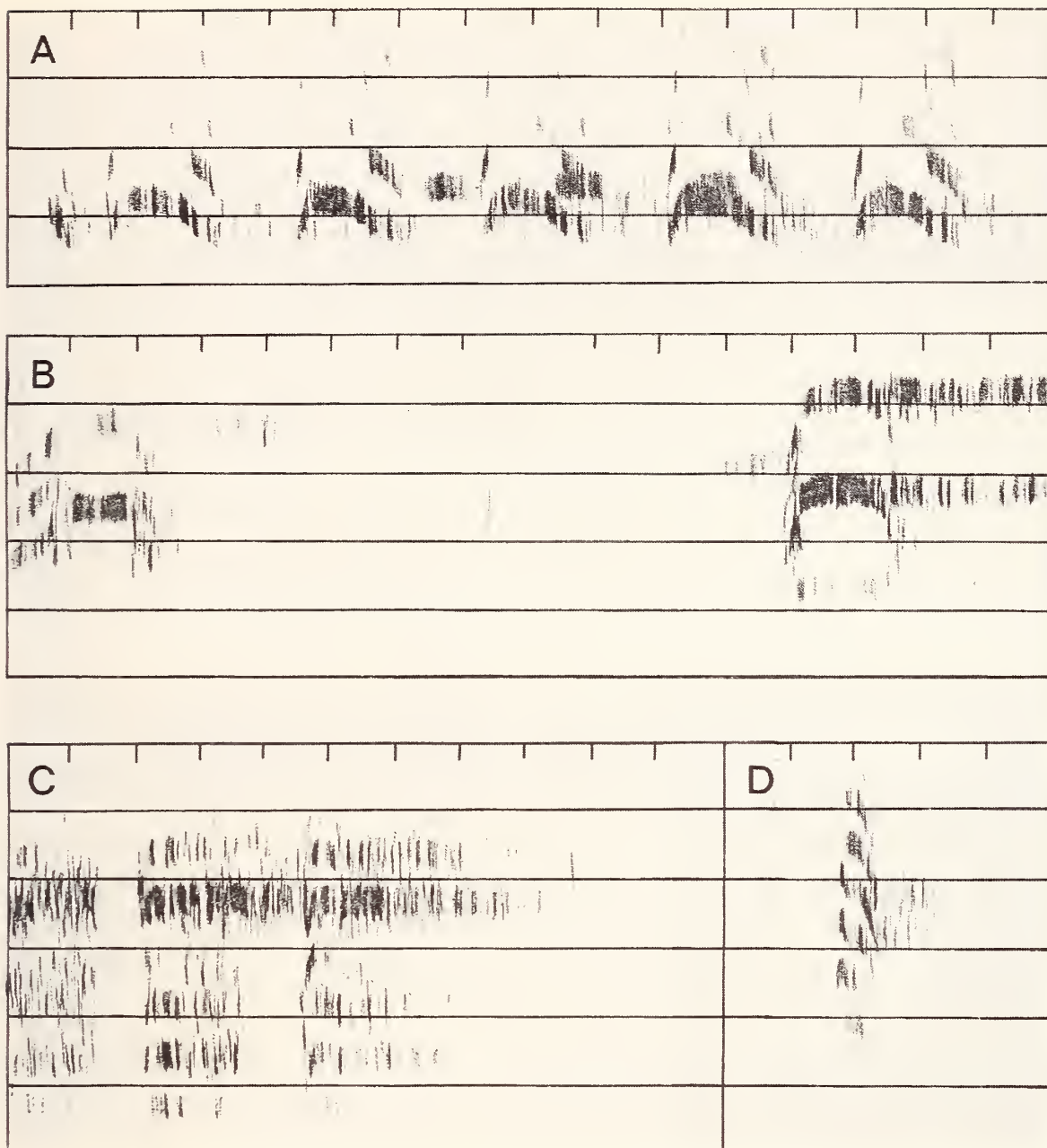


Fig. 11: Sonograms of the loudest calls of *Anorrhinus* and *Penelopides* hornbill species. A — *A. galeritus*; B — *A. tickelli*; C — *P. exarhatus*; D — *P. manilloe*.

adult female and juvenile, white with blue wash especially circumorbitally. Eye colour: adult male, red; adult female, red-brown to orange; juvenile, brown to grey-brown. Leg colour: adult male and adult female, dark grey; juvenile, dark greenish-grey. Loudest call (no recording available): undescribed. Display: none recorded.

