

prove to be the most common in appropriate habitat. Surveys from northern New Mexico to the U.S.-Canadian border (37–49° N latitude) have now revealed that populations of this species are apparently not limited to isolated Pleistocene relicts as suggested by Baldwin and Koplín (1966), but rather appear to form a more continuous distribution throughout the Rocky Mountain range.

Do recent discoveries of Boreal Owls in the North Cascades (Parsons and Kragh in Mattocks 1986) suggest a link to the earlier southern specimen records; and what of the June 1985 Sierran report of a calling Boreal Owl near Echo Summit, California (approximately 39° N latitude; Green in Campbell and Bailey 1985)? Are all these incidents of true vagrancy or the disregarded indicators of other extensive, as yet undetected populations? It would appear that these last major western mountain corridors south of the Canadian border merit a thorough investigation.

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A MODIFIED JAW MUSCLE IN THE MAUI PARROTBILL (*PSEUDONESTOR*: DREPANIDIDAE)¹

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Key words: *Drepanididae*; Hawaiian Islands; jaw muscle; Maui Parrotbill; *Pseudonestor*; skull.

The Maui Parrotbill (*Pseudonestor xanthophrys*) is one of several species of Hawaiian honeycreeper (Drep-

anididae) in which the tip of the upper jaw projects well beyond that of the lower jaw. The bird's resemblance to a parrot is heightened by a deep and strongly decurved upper jaw and a recurved tip on the lower (Fig. 1). Opposite curvature of the tomia in the two jaws is unusual in birds; among passerines it is most highly developed in *Loxia* (crossbills) and *Dysmoredrepanis munroi*, a Hawaiian honeycreeper known only from the type specimen (Perkins 1919; James et al., in

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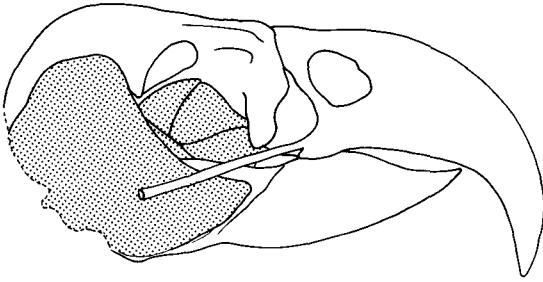


FIGURE 1. Skull of *Pseudonestor xanthophrys* with dried muscles (stipple) and rhamphotheca in place.

press). The upper jaw alone is used in certain foraging behaviors of *Pseudonestor* according to Perkins (1903) and Mountainspring (1987). Mountainspring further remarked that the skull and jaw muscles are peculiar. The following preliminary comments on the skull and jaw muscles of *Pseudonestor* clarify some of these points, pending a more thorough description of better material.

My remarks on *Pseudonestor* are based on a cleaned skull (British Museum [Natural History]: BM S/1961.11.40) and dried muscles on an incomplete skull removed from a mounted skin (Bernice P. Bishop Museum: BBM-240). For this study I examined skulls of 32 species and races of Drepanididae (number of specimens in parentheses); terminology follows Greenway

(1968): *Himatione sanguinea sanguinea* (22); *H. s. freethii* (1); *Palmeria dolei* (1); *Vestiaria coccinea* (17); *Ciriodops anna* (1); *Viridonia virens stejnegeri* (7), *V. v. chloris* (4), *V. v. wilsoni* (4), *V. v. virens* (29), *V. parva* (7), *V. sagittirostris* (1); *Hemignathus obscurus procerus* (1), *H. o. obscurus* (1), *H. lucidus* ssp. (1), *H. wilsoni* (3); *Loxops coccinea coccinea* (2), *L. c. caeruleirostris* (2); *Paroreomyza maculata bairdi* (1), *P. m. mana* (3), *P. m. maculata* (1), *P. m. flammea* (1), *P. m. newtoni* (5); *Pseudonestor xanthophrys* (1); *Psittirostra psittacea* (2); *Loxioides cantans cantans* (15), *L. c. ultima* (5), *L. palmeri* (1), *L. flaviceps* (1), *L. bailleui* (6), *L. kona* (1); *Melamprosops phaeosoma* (1); *Dysmorodrepanis munroi* (1). I follow the anatomical terminology of Baumel et al. (1979) where possible, and of Richards and Bock (1973) and Zusi (1978) for additional features of the palate and braincase.

