

A REVIEW OF THE
SWIFTS OF THE GENUS *HIRUNDAPUS* (AVES: APODIDAE)¹

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DEDICATION

This paper is dedicated to the memory of Dr. David Lack in recognition of his substantial contributions to our present knowledge of the biology of swifts.

ABSTRACT: A review of the literature on the large east Asiatic swifts of the genus *Hirundapus* as well as new data on their osteology indicates that the genus consists of four species (*caudacutus*, *cochinchinensis*, *giganteus*, and *celebensis*) and is generically separable from *Chaetura*. Subspecies limits are reviewed. The typical nest site of *Hirundapus* swifts is a scrape in the detritus at the bottom of hollow trees. Other reported nest sites are largely atypical or attributable to other species. The available information on plumages, body weight, nests, eggs, clutch size, food and behavior are summarized. The common name Needletail is proposed for the genus.

INTRODUCTION

The swifts of the avian family Apodidae are extremely difficult to study under field conditions. Their great mobility and speed of flight preclude periods of prolonged observation and their nest sites, if known, are often in inaccessible holes in trees or rocky crevices. This has led to an accumulation of anecdotal information about species, some based on actual observation, some on hearsay. Often the

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accounts include data which are incorrect or which must, after critical study, be attributed to other species. All too often the paucity of original information has led to the same accounts being repeated, summarized, and rephrased so often that even tenuous original observations gain the semblance of well-substantiated facts. Perhaps nowhere is this more true than for the large swifts of the genus *Hirundapus*.

The purpose of this paper is to review the available information on the breeding biology, distribution, and morphology of these swifts as well as to present new interpretations and some new data relating to species limits in the group and the validity of the genus *Hirundapus*. Although neither of us has had any first-hand field experience with any *Hirundapus* swift, both of us have examined museum material of all species and subspecies recognized in this paper. Additionally we have had extensive field experience with a wide variety of other species of swifts. The classification used in this paper is that of Brooke (1970; 1972) although further comments on generic limits in the Apodidae may be forthcoming after completion of studies now in progress (Collins, *in preparation*).

OSTEOLOGY

Studies of the relationships of the swifts have largely dealt with the much debated affinity between swifts and hummingbirds (Trochilidae) (Lowe 1939; Cohn 1968; Sibley and Ahlquist 1972). Only Orr (1963) has used osteological characters in considering the intrafamilial relationships of swifts. He noted substantial variation in the conformation of the transpalatine process within the Apodidae and that in some members of the genus *Cypseloides*, along with *Hemiprocne*, the postero-lateral border of the palatine is angular and not extended into a wing-like transpalatine process as in most swifts. He agrees (personal communication) with our interpretation that in swifts the shape of the transpalatine process is highly diagnostic at the generic level. Swifts of the genus *Chaetura* had the most well-developed and prominent winglike processes to the palatine in each of the three species he examined (Orr 1963: Fig. 3). He did not examine any specimens of *Hirundapus* in his study.

Since that time skeletal material of *H. caudacutus* (2), *H. giganteus* (1), and *H. cochinchinensis* (1) have become available and were examined (by Collins) as a part of this study. Comparative material representing most genera in the Apodidae and six species of new world *Chaetura* were also examined. The transpalatine process in *Hirundapus* is strongly pointed with only a shallow constriction in the lateral edge (Fig. 1; Morioka 1974: Fig. 1). In this respect it is most similar to *Streptoprocne semicollaris* figured by Orr and to the larger species of *Tachymarpis*. There is no similarity at all to the long and usually blunt wings to the palatine, nor the marked constriction in the lateral edge found in *Chaetura* (Fig. 1; Orr 1963: Fig. 3). Also, the prepalatine bar is narrower and concave in *Chaetura* but broader and convex in *Hirundapus*.

No functional significance has been proposed for these observed differences in palatine and transpalatine process. However as pointed out by Morioka (1974) "since the posterolateral edge and transpalatine process provide the points of origin

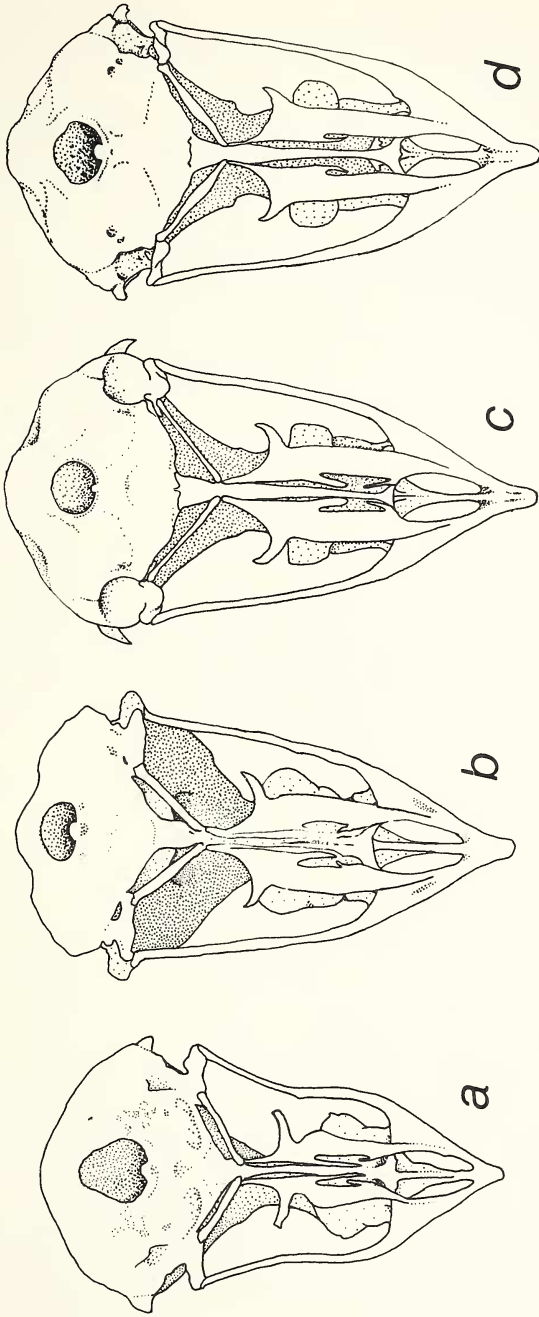


FIGURE 1. Palatine view of swift skulls: a—*Chaetura brachyura*; b—*Hirundapus caudacutus*; c—*H. cochinchinensis*; d—*H. giganteus*. Not to same scale.

for *M. pterygoideus*, one may expect certain variation in the development of this muscle" in those genera of swifts differing in the conformation of the palatine and transpalatine process.

