THE AUK

A QUARTERLY JOURNAL OF

ORNITHOLOGY

VOL. 73 JANUARY, 1956 NO. 1

# A REVIEW OF THE GENERA AND NESTING HABITS OF SWIFTS

BY DAVID LACK

THIS paper was begun as a comparison of the nesting habits of different kinds of swifts (Apodi), the literature on which is very scattered. But as the work progressed, I became dissatisfied with the existing generic classification, as in the last full list by Peters (1940), so I have here revised the genera, in which, incidentally, nesting habits provide a valuable guide, as pointed out by Sick (1947, 1948a, b, 1951). I have not tried to revise the species, though I have made a few suggestions; the species of *Apus* are being reviewed elsewhere (Lack, *in press*).

This paper is based primarily on the published literature, but I have also examined the large collection of swifts in the British Museum (Natural History) and am grateful to Mr. J. D. Macdonald for his friendly help in doing so. I am also most grateful to Dr. A. J. Cain, Dr. E. Mayr, and Mr. R. E. Moreau for their valuable criticisms of the paper in preparation.

*Families and subfamilies.*—In Peters' list, the Apodi are divided into two families, the Hemiprocnidae and Apodidae, and the latter are subdivided into the Apodinae and Chaeturinae. The Hemiprocnidae differ from the Apodidae in the much less modified humerus and the less modified feet, which make it possible for them to perch freely on trees. They agree with *Cypseloides*, but differ from all other Apodidae, in having a diastataxic, not eutaxic, wing, another primitive feature (Stresemann, 1927–1934). They have specialized plumage and nesting habits. The Chaeturinae are separated from the Apodinae by having unspecialized feet, whereas in the Apodinae the hallux is pointed more or less forward (instead of opposed to the other three toes), and the number of phalanges on the third and fourth toes is reduced to three on each (from four and five respectively).

The above subdivision of the family has long been accepted and seems justified on all grounds, including nesting habits. It may be added here that all swifts use saliva for sticking together the materials of their nests, and all, so far as known, have enlarged salivary glands in both sexes in the breeding season. This diagnostic character separates them from the hummingbirds (Trochili), with which they are usually united in one order (for discussion of which see, for instance, Clark, 1906 and Lowe, 1939, who lists previous references). It is probably time that this last question was reopened.

*The nature of the genus.*—The genus is a unit for arranging species in convenient groups, a purpose which is defeated if there are many monotypic genera. It is widely agreed, for instance, that the splitting of *Chaetura* by Mathews (1918) or of *Apus* by Roberts (1940) was not merely unnecessary but undesirable. The genus also denotes affinity and a certain degree of differentiation. Traditionally, morphological characters have been used for the separation of genera and they are usually of value, because closely related species are often more similar in their morphological characters than in color or size. In swifts, however, some of the morphological characters on which reliance has been placed seem highly modifiable, particularly the furcation of the tail and the position and feathering of the toes. When, on the basis of all characters treated together, two species seem closely related, I have put them in the same genus, even if they differ in one of these morphological characters. This brings related species together, but in some cases it makes a genus hard to define.

*Hemiprocnidae.*—There is only one genus with three species, *Hemiprocne comata, longipennis,* and *mystacea,* which are clearly separated by size and color. *H. mystacea,* with a wing-length of over 230 mm., is one of the largest of all swifts. The birds are confined to southeastern Asia and associated islands, one species extending as far as the Solomon Islands.

The nests of all three species have been described (Meyer, 1928; Van Meurs, 1928; Bartels, 1929; Baker, 1934; Lowther, 1949; Gibson-Hill, 1950). The nest is placed on a light branch, commonly 25 to 40 feet above the ground, occasionally much higher, and consists of a cup some one and a half inches across, made of fragments of bark and small feathers. It is literally an egg-cup, since it is just large enough to hold the single egg. The weight of the brooding bird is supported by the branch, and the bird may incubate horizontally or vertically or intermediately (on this point see particularly Lowther, 1949). The egg is glued to the nest with saliva, an adaptation otherwise found only in *Cypsiurus parvus.* In both these birds, the egg presumably has some adaptation not found in other birds to obviate the need for turning during incubation. The nestling is hatched naked, like other swifts, but unlike all others except *Cypsiurus parvus,* it later develops down, which is protectively colored.

The resemblances in nesting biology between *Hemiprocne* and *Cypsiurus* may reasonably be ascribed to convergence. These are the only two genera which have exposed nests (hence the advantage of nestling down) and the only two which have a shallow nest which is liable to sway (hence the advantage of the eggs being fixed).

*Genera of Chaeturinae.*—It is in the genera of Chaeturinae that my arrangement differs most from that of Peters (1940), but it is scarcely new, since with one exception I have returned to that of Hartert (1892).

Peters used nine genera, namely *Collocalia, Hirund-apus, Streptoprocne, Aërornis, Chaetura, Zoonavena, Mearnsia, Cypseloides,* and *Nephoecetes.* Hartert used only three, *Collocalia* (with normal tail feathers), *Chaetura* (with very stiffened rectrices and spiny tips) and *Cypseloides* (with somewhat stiffened rectrices and no spiny tips). *Collocalia* has remained unchanged, and need not be discussed further here. Hartert's *Chaetura* included the species placed there by Peters except for *C. rutila* (which Hartert placed in *Cypseloides*), and it also included the species grouped by Peters in *Hirund-apus, Streptoprocne, Aërornis* (part), *Zoonavena,* and *Mearnsia.* Hartert's *Cypseloides* included the species placed by Peters in *Cypseloides, Aërornis* (part), and *Nephoecetes,* also *C. rutilus* placed by Peters in *Chaetura.*

Most workers in the last fifteen years have brought back *Hirund-apus, Zoonavena,* and *Mearnsia* into *Chaetura,* thus uniting all the species with prominent spiny tips to their tails into the same genus. This leaves *Chaetura* as it was used by Hartert, except for the exclusion of the three species later placed in *Streptoprocne* (*zonaris, biscutata,* and *semicollaris*). No one has disputed that *Hirund-apus, Zoonavena, Mearnsia,* and *Chaetura* (in the narrow sense used by Peters) together form a natural group, the members of which are more closely related to each other than to any other swifts. Hence the further discussions of these birds may be considered later under *Chaetura.*

*Cypseloides* is more difficult. Zimmer (1945, 1953) has restored Hartert's arrangement, bringing back into this genus the species which in Peters' list are referred to as *Aërornis senex, Chaetura rutila,* and *Nephoecetes niger.* By implication, Zimmer retained *Streptoprocne* with its customary three species. On this arrangement, some workers have found it hard to place the species *semicollaris,* the existence of which was Peters' main reason for using *Aërornis*. Together with *senex*, the other species placed by Peters in *Aërornis*, it seems to bridge the gap between *Streptoprocne* and *Cypseloides*. In color pattern and size *semicollaris* is much more like the two other species normally placed in *Streptoprocne* than any other swifts, but it has a square, not forked, tail. The best solution, I suggest, is to transfer the three species of *Streptoprocne* to *Cypseloides*, uniting them with all the species that Hartert and Zimmer placed in that genus.

Summing up, I have returned to the generic arrangement of Hartert except for the transfer of *zonaris*, *biscutata*, and *semicollaris* from *Chaetura* to *Cypseloides*. The three genera may still be defined in terms of the tail feathers, much as they were by Hartert: rectrices normal (*Collocalia*), rectrices stiffened with prominent spiny tips (*Chaetura*), rectrices somewhat stiffened with slightly projecting bare tips, except in one species (*Cypseloides*).

The last group requires further explanation. The exceptional species is *C. niger*, which has normal tail feathers without spiny tips, but in its dark plumage and in nesting habits it agrees so closely with the other species of *Cypseloides* that obviously it is closely related and so should be put with them. All the other species of *Cypseloides* that I have examined (*zonaris*, *biscutatus*, *semicollaris*, *senex*, *rutilus*, and *fumigatus*) have slightly projecting bare tips to the stiffened rectrices (the rectrices seeming to be disproportionately stiffer in the larger than the smaller species). It was because they had bare tips to the rectrices that Hartert kept *zonaris*, *biscutatus*, and *semicollaris* in *Chaetura* and that Peters later transferred *rutilus* to *Chaetura*. But *senex* and *fumigatus* also show this character. Now in all six of these species, the bare tips are much less definite than in any species of *Chaetura* (as used here). Their appearance is as if the barbs had worn away through abrasion, whereas in *Chaetura* (as used here) the spines are prolonged and obviously specialized. Hence *Cypseloides* can still be separated from *Chaetura* by the nature of the bare tips, but this is a less clear-cut character than formerly stated.

A further difficulty for some workers has been that among the species here grouped in *Cypseloides*, the tail is in some species well forked, in others straight or slightly rounded, and in delimiting genera great weight has often been given to this character. In the three species of the *Streptoprocne* group, for instance, the tail is well forked in *zonaris*, slightly forked in *biscutatus*, and not at all forked in *semicollaris*. Seeing that *biscutatus* is intermediate, there seems no good reason for putting *semicollaris* in a separate genus simply on the grounds of this one feature. Of the other species, the tail is forked in *C. niger* and *C. rutilus*, but not in *C. senex, C. fumigatus, C. cherriei*, or *C. cryptus*. The furcation of the tail is evidently a modifiable character which should not be used for generic separation in the *Cypseloides* group.

Fortunately, there are three other characters in which *Cypseloides* (as used here) can be satisfactorily separated from *Chaetura*. First, the wing is described as diastataxic, a primitive feature, and not eutaxic as in all other swifts except the Hemiprocnidae (Clark, 1906; Stresemann, 1927–34). Secondly, as pointed out by Ridgway (1911), in *Cypseloides* (including *Streptoprocne* and *Nephoecetes*) the hallux is longer, more than half as long as the inner toe, whereas in *Chaetura* the hallux is shorter, less than half as long as the inner toe. When a swift clings to a vertical surface, it grips with both feet and tail, and it seems clear that in *Chaetura* the reduction in the length and strength of the hallux has been evolved at the same time as an increase in the length and strength of spiny tips to the rectrices. Thirdly, the nesting habits and clutch-size of *Cypseloides* and *Chaetura* are very different, as discussed later.

*Species of* Cypseloides (*Black or Primitive Swifts*).—The critical morphological characters of the species in this group have been discussed in the previous section. As mentioned, eight species here grouped in *Cypseloides* come from five different genera in Peters' arrangement, but if the tail is regarded as a modifiable character, all can be grouped together, with a ninth species *C. cryptus* described by Zimmer (1945) since Peters' list was published.

