

SPECIALIZATIONS OF SOME CAROTENOID-BEARING FEATHERS

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Certain of the Eurylaimidae (broadbills) and Cotingidae (cotingas) bear feathers of a violet or deep maroon color that is uncommon in birds. These feathers show a number of peculiarities not found in typical feathers colored by melanins or schromochromes (structural colors). I investigated the external and internal morphology of feathers from broadbills, cotingas, and other families in order to determine details of structure, amount of variation between species, and the possible taxonomic value of these specialized feathers.

In a typical feather barb there are rows of barbules present. Cross sections show two layers of cells: a prominent pigmented medulla surrounded by a cortex that usually appears clearer and more or less homogeneous. Desselberger (1930) pointed out that when heavy deposits of lipochromes are present, barbs may be flattened, lack barbules, and be undifferentiated internally. Brush and Seifried (1968) showed a definite correlation between this modified structure and carotenoid deposition in the Gouldian Finch (*Poephila gouldiae*) and several other species.

METHODS

Feathers, obtained from museum skins, were selected on the basis of their color and gloss. The gross structure of barbs and barbules was examined microscopically. Feathers were embedded in nitrocellulose (Parlodion), following generally the methods outlined in Galigher and Kozloff (1964). Paraffin was not used as feathers embedded in it tended to shatter when cut. The entire feather was sectioned transversely on a rotary microtome from the distal towards the proximal end. Sections were made at varying thicknesses, usually about 20 μ . Unless otherwise stated, the descriptions were taken from the modified distal parts of the barbs.

RESULTS

COTINGIDAE

Red-ruffed Fruitcrow. *Pyroderus scutatus*. The throat and upper breast feathers are orange, tipped with a deeper scarlet-orange, and they present a singular crinkled appearance. The distal tips of the barbs lacked barbules, were conspicuously flattened, and it was here that the color was most intense. In distal sections (fig. 1A) the greater part of

the barb was composed of distinct light-colored cells. There was, however, a small area of unorganized dark material at the larger end of the sections. Traced proximally through serial sections, this dark area expanded until, in the region where barbules started to appear, it was discerned as the medulla and was composed of distinct cells (fig. 1B). Further proximally, where the barbules reached their fullest development, the medulla constituted an even larger area (fig. 1C). The cortical cells, which were quite distinct in distal sections, became diffuse and indistinguishable. A thick, wavy layer surrounding the outside of the barb, in which no cells could be discerned, was particularly noticeable in the distal sections. This layer, which was present in all the feathers I examined, is what Strong (1952) mistakenly alluded to as the cortex in *Querula purpurata*. Strong (1902) earlier referred to the possible presence of an "epitrichium" (an inappropriate term for a feather component) surrounding the barb cortex but regarded it as purely an optical effect. That such is not the case is vividly demonstrated in *Dryocopus pileatus* (see below). Hereafter, for want of a better term, I shall refer to this layer as the cuticle.

Guianan Cock-of-the-Rock. *Rupicola rupicola*. In the orange crown of males there is a subterminal band of deep brownish maroon that illustrates particularly well the specializations associated with heavy depositions of carotenoids. Under magnification (fig. 2A), the orange portions of the barbs both proximal and distal to the maroon band were not expanded and bore barbules which were normal in size and number. However, on the maroon band the barbs were flattened and the barbules, although still present, became vestigial. Sections through the maroon portion showed it to consist almost entirely of distinct cortical cells, with only a few dispersed dark granules of melanin indicating the location of the remains of the medulla (fig. 2B). In the orange portions (either proximal or distal), the medullar area increased in size and organization and the cortical cells became less