A brief examination of selected postcranial elements of the smaller species of *Chaetura* as well as of more nearly equal-sized species in the genera *Tachymarptis* and *Streptoprocne* indicates that although there is a closer resemblance between *Hirundapus* and *Chaetura* than between these and other genera examined there are numerous differences equivalent to those existing between other distinct genera of the Apodidae. It further appears that these differences are not the result of the differences in body size. We think that these observed osteological differences, particularly those of the palatines, are of sufficient magnitude to support our view of the generic distinctness of *Hirundapus*. These osteological differences will be considered in greater detail at a later date as part of a proposed study of the intrafamilial relationships of the Apodidae based on their osteology.

GENERIC LIMITS

It is our view that excessive weight has been given to the presence or absence of the projecting shafts of the rectrices and inadequate notice has been taken of other highly distinctive, if not unique, characteristics when setting generic limits in spinetailed swifts. The superficial similarity of the tail spines doubtless indicates a certain community of ancestry within the Apodidae, but the number and extent of the differences in plumage, osteology, and breeding biology between *Hirundapus* and *Chaetura*, as well as in their ectoparasites, suggests that this community of ancestry is not recent and does not warrant generic lumping and *Hirundapus* should be given full generic rank within the Apodidae.

THE GENUS *HIRUNDAPUS*

The swifts of the genus *Hirundapus* form a closely knit group of four very similar species which breed from Siberia, Sakhalin Island, and northern Japan south to Taiwan, the Philippine Islands, the Malay peninsula, India, and parts of Indonesia, but not New Guinea. One species, *H. caudacutus*, is highly migratory, wintering in large numbers in parts of eastern Australia and occasionally New Zealand. It has also been recorded as a vagrant in western Europe (Ferguson-Lees 1960; Vaurie 1955). A second species, *H. cochinchinensis*, migrates a shorter distance to wintering grounds in Java and Sumatra (Mees 1973). *Hirundapus giganteus indicus* has been reported as a winter visitor to Malaya (Glenister 1951) while elsewhere this species has been reported to make only more localized seasonal and weather-influenced movements (Jerdon 1862; Whistler and Kinnear 1935; Deignan 1963). This is probably also true of *H. celebensis*.

All of the species in the genus *Hirundapus* are characterized by great size (wings over 170 mm long) and a doubtless well-deserved reputation for being among the fastest flying birds; speeds as high as 170 km per hour have been reported (Gladkov 1942, in Dementiev et al. 1951). The color patterns are largely similar: dark brown

to blackish above and below except for white undertail coverts and in some, lighter or distinctly white throats, and central portion of back paler than the mantle and rump (Fig. 2). These swifts all have a white flank stripe on either side extending upward and forward from the white undertail coverts (Smythies 1968: Pl. 17; Morse and Laigo 1969: Fig. 1; King and Dickinson 1975:204). These white flank stripes are unique within the family Apodidae, although approximated by the white flank patches occurring in *Aeronautes* and *Panyptila*. They have rarely been mentioned in technical diagnoses because most writers were describing museum specimens in which these stripes are largely hidden by the positioning of the folded wings and the legs. White or whitish spots on the inner webs of the tertials occurs in two species, *H. caudacutus* and *H. cochinchinensis* (Fig. 2), and are quite unlike the whitish edges to all the secondaries found in other genera such as *Aeronautes* and *Panyptila*. The presence of dark tips to the undertail coverts in the juvenal plumage of one species of *Hirundapus* is also unique within the Apodidae. A whitish forehead or white loreal spotting occurs in several populations, as discussed below. As reported for *H. caudacutus* (Baker 1927; Ferguson-Lees, 1960) and *H. cochinchinensis* (Mees 1973) as well as other species of swifts (Collins 1968a), the wings of *Hirundapus* swifts have a distinct gloss or iridescence which appears greenish in fresh plumages but soon wears away to a bluish or purple color and eventually to a lusterless dark brown. This is, of course, particularly noticeable in molting birds when very new and very old feathers can be seen side by side.

Anatomically, *Hirundapus* may be characterized as swifts possessing one carotid artery (Garrod 1873), eutaxic wing, well-developed transpalatine process to the palate, anisodactyl feet, rectrices with projecting spineshaped shafts (see below and Fig. 3), no sexual dimorphism in plumage, and the distinctive plumage patterns mentioned above. *Hirundapus* swifts have not been reported as having greatly enlarged salivary glands during the breeding season as reported for many other swifts which use the glue-like secretions of these glands to cement nest material together. These glands have been considered by several authors, the most recent study being that of Naik and Naik (1969). The absence of such glands in *Hirundapus* would not be surprising as it is a group which usually builds no nest; the eggs are laid in a slight depression in the rubbish at the bottom of hollow trees (this will be considered in detail below).

Beddard (1898:226) reported that while *Chaetura spinicauda* has a biceps sling or loop in the leg, *Hirundapus caudacutus* does not. He also reported that *H. caudacutus* alone among the Apodidae examined has a second thigh muscle in addition to the femoro-caudal that is present in all swifts. Further anatomical study may show these characters to be consistent differences between the genera *Chaetura* and *Hirundapus*.

The rectrices of *Hirundapus* swifts possess extremely stiffened shafts which extend well beyond the vane to produce tail spines similar in most respects to those found in *Chaetura*. The rectrices of some of the larger species of *Cypseloides* and *Streptoprocne* are also stiffened but the vane extends to the tip of the shaft (very attenuated in some forms) and the bare spines are the result of the wearing away of the terminal barbs (Orr 1963; Collins, *personal observation*). In *Hirundapus* the tail spines are most weakly developed in *H. caudacutus* and the tail is nearly square. In *H. giganteus* and *H. celebensis*, however, the central rectrices are noticeably longer, producing a