Subspecies: *P. a. samarensis* Steere, 1890. (19d, 37 [bill].) Plumage differs from *P. a. affinis* in uppertail coverts being pale rufous in adult males (not black in both sexes) and more extensive rufous area on rectrices. Form and softpart colours like *P. a. affinis*. Loudest call (no recording available): undescribed. Display: none recorded.

Subspecies: *P. a. basilanica* Steere, 1890. (19d, 37 [bill].) Plumage differs from *P. a. affinis* in virtual lack of black base to rectrices. Form and softpart colours like *P. a. affinis* except for bill colour: adult male and adult female, upper mandible and casque horn-coloured without black patch at base. Loudest call (no recording available): undescribed. Display: none recorded.

Species: *P. manilloe* (Boddaert, 1783). (—21 b, 36.)

Subspecies: *P. m. manilloe* (Boddaert, 1783). (—21 b, 36.) Plumage differs from *P. p. panini* in being browner above and whiter below, with only a narrow pale rufous band across rectrices. Juveniles show plumage of respective sex from fledging, juvenile females not with plumage like adult male as in *P. panini* (Lieras 1983). Casque form: adult male and adult female, low ridge terminating midway along bill. Bill colour: adult male and adult female, brown with horn-coloured casque and yellow ridges across upper and lower mandible; juvenile, undescribed. Bare skin: smooth, circumorbital and whole of throat: adult male, pink (Lieras 1983); adult female, circumorbital blue, gular pink edged blue; juvenile, undescribed. Eye colour: adult male, dark red; adult female, red-brown or orange (Lieras 1983); juvenile, brown. Leg colour: adult male, dark brown; adult female and juvenile, undescribed. Loudest call (Fig. 11D, locality assumed to be Luzon, Ben King): loud short clear squeak (Frith & Douglas 1978, pers. obs.). Display: none recorded.

Subspecies: *P. m. subnigra* McGregor, 1910. (38.) Larger than *P. m. manilloe* with dark areas of plumage black with a metallic sheen (not dark brown) and pale area on tail broader. Form and softpart colours like *P. m. manilloe*. Loudest call (no recording available): undescribed. Display: none recorded.

Species: *P. panini* (Boddaert, 1783). (21 b, 37 [bill, facial skin].)

Subspecies: *P. p. panini* Reichenbach, 1849. (19d.) Casque form: adult male and adult female, low ridge terminating midway along bill. Bill colour: adult male and adult female, red with yellow ridges across upper and lower mandibles; juvenile, olive-brown. Bare skin: smooth, circumorbital and gular patches just connecting under throat: adult male, flesh-coloured with throat black; adult female, pale blue; juvenile, white tinged blue. Eye colour: adult male, red-brown or brown; adult female, red; juvenile, brown. Leg colour: adult male, dark brown; adult female, undescribed; juvenile, dark greenish-grey. Loudest call (no recording available): undescribed. Display: none recorded.

Subspecies: *P. p. ticaensis* Hachisuka, 1930. (38.) Larger than *P. p. panini* with darker upper-tail coverts and rufous area in rectrices. Form and softpart colours like *P. p. panini*. Loudest call (no recording available): undescribed. Display: none described.

Genus: *Aceros* J. E. Gray, 1844. (9–12, 21 b.)

Subgenus: *Berenicornis* Bonaparte, 1850. (29 b, 31 b, 35, 37 [eye].)

Species: *A. comatus* (Raffles, 1822). (29 b, 31 b, 35, 37 [eye].)