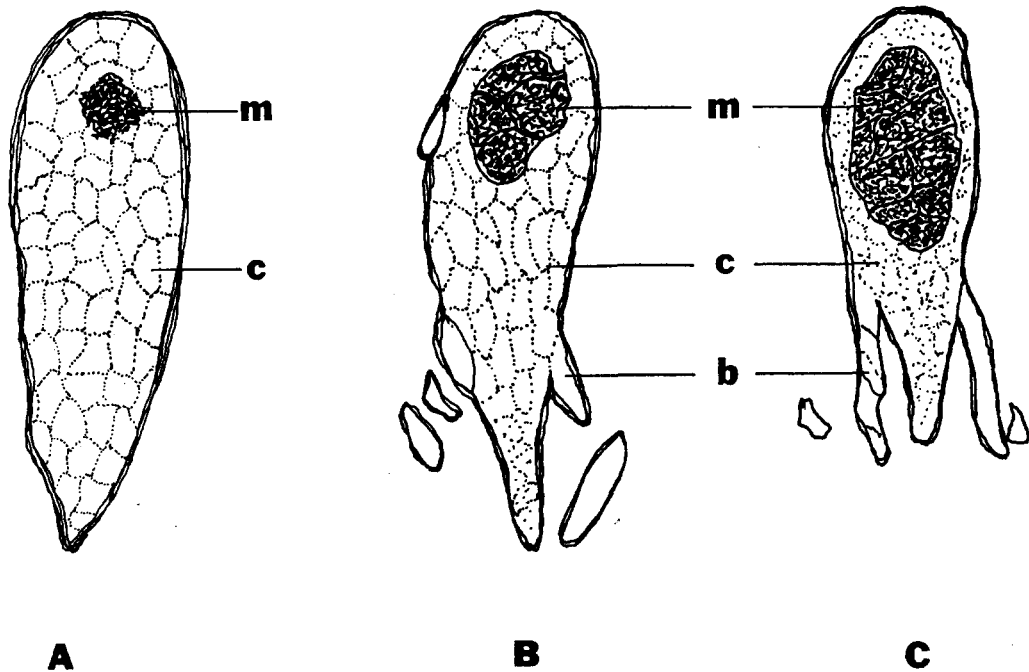


FIGURE 1. Cross sections from a barb of a throat feather of *Pyroderus scutatus*. A. Section from modified distal portion of barb. B. Section taken between A and C approximately where barbules commence. C. Proximal section taken through area of well developed barbules. All sections are shown ventral side uppermost. m = medulla; c = cortex; b = barbule.

distinct (fig. 2C), and in the region of normal barbule development, the medulla assumed its full stature and the outlines of the cortical cells were lost (fig. 2D).

Purple-throated Fruitcrow. *Querula purpurata*. The maroon gorget feathers of the male bear long, flattened, barbuleless barbs. There have been conflicting reports of the internal structure of these barbs. Strong (1952) described cross sections as having a thin outer layer surrounding a "homogeneous, pigmented, central core . . . in which no trace of medullary cells could be found," whereas Mattern (1956) reported cells in the pigmented portions and large air-filled medullary cells in proximal sections. She believed Strong's observations resulted from fading of the pigments in the embedding medium he used, causing the cell outlines to become indistinct. My observations confirm Strong's. I could not distinguish cells in barbs of *Querula* (or *Xipholena*), nor did I find air-filled medullary cells. In a very few sections there were scattered small, dark remnants of medulla, such as illustrated in figure 2B for *Rupicola*. The outer layer mentioned by Strong represents the cuticle, the "core" being the cortex.

Xipholena. The three species of *Xipholena* exhibit perhaps the most extensive develop-

ment of specialized carotenoid-containing feathers of any group of birds. Except for the remiges and rectrices, the males are adorned entirely with glossy feathers ranging from deep maroon to blackish-purple. In the Pompadour Cotinga (*X. punicea*) the barbs were much elongated and lacked barbules for at least two-thirds of their length. Distally, the rachis itself was pigmented and became indistinguishable from the barbs, as at this point the branching became dichotomous, rather than pinnate as is usual in most feathers. As in *Querula*, there was no medulla and the cortex revealed no definite cellular structure.

Cotinga. Males of this genus are bright blue, with patches of deep violet below. The violet throat feathers from the Lovely Cotinga (*C. amabilis*) were glossy with flattened barbuleless barbs. Sections lacked a medulla; distinct cortical cells were present (fig. 3A). Some of the violet feathers, usually those of the belly, did not appear glossy and had normal barbule development. In sections of barbs from them (fig. 3B), a small medullary spot was seen. This consisted of a dark area within a lighter area and contained no distinct cells. The cortical cells were apparent.

