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Systematics and Nomenclature of the Andean Swallow, "*Petrochelidon*" *andecola*

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The Andean Swallow is a relatively little-known species inhabiting the Puna zone (3,100-4,600 m) of the Andes of Peru, northern Chile, and Bolivia, and possibly northwestern Argentina (Fjeldså and Krabbe 1990). It was described by Lafresnaye and d'Orbigny in 1837 from a Bolivian specimen in the Paris Museum and, like most swallow species, was originally placed in the all-encompassing Linnaean swallow genus *Hirundo*, with the specific name *andecola*. It is a medium-sized swallow (mass 14-19 g; Turner and Rose 1989), weakly iridescent bluish or greenish above, and grayish-white below with a brownish throat.

Since its original description, the Andean Swallow has been moved about in a number of genera and its relationships debated. Sharpe (1885) synonymized *andecola* with the Brown-bellied Swallow, which he identified with the *Hirundo cinerea* of Gmelin, 1789, and placed in the genus *Atticora*, then a sort of wastebasket genus for a miscellany of Neotropical swallows. Hellmayr (1935) considered Gmelin's name to be unidentifiable, and used the next oldest species name for the Brown-bellied Swallow (*Petrochelidon murina* Cassin, 1853), while adopting for it the generic name *Orochelidon* proposed by Ridgway (1903). Although Ridgway mentioned only *murina* in differentiating *Orochelidon* from *Atticora*, *Neochelidon*, and *Notiochelidon*, Peters (1960) pointed out that, in a later publication, Ridgway (1904) included *andecola* in his new genus as well. Peters could find no characters to separate *Orochelidon* from *Notiochelidon*, and placed the Brown-bellied Swallow, but not the Andean Swallow, in *Notiochelidon*, where it remains in the modern literature (Turner and Rose 1989).

Meanwhile Berlepsch and Stolzmann (1896) had demonstrated that Sharpe was in error in synonymizing *andecola* with "*cinerea* Gmelin" (= *murina* Cassin), and that *andecola* was a good species. Possibly influenced by Sharpe, they placed *andecola* in *Atticora*. That large genus subsequently has been reduced to the extent that it now includes only two species, *fasciata* and *melanoleuca*, both of which differ from *andecola* in several ways, including possession of long, forked tails.

Chapman (1924) divided *andecola* into two subspecies, naming *oroyae* based on three adults and an immature bird from Oroya and Chipa, Peru, using color characters and the greater bill width of *oroyae* in his diagnosis. With only a pair before him, Hellmayr (1935) was skeptical about the validity of *oroyae*. Zimmer (1955) reexamined the type series and not only

verified Chapman's color characters, but found that *oroyae* had a significantly longer wing, a difference overlooked by both Chapman and Hellmayr.

In his description of *oroyae*, Chapman (1924:12) made the following comments: "The cliff swallows form such an obviously natural group that I hesitate to add to their genus a species that does not wear their distinctive pattern of marking and which is not known to build their peculiar type of nest. But the facts that I cannot find one good generic character separating this species from *Petrochelidon* and that in juvenal plumage *andecola* has the upper tail-coverts strongly tinged with ochraceous-tawny indicate that it may be placed in this genus without undue violence to either systematic or biologic ornithology."

Todd (1929), definitely a "splitter" at the generic level, pointed out that Ridgway (1904; erroneously cited by Todd as 1902) had "dismembered the old genus *Atticora* Boie," placing each species in a monotypic genus except for *andecola*, which, as mentioned above, he placed in his recently described genus *Orochelidon*. Todd completed the dismemberment of the old *Atticora* by creating a new monotypic genus, *Haplochelidon*, for *andecola*. Todd stated he could not follow Chapman in referring this species to *Petrochelidon*, "the very points he brings up arguing against such a disposition." Nevertheless, all subsequent authors have followed Chapman rather than Todd, and kept *andecola* either in *Petrochelidon* (Peters 1960) or in a broadened *Hirundo* that included *Petrochelidon* (Turner and Rose 1989, Sibley and Monroe 1990).