Casque form: adult male, low ridge merging into middle of bill; adult female, only very slight ridge at base of bill. Bill colour: adult male and adult female, black with greenish-yellow base; juvenile, pale yellow. Bare skin: smooth, circumorbital and gular patches connecting across throat: adult male and adult female, matt blue; juvenile, grey with turquoise tinge (Frith & Douglas 1978). Eye colour: adult male and adult female, pale yellow; juvenile, greenish-yellow. Leg colour: adult male and adult female, black; juvenile, grey (Dunselman 1937). Loudest call (Fig. 12A, Sarawak, Alan Kemp): series of mellow hooting phrases repeated ho-ho ho-ho-ho-ho . . ., slowly lowering in pitch. Display: tail slightly raised and lowered while calling (Frith & Douglas 1978), or rocked back and forth under body.

Subgenus: *Aceros* J. E. Gray, 1844. (19d, 20a, 25a b, 26.)

Species: *A. nipalensis* (Hodgson, 1829). (31 b, 36, 39c.)

Casque form: adult male and adult female, low ridge merging into basal half of bill. Bill colour: adult male and adult female, yellow with up to eight black stripes across base of upper mandible; juvenile, undescribed. Bare skin: smooth, circumorbital and extensive inflatable

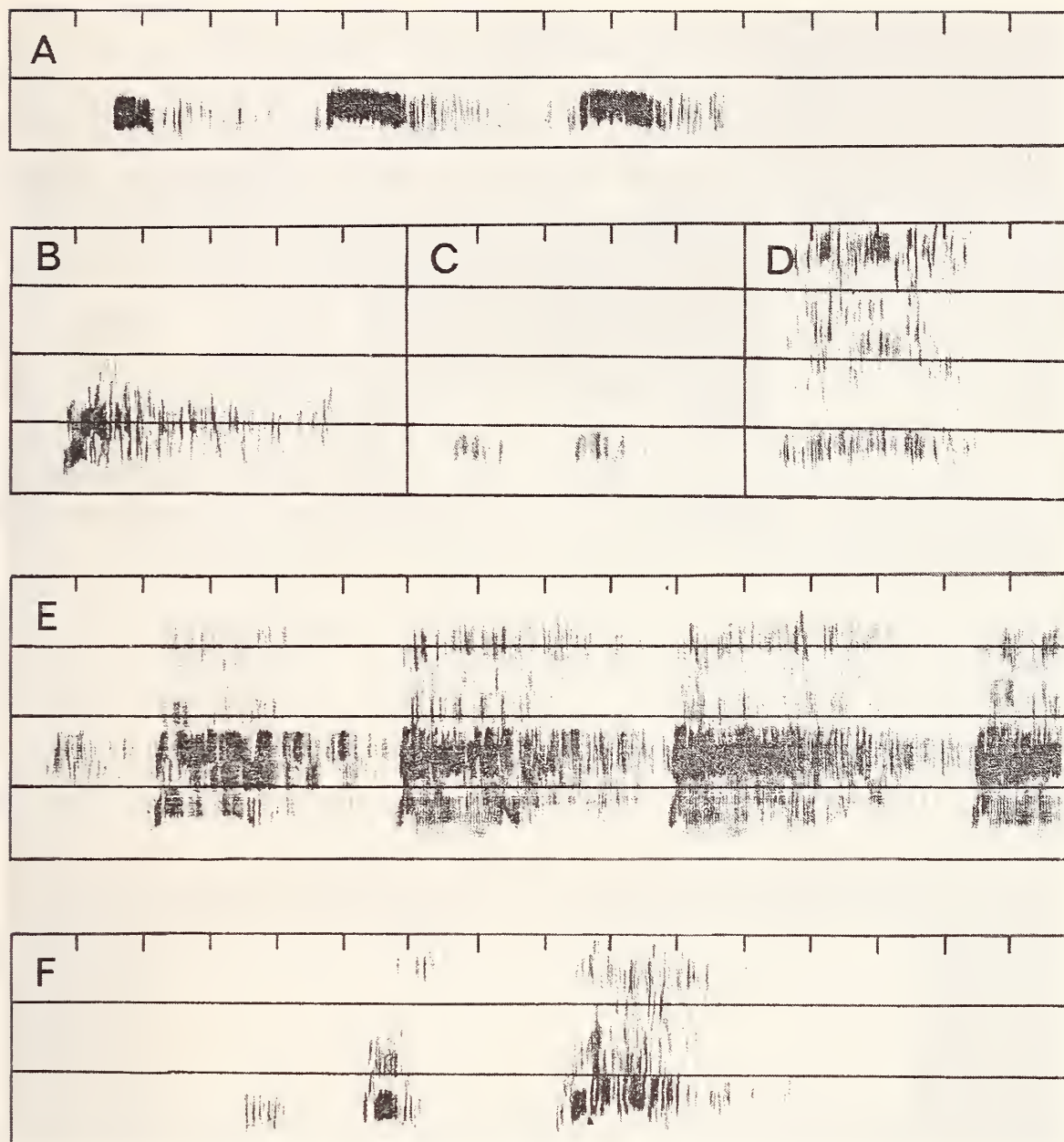


Fig. 12: Sonograms of the loudest calls of *Aceros* hornbill species. A — *A. comatus*; B — *A. cassidix*; C — *A. corrugatus*; D — *A. waldeni*; E — *A. plicatus*; F — *A. undulatus*.

gular area: adult male, circumorbital pale blue, gular scarlet with blue flecks around perimeter; adult female, circumorbital duller blue than male, angle of jaw and across throat dark blue to deep violet, traversing scarlet gular with blue edge (Deignan 1945); juvenile, undescribed. Eye colour: adult male and adult female, red; juvenile, greenish-white. Leg colour: adult male, black, adult female and juvenile, undescribed. Loudest call (no recording available): loud croak (Deignan 1945), various loud roars, croaks, cackles and short bark, female at higher pitch than male (Ali & Ripley 1970). Display: head thrown back, red hair on end, gular skin inflated, bill erect and wide open, wings hanging loosely and quivering slightly, every now and then tail jerked up until almost touches head (Baker in Ali & Ripley 1970).