Phoenicircus. Red crown feathers from males of the Guianan Red-Cotinga (*P. carni-*

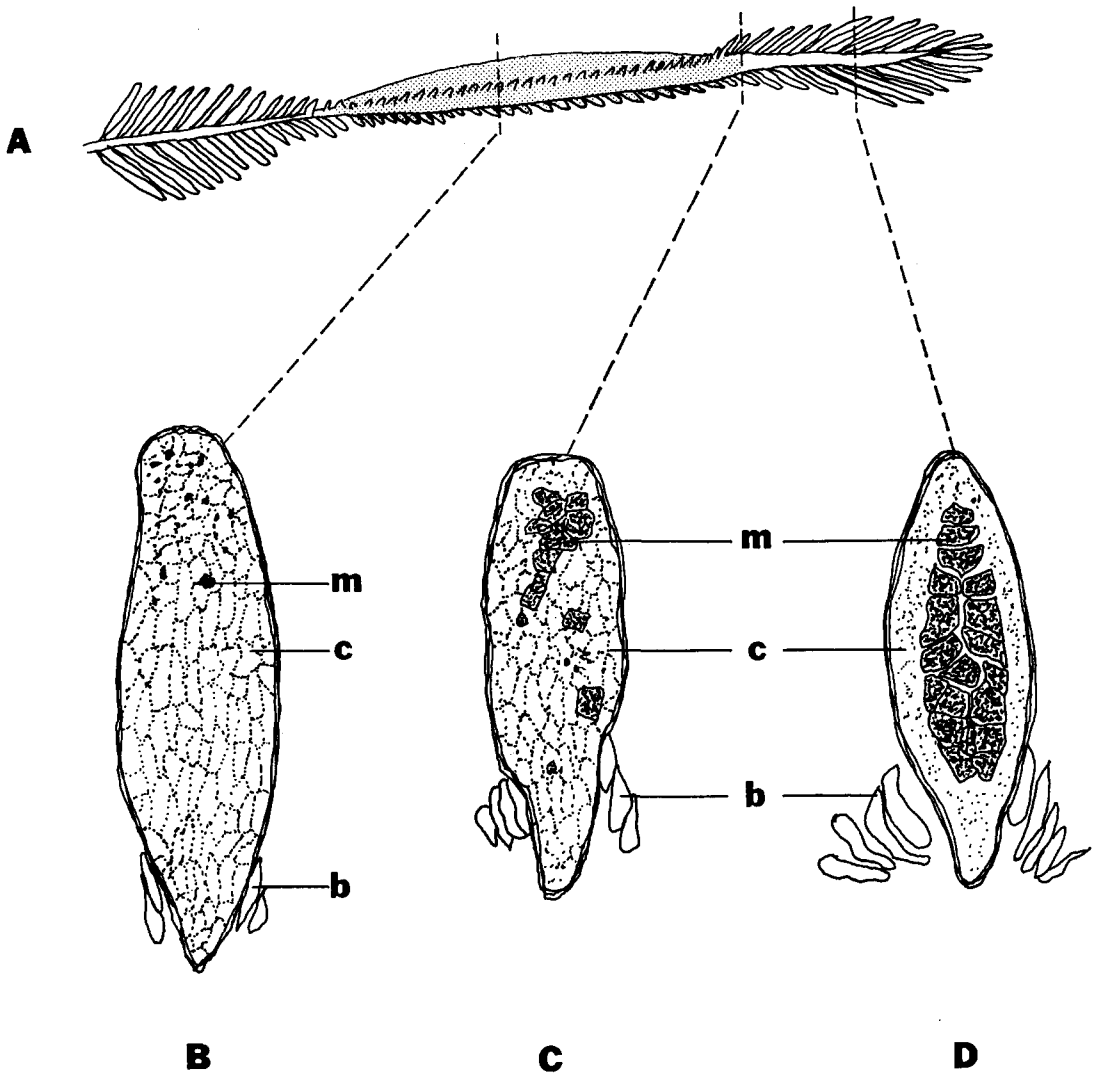


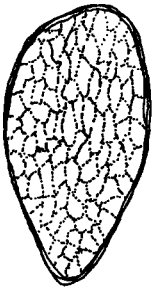
FIGURE 2. A. Distal portion of a single barb from the crown of a male *Rupicola rupicola*; shaded portion is maroon, unshaded portions, orange. B-D. Cross sections of barb; dotted lines show approximate levels of the sections. All sections shown ventral side uppermost. m = medulla; c = cortex; b = barbule.

fex) and the Black-necked Red-Cotinga (*P. nigricollis*) were examined. The distal barbs lacked barbules; proximal barbs bore barbules at the base. No traces of a medulla were found in *P. nigricollis*, while a few proximal sections of *P. carnifex* did show a dark central medullar vestige. Cortical cells were evident in both species.

