

of these observations or comments on an earlier version of this paper. The research was supported by NSF grants DEB-810519 and DEB-761009.

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A Hybrid Between the Orioles *Icterus chrysater* and *I. mesomelas*

STORRS L. OLSON

National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 USA

The Yellow-backed Oriole (*Icterus chrysater*) and the Yellow-tailed Oriole (*Icterus mesomelas*) are broadly sympatric neotropical species of Icteridae that range jointly from southern Mexico through Colombia and parts of Venezuela. The range of *I. mesomelas* also extends south into Ecuador and Peru, whereas *I. chrysater* is strangely absent from Costa Rica. Both species are approximately the same size, and both are largely orange-yellow in color with the gular patch, lores, and most of the wings black. *Icterus mesomelas* differs from *I. chrysater* in that the mantle is black instead of yellow, the secondary coverts and three outer rectrices are entirely or partly yellow instead of black, and there is less black on the forehead than in *I. chrysater*.

In the collections of the National Museum of Natural History, Smithsonian Institution, is a specimen (USNM 403540) that is best interpreted as a hybrid between these two species. It was taken by M. A. Carriker, Jr., on 25 March 1948 at Hacienda Belén, 13 km (8 miles) west of Segovia, Dept. Antioquia, Colombia, at an elevation of 245 m (800 feet). It is labelled as a male, and, although there are no remarks on the condition of the gonads, it appears to be fully

adult, with the feathers of the gular patch entirely black.

The feathers of the mantle of the hybrid are yellow basally, tipped broadly with black in the area that is entirely black in all adult individuals of *I. mesomelas* examined (Fig. 1). Although the back is normally entirely yellow in *I. chrysater*, there was some trace of black in this region in 7 specimens (all males from Colombia) out of about 150 adults from Colombia and Panama. The traces ranged from a few feathers barely tipped with black to a faint scaly pattern in three individuals. In no instance was there any approach to the extreme condition shown by the hybrid.

In adults of *I. chrysater* the tail is entirely black. In the hybrid, however, the outermost rectrix on either side is narrowly edged with yellow and has a fairly wide stripe of yellow along the rachis that expands slightly distally and stops about 5 mm short of the tip of the feather (Fig. 1). The next rectrix inward has a faint yellow margin on the outer web. In *I. mesomelas* these feathers are yellow except at the bases, which are black. In *I. chrysater* the rectrices are typically black, although five specimens I examined had

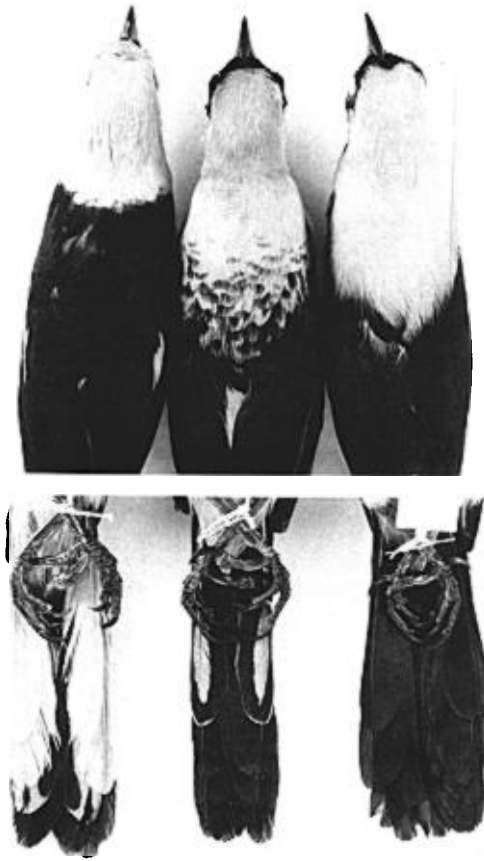


Fig. 1. (Top) Dorsal view of adult males of *Icterus mesomelas* (left), *I. chrysater* (right), and a hybrid between these two species (middle, USNM 403540). (Bottom) Ventral view of the tails of the same specimens.

yellow in the outer rectrix in a manner somewhat similar to that in the hybrid. All of these were clearly subadult birds, however, and the edges of the yellow pattern were more diffuse, sometimes much more so.

In *I. chrysater* the only yellow feathers on the outer surface of the wing are at the very apex of the bend, whereas in *I. mesomelas* the lesser coverts and median secondary coverts are yellow. The hybrid is approximately intermediate, as there is considerably more yellow on the lesser coverts than in *I. chrysater*.

There is much overlap in measurements between *I. chrysater* and *I. mesomelas*, although skins of *I. mesomelas* frequently tend to appear larger, particularly in Carriker's uniformly prepared series. This is the case with the hybrid, which is perhaps what influenced Carriker to enter it in his field catalog as "*Icterus* _____ (?) (near *mesomelas*)."

Yet, if the specimen were not a hybrid, it would probably have to

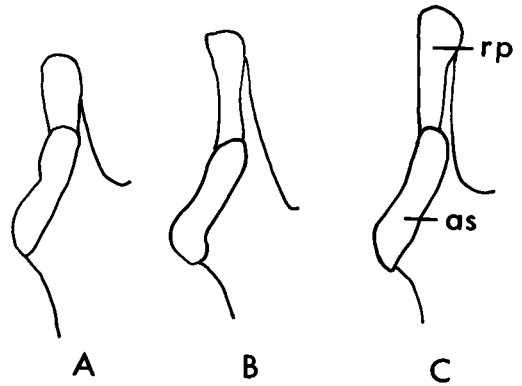


Fig. 2. Camera lucida drawings of the posterior end of the right mandible in dorsal view, showing the degree of development of the retroarticular process (rp): A, *Icterus mesomelas*; B, hybrid; C, *I. chrysater* (as = lateral articular surface of mandible).

be considered an aberrant individual of *I. chrysater* because of the amount of black on the forehead and the occasional occurrence of yellow in the outer rectrix of subadults in that species. On the other hand, if it were an abnormally melanistic individual of *I. chrysater*, one would not expect to find a greater amount of yellow in the bend of the wing.

In comparing skeletons, it may be seen that *I. chrysater* is more highly adapted for gaping and consequently has a noticeably longer retroarticular process of the mandible than does *I. mesomelas*. To check this condition in the hybrid I opened the skin and removed the posterior portion of the right mandible, in which the retroarticular process was fortunately intact. The hybrid is again intermediate, as the retroarticular process is decidedly better developed than in *I. mesomelas* but is shorter than in *I. chrysater* (Fig. 2).

It is difficult to determine what may have lead to this instance of hybridization or why no other instances have been reported elsewhere in the extensive area of sympatry of the two parental species. When Carriker collected at Hacienda Belén, the vegetation consisted mainly of heavily forested hillsides with some old second growth along the river. Apart from one specimen of *I. auricapillus*, Carriker obtained no other orioles during more than 2 weeks at this station; he made no remarks as to whether he observed any that he did not collect. It is possible that a lack of suitable habitat and the consequent scarcity of mates may have been a factor contributing to hybridization. This would be difficult to argue; although *I. mesomelas* tends to prefer edge situations near water, both species may be found in a considerable variety of habitats (Wetmore et al. in press). Furthermore, in Panama, both species tend to breed later than most other icterids, probably beginning in

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.

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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