All nine species have uniformly black upper and under parts. Indeed, they are normally blacker than the species of *Apus*. Zimmer (1945) has pointed out that they differ from all the species of *Chaetura* in America (with which alone they come in contact) in having the rump as dark as the back, whereas in the American species of *Chaetura* the rump is always paler than the back (being slightly paler even in *C. pelagica*). The only interruption of black in their plumage occurs in the region of the head. Thus *C. zonaris* has a complete ring of white round the neck, *C. biscutatus* is white on the hindneck and chest (i.e. the ring is interrupted on the sides of the neck), and *C. semicollaris* is white on the hindneck only. This is another character in which *C. biscutatus* is intermediate between the other two. *C. rutilus* has a rufous collar which in shape is very like the white collar of *C. zonaris*. *C. cherriei* has a white spot on each side of the forehead, *C. cryptus* pale marks on the sides of the forehead and often a white chin, *C.*

*fumigatus* at times a pale chin, *C. senex* a grayish head, but *C. niger* has no white area. (For the descriptions of *C. cryptus* and *C. cherriei* in this account, I have relied on Zimmer, *loc. cit.*)

Otherwise, the species differ mainly in size, the smallest being *C. rutilus* and *C. cherriei* (with wing-lengths around 120–130 mm.) and the largest, the three species formerly placed in *Streptoprocne* (with wing-lengths over 200 mm.). *C. semicollaris*, with a wing-length of over 230 mm., is one of the largest of all swifts.

The group is confined to tropical America except for *C. niger*, which ranges north to southeastern Alaska.

*Nests of* Cypseloides *species.*—The nests of four species, *C. cryptus*, *C. cherriei*, *C. biscutatus*, and *C. semicollaris*, have not been recorded. Those of the other species are closely similar in site, structure, materials, and clutch-size. *C. niger* nests on inland cliffs behind or close to waterfalls, or over a pool, also on steep sea cliffs. The nest is cone-shaped on the outer side, made of mud and moss, and lined with fern tips. The clutch is invariably 1 (Bent, 1940; *cf.* Michael, 1927; Smith, 1928; Knorr and Baily, 1950). *C. rutilus* has been found nesting in a gorge over a stream, also in dark culverts two feet above the water, the nest is again a half-cone, made of mud and moss, and lined with ferns; the clutch (three records) being two (Belcher and Smooker, 1936; also Orton, 1871). *C. senex* nests behind a rock over which water falls (v. Ihering, 1900). *C. zonaris* nests behind waterfalls (Beebe, 1949, citing Todd and Carriker, 1922; also Naumburg, 1930; Sutton, 1951), also on the steep sides of barrancas (Reboratti, 1918) or in holes in rocks or caves (Salmon, cited by Sclater and Salvin, 1879), while an old record strongly suggests that in Jamaica it may also nest on sea cliffs like *C. niger*. (Gosse, 1847, also Taylor, 1955). The cone-shaped nest is made of mud and moss lined with small twigs or fragments of fern (Reboratti, 1918). Mud and moss were also mentioned by Salmon and twigs by Todd and Carriker. The clutch is one or two (Salmon, Reboratti, Todd and Carriker; Reboratti said that one is usual). *C. fumigatus* also nests in steep barrancas, the nest being of the same shape as in the other species and made of mud and moss and lined with fern, the clutch 1 (Reboratti, 1918). (A nest said to have been of this last species was described by Holt, 1927–28, in Brazil, but as it was attached to the brickwork on the inside of a house gable, was made of glued twigs and contained five young, this obviously refers to the nest of some *Chaetura* species.)

Hence all the species of *Cypseloides* for which the nest is reliably known agree in building on steep cliffs, usually in association with water, making a cone-shaped nest of mud and moss lined with fern-tips or twigs, and in laying a clutch of only one or two eggs. In all these characters, they are clearly separated from the species of *Chaetura.* They are also separated from them by their roosting habits. The species of *Chaetura,* so far as known, roost (as they nest) in hollow trees or chimneys, sometimes in great numbers. *Cypseloides zonaris* also roosts as it nests, large numbers flying behind waterfalls (Salvin and Godman, 1888–1904; Davis, 1945; Ribeiro, cited by Sick, 1947). Again, *C. rutilus* roosts clinging to rocks (Beebe, 1949). Incidentally, Beebe's photograph of *C. rutilus* clinging to a vertical surface shows the use of the tail for gripping and the small bare tips to the rectrices. It may be compared with a photograph of *Apus apus,* which also uses the tail for gripping when roosting on a vertical wall, though it has not developed bare tips to the rectrices (J. Markham, in Nicholson, 1951).

Two queries about the breeding of *Cypseloides* may be added. First, how do these birds collect the mud and moss for their nests? All other swifts, so far as known, collect nesting material (other than saliva) in flight. Do the species of *Cypseloides* alight to collect mud, or could they obtain it in flight by skimming over shallows in the way that various swifts skim over water to drink or bathe? The latter seems unlikely, and an observation by Michael (1926) shows that they alight on rocks near waterfalls. Secondly, where, as in *C. zonaris,* the birds actually fly through a waterfall to nest, the first flight of the young swift, through the curtain of water to independence, must be quite something.

*Nesting of* Collocalia *species.*—The species of *Collocalia* comprise a comparatively uniform group of dull gray-brown, sometimes glossy, birds with square or slightly forked tails; most of them have a wing-length of 110 to 140 mm. Some species are easy to recognise from skins, but others, notably those usually placed in or close to *C. francica, C. fuciphaga,* and *C. vestita* in their wide sense, present a bewildering degree of variation, and the specific and racial determinations are confused (*cf.* Mayr, 1937). A specific list has not been attempted here. For clarity, I have in some of the cases which follow used alternative specific names where both have been in frequent use (the subspecific name is often the best guide to the bird intended).

All the species, so far as known, build their nests on the walls of caves, which may be on the sea coast or inland, including high in the mountains. Many species nest in huge colonies, but the White-breasted Swiftlet, *C. esculenta,* usually nests in small groups and, though it nests in caves where present, it also nests in more open rocky sites, occasionally beside a waterfall (E. Sutter, *in litt.*) and also in large hollow trees (Mayr, 1945). This species also uses the buildings of man in various parts of its wide range (Franck, 1926; Spennemann, 1928a; Baker, 1934; Mayr, 1945). The Gray-rumped Swiftlet, *C. inexpectata* (or *francica*) *amechana*, likewise uses buildings in Singapore (Gibson-Hill, 1948), and so does the same species (presumed; it was called *C. francica vestita*) in Java (Franck, 1926; Spennemann, 1928b).

All the species, so far as known, build a small bracket-shaped nest on a vertical wall, in this respect resembling *Chaetura*, but the material is different. The white nests of commerce, made of pure saliva, come primarily from the Gray-rumped Swiftlet, *C. inexpectata* [or *francica*], (Baker, 1934; Banks, 1949; Gibson-Hill, 1948), also from the Brown-rumped Swiftlet, *C. vestita*, (Banks, 1949; Gibson-Hill, 1948), while the Pygmy Swiftlet, *C. troglodytes*, is also said to have an edible nest (McGregor, 1909; Manuel, 1937; Delacour and Mayr, 1946). The other species include much other matter: chiefly moss and lichen, sometimes other vegetable matter in *C. esculenta* (Spennemann, Baker, Banks, Gibson-Hill, *op. cit.*); moss and other vegetable material in the Australian Pale-rumped Swiftlet, *C. spodiopygia* (*francica*) *terrae-reginae*, (Mathews, 1918); moss in *C. whiteheadi* (Delacour and Mayr, 1946); feathers in Robinson's Swiftlet, *C. lowi robinsoni*, (Banks, Gibson-Hill, *op. cit.*) and the related *C. lowi tichelmani* (Stresemann, 1926); vegetable matter in *C. f. fuciphaga* from Java (Stresemann, 1926); grass and feathers in Hume's Swiftlet, *C.* (*fuciphaga*) *innominata*, also in the Plain-rumped Swiftlet, *C.* (*brevirostris*) *unicolor*, and the Himalayan Plain-rumped Swiftlet, *C.* (*fuciphaga*) *brevirostris*, (Baker, 1934), the last species also using moss (Glennie, 1944). In the Solomon Islands, Dr. A. J. Cain (*in litt.*) twice saw *C. esculenta* hovering or turning upside down in the air to snatch at hanging shreds of bark and moss. There are no observations suggesting that the species of *Collocalia* alight to collect nesting material.

The full clutch of most species is two, this applying to the forms *innominata*, *unicolor*, and *brevirostris* just mentioned (Baker, 1934), and to *C. esculenta*, *C. vestita*, and *C. inexpectata* (Stresemann, Baker, Banks, Gibson-Hill, *op. cit.*). But Spennemann (1928a) found some nests of *C. esculenta* with only one well-incubated egg (*cf.* Mayr, 1945). A single egg is normal in *C. lowi robinsoni* (Banks, Gibson-Hill, *op. cit.*) and in *C. lowi tichelmani*, which builds a small nest in proportion to the size of the bird (Stresemann, 1926). Many nests with one egg were also found in the Australian *C. spodiopygia terrae-reginae*, but the original record suggests that laying had only just started at this colony, so this may not have been the full clutch (Mathews, 1918).

*Species of* Chaetura (*Spine-tailed Swifts*).—As already mentioned, I agree with most other workers since Peters in merging *Hirund-apus* (2 or 3 species), *Zoonavena* (1 species) and *Mearnsia* (4 species) with *Chaetura.*

*Mearnsia* has been separated primarily on account of the extremely short tail. But when color pattern is taken into consideration, two species, *C.* (*Mearnsia*) *picina* from the Philippines and *C.* (*M.*) *novaeguineae* from New Guinea, are very like each other but very different from the two other species, *C.* (*M.*) *cassini* and *C.* (*M.*) *böhmi,* both African. In color, the two latter closely resemble each other and also two other African species usually placed in *Chaetura* in the restricted sense (see later), and I therefore suggest that these four African species are related. Finally one of the American species, *C. brachyura,* also has a short tail and so might qualify for a place in *Mearnsia,* but in color pattern it is closest to the other American forms. I therefore suggest that in the spine-tailed swifts a short tail has been evolved separately at least three times, and that it should not be used for generic separation.