Species: *A. cassidix* (Temminck, 1823). (19d, 23, 28a [wrinkled], 37 [facial skin].)

Casque form: adult male, large helmet-like crest from above forehead to abrupt end a third of way along bill; adult female, similar to male but smaller. Bill colour: adult male and adult female, yellow with red-brown casque and orange-brown ridges on bases of both mandibles; juvenile, undescribed. Bare skin: smooth, circumorbital and extensive gular area: adult male,

circumorbital pale blue with dark blue eyelids, gular dark blue with broad black band through lower edge and pale blue-green below band; adult female, like adult male but apparently lacking black band across gular skin (van Bemmél & Voous 1951); juvenile, paler than adults. Eye colour: adult male, red to red-brown; adult female, brown to dark brown; juvenile, dark brown with yellow rim. Leg colour: adult male, black; adult female and juvenile, undescribed. Loudest call (Fig. 12B, Sulawesi, Derek Holmes): single high gruff bark repeated. Display: none recorded.

The populations on the islands of Muna and Buton have been separated as the race *A. c. brevirostris* (van Bemmél & Voous 1951) based on their smaller size and shorter bill. They represent the south end of a cline that decreases in size from north to south across Sulawesi.

Species: *A. corrugatus* (Temminck, 1832) (28a [wrinkled], 37 [bill, throat].)

Casque form: adult male, high wrinkled crest above basal half of bill; adult female, high ridge above basal half of bill. Bill colour: adult male and adult female, yellow with reddish base, red casque and ridges across base of lower mandible, from application of red preen oil; juvenile, undescribed. Bare skin: smooth, circumorbital and extensive inflated gular area: adult male, circumorbital blue, gular pale yellow; adult female, circumorbital and gular blue; juvenile, undescribed. Eye colour: adult male, red; adult female, grey-brown (Riley 1938); juvenile, yellow with brown tinge. Leg colour: adult male, black; adult female, greenish-grey (Riley 1938); juvenile, undescribed. Loudest call (Fig. 12C, Sarawak, Alan Kemp): double hooting notes repeated. Display: none recorded.