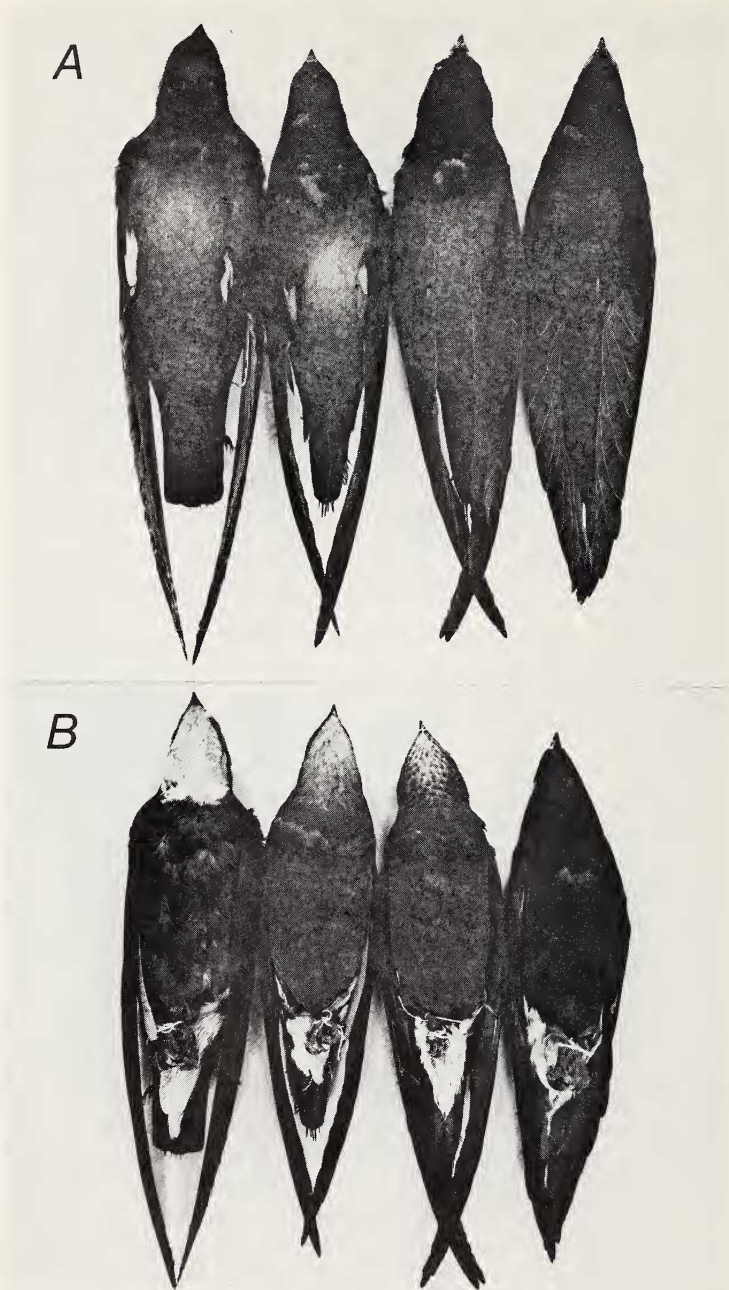


FIGURE 2. Dorsal view (A) and ventral view (B) of *Hirundapus* swifts. Left to right: *H. c. caudacutus*, *H. c. cochinchinensis*, *H. giganteus indicus*, *H. celebensis*.

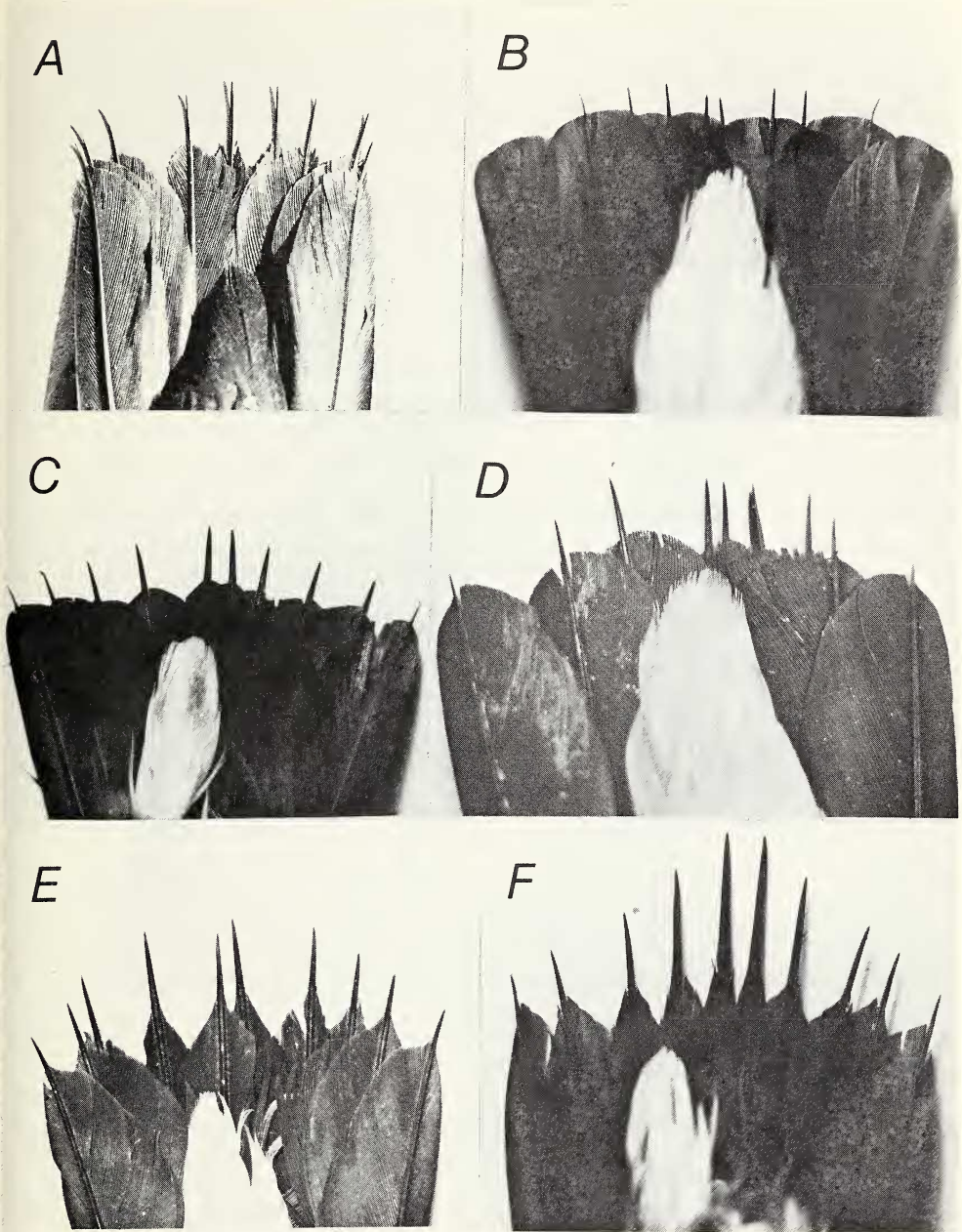


FIGURE 3. Tail spines of *Chaetura* and *Hirundapus* swifts: A—*Chaetura cinereiventris lawrenci*, B—*Hirundapus c. caudacutus*, C—*H. c. cochinchinensis*, D—*H. c. cochinchinensis formosanus*, E—*H. celebensis*, F—*H. giganteus indicus*. Not to same scale.

more rounded tail (Fig. 3). The shafts of these longer central rectices are also larger in diameter; a condition not unlike that found in many woodpeckers (Picidae). The extent to which this stiffened tail is used by these swifts to support themselves when clinging to the inside of their hollow tree nest sites is presently unknown. Roosting sites are known to include hollow trees, deserted factory chimneys and possibly rocky cliffs (Baker 1927).