RESULTS

The interorbital septum of the skull in the Carduelinae and many Drepanididae differs from that of other conical-billed passerines in several ways. It is complete and relatively thick; it forms a broad, and usually flat, floor of the cranial fenestra (fonticulus orbitalis of the braincase); and it separates the optic foramina (Zusi 1978). The most typically cardueline septa among the Drepanididae are those of *Psittirostra* and *Loxioides* (Fig. 2), in which the entire septum is ossified and double-walled, supported by internal trabeculae (two of six specimens of *L. bailleui* had a small interorbital fenestra). The septum is thinner in other members of the family, most of which have a single-walled, flat,

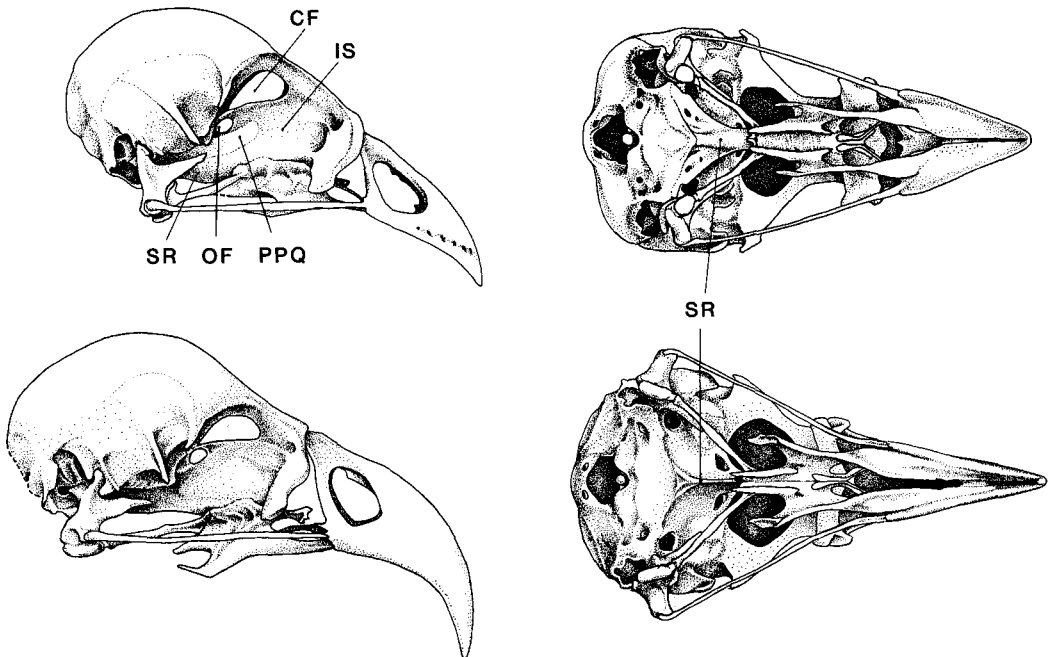


FIGURE 2. Skulls of *Psittirostra psittacea* (above) and *Pseudonestor xanthophrys* (below) in lateral (left) and ventral (right) views. Note knife-like sphenoidal rostrum (S R) of *Pseudonestor*. C F, cranial fenestra; I S, interorbital septum; O F, optic foramen; P P Q, scar of *M. protractor pterygoidei et quadrati*.

