

Systematic notes on Asian birds. 2.¹

A preliminary review of the Eurylaimidae

R.W.R.J. Dekker & E.C. Dickinson

Dekker, R.W.R.J. & E.C. Dickinson. Systematic notes on Asian birds. 2. A preliminary review of the Eurylaimidae.

René W.R.J. Dekker, National Museum of Natural History, P.O. Box 9517, 2300 RA Leiden, The Netherlands. (e-mail: dekker@naturalis.nnm.nl).

Edward C. Dickinson, c/o The Trust for Oriental Ornithology, Flat 3, Bolsover Court, 19 Bolsover Road, Eastbourne BN20 7JG, U.K. (e-mail: asiaorn@fttech.co.uk).

Keywords: broadbills; Eurylaimidae; review.

Recent taxonomic treatments of Asian taxa of broadbills (Eurylaimidae) are discussed and recommendations are made for further evaluation or for awareness of competing hypotheses as to treatment.

Introduction

In preparing the text for a planned 'Synopsis of the Birds of Asia' (see general introduction to the 'Systematic Notes on Asian Birds': this volume) we compare treatment in the Check-list of Birds of the World, in this case of the broadbills (Peters, 1951), with more recent treatments. The changes that have been proposed in such works have been examined, and the context of some proposed changes are clarified. We believe our recommendations are consistent with the conservative tradition of requiring the publication of convincing evidence for change, in as much detail as is needed from case to case. Where our recommendations are at variance with key publications we give the reasons for our views. For the broadbills we are fortunate in having a thoroughly researched and well documented recent book - 'Pittas, Broadbills and Asities' by Lambert & Woodcock (1996) - as a point of reference.

Corydon sumatranus (Raffles, 1822)

There is general agreement that too many subspecies were once recognized. Of the eight subspecies listed in the Check-list of Birds of the World (Peters, 1951) five are now in synonymy (Lambert & Woodcock, 1996), those retained being *sumatranus* (Raffles, 1822) from Sumatra and the Malay peninsula, *brunnescens* Hartert, 1916, of Borneo and the north Natus and *laeensis* Meyer de Schauensee, 1929, of the rest of mainland south-east Asia.

Lambert & Woodcock (1996) placed four forms from mainland south-east Asia named by Deignan (1947) in synonymy. Three of these were placed in synonymy by their author; two, *C. s. morator* Deignan, 1947, and *C. s. ardescens* Deignan, 1947, were explicitly submerged in *C. s. laeensis* 16 years later (Deignan, 1963); the third, *C. s. pallescens* Deignan, 1947, was placed in the synonymy of nominate *sumatranus* as is implicit in his listing of that form instead of *pallescens* for peninsular Thailand. On this

¹ An invitational series arranged by René W.R.J. Dekker and Edward C. Dickinson under the auspices of the National Museum of Natural History, Leiden, The Netherlands, and The Trust for Oriental Ornithology, U.K.

evidence one would expect that by 1963 Deignan would also have treated his extralimital *khmerensis* Deignan, 1947, as a synonym of *laoensis*. It was described as close to that form except for a "concealed dorsal patch as deep and pure a red as in *ardescens*" and, with *ardescens* submerged it could not have been sustained. Peters (1951) listed it as questionably distinct.

In addition, Lambert & Woodcock (1996) placed *orientalis* Mayr, 1938, in the synonymy of *brunnescens*, their argument being that variation within Borneo is more individual than geographic. There are, however, numerous species in which the birds of the extreme north of the island have been claimed to differ from those further south, and the publication of a detailed review of Bornean material, discussing the variability, is desirable if sufficient material from enough locations can be assembled.