The feather lice of the genus *Dennyus* (Mallophaga: Menoponidae) collected from *H. caudacutus* and *H. giganteus* are very different from the lice from other swifts, particularly those from species of *Chaetura*. This has resulted in these lice being placed in the separate subgenus *Takamatsui* Uchida 1926 (J. A. Ledger, personal communication).

The genus *Hirundapus* was proposed by Hodgson 1836, with the type species *Cypselus nudipes* Hodgson 1836. *Hirundapus* has led a checkered career ever since; it has been accepted and used by some workers in each decade while others have felt it was not sufficiently well-differentiated from *Chaetura* Stephens 1826 with genotype *Hirundo pelagica* Linnaeus 1758 or *Acanthylis* Boie 1826 with genotype *Hirundo spinicauda* Temminck 1810 (Brooke 1974). Lack (1956), the last author before Brooke (1970) to review all genera of swifts, considered *Hirundapus* to be a well-marked group within *Chaetura* but stopped short of giving it generic rank. This view has been followed, largely uncritically, by most recent authors. However, Brooke (1970), reflecting the views presented in this paper, recognized the generic status of *Hirundapus*. We feel that the genus *Pallene* Lesson 1837 with type species *Cypselus giganteus* Temminck 1825 should not be recognized merely because of the lack of white areas in the tertials and stronger purple rather than green iridescence (largely a wear phenomenon, see above) though it might serve as a subgenus.

Until recently the Apodidae has been traditionally divided into two subfamilies, Apodinae and Chaeturinae, on the basis of the number of phalanges in the toes (Sclater 1865), and also the positioning of the toes. Brooke (1970) recognized the New World swifts of the genera *Cypseloides*, *Nephoecetes*, and *Streptoprocne* as being a distinctive subfamily but merged the remaining groups, retaining *Hirundapus* in his Chaeturini within the Apodinae on the basis of its having but one carotid artery. He considered that foot formula did not provide an adequate basis for the subdivision of the Apodidae into Chaeturinae and Apodinae; De Roo (1968) found a typical species of the Apodinae, *Schoutedenapus myoptilus*, to have the unreduced number of phalanges typical of the Chaeturinae.

SPECIES LIMITS IN HIRUNDAPUS

Peters (1940) recognized three species in *Hirundapus*: *H. caudacutus* Latham 1801, *H. giganteus* Temminck 1825, and, provisionally, *H. ernsti* M. Bartels, Jr. 1931. *Hirundapus cochinchinensis* was thought to be "almost certainly a subspecies of *H. c. caudacutus*" and *celebensis* was listed as a subspecies of *giganteus* (Peters 1940:232-233).

Several changes must be made in light of more recent findings. The type of *H. ernsti* has been determined to be a wintering specimen of *H. cochinchinensis* (Mees 1971; 1973) and it is not distinct even at the subspecific level. Full species

status for *cochinchinensis* was advocated by Biswas (1951) who pointed out what he felt to be significant body size and color differences and also cited statements (Baker 1927) that it overlaps the breeding range of *H. caudacutus nudipes* in the hills of northern Burma. In our examination of these species we were impressed by not only the arguments of the earlier workers involving plumage color, body size and presumed breeding range sympatry but also by the appearance of the tail spines. In the case of *cochinchinensis* (Fig. 3) they are intermediate in size between the very reduced spines found in both races of *caudacutus* and the larger spines of *giganteus* and *celebensis*. This difference was independently noted by Mees (1973) in his review of the subspecies of *cochinchinensis*. Although expressing some doubts as to its status, Baker (1927:341) and Peters (1940) retained *cochinchinensis* in *caudacutus* while others (Delacour and Jobouille 1931; Vaurie 1955; Mees 1971, 1973) considered them as separate species, a view which we fully support.

The data presented by Mees (1973) based largely on specimens taken on the wintering grounds strongly suggests that *H. c. cochinchinensis* and *H. c. rupchandi* may be nothing more than ends of a cline in coloration or that the specimens of the lighter colored *H. c. rupchandi* are only extremely worn individuals of the nominate race. Although Mees (1973) now considers *H. cochinchinensis* to be monotypic, we believe *rupchandi* should be recognized at least until more material from breeding areas is available for analysis. Our examination of two recently collected and apparently previously unreported specimens from Taiwan (Yale Peabody Museum #40084 and #40085) confirms our earlier belief that the subspecies described by Yamashina (1936) as *H. caudacutus formosanus* is more correctly included in the species *cochinchinensis*. These Taiwanese specimens agree in color, size, and appearance of the tail spines (Fig. 3) with specimens of *cochinchinensis*, as in fact does the type description, as has been independently noted by Mees (1973). A comparison of these Taiwanese specimens with a series from Java reveals only minor, wear-associated, differences in the color of the gloss (Mees, personal communication). Tentatively we continue to recognize *formosanus*, largely on the basis of its geographic isolation from other populations.

Both *H. giganteus* and *H. celebensis* lack the distinctive white in the tertials found in *H. caudacutus* and *H. cochinchinensis* and have dark throats nearly concolorous with the breast, particularly in *H. celebensis* (Fig. 2). Although stated by Hartert (1892) to be "a very distinct species", *H. celebensis* has been considered conspecific with *giganteus* by most subsequent authors. However, we believe the darker overall coloration, stronger purplish iridescence, and near absence of lighter areas of the throat and back of *celebensis* coupled with a near 40% difference in weight (see below) are significant enough to warrant its being separated from *H. giganteus* and given full species status. The existence of three specimens of *H. celebensis* from Palawan (British Museum [Natural History] *vide* C. W. Benson, *personal communication*) indicates a previously overlooked area of sympatry, *H. giganteus* having been long known from this island (DuPont 1971), and further strengthens our view of the specific distinctness of *H. celebensis*.

A number of subspecies have been proposed in *Hirundapus*, not all of which do we believe are distinct. The presence or absence of a white or pale loreal spot

or forehead as well as differences in the general intensity of the color of the body plumage characterize subspecies in *H. caudacutus* and *H. giganteus*. The subspecific differences in *H. cochinchinensis* are based on color intensity differences only and may be clinal in nature. In *H. celebensis* the subspecific differences characterizing *celebensis*, *dubius*, and *manobo* are strictly mensural and based on a very small number of specimens (Table 1). Awareness of this and the fact that a much greater variation in wing length has been observed in a large sample of *H. caudacutus* (Kleinschmidt 1970) and also in specimens of a similar-sized swift, *Tachymarpis melba* (Brooke 1971b), leads us to believe that *H. celebensis* should be considered as monotypic until a more extensive study can be done based on a more adequate series of specimens. Large numbers of these swifts have been captured in the Philippines by natives protecting their apiaries (see below) but it is doubtful if many have made their way into any museum collection despite the rarity of such specimens.