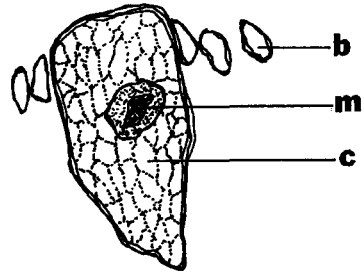
Red-banded Fruiteater. *Pipreola whiteleyi*. Feathers from the reddish-orange breast band of a male revealed flattened distal barbs without barbules. There was a fairly large medullar spot at the larger end of the sections and the cortical cells were in evidence.

Purple-throated Cotinga. *Porphyrolaema porphyrolaema*. Glossy, deep violet feathers

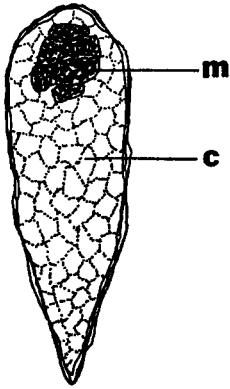
FIGURE 3. A. Cross section of barb from glossy throat feather of *Cotinga amabilis*. B. Cross section of barb from non-glossy breast feather of *Cotinga amabilis*. C. Cross section of barb from cheek feather of *Cymbirhynchus macrorhynchus*. D. Distal end of barb of cheek feather of *Cymbirhynchus macrorhynchus*. E. Cross section of barb from crown of *Pipra aureola*. F. Cross section of barb from red feather of *Phlogothraupis sanguinolenta*. G. Cross section of barb from crest of *Dryocopus pileatus*. None to scale. All sections shown ventral side uppermost. m = medulla; c = cortex; b = barbule; cu = cuticle.



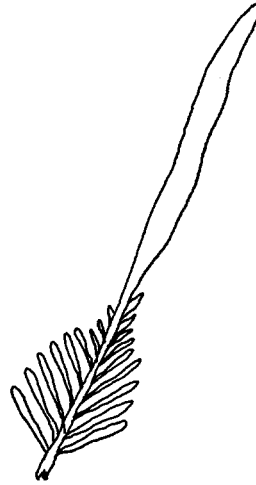
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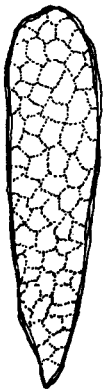
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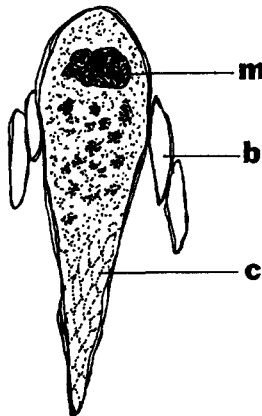
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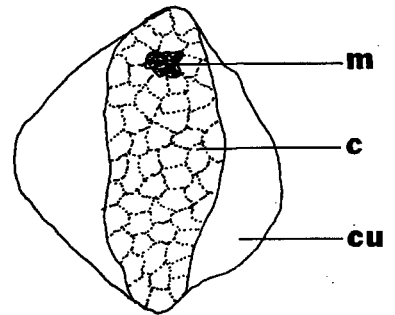
D



E



F



G

δ

from the throat of a male bore flattened barbs lacking barbules distally. Sections appeared more granular than in other species examined. A medullar spot could be found in only a few sections, but cortical cells were distinct in all.

PIPRIDAE

Crimson-hooded Manakin. *Pipra aureola*. Crimson crown feathers from a male bore barbs which were flattened distally and lacked barbules. Cross sections were elongate and pointed at one end. No medullar spot was perceived; cortical cells were obvious (fig. 3E).

Helmeted Manakin. *Antilophia galeata*. The deep crimson feathers from the peculiar crown of males also displayed flattened, barbuleless barbs. In only a few proximal sections was there a vestigial medulla. The cortex was composed of distinct cells.