Cymbirhynchus macrorhynchus (Gmelin, 1788)

Six races were accepted in the Check-list of Birds of the World (Peters, 1951). Lambert & Woodcock (1996) retained four – the nominate, *C. m. affinis* Blyth, 1846, *C. m. malaccensis* Salvadori, 1874, and *C. m. lemniscatus* (Raffles, 1822) and explained their reasons for dropping *C. m. tenebrosus* Meyer de Schauensee & Ripley, 1940, and *C. m. siamensis* Meyer de Schauensee & Ripley, 1940. The latter had been submerged in *malaccensis* in the 'Checklist of the Birds of Thailand' (Deignan, 1963).

It is probably more conservative to conceive of this species as having only three subspecies; a temptation that clearly appealed to Lambert & Woodcock, who recognized that *C. m. lemniscatus* was "very poorly differentiated". Earlier suppression of this form (Mees, 1986) was based on the comparison of "our large material from Sumatra and Borneo" in the National Museum of Natural History, Leiden, which holds 83 specimens from Sumatra and 45 from Java. Lambert & Woodcock (1996) noted that this synonymization was not followed in the 'The Birds of Sumatra' (van Marle & Voous, 1988). This is correct, but it is almost certain that this was not a deliberate rejection. There is no reference to Mees's paper in the 'Note' at the end of the species account, as there is to others that were taxonomically relevant, and Voous closed the manuscript for the checklist (*ibid.* p. 9) only six months after the appearance of the paper by Mees. It is quite probable that its revisionary effects were simply overlooked in this case.

Eurylaimus javanicus Horsfield, 1821

There is less consensus over this species. Five races were accepted in the Check-list of Birds of the World (Peters, 1951), with *E. j. friedmanni* Deignan, 1947, treated as a synonym of *E. j. pallidus* Chasen, 1935a, a judgement not accepted by Deignan (1963), where both *pallidus* of the southern Malay peninsula and *friedmanni* from further north were retained.

Since then there has been general acceptance of *pallidus* in the Malay Peninsula (Medway & Wells, 1976) and that Sumatran *E. j. harterti* van Oort, 1909, is a valid endemic form (van Marle & Voous, 1988). The validity of *friedmanni* has not, to our knowledge been re-examined and the taxon should not be placed in synonymy without review.

As mentioned above the views of Peters (1951) on *friedmanni* were not shared by Deignan (1963), but Lambert & Woodcock (1996) did not discuss *friedmanni* which does not even make their index. They only accepted nominate *javanicus*, *harterti*, and *E. j. brookei* Robinson & Kloss, 1919, and their decision to unite the Sumatran form with the populations of mainland south-east Asia appears to rest on their examination of the material in Tring in which "no clear differences could be found", but the material there although allowing a judgement in respect of *pallidus* is unlikely to be sufficient in itself to allow a review extending to birds from eastern Thailand (the terra typica of *friedmanni*). The proposal by Lambert & Woodcock (1996) to submerge *pallidus* in *harterti* contradicts the views of both Peters (1951) and Deignan (1963), yet no statement was made by Lambert & Woodcock (1996) that the views of Deignan (1963) were examined, and we believe a full review of the various populations of mainland SE Asia remains necessary.

The suppression of the Billiton form, *billitonis* Kloss, 1931, is grounded on a published review (Mees, 1986).

Eurylaimus ochromalus Raffles, 1822

Although Lambert & Woodcock (1996) generally inclined towards a reduction of the number of recognized broadbill subspecies, in this instance they retained the three subspecies historically recognized, which was probably an opportunity missed.

Several authors have reviewed the distinctness of the Bornean form, *E. o. kalamantan* Robinson & Kloss, 1919. In an early review colour differences were not sustained and differences in wing length between Malayan and Sarawak birds bridged by birds from North Borneo (Chasen & Kloss, 1930). This lead, not then but later, to its submergence in nominate *ochromalus* by Mayr (1938). Although this was not followed in the Check-list of Birds of the World (Peters, 1951) such submergence has been supported by evidence from later collecting (Voous, 1961) and comparisons (Mees, 1986).

