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# SCOPATE TOMIA: AN ADAPTATION FOR HANDLING HARD-SHELLED PREY?

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Abstract.—This paper reports the presence of scopate tomia, here defined as brushlike ridges on the cutting edges of the mandibles, in some 30 families of birds, including the Ciconiidae (*Anastomus*) in which tomial brushes were first described by Kahl (1971). The functional significance and biological role of scopate tomia are understood poorly. Tomial brushes probably enhance the holding ability of the bill by increasing its coefficient of friction. Most birds possessing brushes are at least partly insectivorous and have in common a preference for hard-shelled dietary items such as large insects or, as in the case of *Anastomus*, large snails. *Received 7 Oct. 1992, accepted 29 Dec. 1992.*

In the course of a general survey of tomial and other bill modifications in representatives of virtually all of the families of living birds, I came upon a brushlike tomial structure that has received almost no notice in the literature. My examinations over a period of seven to eight years ranged from "spot checks" of a few specimens at the generic level to more intensive study of longer series of specimens of individual species. Here, I present a description of the scopate tomium and its distribution in birds, and discuss its functional and adaptational significance. The material studied is from the extensive skin and alcoholic collections of the American Museum of Natural History (AMNH).

## STRUCTURAL VARIATIONS AND SYSTEMATIC OCCURRENCE

Scopate tomia (from L. *scopa* = brush) consist of brushlike ridges extending along the cutting edges of the mandibular rhamphotheca (Fig. 1). When viewed with a hand lens or a microscope, such brushes have the appearance of a range of densely packed, closely cropped bristles with a cross section usually containing a half-dozen or more individual fibers and suggest an artist's flat oil brush clipped down almost to the ferrule. Bristles are oriented nearly perpendicular to the tomial ridge and represent fine keratinous extensions of the rhamphotheca. In most taxa, brush height is only 0.3 to 0.7 mm and, although often quite visible with a 2 to 9× doublet magnifier, the structure is easily overlooked when examining specimens with the unassisted eye. In extreme examples, brushes are nearly invisible without a microscope and may be only one or a few fibers thick, as in the African Dwarf Kingfisher (*Ceyx lecontei*, Alcedinidae). The modification may occur, although usually not in equal development,

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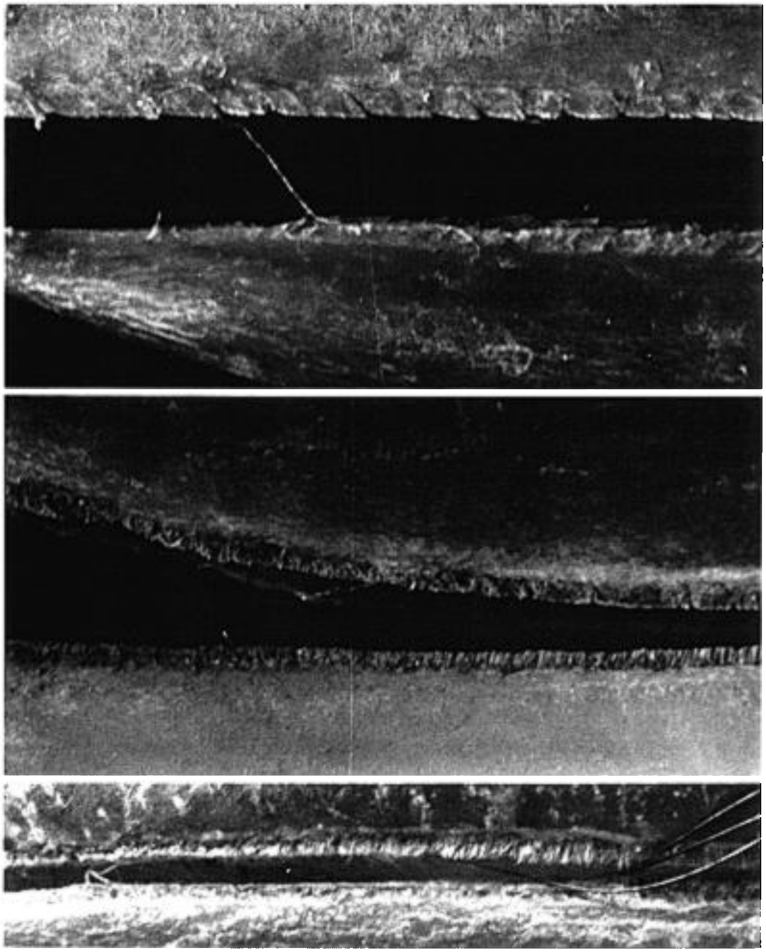

FIG. 1. Tomia in left lateral view. Magnifications about 10×. Top: lacerate tomia of the piscivorous Ringed Kingfisher (*Ceryle torquata* ♂, AMNH 393767). Middle: scopate tomia of the insectivorous Laughing Kookaburra (*Dacelo novaeguineae* ♀, AMNH 703353). Bottom: scopate tomia of the insectivorous and (presumably) frugivorous Crimson Fruitcrow (*Haematoderus militaris* "♂," AMNH 43745).

on both upper and lower mandibles or exclusively on either one. Brushes may extend nearly the full length of a mandible or only part way. Commonly they are most strongly developed distally and diminish proximally. A unique situation prevails among todies (Todidae) and motmots (Momotidae) with denticulate tomia in which brushes are mainly developed on the crests of the individual horny teeth.