Several additional specific names have been proposed for *Hirundapus* swifts, and upon re-examination must be placed in synonymy with earlier-named forms. Examination of Stephens (1817:133-134) leads us to believe that his *Hirundo fusca* may well be the same as what has long been known as *Hirundapus c. nudipes* (Hodgson 1836). Stephens (op. cit.) distinguished his *H. fusca* from *H. caudacuta* Latham by *fusca* having a pale dusky brown forehead and *caudacuta* a white one. Hartert (1892:472) acknowledged the presence or absence of a white forehead as the principal difference between *caudacuta* and *nudipes*, which he recognized as separate species, and yet placed *fusca* as a synonym of *caudacuta*. The type locality of *fusca* is not known and according to Hartert (1892:472) the name had not been used since its proposal. On the other hand *nudipes* has a long history of usage in the primary zoological literature, including many of the sources cited in this paper. We therefore consider *Hirundo fusca* Stephens to be an undoubted nomen oblitum and no change of nomenclature is required.

TABLE 1

Wing lengths in millimeters of *Hirundapus celebensis*.

<i>Mindanao and</i>	
<i>Basilian</i>	211, 211, 216, 217
<i>Negros</i>	211, 211, 212, 214, 214, 216, 216, 216, 216, 218, 218
<i>Mindoro</i>	214, 219, 222, 230, 234
<i>Luzon</i>	226, 222
<i>Palawan</i>	190, 192, 194
<i>Celebes</i>	187 ⁴ , 203, 208

Data from: Clarke 1894; Mearns 1905; Rand 1951, Salomonsen 1953; and specimens measured as part of this study: AMNH (Bobbok, Mindoro); Brit. Mus. (Nat. Hist.) (Palawan), fide C. W. Benson, personal communication. Figures for both sexes have been lumped in view of the small size of the samples and the unlikelihood of their being a significant sexual dimorphism in this measurement. Salomonsen (1953) refers the specimens from Luzon and Mindoro to *H. c. dubia* and those from Mindanao, Basilian, and Negros to *H. c. manobo*.

⁴recent fledgling; wing probably not full length.

As noted by Mees (1973) both *H. klaesii* Buttikoffer 1887 from Sumatra and *H. ernsti* (M. Bartels, Jr. 1931) from Java are attributable to *H. c. cochinchinensis*. The type description of *H. caudacutus bourreti* (David-Beaulieu 1944) as well as a re-examination of the type, collected at Xieng-Khouang, Laos, leaves no doubt that it is correctly referable to *H. c. caudacutus* (Dickinson 1970). Little is known of the exact route taken by *H. c. caudacutus* when migrating from wintering grounds in Australia to northern breeding grounds in parts of Siberia. They are known to reach some parts of their breeding grounds as late as the second half of May or early June (Neufeldt and Ivanov 1960) at which time some are still en route in southernmost areas of China (Dementiev et al. 1951). The date of collection of *bourreti* (24 April 1940; David-Beaulieu 1944) is consistent with its being considered a migrant individual of *H. c. caudacutus* and not part of a resident population. *Hirundo sinensis* Gmelin (1789) seems more likely to refer to a swift than a swallow as has been commonly assumed. It may well refer to *H. caudacutus*, the only member of this taxon to occur in China, but the errors in the description make it indeterminate and it must be considered a nomen dubium. Our view of the genus and its forms can be summarized as follows:

GENUS *Hirundapus* HODGSON

Hirundapus Hodgson 1836, Jour. As. Soc. Bengal, 5:780. Type, by original designation and monotypy, *Cypselus nudipes* Hodgson.

Pallene Lesson 1837, Compl. Buffon, 8:493. Type, by monotypy *Cypselus giganteus* Temminck.

HIRUNDAPUS CAUDACUTUS

Hirundapus caudacutus caudacutus (Latham)

Hirundo caudacuta Latham 1801, Index Orn., Suppl, p. lviii.—New South Wales, Australia.

Hirundo ciris Pallas 1811, Zoogr. Rosso-As., 1:541.—Siberia.

Chaetura australis Stephens 1826, Gen. Zool., 13:76—New South Wales, Australia.

Chaetura macroptera Swainson 1833, Zool., Ill., pl. 42—type locality unknown.

Chaetura caudacuta bourreti David-Beaulieu 1944, Publ. Univ. Indochina, p. 89—Xieng-Khouang, Laos.

Breeds in Siberia, northern China, Sakhalin, and Japan. Migrates through eastern China and Laos, winters in Australia, Tasmania, and rarely New Zealand. Accidental in Europe.

Hirundapus caudacutus nudipes (Hodgson)

Cypselus nudipes Hodgson 1836, Jour. As. Soc. Bengal, 5:779—Nepal.

Hirundo fusca Stephens 1817, Gen. Zool., 10:133—type locality unknown. (Stephens, op. cit.: 134)

Cypselus leuconotus Delessert 1840, Mag. Zool., pl. 20—Bhutan.

Breeds in northeastern Pakistan and Himalayas south and east to Assam and southwestern China.

HIRUNDAPUS COCHINCHINENSIS

Hirundapus cochinchinensis cochinchinensis (Oustalet)

Chaetura cochinchinensis Oustalet 1878, Bull. Soc. Philomath. Paris, 2:52—Saigon, Vietnam.

Hirundapus klaesii Buttikofer 1887, Notes Leyden Mus., 9:40—Sumatra.

Chaetura ernsti M. Bartels, Jr. 1931, Orn. Monatsbr., p. 54—Haliomen Mountains, Java, Indonesia.

Breeds in Assam in India, eastern Thailand, and Indochina. Winters in Sumatra and Java.

Hirundapus cochinchinensis formosanus (Yamashina)

Chaetura caudacuta formosana Yamashina 1936, Orn. Monatsbr., 44:90—Arisan, Taiwan. Island of Taiwan.

Hirundapus cochinchinensis rupchandi (Biswas)

Chaetura cochinchinensis rupchandi Biswas 1951, Ardea, 39:320—Hitaura, Neapl.

Nepal (presumably breeding). Winters in Java and Sumatra.

HIRUNDAPUS GIGANTEUS

Hirundapus giganteus giganteus (Temminck)

Cypselus giganteus Temminck 1825, Pl. col., livr., 61, pl. 364—Bantam, Java.

Breeds in Malaya, Sumatra, Java, Borneo, and the Palawan Island group of the Philippines.

Hirundapus giganteus indicus (Hume)

Chaetura indica Hume 1873, Stray Feath., 1:471—Andaman Islands.

Breeds in India, Bangladesh, Ceylon, Andaman Islands, Burma, Thailand, and Vietnam.

HIRUNDAPUS CELEBENSIS

Hirundapus celebensis (Sclater).

Chaetura gigantea var. *celebensis* Sclater 1865, Proc. Zool. Soc. Lond., p. 608—Menado, Celebes, Indonesia.