If the *Chaetura* group is to be subdivided, I suggest that color provides a truer guide to affinities than the morphological characters usually employed. Supporting this view, a grouping on the basis of color brings the birds of each main region into the same group. The natural subdivisions of the genus are in my view (i) all the American species, (ii) all the African species, that from Madagascar and adding the two white-rumped Asiatic species, (iii) the large species from southeastern Asia sometimes placed in *Hirund-apus,* (iv) the large but short-tailed birds from New Guinea and the Philippines sometimes placed in *Mearnsia* (but the other forms placed in *Mearnsia* belong to group ii).

(i) The American species form a closely knit group of similar size, with dark upper and underparts, and with the rump varying from buff-gray to almost, if not quite, as dark as the back. Peters listed eleven species, *chapmani, pelagica, vauxi, richmondi, gaumeri, nubicola, cinereiventris, spinicauda, martinica, andrei,* and *brachyura.* Of these, *nubicola* is a synonym of *Cypseloides rutilus* (Friedmann *et al.,* 1950), and recent workers have treated *richmondi* and *gaumeri* as subspecies of *vauxi.*

This leaves eight species, but I wonder if further reduction is not desirable. *C. vauxi* and *C. pelagica* are allopatric, and though they do not intergrade, the differences between them, in the shade of the underparts and in size, are of the same order as those separating some of the subspecies in species of *Apus* (*cf.* Lack, *in press.*) *C. chapmani* also appears to belong to the same group as *vauxi* and is again allopatric. Where there is doubt concerning closely related allopatric forms, it is in general better to classify them as subspecies, not species (Mayr *et al.*, 1953), and this has the advantage of indicating their affinity. Is there not sufficient doubt in the case of *chapmani*, *vauxi*, and *pelagica*? Likewise *C. martinica* is allopatric with *C. cinereicauda*, to which it is closely related (Bond, 1936); might it not be regarded as a well-marked insular subspecies? If these suggestions are acceptable, there are only 5 American species of *Chaetura*. Because they are not yet accepted, I have for convenience classified the nesting records for *C. pelagica* and *C. vauxi* separately in the next section.

(ii) Of the African species listed by Peters, *thomensis* is a well-marked race of *C. sabini*. Four of the five good species, *C. sabini*, *C. ussheri*, *C. cassini*, and *C. böhmi*, agree in a characteristic color pattern of dark and slightly glossy upper parts and dark chests, but white rumps and abdomens. The remaining African species, *C. melanopygia*, has a dark rump and abdomen but strongly resembles *C. ussheri* in its scaly chest and seems to belong to the same group. Also two Asiatic species, *C. sylvatica* and *C. leucopygialis*, have somewhat glossy upper parts and mainly white rumps, while *C. sylvatica* also has a pale abdomen like the African species and *C. leucopygialis* has a mainly white tail like *C. sabini*. I think that all these birds are closely related. The Madagascar species, *C. grandidieri*, with dark brown upper parts, a paler rump, and gray-brown underparts, is so similar to *C. sabini*, except in color, that I regard it as closely related.

(iii) The species sometimes grouped in *Hirund-apus*, *C. caudacuta* and *C. gigantea* (with *C. cochinchinensis* as a possible third species—Biswas, 1951), are clearly separated from the subgroups already mentioned by their great size, glossy blue-black wings and rump, brown back and underparts.

(iv) *C. picina* and *C. novaeguineae* resemble the species of group (iii) in plumage more closely than they do any other swifts, since they likewise have glossy blue-black upper parts, including the rump, while *C. picina* also has a prominent white throat like *C. caudacuta* and is of large size. But they differ from the *Hirund-apus* section in various ways, including the short tail, and seem best retained provisionally as a fourth group.

The difference between, say, *C. gigantea* and *C. böhmi* is so great that a case can be made for using further genera. If this is done, I think that the group is best divided into four genera as indicated in groups (i) to (iv). But I see no real need for this, and it is better not to introduce more names than are really needed. Different though some of the species are, I think there is no doubt that they are more closely related to each other than to any other swifts, and this is borne out by the similarity in their nesting, mentioned later.

It is interesting that of the nine genera into which the swifts have been grouped in this paper, *Chaetura* is the only one with representatives in both the Old and New worlds. Even in *Chaetura*, the New World species resemble each other more closely than they do any of the Old World species.

*Nesting of* Chaetura *species.*—All the species of *Chaetura* nest in the same way, as stressed by Sick (1948, 1951), with the partial exception of the *Hirund-apus* subsection (considered in a later paragraph). The nest is in a hollow tree, which the bird normally enters by diving in from above, though it sometimes ascends from below if there is a gap near the roots. The nest is bracket-shaped and attached to a vertical surface, and is made of fine twigs. In *C. pelagica,* and presumably other species, the twigs are broken off by the feet as the bird flies past. This description applies, so far as their habits are yet known, to the North American *C. pelagica* and *vauxi* (Bent, 1940); to the tropical American *C. p.* (or *v.*) *richmondi* (Dickinson, 1951), *C. andrei* (Sick, 1948, 1951), *C. cinereiventris* (Sick, 1948, citing Ribeiro, 1929) and *C. brachyura* (except that the nest was in a cave not a tree; Belcher and Smooker, 1936); also to the Indian *C. sylvatica* (Baker, 1934) and to the African *C. sabini* (Bates, 1911), *C. ussheri* and *C. cassini* (Bannerman, 1933; Chapin, 1939), and *C. böhmi* (except that the nests of the last species were in bore-holes or caves, not trees; Vincent, 1946; confirmed by numerous records *in litt.* from E. L. Haydock in Northern Rhodesia; the nests were up to 25–30 feet below ground level and were made of bark, feathers, and sometimes twigs). This extreme similarity in nesting habits strongly supports the view that all the species here placed in *Chaetura* are closely related and should be united in one genus. As yet, the nests of *C.* (*pelagica*) *chapmani*, *C. spinicauda*, and *C.* (*cinereiventris*) *martinica* in group (i), of *C. melanopygia* and *C. grandidieri* in group (ii), and of *C. picina* and *C. novaeguineae* which together comprise group (iv) have not been described.

Various of the above species, like many other swifts, have found an artificial equivalent to their natural site. The North American

*C. pelagica* now breeds much more often in chimneys than in trees, and chimney-nesting has also been recorded in *C.* (*p.*) *vauxi* in western North America (Bent, 1940), in *C. p.* (or *v.*) *richmondi* in Venezuela (Sutton, 1948), *C. andrei* in Brazil (Sick, 1951), *C. brachyura* in Trinidad (Belcher and Smooker, 1936) and *C. ussheri* in Africa (Bannerman, 1933; Chapman, 1939), while, as noted above, *C. böhmi* has been found nesting in mine-borings. Only *C. böhmi* and *C. brachyura* (Belcher and Smooker, 1936) have been recorded nesting in caves.

The large species in the *Hirund-apus* subsection form a partial, but only partial, exception. *C. caudacuta* regularly nests in large hollow trees (Jahn, 1942; Austin and Kuroda, 1953) and so does *C. gigantea* (Baker, 1934), and both enter in the typical chaeturine way by diving in from above. *C.* (*caudacuta*) *cochinchinensis* has been found breeding in man-made caves in forested country (Baker, 1934). It is stated in various general works that the members of this group also breed in rocky cliffs in high mountains, but I cannot find any definite published records to substantiate this. *C.* (*c.*) *caudacuta* and *C.* (*caudacuta*) *cochinchinensis* build bracket-shaped nests attached to a vertical surface. The nests, however, are made not of twigs but of dried moss and hair; they may be six inches across (Baker, 1934). *C. gigantea,* unlike other *Chaetura* species, makes a simple hollow in the dirt at the bottom of a hollow tree, where the eggs get very stained (Baker, 1934). The large size of this species might make it difficult to construct a sufficiently strong bracket-nest.

Clutch-size in *Chaetura* is greater than in the other genera of swifts except *Aëronautes,* four to five, occasionally three or six, in *C. pelagica* and four to six, occasionally three, in *vauxi* (Bent, 1940); five in *C. cinereiventris* (Sick, 1948, citing Ribeiro, 1929), three in *C. brachyura* (Belcher and Smooker, 1936), four in *C. ussheri* (Chapin, 1939), three in *C. böhmi* (Vincent, 1946), two or three in *C. sabini* (Bates, 1911), three to five in *C. sylvatica* (Baker, 1934), three or four, occasionally two or five, in *C. gigantea* (Baker, 1934), two or three in *C. caudacuta* (Austin and Kuroda, 1953).

*Genera of Apodinae.*—Peters (1940) used seven genera, four of which were monotypic while two included only two species in each. This arrangement derives from Hartert (1892), who divided the Apodinae into two main groups on the basis of the toes; they are:—

| | |
|---|---|
| (i) all directed forward: | *Apus, Aëronautes, Panyptila* |
| (ii) in opposed pairs: | *Tachornis, Cypsiurus, Reinarda,* to which should be added the later-discovered *Micropanyptila* (Sutton, 1928). |

Hartert further subdivided each of these two groups into two, according to whether the toes are bare or feathered. In group (i) they are bare in *Apus* but feathered in *Aëronautes* and *Panyptila;* in group (ii) they are bare in *Tachornis, Cypsiurus,* and *Micropanyptila* but feathered in *Reinarda.*

This division of the group does not, in my view, show the true affinities of the various forms. Instead, I suggest that both the position and the feathering of the toes are highly modifiable characters which should not be used in classifying the Apodinae. In this connection two points may be particularly noted. First, the newly hatched *Apus apus* has the toes in opposed pairs, not all forward (Ingram, 1955), and thus resembles *Tachornis, Cypsiurus,* and *Reinarda* and differs from the adults of its own species. Secondly, the species *andecolus* has bare toes and so has hitherto been placed in the genus *Apus,* but its general appearance, including the distribution of white areas on the plumage, also its geographical range, show that it is related to the two species of *Aëronautes* (also to *Panyptila,* but not to *Apus*), and it is here placed in *Aëronautes.*

For reasons given in detail later, I propose to treat *Tachornis phoenicobia, Reinarda squamata,* and *Micropanyptila furcata* as congeneric, since they show resemblances to each other in color pattern, nesting habits, and geographical range and seem more similar to each other than to any other swifts. *Tachornis* is the oldest available generic name. In the following discussion *Tachornis* covers these three species, not merely *T. phoenicobia.* But, as explained later, *Cypsiurus parvus,* which has sometimes been placed in *Tachornis* in the past, is here retained as a monotypic genus.