The supposed west Sumatran Banjak Islands form, *E. o. mecistus* Oberholser, 1912, has been reviewed and sustained (Ripley, 1944), but solely on size. In fact the wing measurements given: 87.5, 87.5 and 88 mm for *mecistus* (measured by Ripley) versus 74.5-84.5 mm for the nominate form (reported by Ripley as measured by Meyer de Schauensee) did show a difference. However, comparison with earlier results shows that the sample from Borneo (size not stated) must have failed to include specimens from northern Borneo. The wing lengths supplied by Chasen & Kloss (1930), for the combined populations of Sarawak and North Borneo, with a range of 75-89 mm do not support separation of the Banjak birds on wing length. Chasen (1935b) and Mayr (1938) both looked at Bornean skins without finding and supporting a subspecific boundary in Borneo. Monotypic treatment, as proposed by Mees (1986), seems sufficiently well founded to be adopted.

Eurylaimus steerii Sharpe, 1876

The two forms in the Philippines, described in the 19th century as species, were perhaps rather casually lumped in preparation for the 'Birds of the Philippines' (Delacour & Mayr, 1945); a treatment universally followed since.

The population of Mindanao, originally considered to be the nominate form described from Basilan, has been split. In separating *E. s. mayri* Salomonson, 1953, from Mindanao, although not from the Zamboanga peninsula where the population is more akin to Basilan birds, its author did not discuss differences from *E. s. samarensis* (Steere, 1890) from nearby Samar. The Mindanao race, *mayri*, has the darkest crown and nape, and birds of the nominate race to the southwest have this area more purple as indeed does *samarensis* to the north of *mayri* although *samarensis* is in general more distinct. All three forms were listed in 'The Birds of the Philippines' (Dickinson et al., 1991).

Lambert & Woodcock (1996), noting that the two southern forms are much closer to each other than to *samarensis* have preferred to treat this complex as two species, and to accept two subspecies for the southern *steerii*. The distinctions summarized by them for *samarensis* and *steerii* are not convincingly demonstrative of specific differentiation.

Treatment of Philippine speciation is inevitably subjective; there is often allopatry without evidence of contact across straits between major island groups, including especially the gap between NE Mindanao and southern Leyte. The suggested regional distinctions in the Philippine fauna are based on the importance of these physical breaks into groups of islands (Steere, 1894; McGregor, 1920; Inger, 1954; Dickinson et al., 1991). It is entirely typical for populations in the Eastern Visayas (Samar, Leyte and Bohol) to differ from those of Mindanao, but for these to be closer to each other than birds from either Luzon or the Western Visayas (Panay and Negros). For most species occurring in Mindanao and in the Eastern Visayas the appropriate taxonomic treatment seems to be as two, or more, subspecies of one species, but see also the case of the Philippine forms of *Gallicolumba* treated as five allopatric species, within which the forms from Leyte and Samar on one hand and Mindanao as well as Basilan are treated as conspecific (Dickinson et al., 1991).

The treatment of Lambert & Woodcock (1996), which is certainly one hypothetically correct treatment, has been discussed by one of us in preparation for the 'Field Guide to the Birds of the Philippines' (Kennedy et al., in press) but it is not intended to follow them therein. Given the contiguous insular distribution of *samarensis* with the southern population, in a configuration where conspecificity is more normal, the small differences between *steerii* and *mayri*, and the fact that sufficient acoustic evidence is not yet available, it is justifiable to retain the recent, and perhaps more conservative, treatment maintaining a single species, with *samarensis* a very distinct race. The relationships might be appropriately described by treating the two southern forms as a subspecies group. However, the two will probably be found to vary clinally and to intergrade in northwest Mindanao and it may be more helpful to place *mayri* in the synonymy of *steerii* rather than to suggest that there is an equality of difference between the three forms.

The generic name *Sarcophanops* was proposed by Sharpe (1877) for a monotypic genus containing this species. We consider this to have been submerged in the genus *Eurylaimus* without comparative evaluation of the degrees of difference between the other genera of Asian broadbills and a fresh evaluation seems overdue.