The populations of Sumatra and the Malay Peninsula have been described as the race *A. c. rugosus* (Begbie, 1834) since they are larger than the nominate form on Borneo.

Species: *A. waldeni* (Sharpe, 1877). (28a [wrinkled], 37 [bill], 39c.)

Casque form: adult male, high wrinkled crest above basal half of bill; adult female, high ridge above basal half of bill. Bill colour: adult male and adult female, red, including ridges across base of lower mandible; juvenile, undescribed. Bare skin: smooth, circumorbital and extensive inflated gular area: adult male, yellow; adult female, circumorbital black and gular pale yellow; juvenile, undescribed. Eye colour: adult male, red; adult female, red to brown; juvenile, red-brown. Leg colour: adult male, black; adult female, undescribed; juvenile, yellowish-grey. Loudest call (Fig. 12D, locality assumed to be Luzon, Ben King): single mellow barks repeated. Display: none recorded.

Species: *A. leucocephalus* (Vieillot, 1816). (19e, 27c, 28a [wrinkled], 37 [bill].)

Plumage differs from *A. leucocephalus* in head and neck being white with dark brown crown and hindneck (not all red brown), and tail being all white with black tip (not with the basal half also black). There are also differences in softpart colours. Casque form: adult male, high wrinkled crest above basal half of bill; adult female, high ridge above basal half of bill. Bill colour: adult male, red; adult female, red but for dark brown ridges across base of lower mandible; juvenile, undescribed. Bare skin: smooth, circumorbital and extensive inflated gular area: adult male and adult female, bright orange-red with yellow eyelids forming ring round eye; juvenile, undescribed. Eye colour: adult male and adult female, dark brown to red; juvenile, red-brown. Leg colour: adult male and adult female, black; juvenile, undescribed. Loudest call (no recording available): undescribed. Display: none recorded.

Subgenus: *Rhyticeros* Reichenbach, 1849. (19d, 25a, 28a [wreathed].)

Species: *A. everetti* (Rothschild, 1897). (27b, 37 [bill].)

Casque form: adult male and adult female, low series of wreaths across base of bill. Bill colour: adult male and adult female, pale yellow with red-brown patch across centre of both mandibles; juvenile, undescribed. Bare skin: smooth, circumorbital and extensive gular area: adult male, adult female and juvenile, circumorbital dark blue with pink eyelids forming ring

round eye, gular pale blue with dark blue patch under throat. Eye colour: adult male and adult female, red-brown; juvenile, dark brown. Leg colour: adult male, adult female and juvenile, black. Loudest call (no recording available): harsh clucking notes repeated (Ernst Sutter in litt.). Display: none recorded.

Species: *A. narcondami* (Hume, 1873). (37 [eye].)

Casque form: adult male and adult female, low series of wreaths across base of bill. Bill colour: adult male and adult female, white with dark crimson base (Frith & Douglas 1978); juvenile, waxy yellow with base tinged red (Hussain 1984). Bare skin: smooth, circumorbital and extensive partly inflated gular area: adult male and adult female, circumorbital dark blue with red eyelids forming ring round eye, gular white with blue tinge; juvenile, similar to adult but paler. Eye colour: adult male, deep orange-brown with yellow inner rim; adult female, olive-brown with yellow inner rim; juvenile, pale grey in both sexes (Hussain 1984). Leg colour: adult male and adult female, black; juvenile, undescribed. Loudest call (no recording available): loud ka-ka-ka-ka (like cackle of fowl, Ali & Ripley 1970). Display: none recorded.

Species: *A. plicatus* (J. R. Forster, 1781). (37 [bill].)