Chapman (1924) had pointed out that it was not then known whether *andecola* built a typical *Petrochelidon* mud-pellet nest. In a landmark paper, Mayr and Bond (1943) presented a tentative reclassification of the swallows, giving major importance to nest structure as a character. They mentioned the fact that the nesting habits of *andecola* were unknown, and went on to say: "Its nidification should either prove or disprove its relationship with typical '*Petrochelidon*.' If the nesting habits of this swallow are like those of the species included above under 'A', the recognition of Todd's *Haplochelidon* would seem justified." Their category "A" included species with the "nest placed in a crevice among rocks or in a building, hole in a tree, or in a burrow; no mud used in construction."

The first description of the nesting habits of the Andean Swallow appeared in the first Spanish-language edition of *Las Aves de Chile* by Goodall et al.

(1946). In my own translation, their statement was as follows: "As is known, all of the swallows of this genus [i.e. *Petrochelidon*] have the peculiarity of nesting in colonies, in crevices or caves, on the vertical faces of rocky crags or canyons, and it is evident that this species is faithful to this tradition, seeing that we found it nesting thus in Chismisa, although unfortunately on an inaccessible cliff." As Zimmer (1955) pointed out, this seemed to settle the question of whether *andecola* really was a cliff swallow (I use the uncapitalized name "cliff swallow" to refer to members of the genus or subgenus *Petrochelidon* in general), although he also cautioned that one could only infer from the authors' statement that *andecola* built mud nests, as this was not explicitly stated.

Niethammer (1956) described *andecola* as nesting in holes or crevices ("Löchern") in a house wall on a finca in Bolivia, with no further details. This could conceivably but improbably refer to mud nests of the *Petrochelidon* type.

The matter was finally settled when the English-language edition of *The Birds of Chile* appeared (Johnson 1967). The account of the nesting of *andecola* was expanded to read, "Like the related Cave and Cliff Swallow that breed in the northern hemisphere, the Andean Cliff Swallows nest in colonies in crevices or holes in the vertical surfaces of bluffs or escarpments; when the chosen location is soft enough the birds excavate the holes themselves, breaking the surface with their bills, and scraping or pushing the earth away with their feet like the Sand Martins [= *Riparia*] of Europe. Frequently the holes are so high up that they can only be reached with the aid of ropes or ladders." It is obvious that the acceptance of *andecola* as a *Petrochelidon* in *The Birds of Chile* was based solely on the fact that its nesting is colonial, the only thing that *andecola* has in common with cliff swallows.

If the Andean Swallow is not a cliff swallow, what is it? The description of its nesting habits—sometimes in preexisting holes, sometimes in holes it excavates for itself—immediately suggests another Neotropical genus, the rough-winged swallows (*Stelgidopteryx*). Upon making comparisons of external morphology, I found nothing that would be incompatible with a *Stelgidopteryx* relationship for *andecola*, and several points in common, such as the exceptionally large undertail coverts, to which Todd (1929) called attention in his description of the genus *Haplochelidon*. Of course, *andecola* lacks the recurved bars along the outer edge of the outer primary that give the rough-winged swallows their name, but this character is present only in adults, and is better developed in males than in females—its significance as a taxonomic character is uncertain (it also is present in *Psalidoprocne*, an otherwise very different genus of African swallows). The recurved bars are absent in the species generally accepted (Peters 1960, Turner and Rose 1989) as the closest relative of *Stelgidopteryx*, the Tawny-headed Swallow (*Alopochelidon fucata*). This spe-

cies otherwise closely resembles the rough-winged swallows morphologically; it has already been placed in *Stelgidopteryx* by Short (1975), followed by Ridgely and Tudor (1989) and Sibley and Monroe (1990). It is true that the Andean Swallow is the only one of this group to exhibit dorsal iridescence, although it is only weakly developed. However, within the rough-winged swallow superspecies, the exceptionally dark Central American subspecies *S. ridgwayi stuarti* shows a faint iridescence when in freshly molted plumage. There are iridescent and noniridescent swallows already accepted as closely related if not congeneric, such as the *Progne* and *Phaeoprogne* groups of martins and the noniridescent *Ptyonoprocne*, now generally placed in the genus *Hirundo* with many iridescent species. Resemblances among the Andean, Tawny-headed, and rough-winged swallows are further strengthened by comparing juvenile specimens. Chapman (1924) had invoked the reddish-brown rump of juvenile *andecola* as his only evidence for putting the species in *Petrochelidon*. This color, however, is completely compatible with its being a member of the *Stelgidopteryx* group. Within this group there is also a strong tendency for the underparts of juveniles to exhibit a rusty color, or at least a rusty wash. The flanks of juveniles of *andecola* have a light rusty wash not present in adults. I have examined juveniles of all South American swallows, either at Carnegie Museum of Natural History or the American Museum of Natural History (AMNH). None are rustier or redder in juvenal plumage than as adults except *Alopochelidon fucata*, *Stelgidopteryx ruficollis*, and "*Petrochelidon*" *andecola*.