Serilophus lunatus (Gould, 1834)

Except for the north-western part of its range, there is a reasonable degree of consensus over this species, with nine races recognized in the Check-list of Birds of the World (Peters, 1951) and eight or more recognized by Lambert & Woodcock (1996), these authors treating all Sumatran birds as *S. l. intensus* Robinson & Kloss, 1916.

Neither treatment recognized *S. l. aphobus* Deignan, 1948, as distinct as its author continued to maintain (Deignan, 1963). However, Lambert & Woodcock's ninth subspecies, to be found in their map marked 'subspecies uncertain' and shown as two shaded areas should have been changed to agree with their text or have been labelled *aphobus*. The northern of their two shaded areas includes Khao Yai National Park, which incorporates Khao Laem (the type locality of *aphobus*). The southern signals the population of the mountains of south-eastern Thailand where this species may extend into western Cambodia. Deignan (1948) discussed birds from here but left them unnamed. Later he chose to list them under *aphobus* (Deignan, 1963), which may well have remained a provisional treatment for the lack of adequate material. The form is intermediate between *S. l. elisabethae* La Touche, 1921, and *S. l. impavidus* Deignan, 1948, and Lambert & Woodcock appear to have decided in their text, but too late to change the map, that they should follow Peters (1951) and place it in the synonymy of the former. In our view Lambert & Woodcock should have retained the name *aphobus* because the area that on the map is marked 'subspecies uncertain' clearly includes the type locality of *aphobus*.

In Sumatra, Lambert & Woodcock placed *S. l. moderatus* Chasen, 1939, of Atjeh in the synonymy of *intensus* from further south. This view was, in fact, advocated in his general review of the species by Deignan (1948), but not adopted by Peters (1951). That the broadened *intensus* should be united with *S. l. rothschildi* Hartert & Butler, 1898, of the Malay peninsula was considered inappropriate by Deignan (1948), who found that the colour of the lores provided a reliable distinction. But this was thought moot by Lambert & Woodcock (1996) who wrote, of the entire Sumatran population, "there is some doubt as to the validity of this taxon".

The north-western range of the species is more complicated. It consists of northern Thailand and much of Burma, especially the north. It also involves Yunnan, where there is agreement that *elisabethae* occurs in the south-east, but the species also occurs close to the Burmese border where it was originally mapped from its type locality (Mengting) by Cheng (1976) as *S. l. atrestus* Deignan, 1948. The location of Mengting was given as 23°33'N., 99°05'E. (Deignan, 1948). It can be found on the line of the projected Lashio to Kunming railway on the 1945 map of China of the National Geographic Society. Later Cheng (1987, 1994) listed only *elisabethae* from mainland China. It is not known whether Cheng's change in treatment sprang from fresh collection in Yunnan west of the Mekong, from re-examination of the type of *atrestus* or from a decision to follow Peters (1951). It may be significant that post war records from Hsi-Shuan-Pan-Na (Cheng & Cheng, 1962) were assigned to *elisabethae*, because the range given to *atrestus* by Deignan would lead one to anticipate that the demarcation 'west of the Black River-Red River divide' (used in the context of Vietnam) might run northwards into China and provide a boundary between western Yunnan and south-east Yunnan. Whatever the reason no explanation has, to our knowledge,

appeared in western literature. However, Smythies (1953) considered *atrestus* to occur in the Shan States and to have been found at Mogok, central Burma.

Deignan (1948) was unable to borrow topotypical material of nominate *lunatus* and assumed that his specimens from north-west Thailand, which matched those he could examine from Tenasserim (Salween District) would also match those from the Pegu Hills (which are west of the Sittang river). Lambert & Woodcock also treated north-west Thai birds as nominate *lunatus* but did not report having made the comparison that Deignan could not make, although it should now be possible to make it.