I therefore divide the Apodinae into five genera, *Apus* with ten species, all from the Old World, *Cypsiurus* with one species from the Old World, *Aëronautes* (including *andecolus*) with three species from the New World, *Panyptila* with two species from the New World, and *Tachornis* (*sens. lat.*) with three species from the New World.

*Apus* and *Cypsiurus* resemble each other and differ from the three American genera in having dark underparts (save for the pale chin). The only exception is *Apus melba,* which has mainly white underparts, but this condition can easily be derived from *Apus aequatorialis,* in which the corresponding feathers are barred with white. Each of the American species, on the other hand, has a large area of white on the underparts. Further, as compared with *Aëronautes, Panyptila* has a white nape like *A. andecolus,* white sides to the rump like *A. andecolus* and *A. saxatilis,* a white throat and upper chest like *A. saxatilis,* and white bases to the secondaries, like *A. saxatilis.* These resemblances are far too striking to be due to chance, and surely indicate that *Panyptila* and *Aëronautes* (including *andecolus*) are closely related.

At the same time, *Panyptila* shows strong resemblances to *Tachornis* (*sens. lat.*) in nesting habits, since these are the only swifts which suspend a nest from the underside of a tree, the nest being entered from below by a long tube. In both genera, the nesting chamber is a globular sac of plant fibres and feathers, and in *Panyptila* and one species of *Tachornis* the material is worked into a close felt. The main difference between them is that the tubular entrance is formed by hanging leaves or a spathe in *Tachornis* but is made by the bird in *Panyptila*. No other swifts build in anything like this way, which strongly suggests that *Panyptila* and *Tachornis* are closely related. *Cypsiurus parvus*, on the other hand, which has hitherto been thought to be related to *Tachornis phoenicobia*, differs strikingly in nesting habits, building a shallow, spoon-shaped strip to which the eggs are stuck with saliva.

In view of this evidence, I suggest that the main division of the Apodinae is between the Old World forms (*Apus* and *Cypsiurus*) on the one hand, and the New World forms (*Aëronautes*, *Panyptila*, and *Tachornis*) on the other. On this view, either the condition with all the toes forward, or that with the toes in opposed pairs, has been evolved more than once. The latter seems the more specialized condition, and it is in fact confined (in the adult) to the palm-nesting species—*Tachornis* in the New World and *Cypsiurus* in the Old. But it is also found in the nestling *Apus*, which suggests that the same conditions in Palm Swifts may be neotenic.

The furcation of the tail is another morphological character which appears to be highly modifiable in the group. Thus the tail is strongly forked in *Cypsiurus*, *Panyptila*, and two species of *Tachornis*. In all save one of the other species of Apodinae the tail is moderately forked, though to a variable extent, while in some forms of *Apus affinis* it is almost square. For this reason, *affinis* has sometimes been placed in a monotypic genus, but it is closely similar in color pattern and nesting habits to *Apus caffer*, to which it is presumably related.

I do not propose to subdivide *Apus*, or any other genus of the Apodinae. The remaining question is whether as many as five genera are needed for the group. I think that they are. With the transfer of *andecolus* from *Apus* to *Aëronautes*, these two genera can no longer be differentiated, as hitherto, by the presence or absence of feathering on the toes. Indeed, they are extremely difficult to define except in terms of their range, in the Old and New worlds, respectively. On the other hand, I consider that they are less closely related to each other than is each to the other genera in the Old and New worlds, respectively. Hence they must be kept separate. Of the Old World genera, the monotypic *Cypsiurus* is very different from any species of *Apus,* so should be kept separate. Of the New World genera, *Panyptila* might be united with *Aëronautes* on the basis of plumage but is strikingly different in nesting habits; while it might be united with *Tachornis* on the basis of nesting habits, but differs greatly in color. Hence I think it best to retain all five genera.

*The species of* Apus.—A revision of the species of *Apus* is being published elsewhere (Lack, *in press*). The task has proved extremely difficult, owing first to the similarity of some of the species and secondly to the marked differences in pigmentation and size in some subspecies of the same species. As a result, there are several instances in which a subspecies looks less like another race of its own species than like another species. Such convergent resemblances at the specific level are hard to detect.

The following changes, some of them tentative, are proposed from Peters (1940): (i) the transfer of *andecolus* from *Apus* to *Aëronautes,* already discussed, (ii) the elevation of *barbatus* from a race of *A. apus* to a full species, with *mayottensis* and *balstoni* (from *A. apus*), *sladeniae* (from a full species) and *bradfieldi* (from *A. aequatorialis*) as races of it, (iii) the abolition of the species *A. unicolor,* making *unicolor* and *alexandri* races of *A. apus* and *poensis* a race of *A. myoptilus,* (iv) the merging of *A. batesi* as another race of *A. myoptilus,* (v) the transference of the race *niansae* from *A. apus* to *A. pallidus,* (vi) the merging of *A. acuticaudus* as a race of *A. pacificus,* (vii) the merging of *A. toulsoni* as a race or variant of *A. horus,* and (viii) the merging of *A. reichenowi* as a variant of *A. aequatorialis.*

In all, this makes 10 species, *apus, barbatus, pallidus, aequatorialis, melba, myoptilus, caffer, horus, affinis,* and *pacificus.* There seems no case for further genera, as proposed by Roberts (1940), and it is hard to divide the species into subgroups with certainty. However, *A. aequatorialis* and *A. melba* seem very close to each other. So do *A. caffer, A. horus,* and *A. affinis,* as they are similar in color pattern, though *A. caffer* and *A. horus* have well-forked tails, and *A. affinis* a nearly square one.

*Nesting habits of* Apus *species.*—For completeness, I have in the following summary included notes on the nesting of those forms which I have relegated from full species to subspecies. The nests of all ten species as accepted here have been found (but the nests of *myoptilus* [*sens. strict.*], *toulsoni,* and *reichenowi* are unknown). Nine of the ten species have been found nesting in rocks, though some of them also use other sites. The exception is *A. horus*, which (always so far as known) uses holes in banks, usually sandbanks, excavated by swallows, starlings, or possibly bee-eaters (Belcher, 1930; Friedmann, 1930; Roberts, 1940; Taylor, 1949; Clancey and Holliday, 1951; Dickin, 1952). Only one other species of *Apus* has been found nesting in sandy banks, there being one recorded of *A. apus* using the holes of Bank Swallows (*Riparia riparia*) in England (Oakes, 1953).

Of the nine rock-frequenting species, seven use holes or crevices, usually in inland cliffs, namely *A. apus* (Jourdain, 1901; Kelsall and Munn, 1905; Nelson and Clarke, 1907; Oakes, 1953), *A. barbatus* (Van Someren, 1922, who listed it as *A. roehli;* also Roberts, 1940; Benson, 1952), *A. pallidus*, *A. aequatorialis* (Masterson, 1945; Benson, 1952), *A. melba*, *A. caffer* (Roberts, 1939), and *A. pacificus* (Baker, 1934). Rock crevices are also used by various forms treated by previous workers as full species, including *A. apus unicolor* (Volsøe, 1951), *A. apus alexandri* (Bannerman, 1933; Bourne, 1955), *A. pallidus niansae* (Van Someren, 1922, who listed it as *nakuruensis*) and *A. pacificus acuticaudus* (Baker, 1934). On the other hand, *A. affinis* typically builds not in a crevice but under overhanging rocks or under the roof of a cave, and adjacent nests may actually touch each other (Baker, 1934; Roberts, 1939, 1940). *A. caffer*, though at times nesting in natural holes, has been found much more commonly using the old nests of martins and swallows, particularly those of species which build retort-shaped nests (Roberts, 1939, 1940; Vincent, 1946). The nests of hirundines on rocks are also used at times by *A. pacificus* and *A. affinis* (Baker, 1934), and this has been the site of the three recorded nests of *A. myoptilus batesi* (Bates, 1905; Serle, 1954). Holes in sea cliffs are used by *A. apus* in the British Isles (Stevenson, 1866; D'Urban and Mathew, 1895; Ussher and Warren, 1900; Forrest, 1907; Nelson and Clarke, 1907; Baxter and Rintoul, 1953), by *A. apus alexandri* in the Cape Verde Islands (Bourne, 1955) and by *A. pacificus* in China (Cochrane, 1920).

It is interesting that of the nine rock-frequenting species, as many as six also nest on or in buildings. These are *A. apus* in Europe and also *A. apus alexandri* in the Cape Verde Islands (Bourne, 1955); *A. melba* in Europe (Arn, 1945); *A. pallidus* in Europe (Hoffmann *et al.*, 1951) and Asia (Baker, 1927); *A. pacificus* in China but not Japan (Jahn, 1942); *A. caffer* in Africa (Lynes and Vincent, 1939; Roberts, 1939; Moreau, 1942a); and *A. affinis* in Asia (Baker, 1934) and Africa (Moreau, 1942b). The situation of the nest on or in a building varies with the species. Thus the nests of *A. apus* and *A. melba* are normally invisible from outside, each pair of *A. apus* typically having a separate entrance-hole, whereas those of *A. melba* are commonly shared (personal observation). *A. pallidus*, on the other hand, often builds on the upper side of a rafter under the eaves in such a position that the sitting bird can be seen from outside (Hoffmann *et al.*, 1951, also personal observation), though many other nests have been recorded in holes, especially in Egypt and Asia. On a building, as on rocks, *A. caffer* often though not always selects the old nests of hirundines under the eaves (Lynes and Vincent, 1939; Roberts, 1939; Moreau, 1942a), *A. apus* occasionally nests in the same situation in England, using the nests of House Martins, *Delichon urbica*, (Price, 1888; and references there cited), and *A. pallidus* sometimes uses the open nests of Swallows, *Hirundo rustica*, (Hoffman, *et al.*, 1951). *A. affinis* typically builds its nest under the eaves of a house or on the underside of a roof, for instance of a mosque, recalling its natural site under overhanging rocks, and it also may use old martins' nests (Baker, 1934; Moreau, 1942b).

