

April (*ibid.*), so the hybrid was not necessarily taken near its point of origin.

Beecher (1950) considered *I. mesomelas* to be a nectar-feeding derivative of *I. chrysater*, although, if the greater degree of development of the retroarticular process is considered the more specialized condition, then *I. chrysater* could as easily have been derived from *I. mesomelas*. Regardless, the hybrid reported here definitely argues for a close relationship between these two species.

This is contribution Number 14 of the Wetmore Papers, a project supported in part by trust funds

from the Smithsonian Institution for completing unfinished work and study of undescribed material left by the late Alexander Wetmore.

#### LITERATURE CITED

- BEECHER, W. J. 1950. Convergent evolution in the American orioles. *Wilson Bull.* 63: 51-86.  
 WETMORE, A., R. F. PASQUIER, & S. L. OLSON. In press. Birds of the Republic of Panamá. Smithsonian Misc. Coll. 150, part 4.

Received 19 November 1982, accepted 4 February 1983.

### A Reinterpretation of Pamprodactyly in Swifts: a Convergent Grasping Mechanism in Vertebrates

CHARLES T. COLLINS

Department of Biology, California State University, Long Beach, California 90840 USA

Currently, several foot types, based on the number and arrangement of the toes, are recognized in birds. One of these types, the pamprodactyl foot, is characterized as having all four toes ordinarily directed forward (or capable of being turned forward) (Landsborough Thompson 1964, Van Tyne and Berger 1976, Raikow in press). As noted by Newton (1896: 972), however, "earlier ornithologists, having no better characteristics on which to rely, attached to the structure of the toes a value out of all proportion to their real taxonomic importance and thus a superabundance of technical terms was created." Often the definition of terms was based on the appearance of museum specimens and not living birds. Pamprodactyly is a clear example of this, and the mouse birds (Coliidae) and some of the swifts (Apodidae) are among those prominently, but incorrectly, mentioned as exhibiting this type of foot. Pamprodactyly does not describe the observed action of the toes of swifts and colies in life, and it obscures the recognition of a grasping mechanism showing a remarkable convergence toward that found in two other classes of vertebrates.

Although the term pamprodactyl was coined for the Coliidae (Murie 1872, 1873: 190), recent studies have shown that these birds have a very adaptable, flexible foot and can "alter the arrangement of their toes to suit the functional demands of the particular mode of locomotion employed at any time" (Bock and Miller 1959). In my observations of *Colius striatus* and *C. macrourus* in captivity, I have rarely seen them use a configuration approaching pamprodactyly; I exclude instances when they hung by one or two toes, with the remaining toes oriented forward but not involved in grasping. On occasion, they utilized a toe configuration similar to the lateral grasping pattern described below. The myology of the hindlimb and the grasping patterns in the Coliidae have recently been reviewed by Berman and Raikow (1982).

All swifts of the subfamily Chaeturinae (Peters 1940), including the Cypseloidinae (Brooke 1970), have a typical anisodactyl foot (hallux directed posteriorly, toes II, III, and IV directed anteriorly). The Apodinae (Peters 1940), comprising the genera *Apus*, *Cypsiurus*, *Tachornis*, *Reinarda*, *Micropanyptila*, *Aeronautes*, and *Panyptila*, are generally thought to be pamprodactylous. In the course of my field studies of swifts (Collins 1968, 1973a, 1980a, b), I have handled numerous living individuals of one to four species in each of five of these seven genera. In addition, I have observed House Swifts (*Apus affinis*) on a daily basis from hatching to fledging (Collins 1973b). The grasping mechanism in all of these swifts is consistent in that toes I and II (the hallux and innermost toe) are spread medially, together or slightly apart, and oppose toes III and IV (the central and outermost toes), which are spread laterally. This arrangement forms a laterally oriented, pincer-like grasp (Fig. 1) between the two pairs of toes. Hartert (1892) noted that the toes of some swifts (*Tachornis*, *Cypsiurus*, and *Reinarda*) occurred in opposing pairs. Ingram (1955, 1972) and Lack (1956) also noted this condition in the newly hatched *Apus apus* but considered it to be the zygodactyl condition and only typical of young birds; neither of these contentions is supported by the observations presented here.