Smythies drew on Ticehurst, and after his death on Mayr and Deignan, for taxonomic advice (Smythies, 1953: ix) and it seems probable that by 1953 Deignan accepted that *atrestus* reached the Shan States and Mogok, but not north-east Burma, for this is what the distribution tables in Smythies (1953) show. Deignan (1948) had had no specimen before him from north-eastern Burma. Lambert & Woodcock, who mapped the Shan States as occupied by nominate *lunatus*, would have been more correct to say that they split *atrestus* rather than say that they included it in *elisabethae* because they attribute the birds from the Shan States and Mogok to nominate *lunatus*.

Lambert & Woodcock (1996) reminded their readers of the hypothesis of sympathy between *S. l. rubropygius* (Hodgson, 1839) and some other form in northern Burma (Garthwaite & Ticehurst, 1937), resulting in the treatment by Garthwaite & Ticehurst of *rubropygius* as a distinct species. This is one of the most challenging riddles of the family Eurylaimidae because the allopatric forms on the two sides of the Irrawaddy are so distinct.

Lambert & Woodcock (1996) wrote "*S. l. rubropygius* has been collected in the upper Irrawaddy in the Myitkyina district, and Garthwaite collected it in two localities just to the south of there, close to but west of the Irrawaddy: in the Shwebo Forest Division and on the Kaukkwe River, Bhamo Forest Division. *S. l. lunatus* has been collected close to the latter site, in Bhamo, and in view of the lack of intergradation, Ticehurst concluded that these taxa represented two species".

Reference to Garthwaite & Ticehurst (1937) clarifies this considerably. In Garthwaite's text, under the heading *Serilophus rubropygius*, it is stated that three specimens were collected at Nanhlaing Reserve (23°25'N., 96°22'E.), Shwebo Forest Division and one from Hkaungton Reserve, Kaukkwe River, Bhamo Forest Division. The Shwebo birds were shot in August and the Bhamo bird in January.

These four specimens, all females, are in Tring. Those from Nanhlaing Reserve (the labels say 'Chaungzon') were collected on 25 August 1935 (BMNH 1948.803190-3192). The one from Hkaungton Reserve, Kaukkwe River (the label says Hkaungton R.F.) was collected on 2 Mar 1933, not as Garthwaite stated in January (BMNH 1948.80.3189). We identify this locality with Hkaungtung (24°58'N., 96°16'E.) and there is a Kaukkwe Chaung (chaung meaning stream or river) at 24°20'N., 96°34'E., not far south of Myitkyina.

Of *S. l. rubropygius* Ticehurst wrote: "It has been recorded in the Myitkyina district and we now have on the Kaukkwe river and in the Swebo Forest Division, both localities west of the Irrawaddy....." There are five birds in Tring from different localities in the district all collected by J.K. Stanford before 1935. Four of these localities can be traced and these are all west of the Irrawaddy. The fifth seems likely to be so too. In the next paragraph Ticehurst wrote of nominate *lunatus* "it has been recorded in the

Chin Hills otherwise the ranges do not overlap, but as they appeared very near each other in Bhamo and I have seen no sign of intergradation I regard them as representative species." And these two taxa are very distinctive, although *rubropygius* has strong similarities with the Hainan form *polionotus* Rothschild, 1903.

The Bhamo records for *S. l. lunatus* that Ticehurst knew about, and which have puzzled us, can now be shown to have been birds collected in January by Garthwaite, hence the latter's mistaken mention of January. Two males and a female (BMNH 1948.80.3186-88) were all collected on 18 January 1936, which is later than the chronological scope (1932-35) of their paper but 18 months before it was published. The locality appears, from the label, to be Simaw Reserve Forest, Bhamo Forest Division (23°53'N., 97°02'E.). This lies south of Bhamo and south of the bend in the Irrawaddy, and thus on the east bank, lying between it and the border with the Northern Shan States.