Only one species, namely *A. apus*, has been found nesting in trees, this being regular locally in Europe in old woodpecker holes. It nests in old pines in northern Scandinavia and Lapland (many references, and personal observation) and formerly in Scotland (Harvie-Brown and Buckley, 1895), also in Corsica (Jourdain, unpublished *MS* in Edward Grey Institute), and in old broad-leaved trees in parts of Germany and Bohemia (Dresser, 1871–81; Stadler, 1917; Niethammer, 1938) and probably formerly in England (D'Urban and Mathew, 1895). It also uses nesting boxes on trees in Germany (Niethammer, 1938) and in Switzerland (Weitnauer, 1947). In all these situations, the flight in to the nest is more or less horizontal, and the bird does not enter hollow trees by diving in from above, like *Chaetura*. Since *A. apus* has also been recorded nesting in rocks in both inland and sea cliffs, in buildings, the burrows of Bank Swallows, and the nests of House Martins, it has been recorded from more varied nesting sites than any other species of swift. This may be partly because it has been much more studied than any other species.

All save one of the species of *Apus* typically build a simple shallow cup placed on the floor of their crevice or hole (or old martin's nest). *A. affinis* differs from the rest in building a bag-shaped structure with a short tubular entrance attached to the underside of a rock (Baker, 1934; Moreau, 1942b). The only other partial exception is *A. melba*, which at times, but far from always, builds a bracket-shaped nest on a vertical wall, but often, like other species, it builds a simple cup on the floor (Boxberger, 1934, and personal observation).

All the species use as nesting material feathers, dried grass, and other vegetable matter, caught entirely in the air. This material is stuck together with saliva, often rather loosely. But *A. melba* welds bud scales and other small plant remains into a firm hard structure; although it is the largest species, it for the most part selects much smaller plant remains than do smaller species such as *A. apus.* Mud has been reported from the nests of several species, but it may be presumed that this was either a natural accumulation in a crevice or was brought there earlier by a martin.

Clutch-size is remarkably uniform in the genus, two or three eggs being the commonest clutch in every species. This holds for the following species (for which the references are those already given under nesting habits with a few additional sources listed here); *A. apus* (Lack, 1951a), *A. barbatus* (two records of 2, Van Someren, 1922, under the name *A. roehli;* Roberts, 1940), *A. pallidus* (Hoffmann *et al.*, 1951; F. C. R. Jourdain MS in Edward Grey Institute; also Van Someren, 1922, under the name *A. nakuruensis*), *A. melba* (Arn, 1945; Steyn, 1952), *A. myoptilus batesi* (two clutches and one brood of 2), *A. horus, A. caffer, A. affinis,* and *A. pacificus.* For several of these species there is good evidence of geographical variations in clutch-size, two being commonest in some parts of the range, three in others, as shown for *A. apus* (Lack, 1951a), *A. caffer* (Pitman, 1931; Lynes and Vincent, 1939; Moreau, 1942a; Vincent, 1946), *A. affinis* (Baker, 1934), and *A. pacificus* (Baker, 1934). In several of those populations in which three is the commonest clutch, a clutch of four is occasional, including *A. apus, A. melba, A. affinis,* and *A. pacificus.* A clutch of five seems unknown. Since various species of *Chaetura* commonly lay four to five eggs, this might suggest that the *Apus* model is less efficient than the *Chaetura* model at collecting insects quickly.

Cypsiurus (*Old World Palm Swift*).—*Cypsiurus parvus* was for a long time placed in the same genus (*Tachornis*) as the West Indian Palm Swift, *T. phoenicobia.* Yet although I have brought two other American birds, *Reinarda squamata* and *Micropanyptila furcata,* into *Tachnornis,* I have retained *Cypsiurus* as a separate monotypic genus. *C. parvus* particularly resembles *C.* (*Micropanyptila*) *furcata,* since it has the toes opposed in pairs and bare of feathers and a long, forked tail. Nevertheless, I think it probable that *Cypsiurus* is more closely related to *Apus* than to *Tachornis* and that its resemblances to the latter are the result of convergence. As already mentioned, it differs from *Tachornis* in having dark underparts and, more strikingly, in nesting habits.

The nest is a simple strip of feathers or plant fibres, about one and a half inches across, with a small projecting rim at the bottom (Sclater and Moreau, 1932; Townley, 1936; Chapin, 1939, citing many other references; Moreau, 1941). In shape, it resembles the bowl of a spoon, with the longer axis vertical, and it is attached to the vertical side of a a hanging palm leaf on the inner (technically the under) side. Hence the nest is not placed in a narrow tube formed by hanging leaves, it is not sac-shaped, and the entrance is not at the bottom, as it is in *Tachornis.* Further, in *Cypsiurus* the eggs are stuck to the nest with saliva, an adaptation not found (or needed) in *Tachornis phoenicobia* or *T. squamata* with their sac-shaped nests (Belcher and Smooker, 1936; *cf.* Sick, 1947, 1948). The female *Cypsiurus* incubates in a vertical position (Moreau, 1941). The nestling hatches naked like other swifts, but develops down, which, so far as known, is not found in *Tachornis* or any other swift except *Hemiprocne.* The clutch is two or three. It may be added that *Cypsiurus,* like so many other swifts, has adapted its nesting habits to man, and in Asia it often nests in the roofs of native houses, especially those made of palm leaves or thatch (Baker, 1934).

As already mentioned, *Hemiprocne* resembles *Cypsiurus* in attaching the egg with saliva, in having nestling down, and in its long forked tail, but all these resemblances can be attributed to convergence.

Aëronautes (*White-throated and allied Swifts*).—As already mentioned, *Aëronautes saxatilis* was separated from *Apus* because its toes are somewhat feathered. It was later found that another American species, *montivagus,* until then placed in *Apus,* had some feathering on the toes, so it also was transferred to *Aëronautes.* This left only one American species, *andecolus,* in the genus *Apus,* and as already discussed, I consider that this likewise belongs to *Aëronautes.* This makes *Aëronautes* hard to define, since *andecolus* has unfeathered toes. The two main differences from *Apus* are the New World distribution and the presence of white on the underparts (though *Apus melba* has mainly white underparts). Also, Ridgway (1911) pointed out that in *Aëronautes saxatilis* the tail is moderately forked, but the outermost pair of rectrices is only slightly longer than the next pair. This also holds for *A. andecolus* (I have not seen *A. montivagus*) and it further helps to separate *Aëronautes* from *Apus,* since in many species of *Apus* the outermost pair of rectrices is decidedly longer than the next pair; but *Apus affinis* is an exception, with a nearly square tail, and the difference is small in some of the other species (Lack, *in press*).

*Aëronautes* consists of three species, all found on the western side of

America, and mainly between the high mountains and the sea. Their plumage is dark with patches or bands of white. In *A. montivagus*, which is the smallest and darkest species, white occurs on the throat and lower abdomen, while the breast and center of the abdomen are whitish. In *A. saxatilis*, white occurs on the throat and chest, the center of the upper abdomen, the flanks near the rump, and the tips of the secondaries. In *A. andecolus*, the whole of the underparts are white, and so are the neck and rump, including the flanks near the rump.

*A. saxatilis* builds in rock crevices on steep cliffs. It has also taken to using holes in buildings, occasionally in the old nest of a hirundine (Bent, 1940; Pitelka, 1944). The nest is a simple cup, which is sometimes attached to a vertical wall. The materials are feathers and dried vegetation. In all these respects, this species closely resembles the species of *Apus* (in which one species, *A. melba*, sometimes builds a bracket-nest on a vertical wall). But the recorded clutch of *A. saxatilis* is larger than that of *Apus*, being four, five, or six eggs (Bent, 1940; Bradbury, 1918; Rett, 1946). Since clutch-size is characteristic for each genus of Apodi, this reinforces the arguments given earlier for separating *Aëronautes* and *Apus*. The nests of *A. montivagus* and *A. andecolus* have not been found, but they are thought to be in holes in rocks in mountains (Taczanowski, 1884).

Panyptila (*Scissor-tailed Swifts*).—As discussed earlier, *Panyptila* stands between *Aëronautes*, which it strongly resembles in color pattern, and *Tachornis*, which it strongly resembles in nesting habits and to some extent in plumage. In color *Panyptila* is a rich glossy bluish black with white on throat and chest, nape, sides of rump, tips of secondaries, and a spot on each side of the forehead. The two species, *P. cayennensis* and *P. sancti-hieronymi*, differ only in size, but though allopatric they are placed in separate species. *P. sancti-hieronymi* breeds in Guatemala, also in Honduras (Carr and Dickinson, 1951) and probably in western Mexico (Selander, 1955). *P. cayennensis* occurs in eastern Mexico (Friedmann *et al.*, 1950) and to the south of the range of *P. sancti-hieronymi*, occurring over much of northern South America. The difference in size is remarkable for two forms otherwise so similar; Ridgway (1911) gives the wing-length of *P. cayennensis* as 116–120 mm. and that of *P. sancti-hieronymi* as 180–195 mm.

*Panyptila* builds an extraordinary nest, a long tubular structure which may be over two feet long even in the smaller species, though sometimes as short as seven inches. The entrance is at the lower end, and the eggs are in a lateral pocket or shelf near the top of the tube, which is wider than the rest. In both species the nest is suspended under either a high branch of a tree or an overhanging rock. The material consists of dried feathery tufts of plant seeds and often of feathers, and the whole is worked with saliva into a close felt. (For *P. sancti-hieronymi,* see Salvin, 1863; Salvin and Godman, 1888–1904; Carr and Dickinson, 1951: for *P. cayennensis,* see Sclater, 1897; Richmond, 1898; Williams, 1922; Belcher and Smooker, 1936; Sick, 1947). The original nest described by Salvin apparently had a false entrance, but this has not been mentioned by any other observer.

*Panyptila,* like other swifts, nests in a hole, but the hole is of its own construction. Like other swifts, also, it has taken to nesting on buildings, *P. cayennensis* hanging its nest from the ceilings of houses (Sclater, 1897; Beebe, 1910; Williams, 1922; Greenway, 1934). The nest described by Beebe was alongside that of a wasp, but other observers have not mentioned this, so it may have been a chance association. *Panyptila* further resembles other swifts in using the same site in successive years, an extra shelf being added to the same tube (Belcher and Smooker, 1936). One nest of *P. cayennensis* contained three eggs (Belcher and Smooker, 1936); a group of three young of *P. sancti-hieronymi* brought to Carr suggests that the clutch of this species may also be three (Carr and Dickinson, 1951). The birds are also said to use the nest for shelter during rain (Salvin, 1863; Salvin and Godman, 1888–1904; Richmond, 1898).

Tachornis (*New World Palm Swifts*).—As already mentioned, I consider the species listed by Peters as *Tachornis phoenicobia, Micropanyptila furcata,* and *Reinarda squamata* to be more closely related to each other than to any other swifts and therefore think it desirable to unite them in one genus, instead of having three monotypic genera. As can be seen from the following notes, they show various resemblances to each other (and at times also to *Panyptila*) in both color pattern and nesting habits.