Chaetura dubia McGregor 1905), Bureau Govt. Labs., Manila, 34:15—Mindoro, Philippines.

Chaetura gigantea manobo Salomonsen 1953, Vidensk. Medd. Dansk. Naturh. Foren., 115:239—Malaybalay, Bukidnon Prov., Central Mindanao, Philippines.

Occurs (presumably breeding) in Celebes, and Philippines including Palawan Island group.

The order of species presented here assumes the increasing specialization of the tail spines to be the most important phylogenetic trend in the genus. If however, increasingly patterned and colored plumage were held to be the most important trend the sequence might be nearly the reverse. This matter cannot be considered further until a phylogenetic analysis of the Apodidae has been undertaken.

AGE ASSOCIATED DIFFERENCES IN PLUMAGE

Although no sexual differences in plumage have been detected in any *Hirundapus* species, some age associated differences have been recorded. The juvenal plumage of *H. caudacutus*, as mentioned earlier, has dark tips to the white under-tail coverts. This species is also noted as having the ends of the "white lower wing coverts spotted with black-brown markings" (Dementiev et al. 1951), a feature we have not been able to confirm as these coverts are all uniform brown in the specimens of *H. caudacutus*, *H. cochinchinensis*, and *H. giganteus* we have examined. Comment has also been made that in juvenal plumaged birds the white forehead of *H. caudacutus* and the white loreal spots in *H. giganteus indicus* are less extensive,

or dusky or "mouse colored" (Dementiev et al. 1951; Abdulai 1964), characters we have been unable to confirm in this study. One specimen of *H. celebensis* (USNM 247744) has distinctly brownish loreal spots and may well be the basis for the statement by Salomonsen (1953:240) that this race has the "loreal spot sooty grey (possibly due to staining)". However, two syntypes of *H. celebensis* have "pure white and very conspicuous" loreal spots (G. F. Mees, *personal communication*). Closer examination of the brown lored specimen, a male, shows it to be in very fresh unworn plumage with all of the primaries ensheathed at the base, a condition which can only be found in a nestling or recently fledged juvenal plumaged bird; adults would only have one or two primaries in molt at one time. The undertail coverts of this specimen are white and lack the dark tips of juvenals of *H. caudacutus*. The loreal spot is dusky or brownish in color and since this color includes the full length of the loreal feathers and not just the tips it is unlikely to be the result of staining. The edges of the underwing secondary coverts in this specimen are broadly dusky grey-brown and not whitish as true in adult specimens. Meyer and Wigglesworth (1898) also report brown lores for a "♀ juv." specimen thus making it clear that this condition represents an unreported juvenal plumage character of *H. celebensis*, not shared with *H. giganteus*, rather than a racial character or sexual dimorphism in plumage, the latter being uncommon in swifts and otherwise unknown in *Hirundapus*. Further study is needed before a juvenal plumage can be characterized for *H. giganteus* and *H. cochinchinensis*.

BODY WEIGHTS

Information on body weight in *Hirundapus* swifts is scarce. Neufeldt and Ivanov (1960) present data for *H. c. caudacutus* obtained from specimen labels in the Leningrad Museum; 11 males ranged from 109 to 140 gm (average 122.2) while 5 females ranged from 101 to 125 gm (average 113.7). The male type of *H. c. nudipes* weighed 4½ oz (± 127 gm) (Hodgson 1836). In Thailand, body weights of two males of *H. giganteus indicus* were 134.0 and 124.5 gm and an unsexed specimen weighed 123.0 gm while a third male of this species which was "very fat" was appreciably heavier (167.0 gm) (J. T. Marshall, *personal communication*). Body weights for a male and an unsexed specimen of *H. c. cochinchinensis* also from Thailand were respectively 76.1 and 85.5 gm (J. T. Marshall, *personal communication*). It is interesting to note that although *H. cochinchinensis* is only slightly shorter winged than *H. caudacutus* it appears to be significantly lighter in weight. If this is borne out by additional data it would imply an appreciably different wing loading for this species and perhaps equally different foraging procedures, enhancing its capacity to maintain syntopy with its heavier congeners which sometimes forage with it in the same flock (Delacour and Jabouille 1931:288). The data presented by Morse and Laigo (1969) for *Chaetura dubia* (= *H. celebensis*) in the Philippines indicate that it ranges in weight from 170 to 203 gm (22 unsexed specimens; 2—27 February 1968) and averages 179.6 grams. From these limited data it appears that on an average *H. celebensis* is possibly as much as 40 per cent heavier than *H. giganteus* with all recorded individuals of *H. celebensis* being heavier than

even the heaviest *H. giganteus*. These data further support the specific distinctness of *H. celebensis*. In summary, *Hirundapus caudacutus* weighs 101-140, *H. cochinchinensis* 76-86, *H. giganteus* 123-167, and *H. celebensis* 170-203 grams.

The apparent sexual dimorphism in body weight in *H. caudacutus* may only be due to the size of the samples used and may not be significant. The available data for some larger African species of *Apus* show near equality in body weight with the heaviest birds being individual females (Brooke 1969). A slight but significant sexual dimorphism in body weight has been shown for two small neotropical species, *Cypseloides rutilus* and *Aeronautes montivagus*, with males being heavier than females in both cases (Collins 1968b, 1972).

NESTS AND NEST SITES

Lack (1956) has shown that in the Apodidae, genera are usually characterized by distinctive nesting habits and, frequently, clutch sizes. There is no reason to doubt the application of this observation in *Hirundapus*. A number of nests have been found in a wide variety of locations and attributed to members of this genus. Few of these were authenticated by specimens or other satisfactory evidence. In some cases the assumed attribution seems to have been based on little more than the observation of *Hirundapus* swifts in an area where unidentified nests were found.

In one of the earliest accounts (Baker 1897), nests attributed to *H. giganteus indicus* were found on the walls of dark cavelike passages in deserted lime quarries in North Cachar, Assam, India. The nests were masses of mossy plant material and bear hair collected from an adjacent bedding area of the bears and held together with mud; later accounts of these same nests also mention the use of saliva in the nests (Baker 1927; 1934). Adult swifts were seen nearby and were flushed from the nest area but none appear to have been collected. One of the three nests, however, contained three nearly fledged young which showed the tail spines and white loreal spot of the adults. In a later account, however, these nests are re-attributed to *H. cochinchinensis* (Baker 1927); a change which is not clearly explained or consistent with the previous description of the young as having a white loreal spot. Such a spot is present in *H. giganteus* but lacking in *H. cochinchinensis*! and in still another account Baker (1934) expresses the opinion that the nests were more likely to be those of *Micropus subfurcatus* (= *Apus affinis nipalensis*) and that the *Hirundapus* swifts had taken over the nests of the smaller species. Even so, the description of the nests is unlike those of *A. affinis* anywhere in its range but is typical of cave swiftlets of which only one, *Aerodramus brevirostris* breeds in the area (Ali and Ripley 1970). Baker (1934) also expresses the view that:

it is probable that the above instance of Spinetails breeding in a cave may be exceptional, as I never got others, though we worked very hard for them. The whole of this country for miles upon miles was open park-land dotted over with great black Oaks, a very large percentage of which were hollow, so it seems more probable that such trees formed the normal breeding places for the Spinetails.