These records are, as far as we have traced them, nearly consistent with Smythies (1953) who, of the 'species' *lunatus* said "it seems to be confined to the area south of the Shweli river and east of the Irrawaddy, except for Hopwood and Mackenzie's record from the Chin Hills. It has not been observed in north-east Burma, the most northerly record being a specimen obtained at 3,700 feet near Mogok". The slight inconsistency is, that with the limited maps at our disposal, we think that the Simaw Forest Reserve lies north of the Shweli river. The specimen from Mogok (BMNH 1948.80.3185 collected by Garthwaite on 4 March 1934) is a good match for the birds from Simaw and it seems this form, whatever it may be named and this must be what Smythies and Deignan believed to be *atrestus*, ranges a little further north but still not into north-east Burma north of Bhamo and east of the Irrawaddy. The type locality of *atrestus* (Menting, Yunnan) is nearly due east of Mogok and there seem to be no records from Yunnan west of the Salween.

However, Smythies (1953) listed *rubropygius* from north-east Burma and said "it is found all over the foothills of north-east Burma, to 4,000 feet, and extends then west of the Irrawaddy to Arakan". This seems to imply that he knew of its occurrence east of the Irrawaddy (although evidently not far enough south to occur in sympatry with *lunatus*).

We suggest therefore that there is no record of overlap between *rubropygius* and paler forms (nominat *lunatus* or *atrestus*) except for the single record from the Chin Hills, which needs to be reinvestigated. This is true even if *rubropygius* occurs in north-east Burma to the east of the Irrawaddy (for which we have not seen evidence).

In spite of the very different appearance of these parapatric forms, to which, if *rubropygius* fails to cross it, the Irrawaddy appears to represent a significant barrier to gene flow, the species *lunatus* may or may not include *rubropygius*. The similarity to the Hainan population gives cause for hesitation before splitting and as a provisional treatment no doubt Lambert & Woodcock are right to see *rubropygius* as a form of this species.

Psarisomus dalhousiae (Jameson, 1835)

Except that Lambert & Woodcock (1996) did not find evidence to support *P. dalhousiae divinus* Deignan, 1947, which they erroneously spelled *davinus*, their arrange-

ment is consistent with that of the Check-list of Birds of the World (Peters, 1951). They reserved their position over central Vietnamese birds, separation of which would require a reappraisal of *divinus* and of *P. d. assimilis* Hume, 1875, as these names have been applied in Indochina (Delacour, 1951).

Calypdomena viridis Raffles, 1822

A race *caudacuta* Swainson, 1838, was doubtfully included in the Check-list of Birds of the World (Peters, 1951) occupying the southernmost part of the Malay peninsula. In reality mainland south-east Asian *C. v. continentis* Robinson & Kloss, 1923 (type locality Ban Tha San, Chumphorn Province, Thailand), is very close to nominate *viridis* Raffles, 1822, from Sumatra. It differs essentially only in wing length (where there is in any case a degree of overlap), although mainland birds may be slightly paler. If southern Malayan birds differ from *continentis*, apparently this is because they have seemed inseparable in size from the nominate form.

In a review of this, the evidence put forward, not separated by sex, suggested that birds from Malacca and Johore might be better treated as the nominate form (Wells & Medway, 1976), but later the same year this was not adopted due to continuing doubts (Medway & Wells, 1976).

Lambert & Woodcock (1996) recognized a difference, although calling it marginal. They drew their boundary south of the birds of Malacca and Johore and apparently of Singapore (as their text suggests), and gave wing measurements by sex in which they found a small overlap in males and no overlap in the case of females. They treated all peninsular birds as *continentis*, and by drawing their border south of Singapore made *caudacuta* Swainson, 1838, which has a Singapore type locality, a senior synonym of *continentis* and so unless further research was done they should have used Swainson's name. This problem has previously been avoided by treating the population of the tip of the peninsular as representative of the nominate form and drawing the border further north (Chasen, 1935b; Medway & Wells, 1976), or by placing *continentis* in the synonymy of the nominate form (Wells & Medway, 1976). Singapore birds are thought not to differ from those of Malacca and Johore (Wells & Medway, 1976), and we have been advised (D.R. Wells, in litt.) that Singapore birds should be included with those of the Malay peninsula. The name *caudacuta* must therefore be used in place of *continentis*. The type locality of *caudacuta* stands as Singapore, which was proposed as a correction of 'India'. Only if the type, now in Cambridge, does not match Singapore birds will it be possible to re-restrict the type locality and permit retention of the name *continentis*.