The only published mention of scopate tomia that I have found refers to their occurrence in open-billed storks (*Anastomus,* Ciconiidae) where the structure is relatively conspicuous. Kahl (1971) described the modification as consisting of 20 to 30 leathery, columnar pads, about 2 to 4 mm wide by 1 to 2 mm high, extending along the distal half of the tomium of the upper mandible. Anteriorly, the fibers comprising these "pads" are closely compacted, but posteriorly the structure is more openly brushy.

Additional factors, besides their small dimensions, may account for tomial brushes having escaped attention previously. Most museum skins are made up with the mouth closed, if not tied shut. Thus, the tomia of at least the lower jaw are often not easily examined and, in fact, cannot be examined without risk of damaging the specimen. There are other investigational difficulties including ones touching on the question of whether brushes might be an artifact of wear or of drying. While these questions can only be answered unequivocally by examination of living or fresh material, their occurrence unaltered in alcoholic specimens would appear to eliminate the possibility of scopate tomia arising as artifacts of drying. The dimensional regularity of the structures argues against their origin by random injury as does their consistent occurrence in certain taxa and not in others. Also, as Walter J. Bock has pointed out to me (pers. comm., 25 June 1991), "the rhamphotheca is constantly growing from its germinative layer and is worn away at its tip, and the fact that one [often] sees the tomial brush along much of the length of the bill suggests that it is a normal part of bill structure."

It may be further noted that tomial modifications are commonly damaged or obliterated by wear. The lower mandibles of flickers (*Colaptes* spp., Picidae), for example, are clearly scopate, but many individuals have their brushes damaged or worn to such a degree that they appear brushless. Among cuckoos (Cuculidae), brushes appear to be truly absent in Cuculinae, and although present in Phaenicophaeinae and other subfamilies, they are commonly worn or damaged. This family, in particular, demonstrates the ease with which "spot checks" of only a few specimens may fail to demonstrate the structure's presence in individual genera or species. With regard to *Anastomus* Olson and Feduccia (1980) suggested that scopate tomia are an adventitious phenomenon due to a *lack* of abrasion.

Different problems affect the recognition of brushes in some other avian groups. Their existence as bona fide structures appears unequivocal when they are well and clearly developed. However, this is not always the case. In many icterid genera, for example, the tomia are certainly modified in that a narrow, somewhat irregular, differentiated ridge is present along the cutting edge, but these "pseudoscopate" brushes have a vitreous appearance suggesting a brush clotted with hardened varnish. The tomia of

TABLE 1
TAXA WITH SCOPATE TOMIA

| | |
|---|---|
| Ardeidae | *Nyctanassa* |
| Ciconiidae | *Anastomus* |
| Aramidae | * |
| Dromadidae | *Dromas* |
| Cuculidae | Phaenicophaeinae, Crotophaginae, Neomorphinae, Centropodinae |
| Alcedinidae | *Ceyx, Dacelo, Clytoceyx, Halcyon* |
| Todidae | All genera |
| Momotidae | All genera |
| Meropidae | All genera |
| Coraciidae | All genera |
| Brachypteraciidae | All genera |
| Galbulidae | All genera |
| Bucconidae | Most genera |
| Capitonidae | * |
| Indicatoridae | *Prodotiscus* |
| Picidae | Picinae |
| Eurylaimidae | *Eurylaimus* |
| Dendrocolaptidae | Most genera |
| Furnariidae | * |
| Formicariidae | *Sakesphorus, Thamnophilus, Megastictus, Thamnistes* |
| Cotingidae | *Haematoderus* |
| Tyrannidae | Some Elaeninae, Fluvicolinae, Tyranninae |
| Philepittidae | *Neodrepanis* |
| Campephagidae | *Coracina, Pericrocotus* |
| Pycnonotidae | *Nicator* |
| Irenidae | *Irena* |
| Muscicapidae | *Peltops* |
| Meliphagidae | *Acanthorhynchus, Anthochaera, Prosthemadera, Promerops* |
| Icteridae | * |
| Sturnidae | *Speculipastor, Buphagus* |
| Artamidae | * |

* Scopate tomia, when present, weakly developed (see text).

the Aramidae and Artamidae present similar uncertainties. In view of these difficulties the following table must be regarded as provisional.