All three species have the toes opposed in pairs, but *T. squamata* differs from the other two in having feathered, not bare, toes (which links it with *Panyptila,* in which, however, all the toes point forward). The tail is strongly forked in *T. squamata* and *T. furcata* (also in *Panyptila*), but weakly forked in *T. phoenicobia.* The upper parts are glossy blue-black in *T. squamata* (thus linking it with *Panyptila*), but the feathers have white edges; the upper parts are rather glossy in *T. furcata,* dull sooty in *T. phoenicobia.* The underparts of all three species are pale, darker on the flanks, while *T. furcata* and *T. phoenicobia* have a dark bank across the chest. The rump is dark in *T. squamata* and *T. furcata,* but white on the sides in *T.*

*phoenicobia* (recalling *Panyptila*). The secondaries are narrowly tipped with white in *T. furcata* (recalling the broad white tips of *Panyptila*). (I have taken the description of *T. furcata* from Sutton, 1928.)

*T. squamata* nests in the long tube formed by the hanging leaves of a palm (Belcher and Smooker, 1936; Sick, 1948). In design, as pointed out by Sick, the nest closely resembles the hanging pocket or shelf which forms the upper part of the tubular nest of *Panyptila*, but the lower part of the tube is, in *T. squamata*, part of the plant, and is not made by the bird. The nest is a thin-walled sac, but the feathers are not worked into a felt, so that from outside it looks like a loose bundle of feathers. The entrance is from below. The clutch is "usually 3" (Belcher and Smooker, 1936; and one record by Sick, 1948). *T. phoenicobia* likewise builds a globular nest with the entrance at the bottom, placed in a hollow palm spathe or under a drooping palm frond, and it is made of vegetable fibres or feathers, compacted into a felt (as in *Panyptila*). The clutch is two or three (Gosse, 1847; Bond, 1936). The nest of *T. furcata* is unknown.

*The critical taxonomic characters.*—The foregoing review indicates that some of the morphological characters previously relied upon for classifying swifts give misleading results. In particular, the furcation of the tail and the feathering of the toes seem highly modifiable, and the species which share these characters need not be closely related. Even the position of the toes in opposed pairs has probably been evolved independently in two groups. It is not that morphological characters as such are likely to give misleading results, but that various earlier workers have given too much weight to single characters considered in isolation. Certain morphological characters, such as the diastataxic wing in *Cypseloides*, taken together with other features, have proved valuable in delimiting genera.

Color pattern has often been considered a less reliable guide than morphological characters in delimiting genera and in determining the relationships between genera, but in swifts it tends to be characteristic for each main group of species. Presumably, in the Apodi, the color of the plumage has been more conservative in evolution than have various morphological features affecting toes and tail. Thus similarity in color helps to unite all the species here placed in *Cypseloides*, it links the African species of *Chaetura* (two of which were formerly separated in *Mearnsia*), it relates *Apus affinis* to the other members of that genus, it helps in the transference of *andecolus* from *Apus* to *Aëronautes*, and it shows the affinity between *Aëronautes* and *Panyptila*.

Size is not a good taxonomic character in swifts and within some genera, such as *Chaetura*, *Apus*, and *Panyptila*, it is very variable.

The evidence from geographical range supports conclusions based on color pattern, notably in bringing *andecolus* into *Aëronautes* and in separating *Cypsiurus parvus* from *Tachornis*. Most of the genera are restricted to the New or the Old World, while in *Chaetura*, which occurs in both, the species of the New World seem more closely related to each other than to any of those in the Old World.

Nesting habits have proved an extremely useful guide. By themselves they might be as untrustworthy as any other character taken singly for denoting affinities, but in the Apodi they strikingly support the evidence of plumage, of some morphological characters and of geographical range, in the division of the group into nine genera as in this paper. More surprisingly, clutch-size has also proved characteristic for each genus. The nesting habits of each genus are summarized in Table 1.

TABLE 1. NESTING HABITS OF SWIFTS

| *Genus* | *Situation* | | | | |
|---|---|---|---|---|---|
| | *general* | *particular* | *Shape* | *Main material* | *Typical clutch* |
| *Hemiprocne* | small high branch | on top | tiny cup | bark and feathers | 1 |
| *Cypseloides* | rocks by water | vertical surface | large cone | mud and moss fern tips | 1 (2) |
| *Collocalia* | cave | vertical surface | bracket | saliva<br>plant fibres<br>feathers | (1) 2 |
| *Chaetura* | hollow tree | vertical surface | bracket | twigs | 3 to 5 |
| *Apus* | cliffs | crevice | open cup | plant fibres and feathers | 2 to 3 |
| *Cypsiurus* | palm leaf | vertical surface | shallow shelf | plant fibres and feathers | 2 to 3 |
| *Aëronautes* | cliffs | crevice | open cup | plant fibres and feathers | 4 to 5 |
| *Panyptila* | rock or high branch | suspended under | long tube | plant fibres and feathers | 3 |
| *Tachornis* | folded palm leaves or spathe | up long tube | sac | plant fibres and feathers | 2 to 3 |

It is interesting to find that Mayr and Bond (1943) in classifying the swallows (Hirundinidae) reached a similar general conclusion for this group, namely that nesting habits are a valuable taxonomic character, while the feathering of the tarsus and the furcation of the tail are highly untrustworthy in delimiting genera. In the Hirundinidae, color pattern is in various respects unreliable, though these authors stress its general helpfulness in the classification of genera.

*Geographical conspectus.*—*Chaetura* is the most widespread genus of swifts, with breeding species in most of America (including the Nearctic), in the southern half of Africa, in Asia (including the Palaearctic), and in New Guinea. *Apus* is fairly widespread, with breeding species in the Palaearctic, in Africa, and in tropical Asia. The other genera are much more confined, *Hemiprocne* to southeastern Asia and adjoining archipelagoes, *Cypseloides* to tropical America with one species in northwest America, *Collocalia* to southeastern Asia and the islands of the Indian and Pacific oceans, *Cypsiurus* to tropical Africa and Asia, *Aëronautes* to the western mountains and seaboard of America, *Panyptila* and *Tachornis* to tropical America.

Only six species of swifts breed in appreciable numbers north of about latitude 50° N., *Apus apus* in Europe and western Asia, *Chaetura caudacuta* and *Apus pacificus* in eastern Asia, *Chaetura (p.) pelagica* in eastern North America, *Cypseloides niger* and *Chaetura (p.) vauxi* (and perhaps *Aëronautes saxatilis*) in western North America. These migrate south for the winter.

Most of the world's swifts are found in, and many are confined to, the tropics. Thus the mainland of tropical Africa supports 17 species (5 of *Chaetura,* 11 of *Apus,* 1 of *Cypsiurus*) and Madagascar and the Seychelles bring in 2 more (1 of *Collocalia,* 1 of *Chaetura*). Tropical Asia supports more than 20 species (3 of *Hemiprocne,* perhaps 10 of *Collocalia,* 5 of *Chaetura,* 3 of *Apus,* 1 of *Cypsiurus*). Tropical America, again, has 22 species (9 of *Cypseloides,* 5 of *Chaetura,* 3 of *Aëronautes,* 2 of *Panyptila,* 3 of *Tachornis*). In any one tropical country, however, there are at least as many species in Africa as elsewhere, as more of the Asiatic and American species replace each other geographically. Thus the number of breeding species in Mexico is 7 (Friedmann *et al.,* 1950), Colombia 10 (de Schauensee, 1948–49), Venezuela about 11 (that number has been recorded, but not all breeding at Rancho Grande alone, Schäfer and Phelps, 1954), former British India 11 (Baker, 1934), the whole of Malaysia including many archipelagoes 12 (Delacour, 1945), the Union of South Africa 9 (based on Roberts, 1940), Kenya about 11 (Praed and Grant, 1953), and the Belgian Congo about 15 (Chapin, 1939). Some of these figures are approximate as the exact status of some species is doubtful. In Kenya, Meinertzhagen (1937) once shot nine different forms from a single flock.

New Guinea, so rich in certain kinds of birds, has only 6 breeding species of swifts (1 of *Hemiprocne,* 4 of *Collocalia,* 1 of *Chaetura*). Surprisingly, Australia is almost devoid of resident swifts. Two species of *Collocalia* breed in the extreme northeast and that is all, though two migrants from Asia, *Chaetura caudacuta* and *Apus pacificus*, are widespread in winter.

*Size limits.*—The smallest swifts are found in the genera *Collocalia* and *Tachornis*, with wing-lengths around 90 mm., while the largest are *Hemiprocne mystacea*, the *Streptoprocne* section of *Cypseloides*, the *Hirund-apus* section of *Chaetura*, and *Apus melba*. In three species, *Hemiprocne mystacea*, *Cypseloides semicollaris*, and *Apus melba*, the wing-length may exceed 230 mm. It may be tentatively suggested that these size limits are imposed by the food supply. For catching very small insects, it is perhaps less necessary to travel so fast through the air but more necessary to be able to check and turn in flight. Anyway, below the lower limit of size in swifts, the swallows (Hirundinidae) take over, with their shorter and less specialized wing, slower speed but greater ability to check and turn. At the other extreme, swifts larger than those that exist might be unable to find enough large insects that are air-borne in daytime, at least during part of each year. Many larger insects take wing at night, but at dusk the nightjars (Caprimulgidae) take over, many of which are larger than swifts, while they also possess a greater ability in turning and hovering, and the eyes are modified for seeing in a dim light.

*Summary.*—1. The Apodi are here classified in 9 genera as follows, the number of species being placed in brackets: *Hemiprocne* (3), *Cypseloides* (9), *Collocalia* (not specified), *Chaetura* (17), *Apus* (10), *Cypsiurus* (1), *Aëronautes* (3), *Panyptila* (2), *Tachornis* (3). (See check-list which follows.)

2. The main changes from Peters are (i) a return to Hartert's (later Zimmer's) arrangement of *Cypseloides* but with the addition of *Streptoprocne*, (ii) the transfer of *andecolus* from *Apus* to *Aëronautes*, (iii) the grouping of *Reinarda* and *Micropanyptila* in *Tachornis*.

3. Color pattern is a helpful taxonomic character in swifts, but the furcation of the tail and the feathering of the toes are highly modifiable.