Casque form: adult male and adult female, low series of wreaths across base of bill. Bill colour: adult male and adult female, pale yellow with red-brown base, casque darker and browner; juvenile, undescribed. Bare skin: smooth, circumorbital and extensive inflated gular area: adult male and adult female, circumorbital pale blue with flesh-coloured eyelids forming ring round eye (Gillard & LeCroy 1966), gular white with blue tinge; juvenile, undescribed. Eye colour: adult male, red to red-brown; adult female, brown; juvenile, undescribed. Leg colour: adult male, black; adult female and juvenile, undescribed. Loudest call (Fig. 12E, Biri Island, Jared Diamond): loud raucous grunts (Coupe 1967), continuous honking in flight ka-ka (Gillard & LeCroy 1967). Display: none recorded.

The fragmented insular distribution of this single Australasian species is evident in the local variations that have been reported, mainly in size and intensity of rufous colouration of the head and neck in juveniles and adult males. Eye colour also appears to be variable, but the extent to which this is related to age, sex or local variation is unresolved. Colours of the bill and bare facial skin, and calls, appear to remain constant across the range of the species. The nominate race described above occurs on the islands of Ceram and Ambon. The race *A. p. ruficollis* (Vieillot, 1816), with the head and neck golden-brown in adult males, occurs on the islands of Morotai, Halmahera, Batjan, Kasiruta, Obi, New Guinea west of Humboldt Bay and the Digul River and adjacent islands of Misool, Salawati, Bataqata, Gebe and Waigeo. It intergrades with *A. p. jungei* Mayr, 1937 which is larger than *A. p. ruficollis* and extends through eastern New Guinea and the adjacent islands of Japen and the d'Entrecasteaux Islands. *A. p. dampieri* Mayr, 1934, which is smaller than *A. p. ruficollis* with a lighter bill and the head and neck yellow-brown in adult males, occurs on New Hanover, New Ireland and New Britain in the Bismarck Archipelago. *A. p. harterti* Mayr, 1934, with the head and neck of adult males buff, occupies the western Solomon Islands of Buka, Bougainville, Fauro and Shortland. Finally, *A. p. mendanae* Hartert, 1924, which is smaller than *A. p. harterti* and has ridges on the base of the bill (Lint 1972), occurs on the southern Solomon Islands of Choiseul, Santa Isabel, Vangunu, Malaita, and Guadalcanal.

Species: *A. subruficollis* (Blyth, 1843). (37 [throat].)

Casque form: adult male and adult female, low series of wreaths across base of bill. Bill colour: pale yellow with red-brown base and narrow black base to lower mandible (Riley 1938), mandibles without ridges across base. Bare skin: smooth, circumorbital and extensive inflated gular area: adult male, circumorbital reddish-purple (Riley 1938), gular yellow; adult female, circumorbital undescribed, gular blue (possibly with black bar across centre, Riley

1938); juvenile, undescribed. Eye colour: adult male, red to red-orange; adult female, dark orange-brown (Riley 1938); juvenile, undescribed. Leg colour: adult male and adult female, black in front and dull grey behind (Riley 1938); juvenile, undescribed. Loudest call (no recording available): undescribed. Display: none recorded.

The descriptive details and distribution of this species are difficult to determine due to its early classification as a close relative or form of *A. plicatus* and its later inclusion as a form of *A. undulatus* (Sanft 1953, 1960). Elbel (1969, 1977) reported inconsistencies between the relationships of the Mallophaga and the proposed classifications of these hornbills, suggesting that *A. subruficollis* was a full species. Hussain (1984) also examined the radiation of the subgenus *Rhyticeros* when discussing the relationships of *A. narcondami*. The colouration of the gular skin suggests that *A. subruficollis* is most closely related to *A. undulatus* but is consistently distinguished by the unmarked yellow gular skin of adult males (there being an interrupted blue-black band across the gular skin in adult males and juveniles of both sexes of *A. undulatus*). Adult female *A. subruficollis* also often lack a dark blue band across the gular skin, which is always present in *A. undulatus*, but this is less obvious as the gular skin is also blue, although of a lighter tone. There is also a significant and consistent size difference between adults of *A. subruficollis* and the larger *A. undulatus* (Table 4) which supports their separation. Furthermore, all adult male and juvenile *A. subruficollis* have their heads coloured more rufous than those of *A. undulatus*.