## FUNCTION AND BIOLOGICAL ROLE

In searching for an adaptive purpose for scopate tomia several possibilities come to mind. These ideas are presented with the warning that they are largely speculative and require further investigation. The likelihood that no single interpretation may suffice to cover all occurrences of scopate tomia in birds should also be borne in mind.

*Function.*—Mechanically, a brushy ridge might enhance the holding ability of the bill by increasing the coefficient of friction of the tomial surface. Brushes may be expected to be more malleable than the unmodified, hard-edged tomial crest and, therefore, to be able to conform more closely with the shape of the object seized by the bill, maintaining a broader area of frictional contact than is possible with point-to-point contacts between two rigid surfaces. This feature could be important in establishing a firmer grip on an object that must be seized and held briefly during the initial grasp by the bill. Birds commonly first grab an object with their bill tip, and this is where brushes are often best developed.

*Biological role.*—Scopate tomia occur in birds with widely disparate feeding habits as a few examples will demonstrate.

Both todies and motmots have brushes, but todies glean prey from the underside of leaves and twigs while hovering or sitting on a perch (Kepler 1977), whereas motmots usually sally from an overhead lookout or drop down to seize prey on the ground. Among rollers (Coraciidae), *Coracias* spp. are also "perch and pounce" feeders, while *Eurystomus* spp. take prey on the wing. Bee-eaters (Meropidae) and their New World ecologues, the jacamars (Galbulidae), are also aerial hawkers as is the Swallow-winged Puffbird (*Chelidoptera tenebrosa,* Bucconidae) according to Fry (1970, 1984) and Burton (1977). *Malacoptila* spp. and probably most other puffbirds use the "perch and pounce" technique (Skutch 1948, 1983). Most kingfishers (Alcedinidae) are also perch and pounce foragers, a method that Fry (1980a) concluded was primitive in coraciiforms generally. On the other hand, the highly aberrant Shovel-billed Kingfisher (*Clytoceyx rex*), which has well developed brushes, digs for earthworms. Woodpeckers (Picidae), whose varied feeding techniques were summarized by Short (1982), and the scansorial dendrocolaptids provide additional examples of the diversity of feeding habits among taxa with scopate tomia. Fitzpatrick's (1980) review of tyrant flycatcher (Tyrannidae) behavior suggests a positive correlation between bill type, feeding behavior, and scopate tomia. The modification is generally absent in narrow-billed, warblerlike flycatchers that feed mainly as gleaners, and occurs more frequently in broad-billed "typical" flycatchers; thus, I found brushes in only four of 36 genera of Elaeninae, most of which are small to medium sized gleaners, while just over half the genera of "flycatching" Fluvicolinae and Tyranninae have scopate tomia. This correlation does not appear to extend to Old World muscicapid and monarchid "flycatchers," since I failed to find any unambiguous examples of scopate tomia even in the more flycatcherlike genera; *Peltops,* a genus with uncertain affiliations, is a possible exception. Brushes seem to be generally absent in gleaners, including vireos (Vireonidae) and the various families of "warblers," "creepers," "wrens," and "tits" in both hemispheres. These birds, like the elaenine flycatchers, are mostly small in size and presumably prey mainly on small arthropods.

*Food preference.*—There is some circumstantial evidence that "hard-shelled" dietary items, such as snails and large insects, provide a common denominator linking scopate tomia to feeding habits.

Open-billed storks feed preferentially on aquatic snails of the genus *Pila* (Kahl 1971). The globular shells of these snails are large in proportion to the bird's bill; an example of *Pila* in the ornithological collection of the American Museum of Natural History, picked up under an *Anastomus* roosting tree by R. C. Murphy, has a columellar length of 57 mm, making the shell about the size of a small lemon while the culmen length of this stork is only about 240 mm. The lower mandible is not scopate; distally it is laterally compressed to the sharpness of a dull letter opener, and in the Asian Openbill (*A. oscitans*), as Kahl noted, the tip is commonly bent to the bird's right. This deformation includes a twist in the dorsoventral axis away from true vertical to produce a somewhat spooned effect. The lower mandible in the African Openbill (*A. lamelligera*), the second species of the genus, is compressed but lacks this twist.

Brown (1982:176–177) observed that open-billed storks hold their prey underwater against the bottom with the tip of the upper bill, while the bladelike lower mandible is used to extract the snail from its shell. The snails are handled in the distal part of the bill and are not crushed as was once supposed when the gap between the upper and lower mandibles was attributed to wear (the opposite of Olson and Feduccia's suggestion, previously noted). The cited specimen of *Pila,* which has a rather thin-walled shell, is undamaged except for minor breakage along the outer rim. Another well known snail-eater, the Limpkin (*Aramus guarauna,* Aramidae), does not have scopate tomia, although the tip of the upper jaw is obscurely denticulate.