4. The situation and construction of the nest are characteristic for each genus, and so is clutch-size (See Table 1).

5. Many species now nest on buildings, including *Collocalia* (2 spp.), *Chaetura* (5 spp.), *Apus* (6 spp.), *Cypsiurus* (1 sp.), *Aëronautes* (1 sp.), and *Panyptila* (1 sp.).

## CHECK-LIST OF APODI

The changes from Peters (1940) are indicated in brackets. I have also changed Peters' order, conforming to the modern practice of putting first those genera with more primitive features.

### HEMIPROCNIDAE

*Hemiprocne* (Crested Swifts)

- *longipennis*
- *mystacea*
- *comata*

### APODIDAE

#### CHAETURINAE

*Cypseloides* (Primitive Swifts or Black Swifts)

- *zonaris* (transferred from *Streptoprocne*)
- *biscutatus* (transferred from *Streptoprocne*)
- *semicollaris* (transferred from *Aërornis*)
- *senex* (transferred from *Aërornis*)
- *rutilus* (transferred from *Chaetura*)
- *fumigatus*
- *cherriei*
- *cryptus* (described by Zimmer, 1945)
- *niger* (transferred from *Nephoecetes*)

*Chaetura* (Spine-tailed Swifts)

(i) *pelagica* (tentatively including *vauxi, gaumeri, richmondi, chapmani*)
*cinereiventris* (tentatively including *martinica*)
*spinicauda*
*andrei*
*brachyura*
(ii) *sabini* (including *thomensis*)
*ussheri*
*melanopygia*
*cassini*
*böhmi*
*sylvatica*
*leucopygialis*
*grandidieri*
(iii) *caudacuta*
(*cochinchinensis*?) (see Biswas, 1951)
*gigantea*
(iv) *picina*
*novaeguineae*

*Collocalia* (Cave Swiftlets) (species not listed)

#### APODINAE

*Apus* (Typical Swifts)

- *apus* (including *unicolor* and *alexandri*)
- *barbatus* (including *sladeniae, balstoni, mayottensis* and *bradfieldi*)
- *pallidus* (including *niansae*)

  *aequatorialis* (including *reichenowi*)
  *melba*
  *myoptilus* (including *poensis* and *batesi*)
  *caffer*
  *horus* (including *toulsoni*)
  *affinis*
  *pacificus* (including *acuticaudus*)
*Cypsiurus* (Old World Palm Swift)
  *parvus*
*Aëronautes* (White-throated and allied swifts)
  *saxatilis*
  *montivagus*
  *andecolus* (transferred from *Apus*)
*Panyptila* (Scissor-tailed Swifts)
  *sancti-hieronymi*
  *cayennensis*
*Tachornis* (American Palm Swifts)
  *phoenicobia*
  *furcata* (transferred from *Micropanyptila*)
  *squamata* (transferred from *Reinarda*)

## LITERATURE CITED

ARN, H. 1945. Zur Biologie des Alpenseglers *Micropus melba melba* (L.). Schweiz. Arch. Ornith., **2:** 137–181.

AUSTIN, O. L., and N. KURODA. 1953. The birds of Japan, their status and distribution. Bull. Mus. Comp. Zool., **109:** 478–480.

BAKER, E. C. S. 1927. The Fauna of British India. (Taylor and Francis, London.) Vol. 4: pp. 322–357.

BAKER, E. C. S. 1934. The Nidification of the Birds of the Indian Empire. (Taylor and Francis, London.) Vol. 3: pp. 452–477.

BANKS, E. 1949. A Naturalist in Sarawak. (Huchins, London). pp. 5–12.

BANNERMAN, D. A. 1933. The Birds of Tropical West Africa. (The Crown Agents for the Colonies, London.) Vol. 3: pp. 179–204.

BARTELS, M. 1929. De bouwhouding van *Hemiprocne longipennis longipennis* (Rafin.). Org. Cl. Nederl. Vogelk., **1:** 139.

BATES, G. L. 1905. Field-notes on the birds of Efulen in the West-African colony of Kamerun. Ibis, 1905: 91.

BATES, G. L. 1911. Further notes on the birds of Southern Cameroon. Ibis, 1911: 517.

BAXTER, E. V., and L. J. RINTOUL. 1953. The Birds of Scotland. (Oliver and Boyd, Edinburgh.) pp. 244–246.

BEEBE, M. B., and C. W. BEEBE. 1910. Our Search for a Wilderness. (Constable, London.) p. 143.

BEEBE. W. 1949. The Swifts of Rancho Grande, North-central Venezuela, with special reference to migration. Zoologica, **34:** 53–62.

BELCHER, C. F. 1930. The Birds of Nyasaland. (The Technical Press, London.) pp. 150–155.

BELCHER, C., and G. T. SMOOKER. 1936. Birds of the Colony of Trinidad and Tobago. Ibis, 1936: 24–28.

BENSON, C. W. 1952. Further breeding notes for Nyasaland. Bull. Brit. Ornith. Club, **72**: 63–64.

BISWAS, B. 1951. On some larger Spine-tailed Swifts, with the description of a new subspecies from Nepal. Ardea, **39**: 318–321.

BOND, J. 1936. Birds of the West Indies. (Academy of Natural Sciences of Philadelphia.) p. 202.

BOURNE, W. R. P. 1955. The Birds of the Cape Verde Islands. Ibis, **97**: 543.

BOXBERGER, L. v. 1934. Aus der Brutbiologie des Alpenseglers. Beitr. Fortpfl.-biol. Vög. **9**: 30–31.

BRADBURY, W. C. 1918. Notes on the nesting habits of the White-throated Swift in Colorado. Condor, **20**: 103–110.

CARR, M. H., and J. C. DICKINSON. 1951. The San Geronimo Swift in Honduras. Wilson Bull., **63**: 271–273.

CHAPIN, J. P. 1939. The Birds of the Belgian Congo. Pt. 2. Bull. Amer. Mus. Nat. Hist., **75**: 441–469.

CLANCEY, P. A., and C. S. HOLLIDAY. 1951. The Horus Swift, *Micropus horus* (Salvadori and Antinori) breeding in Natal. Ostrich, **22**: 122.

CLARK, H. L. 1906. The feather tracts of swifts and hummingbirds. Auk, **23**: 68–91.

COCHRANE, H. L. 1920. Nesting of White-rumped Swift (*Cypselus pacificus*). Emu, **19**: 176–178.

DAVIS, W. B. 1945. Notes on Veracruzan birds. Auk, **62**: 275–276.

DELACOUR, J. 1947. Birds of Malaysia. (Macmillan, New York) pp. 138–145.

DELACOUR, J., and E. MAYR. 1946. Birds of the Philippines. (Macmillan, New York.) pp. 124–130.

DICKIN, M. L. 1952. Nesting of the Horus Swift at Queenstown, Cape Province. Ostrich, **23**: 130.

DICKINSON, J. C. 1951. A nest of *Chaetura vauxi richmondi* in Central Honduras. Wilson Bull., **63**: 201–202.

DRESSER, H. E. 1871–1881. A History of the Birds of Europe. Vol. **4**: 583–589.

D'URBAN, W. S. M., and M. A. MATHEW. 1895. The Birds of Devon. (R. H. Porter, London). p. 106.

FORREST, H. E. 1907. The Fauna of North Wales. (Witherby, London.) p. 193.

FRANCK, P. FR. 1926. Ueber die Lebens- und Nistweise von *Collocalia francica vestita* (Lesson). Orn. Monatsb., **34**: 99–103.

FRIEDMANN, H. 1930. Birds collected by the Childs Frick expedition to Ethiopia and Kenya Colony. Pt. 1. U. S. Natl. Mus. Bull. 153, p. 317.

FRIEDMANN, H., L. GRISCOM, and R. T. MOORE. 1950. Distributional Check-List of the Birds of Mexico. Pt. 1. Pac. Coast Avif., **29**: 158–161.

GIBSON-HILL, C. A. 1947. Natural History of Christmas Island. Bull. Raffles Museum, **18**: 150–152.

GIBSON-HILL, C. A. 1948. The Malayan Swiftlets. Malayan Nature Journ., **3**: 190–200.

GIBSON-HILL, C. A. 1950. A note on the Crested Tree-Swift. Malayan Nature Journ., **5**: 5–8.

GLENNIE, E. A. 1944. Note on the nesting of the Himalayan Swiftlet (*Collocalia fuciphaga*). Journ. Bombay Nat. Hist. Soc., **44**: 593–597.

GOSSE, P. H. 1847. The Birds of Jamaica. (John Van Voorst, London.) pp. 58–63.

GREENWAY, J. C. 1934. *Panyptila cayennensis* (Gmelin) nesting in a house. Auk, **51**: 377–379.

HARTERT, E. 1892. Catalogue of the Birds in the British Museum, **16**: 434–518.

HARVIE-BROWN, J. A. and T. E. BUCKLEY. 1895. A Vertebrate Fauna of the Moray Basin, **2**: 298.

HOFFMANN, L., et al. 1951. Nouvelles observations sur les martinets pales. L'Oiseau, **21**: 304–309.

HOLT, E. G. 1927–1928. An ornithological survey of the Serro do Itatiaya, Brazil. Bull. Amer. Mus. Nat. Hist., 57: 287.

IHERING, H. VON. 1900. Catalogo critico-comparativo dos Ninhos e Ovos das Aves do Brazil. Rev. Mus. Paulista, **4**: 254–255.

INGRAM, C. 1955. The foot of the young Swift *Apus apus.* Ibis, **97**: 149–150.

JAHN, H. 1942. Zur Oekologie und Biologie der Vögel Japans. Journ. für Ornith., **90**: 207–209.

JARDINE, W. 1839. The Birds of Great Britain and Ireland. (W. H. Allen, London.) Vol. **2**: p. 406.

JOURDAIN, F. C. R. 1901. On the breeding habits of the Swift in Derbyshire. Zool., ser. 4: **5**: 286.

KELSALL, J. E., and P. W. MUNN. 1905. The Birds of Hampshire and the Isle of Wight. (Witherby, London.) p. 99.

KNOOR, O. A., and A. L. BAILY. 1950. First breeding record of Black Swift, *Nephoecetes n. borealis*, in Colorado. Auk, **67**: 516.

LACK, D. in press. The species of *Apus.* Ibis (1956).

LACK, D., and E. LACK. 1951a. The breeding biology of the Swift *Apus apus.* Ibis, **93**: 542–543.

LACK, D., and E. LACK. 1951b. Découverte de la reproduction d'*Apus pallidus* en France. Alauda, **19**: 49.