Unfortunately Baker's later reassessments as to the actual builders of these nests and the unusual, if not unique, positioning of these nests have not been incorporated

by subsequent authors. This has led to paraphrased accounts of the earlier conclusions being repeated widely even in recent literature, and a rocky cliff nest site with a nest of moss and saliva being considered typical of *H. cochinchinensis* and distinctive within the genus. What may have happened is that *H. giganteus* used a pre-existing nest of *A. brevirostris*, an atypical if not unique situation.

The best account of breeding in *Hirundapus*, accompanied by photographs of the nest site, is that by Neufeldt and Ivanov (1960) summarizing the information of Gizenko (1955) and Lobko-Lobanovski (1956), for *H. caudacutus* in Siberia and on Sakhalin Island. Its fullness of data and the care for identification with which it was obtained warrant taking this information as the standard of comparison for additional nesting records of *Hirundapus* swifts. Jahn (1942) and Austin and Kuroda (1953) show that there is no significant difference in the breeding of this species in Japan. The basic feature of these accounts is that nests are mere depressions or scrapes in the rubbish and detritus in the bottom of large hollow trees. These authors found no evidence that these large swifts bring any nest material to the site; they simply scrape or utilize a shallow depression in the nest site substrate, as is also true of the largest new world species, *Streptoprocne semicollaris*, which lays eggs on bare sandy ledges in caves (Rowley and Orr 1962).

Baker (1934) describes similar nests and nest sites for *H. giganteus indicus* on the basis of observations provided by J. Stewart who apparently examined numerous such sites, including eggs as well as young and adults captured in the hollow trees. Baker (1934:466) states that "although the birds roost in hollow trees in quite big flocks, only one, rarely two, or at the outside three, pairs will breed in the same tree." In an earlier account that he himself published Stewart (1913) describes in greater detail the finding of three nest scrapes in the bottom of one tree, *only one of which contained eggs or young!* He also mentions finding in another tree, two nests each of which contained two fresh eggs. No other account of *Hirundapus* breeding mentions the use of a single hollow tree by more than one pair at one time. By their own admission (Stewart 1917; Baker, 1934) the presence of more than one active nest per tree is very unusual. It is distinctly probable that both theirs and all subsequent references in the literature to this day of more than one pair breeding in the same tree are based on these two incidents. It is quite possible that the additional scrapes observed in the first incident represented nest scrapes of previous years or trial scrapes made early in the present nesting season and that only one was active at the time. It is also possible that the one recorded case of two sets of two eggs in a single tree could represent a more normal clutch of four accidentally divided between two scrapes. Such accidental occurrences are not unusual in birds. It is very doubtful that there are any valid records of two pairs ever nesting in the same tree at the same time. The suggestion that three nests per tree is possible, attributed to Stewart by Baker (1934; see quote above) is almost certainly based on the single incident mentioned above and is not consistent with the previously published statement that he had "not found more than *two* pairs breeding in one tree" (Stewart, 1913). The inconsistencies in these various accounts are compounded by the feeling stated by Ali (1953:13) that some of the notes and discoveries by Stewart as reported by Baker were "unfortunately of not unimpeachable authenticity."

Stewart (1913) also mentions that the nest scrapes of *Hirundapus giganteus indicus* were "lined with dry leaves and straw", a feature not noted in any other account of *Hirundapus* nests. However, there has been one recorded observation of this species "flying with a straw in its mouth" (Bourdillon, *in* Fergusson 1904: 661) during the suspected breeding season.

Allen (1960) reported a nest of *H. g. giganteus* found on a ledge behind a waterfall in Malaya. The similarity of this nest and eggs to those of *Hydrochous gigas*, another large swift of that part of Malaya, was independently noted by ourselves in this study and Somadikarta (1968). This view has been confirmed by Becking (1971) who examined feathers adhering to the brim of this nest, glued there by saliva used in nest construction.

The nests of *H. celebensis*, as well as those of other races of the other three species of *Hirundapus* remain undescribed. The suggestion that *H. celebensis* "builds its nests in caves" on the Island of Negros in the Philippines (Clarke 1898) is based on information gained from natives by his collector. Such hearsay evidence from natives who, in our experience, frequently do not differentiate between the several species of swifts present in an area, is extremely uncertain. Thus this suggested sea-cave nest site is considered by us to be an unlikely possibility both in the light of the amount of well-documented information presented above for other species and the distinct possibility that they were referring to a cave nesting species of the Collocaliini and not a member of the genus *Hirundapus*. Jerdon (1862) was led to search sea caves and cliffs for nests or roosts of *H. g. indicus* with no success at all.

Despite the prevalence of information in *original sources* supporting hollow tree nest sites for *Hirundapus* swifts most recent works considering these swifts continue to mention rocky cliff nesting and/or roosting sites. The original sources for these statements are usually not mentioned and in some cases appear to be based on the atypical nesting situation of *H. g. indicus* discussed at length above. Colonial nesting in steep rocky banks is reported for *H. caudacutus* (Johansen 1915; *in* Dementiev, et al 1951). The same species is also reported to roost in great numbers on the vertical faces of limestone cliffs (Baker 1927:342) or in "hollows or cracks in the rocks" (Dementiev, et al 1951). In both of these cases no details were presented to substantiate this and we believe they should be questioned and may well be based on observations of other species of swifts. The account of LeSouef (1907) of *H. caudacutus* nesting on ledges near a waterfall in Japan is accompanied by detailed observations but no specimen was collected. However, as mentioned above, other accounts of the nesting of *H. caudacutus* in Japan are in agreement with a hollow tree nesting site and thus the observations of LeSouef are certainly atypical if correctly attributable to this species.

Although it is not yet possible to exorcise from the literature the numerous general accounts of rocky cliff nesting and roosting sites for *Hirundapus* swifts, it is hoped that all future authors dealing with this point will carefully examine the arguments presented here and also the few original sources available and not simply repeat what others have said and thus perpetuate the uncritical and frequently erroneous accounts of their predecessors.

We are strongly of the opinion that descriptions of rocky cliff nesting and roosting sites for *Hirundapus* swifts are atypical at best, and frequently erroneous. We do not agree with recent statements such as that by Harber (1955) that "nesting in cliffs has been disputed but is now established for certain localities."