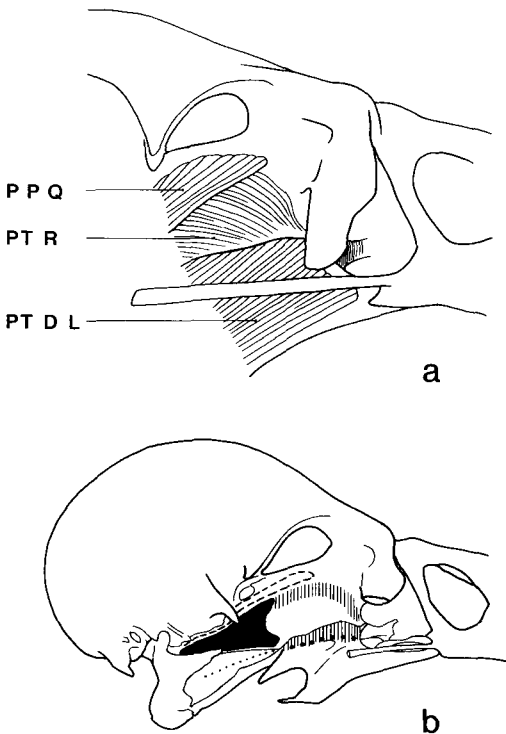


FIGURE 3. Skull and jaw muscles of *Pseudonestor xanthophrys*. (a) Dried muscles of BBM-240, male: P P Q, protractor pterygoidei et quadrati; PT D L, pterygoideus dorsalis lateralis; PT R, pterygoideus retractor. (b) Skull of BM S/1961.11.40, female, showing muscle attachments: dashed outline is protractor pterygoidei et quadrati; vertical hatching shows known attachment of pterygoideus retractor, and black area indicates inferred attachment. Large dots indicate attachment of an aponeurosis and small dots an inferred aponeurotic extension.

translucent, central portion of the septum. Many of these species have a fenestra in the single-walled portion. The presence and size of both of these features of the septum are variable within and between species.

Another feature of the interorbital septum in many birds is the scar of the protractor muscle (*M. protractor pterygoidei et quadrati*)—a somewhat roughened, oblong depression ventral to the optic foramen and cranial fenestra (Fig. 2). This is the only jaw muscle that typically originates, at least in part, from the interorbital septum in passerine birds.

In *Pseudonestor* the caudolateral surfaces of the sphenoidal rostrum are excavated (concave) caudally almost to the basitemporal plate (lamina basiparasphe-noidalis). The midventral portion of the caudal half of the sphenoidal rostrum is consequently narrow and knife-like (Fig. 2). The concavity extends forward and expands over most of the interorbital septum, which is unusually thin and flattened for a heavy-billed drepanidid. Most of the septum is single-walled, but thicker than the translucent portions of other species. I found no scar of the protractor muscle on the interorbital septum (Fig. 2).

Examination of dried muscles on a skull (BBM-240, male) revealed that, unlike other passerines, a major portion of the interorbital septum in *Pseudonestor* is occupied by a muscle (Fig. 3). This muscle originates fleshy from the flattened, single-walled depression of the interorbital septum; the complete origin is unknown because the caudal portions of both muscles and of both orbits, the basitemporal plate, and the caudal portion of the sphenoidal rostrum had been removed. Fibers pass rostroventrally to insert on the lateral surface of the palatine hasp and on an aponeurosis that attaches along the ventrolateral surface of the hasp (Fig. 3). The rostral limit of this aponeurosis is a lateral ridge on the rostral edge of the palatine at its junction with the vomer. Here the aponeurosis has a more dorsally oriented wing that receives fibers from the rostral portion of the muscle. Because the pterygoideus and caudal end of the palatines had been removed, I could not determine the full extent of the origin and insertion. The belly on the septum is rather flat and thin; it becomes thicker caudally, where it was cut off. The orientation of fibers in the incomplete, caudal portion was not clear because the muscle appeared to have dried in a distorted position. The rostral portion of the muscle is unipennate.

My interpretation of this muscle, based in part on the structure of the complete skull, is that it represents an expanded *M. pterygoideus retractor*. The retractor portion of the pterygoideus muscle is widely present within passerines (Fiedler 1951, Bock 1960). In most species it originates from the ventral portion of the braincase rostral to the basitemporal plate, between the bony opening of the pharyngotympanic tubes and the caudal portion of the origin of *M. protractor pterygoidei et quadrati*. Fibers pass rostrally along the sphenoidal rostrum to insert on the rostradorsal portion of the pterygoid and the pterygoid process of the palatine. Pars retractor represents only a small part of the entire pterygoideus complex.