LOWE, P. R. 1939. On the systematic position of the Swifts (Suborder Cypseli) and humming-birds (Suborder Trochili), with special reference to their relation to the order Passeriformes. Trans. Zool. Soc. Lond., **24**: 307–346.

LOWTHER, E. H. N. 1949. A Bird Photographer in India. (Oxford University Press.) pp. 1–10.

LYNES, H., and J. VINCENT. 1939. The White-rumped Swift, *M. caffer*, beginning to breed under the eaves of houses. Ostrich, **10**: 75–84.

McGREGOR, R. C. 1909. A Manual of Philippine Birds. (Bureau of Printing, Manila.) Pt. 1. pp. 355–356.

MANUEL, C. G. 1937. Beneficial Swiftlet and edible birds' nest industry in Bacuit, Palowan. Philipp. Journ. Sci. Minch, **62**: 379–391.

MASTERSON, H. B. 1945. The Mottled Swift. Ostrich, **16**: 70–72.

MATHEWS, G. M. 1918. The Birds of Australia. (Witherby, London.) Vol. 7: pp. 246–268.

MAYR, E. 1937. Birds collected during the Whitney South Sea Expedition 33. Notes on the genus *Collocalia.* Amer. Mus. Novit. 915, 19 pp.

MAYR, E. 1945. Birds of the Southwest Pacific. (Macmillan, New York.) p. 77.

MAYR, E., and J. BOND. 1943. Notes on the generic classification of the swallows, Hirundinidae. Ibis, **85**: 334–341.

MAYR, E., E. G. LINSLEY, and R. L. USINGER. 1953. Methods and Principles of Systematic Zoology. (McGraw-Hill, New York.) p. 104.

MEINERTZHAGEN, R. 1937. Some notes on the birds of Kenya Colony. Ibis, 1937: 756.

MEYER, P. O. 1928. Zur Nistweise des Baumseglers, *Hemiprocne mystacea aëroplanes* Stres. Ornith. Monatsb., **36:** 137–138.

MICHAEL, C. W. 1927. Black Swifts nesting in Yosemite National Park. Condor, **29:** 89–97.

MICHAEL, E. 1926. The habits of the Swifts in Yosemite Valley. Condor, **28:** 109–114.

MOREAU, R. E. 1941. A contribution to the breeding biology of the Palm-Swift, *Cypselus parvus.* Journ. East Africa and Uganda Nat. Hist. Soc., **15:** 154–170.

MOREAU, R. E. 1942a. The breeding biology of *Micropus caffer streubelii* Hartlaub, the White-rumped Swift. Ibis, 1942: 27–49.

MOREAU, R. E. 1942b. *Colletoptera affinis* at the nest. Ostrich, **13:** 137–147.

NAUMBURG, E. M. B. 1930. The birds of Matto Grosso, Brazil. Bull. Amer. Mus. Nat. Hist., **60:** 143.

NELSON, T. H., and W. E. CLARKE. 1907. The Birds of Yorkshire. (A. Brown, London.) Vol. 1, p. 263.

NICHOLSON, E. M. 1951. Birds and Men. (Collins, London.) photo by J. Markham opp. p. 224.

NIETHAMMER, G. 1938. Handbuch der deutschen Vogelkunde. (Akademische Verlagsgesellschaft, Leipzig.) Vol. 2, p. 44.

OAKES, C. 1953. The Birds of Lancashire. (Oliver and Boyd, Edinburgh). p. 154.

ORTON, J. 1871. Notes on some birds in the museum of Vassar College. Amer. Nat., **4:** 713.

PETERS, J. L. 1940. Check-list of Birds of the World. (Harvard University Press, Cambridge.) Vol. 4: pp. 220–259.

PITELKA, F. A. 1944. White-throated Swift breeding with Cliff Swallows at Berkeley, California. Condor, **46:** 34–35.

PITMAN, C. R. S. 1931. The eggs of *Micropus caffer streubelii* (Hartl.)—The White-rumped Swift. Ool. Rec., **11:** 44–45.

PRAED, C. W. M., and C. H. B. GRANT. 1953. Birds of Eastern and North Eastern Africa. (Longmans, Green, and Co., London) pp. 776–792.

PRICE, F. W. 1888. Swifts laying in Martins' nests. Zool., ser. 3: **12; 68:** (also Zool., ser. 3: **11:** 348, 391, 428).

REBORATTI, J. H. 1918. Nidos y huevos de vencejos. Hornero, **1:** 193.

RETT, E. Z. 1946. An unusual nest of the White-throated Swift. Condor, **48:** 141.

RICHMOND, C. W. 1898. The Cayenne Swift, *Panyptila cayennensis* (Gmelin). Auk, **15:** 7–10.

RIDGWAY, R. 1911. The Birds of North and Middle America. Bull. U. S. Natl. Mus. 50, Pt. 5: 681–729.

ROBERTS, A. 1939. Swifts and other birds nesting in buildings. Ostrich, **10:** 85–99.

ROBERTS. A. 1940. The Birds of South Africa. (Witherby, London.) 154–158.

SALVIN, O. 1863. Descriptions of thirteen new species of birds discovered in Central America by Frederick Godman and Osbert Salvin. Proc. Zool. Soc. Lond., 1863: 190–192.

SALVIN, O., and F. D. GODMAN. 1888–1904. Biologia Centrali-Americana. (Taylor and Francis, London.) Aves, **2:** 366–81.

SCHÄFER, E., and W. H. PHELPS. 1954. Aves de Rancho Grande. Bol. Soc. Venez. Cienc. Natur. **16:** 68–71.

SCHAUENSEE, R. M. DE. 1948–1949. The Birds of the Republic of Colombia. Pt. 1. Caldasia, **5:** 514–517.

SCLATER, P. L. 1897. (Nest of *Panyptila cayennensis* from house.) Ibis, 1897: 262.

SCLATER, P. L., and O. SALVIN. 1879. On the birds collected by the late Mr. T. K. Salmon in the State of Antioquia, United States of Colombia. Proc. Zool. Soc. Lond., 1879: 486–550.

SCLATER, W. L., and R. E. MOREAU. 1932. Taxonomic and field notes on some birds of northeastern Tanganyika Territory. Ibis, 1932: 657–658.

SELANDER, R. K. 1955. Great Swallow-tailed Swift in Michoacán, México. Condor, **57**: 123–125.

SERLE, W. 1954. A second contribution to the ornithology of the British Cameroons. Ibis, **96**: 58.

SICK, H. 1947. O ninho de "*Panyptila cayennensis*" (Gmelin) e algumas observações compilatórias sôbre a ecologia de outros andorinhões brasileiros. Rev. Brasil. Biol., **7**: 219–246.

SICK, H. 1948a. The nesting of *Reinarda squamata* (Cassin). Auk, **65**: 169–174.

SICK, H. 1948b. The nesting of *Chaetura andrei meridionalis*. Auk, **65**: 515–520.

SICK, H. 1951. Umstellung der Nistweise beim Stachelschwanz-Segler *Chaetura andrei*. Journ. für Ornith., **93**: 38–41.

SMITH, E. 1928. Black Swifts nesting behind a waterfall. Condor, **30**: 136–138.

SPENNEMANN, A. 1928a. *Collocalia esculenta linchi* (Horsf.) Beitr. Fortpfl.-biol. Vög., **4**: 53–58, 98–103.

SPENNEMANN, A. W. 1928b. Die essbaren Vogelnester von Grissee. Ornith. Monatsb., **36**: 111–112.

STADLER, H. 1917. Vom Zug der Mauersegler (*Micropus apus apus* (L.)) im Maintal 1916. Verh. Ornith. Ges. Bayern, **13**: 74–86.

STEYN, P. B. 1952. The nesting of the African Great Swift. *Apus melba africanus*. Ostrich, **23**: 221–222.

STEVENSON, H. 1866. The Birds of Norfolk. (John Van Voorst, London.) p. 343.

STRESEMANN, E. 1926. Zur Kenntnis der Salanganen SO-Borneos. Orn. Monatsb., **34**: 104–108.

STRESEMANN, E. 1927–1934. Aves. Handbuch der Zoologie. ed. W. Kükenthal. (Walter de Gruyter, Berlin and Leipzig.) Vol. 7, pt. 2, pp. 834–837.

SUTTON, G. M. 1928. A new swift from Venezuela. Auk, **45**: 135–136.

SUTTON, G. M. 1948. Breeding of Richmond's Swift in Venezuela. Wilson Bull., **60**: 189–190.

SUTTON, G. M. 1951. Mexican Birds: First Impressions. (University of Oklahoma Press.) pp. 211–212.

TACZANOWSKI, L. 1884. Ornithologie du Perou. (A. Rennes, Paris.) Vol. 1: 229–235.

TAYLOR, J. S. 1949. Notes on the martins, swallows and swifts: Fort Beaufort, C. P. Ostrich, **20**: 26–28.

TAYLOR, LADY. 1955. Introduction to the Birds of Jamaica. (Institute of Jamaica, Macmillan, London.) p. 82.

TOWNLEY, D. 1936. Field notes on little-known Southern Rhodesian birds. Ostrich, **7**: 104–106.

USSHER, R. J., and R. WARREN. 1900. The Birds of Ireland. (Gurney and Jackson, London.) pp. 102–103.

VAN MEURS, H. 1928. Een nidologisch probleem dat om oplossing vraagt. Org. Club Nederland. Vogelkund, **1**: 23–70.

VAN SOMEREN, V. G. L. 1922. Notes on the birds of East Africa. Novit. Zool., **29**: 87–89.

VINCENT, A. W. 1946. On the breeding habits of some African birds. Ibis, **88**: 317–318.

VOLSØE, H. 1951. The breeding birds of the Canary Islands. Vidensk. Medd. Dansk naturh. Foren. 113: 61.

WEITNAUER, E. 1947. Am Neste des Mauerseglers, *Apus apus apus* (L.). Ornith. Beob., **44**: 135.

WILLIAMS, C. B. 1922. Trinidad Birds. Notes on the food and habits of some Trinidad birds. Trinidad and Tobago Bull,. **20**: 165–166.

ZIMMER, J. T. 1945. A new Swift from Central and South America. Auk, **62**: 586–592.

ZIMMER, J. T. 1953. Studies of Peruvian birds No. 64. The Swifts: Family Apodidae. Am. Mus. Novit. 1609. 20 pp.

*Edward Grey Institute of Field Ornithology, Oxford, England. December 19, 1954.*