The number of phalanges is reduced in toes III and IV of the Apodinae (Sclater 1865) through the fusion of elements (Zehntner 1890), making all the toes more equal in length, which would seem requisite for efficient lateral grasping of the type observed. Only when the toes fail to gain purchase, as on a smooth hard surface, and the swift begins to slide downward do they tend to assume the pamprodactylous condition so widely attributed to them; this toe position is also assumed in the relaxed foot and thus easily seen in museum specimens. The lateral grasping action seems particularly well adapted to holding on to the

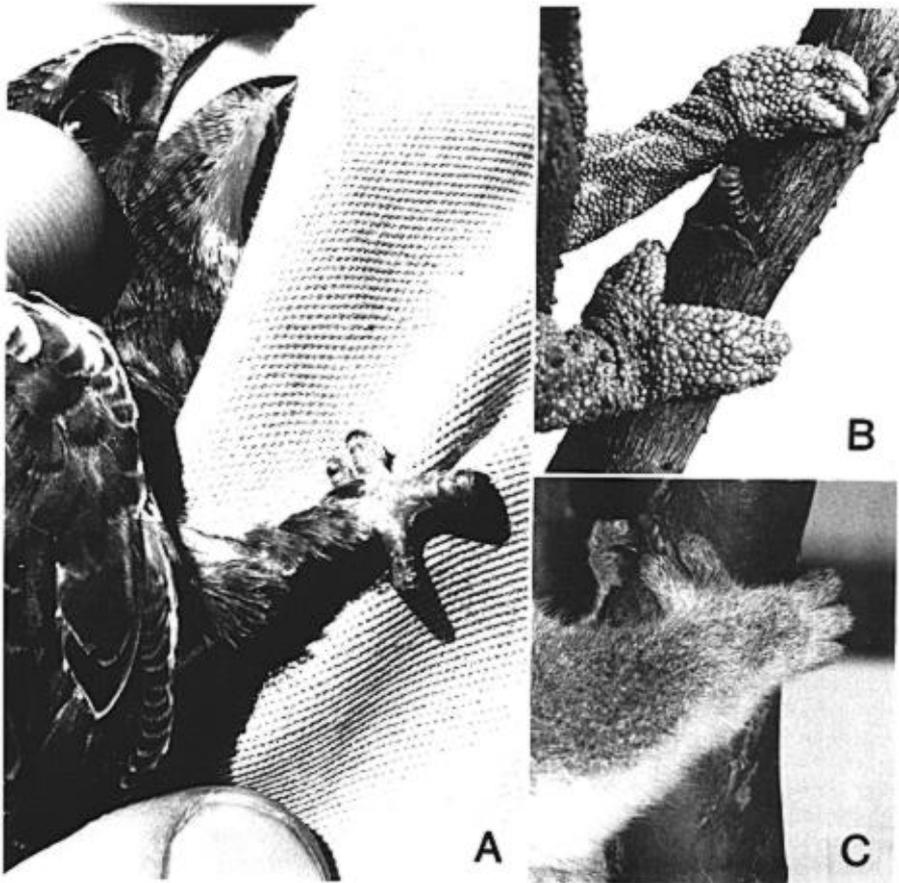


Fig. 1. Convergent lateral grasping mechanism in climbing vertebrates; (A) nestling House Swift, *Apus affinis* (Aves: Apodidae); (B) left and right forelimbs of Jackson's chameleon, *Chamaeleo jacksoni* (Reptilia: Chamaeleonidae); (C) right forelimb of koala, *Phascolarctos cinereus* (Mammalia: Phascolarctidae).

soft material, mostly plant floss and feathers, that makes up the nest of these swifts or to the palm-frond nest substrate of the four genera of palm swifts. Some of these swifts also roost in or on the nests in the nonbreeding season; none is known to utilize perch or roost substrates where lateral grasping would be at a disadvantage.

Other birds mentioned as having a pamprodactyl foot are some nightjars, including *Steatornis* (Ingram 1958), and the parrots of the genus *Micropsitta* (Bock and Miller 1959). Recent observations have shown that pamprodactyly is not typical of either *Steatornis* (Bock and Miller 1959) or *Micropsitta* (R. Orenstein pers. comm.). That any birds predominantly or even regularly use this toe configuration in the wild should be considered doubtful.

Zygodactyl and heterodactyl in the ornithological literature have more restricted definitions (Landsborough Thompson 1964, Van Tyne and Berger 1976, Raikow in press) than simply the "yoke-toed" con-

dition noted for reptiles and mammals. In the zygodactyl foot of birds, toes I and IV oppose II and III; in the heterodactyl foot, toes I and II oppose III and IV. Thus, the type of foot described here for the Apodinae corresponds in toe arrangement (toes I and II opposing III and IV), but not orientation (lateral rather than anterior-posterior), to the heterodactyl foot of trogons (Trogonidae).

A similar, laterally oriented, grasping mechanism can be seen in the "specialized 'zygodactylous' grasping feet" (Romer 1956) of the chameleons (Fig. 1) (Reptilia: Chamaeleonidae) and the forelimbs of numerous species of the phalangeroid mammals (Vaughn 1972), particularly the koala (*Phascolarctos cinereus*; Degabriele 1980) (Fig. 1). The Chamaeleonidae and phalangeroid mammals have pentadactylous feet. In the chameleonid manus, toes I, II, and III oppose IV and V, while in the pes toes I and II oppose III, IV, and V. In the manus of *Phascolarctos* (Degabriele 1980), toes I and II oppose III, IV, and V,

while in the pes toe I opposes II-V, with II and III being syndactyl.