Although the scar of *M. protractor pterygoidei et quadrati* is not evident in skulls of *Pseudonestor*, the muscle is well developed. The ventral border of its origin has been displaced dorsally by the expanded retractor (Fig. 3). The origin is from the laterally flared interorbital septum between the dorsal border of *M. pterygoideus retractor* and the cranial fenestra and optic foramen. The caudal portion of the muscle had been removed.

Among the Carduelinae, the palatine retractor is enlarged in *Coccothraustes coccothraustes* (Fiedler 1951, p. 259; Nekrasov 1978, fig. 25A), and probably throughout the genus (enlarged in *C. hesperiphona* based on dissection, and in *C. migratorius*, *C. personata*, *C. melanozanthos*, and *C. carnipes* based on skull structure; Zusi, pers. observ.). In *C. hesperiphona* the muscle originates from the ventral portion of the braincase rostral to the basitemporal plate, from the excavated, caudolateral portion of the sphenoidal rostrum and from the adjacent portion of the interorbital septum opposite the full length of the pterygoid bone. It inserts on the dorsocaudal surface of the pterygoid process of the palatine and on the medial surface of a long aponeurosis from the rostradorsal edge of the pterygoid. The aponeurosis extends caudally between the pterygoid and cranium to the level of the dorsal process of the pterygoid. Its lateral surface is occupied by fibers

of part of *M. pterygoideus dorsalis medialis* (posterior part). *M. protractor pterygoidei et quadrati* and its long aponeurosis from the dorsal process of the pterygoid lie caudodorsal and parallel to the pterygoid retractor. The midventral line of the sphenoidal rostrum is ridge-like and the rostrum and ventral portion of the interorbital septum are unusually narrow; these surfaces are occupied by fibers of the palatine retractor. The ventral border of the protractor scar is poorly defined and displaced dorsally by the palatine retractor. However, rostral expansion of the muscle and modification of the main portion of the septum as seen in *Pseudonestor* are absent.

Morphological evidence from both *Pseudonestor* and *Coccothraustes* indicates that the following skeletal features accompany maximum enlargement and expansion of the palatine retractor: narrowing and lateral excavation of the sphenoidal rostrum and adjacent braincase; a ridge-like midventral contour of the caudal portion of the sphenoidal rostrum; flattening and excavation of the interorbital septum; and dorsal constriction of the protractor muscle scar. These features are lacking in the drepanidid species listed at the outset of this paper, with the following exceptions: the first two features are present in *H. wilsoni* and to a lesser extent in *H. lucidus*, and all four are present in *Pseudonestor*. In *H. wilsoni* the caudolateral portion of the sphenoidal rostrum is excavated (concave) such that its midventral portion is narrow and ridge-like. Further rostral the ridge gives way to a typically rounded rostrum. The scar of the protractor muscle is well-defined and the interorbital septum is not modified. These features suggest an enlarged palatine retractor in this species, with no great deviation from the normal structure of the muscle.

Sims (1955) described two muscles in *C. coccothraustes* (ethmo-mandibularis; pterygoideus dorsalis medialis) as arising on the rostral portion of the interorbital septum and inserting on the mandible. From my examination of a skull of that species and dissection of *C. vespertinus*, and illustrations of *C. coccothraustes* in Nekrasov (1978, fig. 25A), I judge that "ethmo-mandibularis" is a part of *M. pterygoideus dorsalis lateralis*, and that the alleged attachments of both muscles on the interorbital septum are in error. Sims (1955) did not mention the retractor portion of *M. pterygoideus*.

Structure of *M. pterygoideus* in several drepanidids is well described in Richards and Bock (1973). The bulk of this complicated muscle connects the palatine and pterygoid with the ramus of the lower jaw. Both attachments are moveable relative to the cranium and the muscle therefore has a dual function—depression of the upper jaw by retraction of the palate and adduction of the lower jaw. Only one small part, the retractor portion of *M. pterygoideus*, attaches on the braincase and its sole action is retraction of the palate. This is the only jaw muscle that serves to depress the upper jaw without direct effect on the lower jaw as well. The function of the highly modified muscle in *Pseudonestor* would be the same.