EURLAIMIDAE

Black and Red Broadbill. *Cymbirhynchus macrorhynchus*. On the rump, lower throat, and abdomen are glossy feathers of a deep maroon color. The distal portions of the barbs lacked barbules and in the cheek region, where these feathers are very plush and glossy, the barbuleless parts are markedly expanded and flattened (fig. 3D) There was a distinct, fairly large medullar area (fig. 3C) although this varied in size and was absent in some sections. Cortical cells were apparent in all sections.

Wattled Broadbill. *Eurylaimus steerei*. The crown and upper rump feathers are a deep purplish-maroon, almost brownish in appearance. The barbs of the rump feathers were not as flattened as those of the crown. In both, barbules were absent, a small medullar spot was present, and the cortical cells were very distinct.

Banded Broadbill. *Eurylaimus javanicus*. In some barbs of the dark brownish-maroon crown feathers barbules were lacking, while in others they extended to the tip of the barb. The sections were more rounded in shape than for other barbs seen. No trace of a medulla could be found, though cortical cells were in evidence.

TYRANNIDAE

Vermilion Flycatcher. *Pyrocephalus rubinus*. Barbs of the glossy vermilion feathers from the crown of a male lacked barbules distally. No vestige of a medulla was found in any of the sections.

THRAUPIDAE

Crimson-collared Tanager. *Phlogothraupis sanguinolenta*. The glossy red feathers of this species presented somewhat flattened barbs with at least rudimentary barbules throughout their length. Cross sections revealed a definite dark medullar spot. Outlines of cortical cells could be distinguished only in the pointed end of the sections (fig. 3F).

PICIDAE

Pileated Woodpecker. *Dryocopus pileatus*. The glossy red crest feathers bear very long, barbuleless barbs. In section these presented a most singular appearance. There was an area of distinct cortical cells which in some of the sections contained a small, dark medullar spot. Surrounding this cortex was a greatly enlarged and thickened cuticle (fig. 3G) which appeared to be tinted purplish in reflected light. In this translucent cuticle, no structures were seen that would indicate any cellular composition.

DISCUSSION

Völker (1952, 1954) and Brush (1969) found that various carotenoids are responsible for the red and violet colors in cotingas. Desselberger (1930), Frank (1939), Brush and Seifried (1968), and others have correlated heavy carotenoid depositions with a highly modified feather structure in which barbs are markedly flattened and lack barbules. This condition was found in most of the glossy, highly pigmented feathers I examined. The loss or reduction of barbules and the expansion and flattening of the barb are specializations that presumably accomplish a more effective display of the pigments than could be gained with typical feather structures. Frank (1939) noted that lipochromes are primarily deposited in barbs as opposed to melanins which are commonly found in barbules.

There are corresponding internal modifications of the barb where these external specializations are found. Serial sections of barbs from *Pyroderus scutatus* and *Rupicola rupicola* showed that the medulla, which plays an important role in structural coloration, becomes vestigial or is lost altogether in the carotenoid-bearing portions of these barbs. In the other species investigated, the medulla was either absent or appeared sporadically as a small vestigial structure. The carotenoid pigments seem to be deposited exclusively in the cells of the cortex. In the modified tips of the secondaries in the Cedar Waxwing

(*Bombycilla cedrorum*), the carotenoid pigments are also deposited in the cortex of the rachis (Brush and Allen 1963). Strong (1902: 161) stated that in the fully cornified feather barb "there is little or no evidence of" the "former cellular nature" of the cortex. This, however, seems to apply mainly to schemochromatic or melanin-pigmented feathers, whereas in carotenoid-containing feathers the cortical cells are usually quite evident. In some forms (e.g., *Querula*, *Xipholena*) the cellular composition of the cortex seems to be abrogated. Serial sections of *Pyroderus* and *Rupicola* barbs show that the cortical cells degenerate progressively as the medulla increases in size. This may indicate that the presence of the medulla in some way suppresses the formation of cortical cells or causes them to degenerate. Conversely, the presence of great quantities of carotenoids may inhibit formation of the medulla.