Several crab-eating birds have scopate tomia, including the Yellow-crowned Night Heron (*Nyctanassa violacea*) which, alone among ardeids, has clearly developed brushes, as does the Crab Plover (*Dromas ardeola,* Dromadidae).

With the exception of the specialists just mentioned, most birds with tomial brushes are insectivorous to some degree, and, significantly perhaps, large insects are specified in published food lists for some of these birds. Examples are found among jacamars and bee-eaters (Burton 1977; Fry 1969, 1970, 1984; Skutch 1983, Wetmore 1968), African coraciids (Fry 1988), motmots (Skutch 1964, 1971, 1983), and rollers (Cracraft

1971, Rand 1936). With regard to rollers, Cracraft (1971) noted that *Coracias,* in contrast to other members of the family, has a relatively strong jaw apparatus adapted for "crushing," suggesting that it feeds on larger prey. Feduccia (1970) contrasted woodhewers (Dendrocolaptidae) with their ovenbird relatives (Furnariidae) by noting that dendrocolaptids commonly take larger, harder shelled prey. Most dendrocolaptid genera have brushes, whereas furnariids either lack them or have them weakly developed.

The prevalence of scopate tomia in Piciformes and Coraciiformes suggests that a consideration of the foods of brushless piciforms and coraciiforms may be instructive. Thus, among piciforms brushes are absent in the largely frugivorous toucans (Ramphastidae) as they are in the somewhat analogous hornbills (Bucerotidae) among coraciiforms. Additional piciform exceptions include the barbets (Capitonidae auct.), in which scopate development is poorly expressed or absent; these birds are also strongly frugivorous (England 1985). Brushes appear to be absent in Indicatoridae except in *Prodotiscus* spp.; Friedmann (1955) described this as the "most divergent" genus of the family in being largely insectivorous and the only honeyguide that does not eat bee comb. Among coraciiforms, scopate tomia are also absent in ground feeding hoopoes (Upupidae).

A few non-insectivores have scopate tomia. Examples include fairy bluebirds (*Irena* spp., Irenidae) and sugarbirds (*Promerops,* Meliphagidae) which supplement their diets with insects but which are otherwise frugivores and nectarivores (*Irena*; Ali and Ripley 1971, Smythies 1981) or specialized nectarivores (*Promerops,* Skead et al. 1967). The presence of brushes in only one cotingid, the Crimson Fruitcrow (*Haematoderus militaris*) (Fig. 1Bottom), is puzzling; while it is thought to be frugivorous, the only foods recorded as stomach contents are beetles, including a 35 mm long buprestid (Snow 1982). *Buphagus* may occupy a similarly exclusive position among starlings (Sturnidae), although the lower mandibles of *Speculipastor* may be scopate; the modification in oxpeckers (*Buphagus* spp.), which feeds on external parasites on ungulates, is atypical.

## RELATIONSHIP BETWEEN LACERATE AND SCOPATE TOMIA

Lacerate tomia (from L. *laceratus,* past part. of *lacerare* = to lacerate) have the tomial margin more or less deeply and irregularly cut or incised. Miller (1912:267) used the term "serrate" to describe this tomial modification in kingfishers.

The alcedinids are noteworthy both because of the diversity of feeding habits among family members and because structural variations among halcyon kingfishers bridge the structural gap between lacerate and scopate tomia (cf Figs. 1Top, 1Middle). Forshaw (Forshaw and Cooper 1983, 1985) and Fry (1980b) reviewed the literature on kingfisher diets. Nonpiscivorous species, which make up more than three-quarters of the family, are nominally insectivores, although a broad diversity of prey including small vertebrates appears in most food lists. Frequently, preferences are biased by habitat choice and opportunity, but there are specialists. Earthworms figure prominently in the diets of *Melidora* and *Clytoceyx.* Among the halcyons, Pacific Kingfisher (*Halcyon tuta*), Tahiti Kingfisher (*H. venerata*), and Tuamotu Kingfisher (*H. gambieri*) have bills modified for "flycatching," while the Black-capped Kingfisher (*Halcyon pileata*), reportedly the most piscivorous of the genus, and the White-throated Kingfisher (*H. smyrnensis*), which is strongly piscivorous seasonally (Mukherjee 1976), have sharp-edged, lacerately toothed tomia. At the other extreme, the Beach Kingfisher (*H. saurophaga*), the White-collared Kingfisher (*H. chloris*), and the Micronesian Kingfisher (*H. cinnamomina*) have conventional brushes forming a bluntly fibrous ridge in cross section. Within *Halcyon,* the range from one structural extreme to the other is fairly continuous. The lacerate toothing of the large fish-eating alcedinids *Megaceryle* and *Pelargopsis* appears distinctly fibrous under magnification.

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