Specimens which seem to be *A. subruficollis* (and which include those described as *A. u. ticehursti* (Deignan, 1941) have been collected from at least the following localities (original localities from labels in brackets): India (Magherita in upper Assam, American Museum of Natural History); Burma (Kyaikkami (Amherst), Lower Pegu, Ateran River, American Museum of Natural History; Three Pagodas Pass, Hans Bartels in litt.; Myawadi (Meeyawad-die) on the upper Thoungyeen (Thaungyin) River, Bingham 1879; Kadan Kyum (King Island) in the Mergui Archipelago, Anderson 1887; Telok Krang, Telok Besar and Letsok-aw Jyun (Domel Island), Riley 1938); Thailand (Petchaburi Province, Riley 1938; Karnchanaburi Province, Pilai Poonswad in litt.; Mai Lem River, reported as common in north, Riley 1938; D. C. Dickinson in litt. to David Wells identified a specimen from Ranong, Peninsular Thailand); Sumatra (Deli District around Medan, Boelse, American Museum of Natural History; Tebingtinga, Pematang Siantar on the road from Medan to Lake Toba, Hans Bartels in litt.). Riley (1938) also includes Borneo and the Malay States in the range of the species, but specimens checked so far from these regions have the band across the gular skin typical of *A. undulatus* (see also that species below). These records are sufficient to establish that *A. subruficollis* is sympatric with *A. undulatus* in several areas of the Asian mainland.

Species: *A. undulatus* (Shaw, 1811). (18, 20a, 37 [throat].)

Casque form: adult male and adult female, low series of wreaths across base of bill. Bill colour: adult male and adult female, pale yellow, more orange at base and including ridges

Table 4: Measurements of adult specimens of *Aceros subruficollis* and *A. undulatus*, with three or more wreaths on their casques, from the Asian mainland.

Species and sex		Measurements, (sample) mean (range), in mm			
		Bill length	Wing length	Tail length	
Males					
<i>subruficollis</i>	(10)	169 (138–177)	(10) 419 (395–450)	(10)	247 (237–267)
<i>undulatus</i>	(27)	202 (180–225)	(25) 497 (472–527)	(25)	298 (270–333)
Females					
<i>subruficollis</i>	(9)	137 (131–143)	(9) 381 (363–400)	(9)	221 (190–266)
<i>undulatus</i>	(19)	162 (144–190)	(15) 454 (418–490)	(14)	267 (245–288)

across base of mandibles; juvenile, pale yellow to white (Bell & Brunning 1979). Bare skin: smooth, circumorbital and extensive inflated gular area: adult male, circumorbital red with pink eyelids, gular bright yellow with interrupted blue-black band across centre; adult female, circumorbital flesh-coloured and gular blue with interrupted blue-black band across centre; juvenile, like adult male with lighter band across throat. Eye colour: adult male, dark red with narrow yellow inner rim (Bartels & Bartels 1937); adult female, dark brown with narrow blue inner rim (Bartels & Bartels 1937), juvenile, pale blue (Frith & Douglas 1978, Bernstein 1861, pers. obs.). Leg colour: adult male and adult female, dark olive-grey (Deignan 1945); juvenile, undescribed. Loudest call (Fig. 12F, Sarawak, Alan Kemp): phrases of two, rarely three, short raucous grunts, the first softer, uttered in series of 3–4 phrases. Display: throat inflated, tail drooped, bill jerked skywards to vertical with each phrase and then lowered again (Ali & Ripley 1970, pers. obs.).

The Bornean population has been separated as the race *A. u. aequabilis* Sanft, 1960 on its smaller size and lesser development of ridges across the base of the mandibles. Form, softpart colours, calls and displays appear to be constant across the range of the species.

Genus: *Ceratogymna* Bonaparte, 1859. (7–12, 20b, 22, 29a, 33, 40.) (Species: *bucinator*, *fistulator*, *brevis*, *subcylindricus*, *cylindricus*, *atrata*, *elata*.) Afrotropical genus.

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