Concerning the development of these types of feathers, Voitkevitch (1966:29) noted that, "Where great quantities of lipochromes accumulate during structure differentiation, the cell material of the first order barbs [=barbs] is stimulated to a more intensive growth than that of the second order barbs [=barbules]. Consequently, the parts of the first order barbs colored by lipochromes (or with melanins) are relatively more bulky." However, contrary to what is stated, this does not apply to melanins.

The lack of barbules, at least in some species, is a factor of wear. Dwight (1900) showed that in *Carpodacus purpureus* and *Loxia curvirostra* the feathers of the bright definitive male plumage bear barbules that are worn away to expose the flattened barb during the breeding season. Desselberger (1930) described weak deciduous barbules that are soon lost from the red mask of the European Goldfinch (*Carduelis carduelis*). While wear is responsible for the barbuleless condition in some species, in others the barbs apparently develop without barbules. For instance, the barbs of the gorget feathers of *Querula* show no trace of barbules, even while still in their sheaths.

Surrounding the cortex is a clear, cuticular layer of varying thickness. This cuticle is not an effect of optics as suspected by Strong (1902). In the crest feathers of *Dryocopus pileatus* the cuticle constitutes a major portion of the barb. A cuticle was also observed in the specialized waxy portions of the secondaries of the Cedar Waxwing (Brush and Allen 1963). Although I could not distinguish

cells in the cuticle of any of my specimens (even *Dryocopus*), Auber and Appleyard (1951) have described and pictured the surface layer of the cortex as composed of flattened cells resembling the cuticle of mammalian hair. They also found (1955) a cellular cuticle in the honeycreepers *Chlorophanes* and *Iridophanes*. The presence of a well-developed cuticle in carotenoid-laden feathers probably explains their high gloss.

Many carotenoid-bearing feathers have a propensity to change color with heat or pressure. This was first reported by Quelch (1896) in *Cotinga* and *Xipholena*. Color change was reported by Frank (1939) for *Picus viridus*, by Strong (1952) for *Querula*, by Mattern and Völker (1955) and Mattern (1956) for a number of other species. This change is not marked in reddish or orange feathers, which only become lighter orange. However, deep maroon or violet feathers such as found in *Xipholena*, *Querula*, *Cotinga*, *Porphyrolaema*, and *Cymbirhynchus*, when heated near a flame, change dramatically to a light yellowish-orange. The nature of violet coloration in cotingas has been subject to dispute. Görnitz and Rensch (1924) attributed this color to a pigment which they called "cotingin." However, the extracted pigment from violet feathers of *Xipholena punicea* is brick red and consists of a complex of several carotenoids (Brush 1969). The pigments themselves are not violet and there is no typical schemochromatic medullary structure present in violet feathers to account for the blue portion of the color. Mattern (1956) and Schmidt (1956) reported that violet color is a result of the alignment of small granules of pigment. Heat destroys the granules and pressure causes them to realign, producing the change in color. Brush (1969) observed that the red extract of feathers of *Xipholena punicea* changed to yellow when treated with sodium borohydrate and that the keto-carotenoid curve observed prior to treatment changed to one typical of hydroxy-carotenoids. This may explain why heated feathers turn yellowish rather than red. I can find nothing in the literature or my own observations to support Brush's (1969:431) statement that "the violet coloration of certain species (e.g., *Cotinga cotinga*) is considered to be produced structurally and is not a true pigment." The violet feathers from *Cotinga* are similar to those of *Xipholena* in appearance and physical behavior; i.e., they change color when heated or subjected to pressure. I should emphasize that not all feathers that contain carotenoids

are necessarily specialized in the manner of those discussed in this paper. Many appear to have no external modifications. The specializations described seem to be associated with very heavy depositions of carotenoids in distinctive patterns of display, although again there are exceptions. The presence of these specialized feathers in a number of unrelated avian taxa indicates that this feature carries little or no taxonomic significance.

SUMMARY

Certain feathers with heavy depositions of carotenoids exhibit distinctive modifications. The barbs are flattened and usually lack barbules. The internal structure of the barbs differs from schemochromatic feathers in that the medulla is reduced or absent, there are distinct cortical cells which contain the pigments, and a thickened exterior cuticle is present, giving the barbs a glossy appearance. These modifications are believed to increase the effectiveness of carotenoid display. They are found in many groups of birds and do not indicate phylogenetic affinity.

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