Zimmer (1955), while admitting that "the generic separation of *Alopochelidon* from *Stelgidopteryx* is not very marked" except for the structural modification of the primaries of the latter, added a second character to "help maintain the genus [*Alopochelidon*] as at present recognized." He stated that the bill of *Alopochelidon* is notably weaker than that of *Stelgidopteryx*. However, this difference is bridged by the two subspecies of *andecola*. The bill of *oroyae* is even stronger than that of *Stelgidopteryx*, whereas that of nominate *andecola* is much weaker and approaches that of *Alopochelidon*.

In view of the evidence afforded by nesting habits and morphological characters, I regard the Andean Swallow as a member of a group that includes the Tawny-headed and rough-winged swallows. In view of the gaps between other recognized genera of swallows, I propose to include all of these in an expanded genus *Stelgidopteryx*—those who wish to call attention to the distinctive characters of the three components may consider the genus to consist of three subgenera, namely *Stelgidopteryx*, *Alopochelidon*, and *Haplochelidon*.

One might ask whether there is anything particularly important about shifting the generic affiliations of a rather obscure South American swallow.

This question leads to an aspect of the question of the relationships of the Andean Swallow not yet considered, namely zoogeographic implications. In recent years there has been interest in a synthetic approach that includes deductions about zoogeographic relationships among entire avifaunas, and about origins and movements of families and genera of birds. Every species that is wrongly classified creates noise in the system, and can lead to unwarranted conclusions. For example, whether *Petrochelidon* is considered as a valid genus or as a subgenus of *Hirundo*, it is a group that is virtually worldwide in distribution, but certainly of Old World origin. By the removal of *andecola* from *Petrochelidon*, the only representative in South America (other than North American migrants) of the entire *Hirundo* complex is the isolated population in Peru and Ecuador of the essentially Caribbean Cave Swallow, *H. (Petrochelidon) fulva*, considered an allospecies, *H. rufocollaris*, by some authors (Ridgely and Tudor 1989). More plausible zoogeographically is the placement of *andecola* in a wholly Neotropical radiation of swallows, one member of which (*Stelgidopteryx serripennis*) has reached the North Temperate Zone relatively recently. Along the same line of the effect of classification on zoogeographic analyses, Earlé (1987) mentioned in passing in a paper on the affinities of the African *Hirundo (Petrochelidon) fuliginosa* that *andecola* might not be a cliff swallow, and went on to say that it "may be a *Riparia* or close to it, since, though it is a colonial nester, apparently it does not use mud for nest building (Zimmer 1955, Johnson 1967)." This lumping was actually carried out by Phillips et al. (1964), who placed the rough-winged swallow (without discussion) in *Riparia*, the genus of the Bank Swallow or Sand Martin. As the classification now stands, the only representative of *Riparia* in the New World, *R. riparia*, is such a recent immigrant from the Old World that the New World population is considered by most authors to be subspecifically identical with the European population. The addition of the Neotropical *Stelgidopteryx* to *Riparia* would, of course, necessitate a completely different interpretation of the distributional history of *Riparia*. There are considerations other than zoogeographical against this particular lumping. Shortly after the publication of Phillips et al. (1964), Gaunt (1965), who assessed fossorial adaptations in the anatomy of *Riparia riparia*, showed that the resemblances between the Bank and rough-winged swallows were superficial and the differences major. More recently, Monson and Phillips (1981) reverted to using *Stelgidopteryx* for the rough-winged swallows. After the publication of Earlé's paper I sent him a copy of the script of my 1976 oral presentation on this subject, whereupon Dr. Earlé wrote me (letter of 18 December 1987), "I enjoyed reading the copy of your oral paper, more so as it was an exact reflection of my thoughts on the position of *andecola*."