This lateral grasping mechanism appears to be a particularly clear but overlooked case of convergence among these three classes of climbing vertebrates. It is doubtful that a single name can be usefully applied to this type of grasping foot. The further elucidation of the underlying tendon and muscle arrangements of the respective groups in which this grasping mechanism appears is a fertile area for further study.

My field studies have been generously supported by the F. M. Chapman Fund, American Museum of Natural History, the California State University (Long Beach) Foundation, and Cyril K. Collins. The study of *Apus affinis* was made possible by a Senior Fulbright Research Fellowship to India and the kindness of R. M. Naik, S. L. Warter, G. L. Callison, D. G. Huckaby, and R. J. Raikow made helpful comments on earlier versions of this paper.

#### LITERATURE CITED

- BERMAN, S. L., & R. J. RAIKOW. 1982. The hindlimb musculature of the mousebirds (Coliiformes). *Auk* 99: 41-57.
- BOCK, W., & W. DEW. MILLER. 1959. The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. *Amer. Mus. Novitates* 1931: 1-45.
- BROOKE, R. K. 1970. Taxonomic and evolutionary notes on the subfamilies, tribes, genera and subgenera of the swifts (Aves: Apodidae). *Durban Mus. Novitates* 9: 13-24.
- COLLINS, C. T. 1968. The comparative biology of two species of swifts in Trinidad, West Indies. *Bull. Florida State Mus.* 11: 257-320.
- . 1973a. Notes on survival and band wear in White-throated Swifts. *Western Bird Bander* 48: 20-21.
- . 1973b. Development of temperature regulation in the House Swift. *Pavo* 11: 1-11.
- . 1980a. The biology of the Spot-fronted Swift in Venezuela. *Amer. Birds* 34: 852-855.
- . 1980b. Notes on the food of the Horus Swift *Apus horus* in Kenya. *Scopus* 4: 10-13.
- DEGABRIELE, R. 1980. The physiology of the koala. *Sci. Amer.* 243: 110-117.
- HARTERT, E. 1892. Catalogue of birds of the British Museum, vol. 16. London, Trustees of the Brit. Mus.
- INGRAM, C. 1955. The foot of the young swift *Apus apus*. *Ibis* 97: 149-150.
- . 1958. Notes on habits and structure of the Guacharo *Steatornis caripensis*. *Ibis* 100: 113-119.
- . 1972. The feet of young swifts *Apus apus*, *caffer* and *affinis*. *Bull. Brit. Ornithol. Club* 92: 96.
- LACK, D. 1956. A review of the genera and nesting habits of swifts. *Auk* 73: 1-36.
- LANDSBOROUGH THOMPSON, A. 1964. A new dictionary of birds. London, T. Nelson and Sons.
- MURIE, J. 1872. On the genus *Colius*, its structure and systematic place. *Ibis* 3 (3rd ser.): 262-280.
- . 1873. On the Upupidae and their relationships. *Ibis* 4 (3rd ser.): 181-208.
- NEWTON, A. 1896. A dictionary of birds. London, A. & C. Black.
- PETERS, J. L. 1940. Checklist of birds of the world, vol. 4. Cambridge, Harvard Univ. Press.
- RAIKOW, R. J. In press. The locomotor system. In *Form and function in birds*, vol. 3 (A. S. King and J. McClelland, Eds.). London, Academic Press.
- ROMER, A. S. 1956. Osteology of the reptiles. Chicago, Univ. Chicago Press.
- SCLATER, P. L. 1865. Notes on the genera and species of Cypselidae. *Proc. Zool. Soc. (London)* 39: 593-617.
- VAN TYNE, J., & A. J. BERGER. 1976. Fundamentals of ornithology. New York, J. Wiley and Sons.
- VAUGHN, T. A. 1972. Mammalogy. Philadelphia, W. B. Saunders Co.
- ZEHTNER, L. 1890. On the development of the feet of *Cypselus melba*. *Ibis* 1890: 196-200.

Received 15 October 1982, accepted 21 March 1983.

### The Raising of a Ghost—*Spinus cucullatus* in Puerto Rico

HERBERT A. RAFFAELE

Department of Ecology and Evolution, State University of New York at Stony Brook,  
Stony Brook, New York 11794 USA

The Red Siskin (*Spinus cucullatus*) has been referred to in most major works on the birds of Puerto Rico ever since it was first listed by Sundevall (1869). Recent references have repeated Gundlach's (1878: 207) statement that the collector of the bird told him that the specimen was not taken in the wild but was a cage bird. Weary of the unwarranted inclusion of the

species in the island's bird lists, Leopold (1963: 6) stated, "Surely, after nearly a hundred years, it is time that this ghost be laid."

Despite Leopold's lament, the ghost of the Red Siskin was not to succumb feebly. Biaggi (1970) retained *S. cucullatus* in the main text rather than placing it in the appendix of doubtful reports, a puzzling inclu-