Both Peters (1951) and Lambert & Woodcock (1996) treated Bornean and Sumatran birds as one taxon although *gloriosa* had been maintained by Deignan (1961) despite the footnote by Peters (1951) noting that the separation had been based solely on Bornean birds without reference to the Sumatran population. Our limited material in Leiden suggests that Lambert & Woodcock were right to submerge this, but on fresher material in greater quantity the difference may well appear constantly.

Generic treatment

It is not within the scope of these papers to review generic limits although we

acknowledge that too much lumping has occurred in some families, but we shall sometimes offer some limited comments. In the specific case of the genera of broadbills we believe that the merit of *Sarcophanops* Sharpe, 1877, may deserve closer review. The distinctness of *steerii* from the species *javanicus* and *ochromalus* has been remarked by Olson (1971), and the most evident characteristic is the wattle of the Philippine bird, which characterized the genus (Steere, 1877).

General comments

In their treatment of the different species Lambert & Woodcock, when their own material has been inadequate have sometimes accepted the careful reviews of others and sometimes not (e.g. Mees's conclusions on *E. j. billitonis* are accepted, but his work on *E. o. kalamantan* is not). Because no prior detailed review was published giving the numbers of specimens examined and the distribution of those over the range of the forms examined, it is not clear just how adequate their material was. Perhaps partly on account of these factors the coherent philosophy of measured reduction of subspecies that these authors seem to hold is not consistent. In *Eurylaimus javanicus* there is a substantial reduction, but in *Eurylaimus ochromalus* the treatment appears to run counter to this.

A general point must be made here. Some museum collections are rich in material, but each tends to be rich for different geographical areas. Deignan (1947) was able to perceive distinctions in broadbills partly because, in Washington, he had substantial fresh material from mainland south-east Asia. Mees (1986), at Leiden, had plentiful material from much of Indonesia and particularly good fresh material from Java. The Natural History Museum in Tring, although it has a remarkable overall coverage, has very limited material from much of Asia. Sometimes it has only old material that is unsexed and not dated to month of collection. On this basis definitive studies, which may demand the separation of males from females and of fresh plumaged birds from worn, are impossible. Serious revisionary studies require extensive material to be gathered representative of as much of the range as possible. In the case of *Eurylaimus javanicus* specimens from Thailand, and perhaps parts of Indochina, should be borrowed from other museums.

The broadbills in Asia have presumably had their ranges, and the evolution of their subspecific distinctness, influenced by essentially the same factors. But there are riddles posed by the presence on Java of only one species compared with four on Sumatra and six on Borneo. Although the distinctness of the genera suggests a very old family, the ranges of the species will have been affected in more recent times by sea levels and concurrent climatic effects on vegetation patterns. A major formative influence must have been the periodicity of connection of the different parts of the Greater Sundas to mainland Asia between glacial maxima. A coherent approach at the subspecific level assists in the development of zoogeographic hypotheses.

Acknowledgements

We are most grateful to Robert Prys-Jones, Michael Walters, Mark Adams and Frank Steinheimer at the Natural History Museum, Tring, U.K. and to George Bar-

rowclough, Mary LeCroy and Paul Sweet at the American Museum of Natural History for access to specimens in their care. Mrs. F. E. Warr has helped us very substantially with library research at the Natural History Museum, Tring. Robert Prys-Jones kindly allowed us access to information on type specimens in the Cambridge University Museum of Zoology. We are also indebted to David Wells for an interesting discussion of the genus *Calyptomena* and subsequently reading this paper in draft and commenting.

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Received: 20.iii.1999 (first draft); 20.ix.1999 (final draft)

Accepted: 24.i.2000

Edited: C. van Achterberg