A shorter version of this paper was presented at

the 1976 meeting of the American Ornithologists' Union. Its conclusions were made known to several ornithologists, as suggested by the "pers. comm." in Sibley and Monroe (1990), although those authors appear to credit me with a statement that the vocalizations of *andecola* resemble those of other *Stelgidopteryx*. I have made no such observations. Indeed, Ridgely and Tudor (1989), although expressing doubt that *andecola* truly belongs to the *Hirundo/Petrochelidon* complex, left it there "in light of reported voice similarities to other *Petrochelidon* (fide T. Parker)."

The enlarged *Stelgidopteryx* may be defined as a group of primarily Neotropical swallows that excavate nest holes or nest in previously existing cavities. They differ from other swallows in the Neotropical radiation (*Atticora*, *Neochelidon*, *Pygochelidon*, *Notiochelidon*) in having more or less rusty coloration in the juvenal plumage, and essentially square-ended, not forked tails (difference in length between outermost and central rectrices of unworn adult males less than 6 mm vs. 11–42 mm in other genera). The rectrices are also relatively broader, although approached by *Notiochelidon murina* in this respect. The undertail coverts are relatively long and broad. Zimmer (1955) has already shown that the toe characters used by Ridgway (1904) are not consistent.

A referee has suggested that the relationships of *andecola* lie with *Notiochelidon murina* rather than with *Stelgidopteryx*. The resemblances between *murina* and *andecola*, however, are superficial. In addition to the tail shape and color of juvenal plumage characters cited above, the wing shapes of the two genera are quite different. All *Stelgidopteryx* species in the sense of this paper have broad tertials, and their primaries extend beyond the tertials by only 40 to 45% of wing length. In *N. murina* the tertials are narrow and the primaries long, extending beyond the tertials 51 to 56% of wing length. The undertail coverts of *Stelgidopteryx* are white (*serripennis*, *fucata*), white with a subterminal black band (*ruficollis*, *ridgwayi*), or pale to dark gray with a white tip (*andecola*). Those of *N. murina* are jet black, with iridescent tips, quite unlike those of *Stelgidopteryx*. The tertials and undertail coverts of two other species placed by Sibley and Monroe (1990) in *Notiochelidon*, *cyanoleuca* and *pileata*, match those of *murina* (I have not examined *N. flavipes*).

As a peripheral aspect of this study, I investigated the validity of Chapman's (1924) subspecific division of *Stelgidopteryx andecola*. I examined the four specimens (including holotype) at the AMNH, assigned by Chapman to his new subspecies *oroyae*. The three specimens from La Oroya, Junín, appeared to be intergrades between *andecola* from farther south and a form represented by AMNH 174,266 from Chipa, Pasco, farther north. The Chipa specimen is distinctly more sooty, less pale gray, on the abdomen, and has blackish undertail coverts, tipped with buff. In *andecola* the abdomen is whitish to very pale gray, and the shorter (anterior) undertail coverts are whitish,

the longer ones varying from equally whitish to light brownish gray. In the birds from La Oroya, the undertail coverts and belly are darker than in *andecola*, but the undertail coverts are still no darker than brownish gray. In the Chipa bird, the undertail coverts are distinctly darker than any other area of the underparts, even the throat. The Chipa specimen matches the description of *oroyae* and the La Oroya specimens in the slightly more purplish (less greenish) blue of the dorsal iridescence, and in having pale shafts to the primaries. As the species has been recorded as far north as Ancash (FjeldsÅ and Krabbe 1990), an effort should be made to obtain more northern specimens to see whether they match that from Chipa.

The reexamination of avian classification at higher levels has received much attention in recent years, and has had an impact on attempts to construct plausible distributional histories of major taxa. The swallow cases considered here indicate that the erroneous classification of even a single species can have a significant effect on zoogeographic conclusions. "Cleaning up" such errors will improve the basic distributional data fundamental to future synthetic studies of several kinds.

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