DISCUSSION

The remarkable enlargement of the pterygoid retractor in *Pseudonestor* probably evolved by expansion of the

origin rostrally along the sphenoidal rostrum and then onto the interorbital septum. At the same time, the insertion expanded from the pterygoid-palatine junction rostrally to the anterior limit of the palatine hasp. Aponeuroses supplemented the palatine hasp for insertion of the new muscle fibers. *M. pterygoideus, pars retractor*, could anchor the upper jaw on the cranium against forces that would raise the jaw, depress the upper jaw independent of motion of the lower, combine with other muscles to enhance the force of biting, or retract the whole jaw apparatus relative to the cranium. All but the last of these actions appear to play an important role in the feeding behavior of this species. Perkins (1903) and Mountainspring (1987) describe its methods of exposing beetle larvae hidden in hard wood. The birds dig into cracks or borer tunnels with the tip of the upper jaw and then pry or tug on the wood. The upper jaw is also used for ploughing or scraping of old wood, and for pecking. Both jaws are used to seize prey and to split hard branches containing borer tunnels. Wrenching motions of the head may enhance the effect of the grip. These descriptions imply extensive use of the upper jaw alone in forceful actions, as well as a need for a powerful grip by both jaws.

Males of *Pseudonestor* are larger than females and have notably larger bills (Amadon 1950). Mountainspring (1987) discussed foraging differences between the sexes and concluded that males excavated deeper and probed and plucked more frequently than females; both sexes engage in the strenuous activities of excavating and twig splitting. Enlargement of the retractor muscle is present in both sexes (observed on skull of male; inferred from interorbital septum of female).

Bock (1970) regarded *P. xanthophrys* as intermediate between the thin-billed *Loxops* and *Hemignathus* and the heavy-billed *Psittirostra*, and stated that *Psittirostra psittacea* could have evolved from *Pseudonestor*. Discovery of the unique character complex involving morphology of at least the bill, skull, and jaw muscles, however, indicates that *Pseudonestor* was not "ancestral" to other known groups.

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OBSERVATIONS OF THE RED-BILLED GROUND-CUCKOO
(*NEOMORPHUS PUCHERANII*) IN ASSOCIATION WITH
TAMARINS (*SAGUINAS*) IN NORTHEASTERN
AMAZONIAN PERU¹

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Key words: Commensalism; Amazonia; Neomorphus; Saguinas; nutrition; ornithology; ecology.

The neotropical ground-cuckoos (*Neomorphus*), reviewed by Haffer (1977) are rare, terrestrial birds which range from Nicaragua to southeastern Brazil. In Amazonian Peru, they inhabit forested, hilly areas including terra firme forest with palms. Their postures and shape remind one of the better-known *Geococcyx* road-runners of the arid scrub regions of Mexico and southwestern United States. Ground-cuckoos are nonparasitic, utilizing their own nest and investing in offspring (Sick 1949, 1962; Roth 1981). These birds are known to associate with army ant swarms, eating exposed insects and small vertebrates in a manner similar to several formicariid antbirds (Willis and Oiniki 1978, Willis 1982). In many parts of their range, ground-cuckoos are commonly called "peccary-birds," because of their

habit of following bands of forest pigs, *Tayassu* sp. (Sick 1949; Haffer 1977; J. P. O'Neill, pers. comm.). In southern Peru, Rufous-vented Ground-Cuckoos (*Neomorphus geoffroyi*) are known to associate with primates such as *Saimiri* and *Cebus* (Terborgh 1983, p. 173). The authors opportunistically observed an adult Red-billed Ground-Cuckoo (*N. pucheranii*) in temporal association with a mixed-species troop of tamarins (*Saguinas*) while conducting other long-term studies in the forest understory at the Estación Biológica Quebrada Blanco (EBQB) in northeastern Amazonia Peru.

STUDY SITE

The EBQB stands on moderately hilly, well-drained soils on the eastern margin of the Amazon River, approximately 70 km south of Iquitos (04°23' S, 73°17' W). The principal tributaries are the whitewater Quebrada Blanco and its effluent, the clear-water Quebrada Choroy. Annual temperature averages 25.7°C, with annual and monthly variations of 2°C. Annual mean precipitation is over 2,600 mm with annual variations

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