EGGS AND CLUTCH SIZE

The eggs of *Hirundapus* swifts, like those of nearly all other swifts, are pure porcelain white but frequently become discolored during incubation. The average dimension of 28 eggs of *H. c. caudacutus* from Sakhalin Island were 32.27×22.34 mm (Neufeldt and Ivanov 1960) while a single egg removed from the oviduct of *H. caudacutus nudipes* measured 31.2×22.4 mm (Baker 1927). Eggs of *H. c. caudacutus* from Japan (Austin and Kuroda 1953) are similar in length (27.5 to 31.2 mm) but appear to be somewhat smaller in width (17.5 to 19.3 mm). A single egg from the oviduct of *H. c. cochinchinensis* measured 28.1×21.0 mm while a sample of 100 eggs of *H. giganteus indicus* averaged 29.6×22.2 mm; maxima 32.1×22.5 and 31.2×23.5 mm; minima 28.8×22.0 and 29.9×20.0 mm (Baker 1927). Nine fresh eggs of *H. c. caudacutus* weighed between 7.95 and 8.93 grams (Neufeldt and Ivanov 1960).

The clutch size in *Hirundapus* ranges from two to seven eggs and incubation, in *H. caudacutus* at least, is said to start with the first egg (Neufeldt and Ivanov 1960). This is a common feature in the reproductive strategy of raptors for which the ease of finding food for the young varies greatly in different years, but an adaptation otherwise unknown in the Apodidae.

BEHAVIOR

Observations of display behavior of swifts are fragmentary and generally hampered by the extreme mobility of these birds and the resultant short periods of continuous observation. On its wintering grounds in Australia, several apparent displays by *H. caudacutus* have been recorded and which appear to be unique in the family. On several occasions individuals have been noted to "tumble," "dive," or "gravity drop" from a flock circling high over head (Simpson and Noonan 1967; d'Ombraïn 1934). After vertical drops of from six to nine meters up to 30 m or more the birds quickly rose to join the circling flock. Although several members of the flock were engaged in these activities, repeated performances by more than one of these individuals were recorded. The significance of this activity is not understood but a sexual display function is suggested (Simpson and Noonan 1967) though this seems unusual for birds in winter quarters. Steep dives at high speed to nearly ground level have also been recorded as part of feeding activities (Cameron 1968) on the wintering grounds and similar dives have been observed on the breeding grounds by Gladkov (1942; in Dementiev et al. 1951).

Flocks of both *H. caudacutus* and *H. giganteus* feeding over water have been observed to fly low over the surface in a tight circle, with individuals occasionally dipping down to drink or possibly bathe (D'Ombraïn 1934; Cameron 1968; Smythies

1968; Ali and Ripley 1970:37). Drinking and bathing on the wing in a similar fashion have been observed for single individuals, but not flocks, of *Chaetura pelagica* (Vaurie 1947) and for several other species of New World and Ethiopian swifts (Collins, *personal observation*; Brooke 1973). Such activities are apparently risky maneuvers as on two occasions, both in Australia, individuals of *H. caudacutus* have been seen to crash into the water (Cameron 1968; G. Bennett, *personal communication*) possibly from having inserted the mandible too deeply in the water when flying at such high speeds. In both cases the birds did not swim and were not successful in rising from the water but flew away strongly when thrown aloft. Wounded individuals of *Tachymarptis melba africana* and *Apus b. bradfieldi* which fell in the water were observed to swim strongly with their wings outstretched (Brooke, *personal observation*).

Smythies (1953:365) also reports that in Burma *H. giganteus* can be heard to make a distinct drumming sound while drinking "not unlike the drumming of a snipe" and "when rising from the water the wings are brought together over the back with an audible smack". Ali and Ripley (1970:36) state that "the wings (of *H. giganteus*) produce a loud twanging sound (as of a harp string) as the birds hurtle past overhead". Such noise-making is uncommon among swifts. Bednall (1963) records a similar "drumming" noise made by a spreading and twisting of the tail at the start of a dive by *Tachymarptis aequatorialis*. Several *Chaetura* species make wing-clapping noises as a threat display at roosts but not in flight (Collins 1968a, 1968b).

The vocalizations of *Hirundapus* swifts as described by numerous authors include a loud squeaking or screaming cry uttered in flight and also a sharp clear note. It is presumably the latter vocalization that is referred to in Smythies (1968) as a "harsh loud call like a magnified flowerpecker".

In *Apus apus*, nonbreeding birds ascend high in the air, sometimes over the sea, at dusk, and remain on the wing all night. This has been discussed by numerous authors and most recently reviewed by Eastwood (1968) and Lockley (1971). This also has been observed for *Streptoprocne zonaris* in Trinidad (Snow 1962; Collins, *personal observation*) and been attributed to all old world swifts away from their breeding grounds by Brooke (1971a). It appears that this also occurs in *H. giganteus indicus*: Jerdon (1862) observed an enormous flock, presumably of non local breeding birds, heading out to sea at dusk on the Malabar coast of India. He made a search for a roost and/or breeding site along the coastal cliffs and an offshore islet but without success.

FOOD

The diet of *Hirundapus* swifts has not been studied in detail although some food items, all insects, have been listed for each of the four species. The orders and families of insects involved include: Ephemeroptera, Orthoptera, Hemiptera, Odonata, Diptera (Phoridae), Coleoptera (Scolytidae, Coccinellidae), Hymenoptera (Vespididae, Formicidae, Apidae, Ichneumonidae, Bombidae).

In the Philippines, *H. celebensis* has become an important predator of the workers and drones of honey bees (3 species of *Apis*) (Morse and Laigo 1969). The swifts are collected in large numbers by the natives when they are flying low over fields near the apiaries; approximately 450 were so captured between January and March 1968. Bee eating has also been recorded for *Tachymarpis aequatorialis* (Brooke 1973) in Africa and may be common among swifts.

Although on occasion they forage near ground level or over water, *Hirundapus* swifts usually forage high above the ground, frequently utilizing updrafts associated with cliffs and escarpments. It is probably this latter habit that has so often and, we believe erroneously, led to their being associated with these cliffs for nesting and roosting as is the case with some more familiar swifts, particularly those of the genus *Apus*.

ENGLISH NAMES

Despite the objections which can be raised we consider that "needletail" would make the best group name; it has only been used for members of this genus and it does draw attention to the remarkably long, large projecting shafts of the rectrices. This recommendation has been recently adopted by King and Dickinson (1975). As for the species names, White-throated and Brown-throated have long been in use, particularly in India, and are also diagnostic species characters as shown above. King and Dickinson (1975) however, use White-throated, Brown, and White-vented for the three species they consider. The literature does not provide a suitable name for *H. celebensis* which we propose to call the Purple Needletail. In short:

White-throated Needletail	<i>H. caudacutus</i>
White-vented Needletail	<i>H. cochinchinensis</i>
Brown-throated Needletail	<i>H. giganteus</i>
Purple Needletail	<i>H. celebensis</i>

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