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THE DIAGNOSTIC SIGNIFICANCE OF THICKENED AND PRONGED HAMULI IN FEATHERS

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ABSTRACT

The taxonomic distribution of thickened and/or pronged hamuli (hooklets) on distal barbules in the pennaceous part of feathers was studied with light microscopy (LM) and scanning electron microscopy (SEM) in order to assess the diagnostic significance of these structures. Comparison of the LM and SEM appearance of these structures indicates that thickened hamuli are artifacts, arising from the misinterpretation of rotated tape-like structures. Pronged hamuli, on the contrary, are non-artifacts. However, these structures have a much wider taxonomic distribution than was reported by earlier workers and prongs do not seem to be useful for identifying feather fragments.

Key Words: feather structure, SEM, pennaceous barbs, hamuli, prongs, diagnostic significance of feather structures

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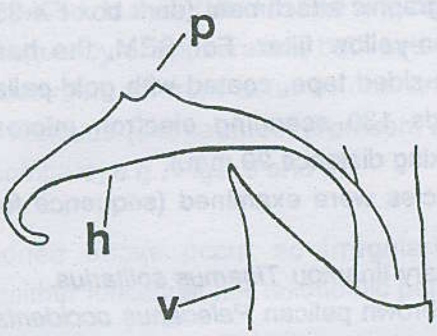
Messinger (1965: fig. 14) suggested that "pronglets" on the hamuli of flight-feathers distinguish the mourning dove *Zenaidura macroura* from the passenger pigeon *Ectopistes migratoria*, but he considered the thickening of the proximal-most hamuli typical of all Columbiformes (Fig. 1).

FIGURE 1. Schematical drawing of pronged and thickened hamulus in flight-feather of mourning dove - *Zenaidura macroura* (redrawn from Messinger 1965); h = hamulus, p = prongs, v = ventral tooth.



In summary, aforementioned light microscopy (LM) studies have reported thickened and/or pronged hamuli in albatrosses, petrels, ducks, swans, pigeons, parrots, and cuckoos.

Considering the - sometimes contradictory - descriptions of pronged and/or thickened hamuli and the fragmentary known taxonomic distribution of these structures, it is evident that the occurrence of these structures needs to be studied in greater detail. Might these structures be characteristic of the Columbiformes (cf. Messinger 1965), this finding would have diagnostic significance.

Pigeons and doves are notoriously dangerous with regard to flight safety and constitute a major category in bird strike statistics (e.g., Brom 1984, 1988). When identifying feather remains after collisions between birds and aircraft, the microstructure of the downy part of feathers is commonly used (e.g., Reaney *et al.* 1978, Laybourne 1984, Brom 1986). The columbids have highly characteristic downy barbules (Messinger 1965: 214, Brom 1986), but in case downy barbs are not available for examination, fragments of pigeon feathers may be more difficult to identify. Since the early publications by Mascha (1905) and Chandler (1916), hardly any studies have been dedicated to the morphology of the pennaceous part of feathers (cf. Dyck 1985). Therefore, diagnostic characters found in this part would facilitate the identification by providing an additional and independent character set.

In the present study, for the first time the morphology and taxonomic distribution of pronged and/or thickened hamuli is examined with scanning electron microscopy (SEM), and comparisons are made with LM observations.

INTRODUCTION

Recently, several characteristics in the microstructure of feathers have been studie establish their diagnostic and phylogenetic significance (Brom 1986, 1990, 19 1991b, Brom & Visser 1989). In this paper, the structure and taxonomic distributio another ptilological characteristic, thickened and pronged hamuli, is evaluated.

Hamuli (or hooklets) are encountered in all avian taxa except the ratite birds (ost rhea, emu, cassowary, kiwi, moa) - which have a loose feather texture - and ma considered basic components of the interlocking system of feathers (Wray 1887). T are located on the reverse edge of the distal barbules of pennaceous barbs (Sick 1 Fig. 1 and 4) and contribute to the strength and cohesiveness of the vanes by loc into the recurved obverse edge of the proximal barbules of the adjacent barbs (Luc Stettenheim 1972: fig. 168; Dyck 1985: fig. 9).

In several taxa, thickened and pronged projections occur on the dorsal surface of middle portion of the hamuli, which have been termed "kleine Spitzen" (Mascha 1 631), "prongs or horns" (Chandler 1916: 359), "Abstemm-Höcker" or "Abstemm-Do (Sick 1937: 330), "pronglets" (Messinger 1965: 215), and "tiny pointed bumps "prickles" (Lucas & Stettenheim 1972: 249). It has been suggested that these pro have the function of "fine-tuning" the proximal and distal barbules and hence, fur increase the cohesiveness of the vanes (Sick 1937: 330).

Earlier studies have suggested that thickened and/or pronged hamuli have a lim taxonomic distribution, which could mean that these structures might have a diagno significance.

Mascha (1904: 631, figs. 16 &17) encountered prongs irregularly distributed over hamuli of the distal barbules of flight-feathers of two species of cuckoos, but did not these structures in other taxa. Chandler (1916: 359, 364, figs. 69a, 67a, 72f, 7 observed such prongs on distal barbules of contour feathers of pigeons and doves, added that these prongs may sometimes be found on the hamuli of parrots and cucko Furthermore, he depicted similar prongs on hamuli of the wandering albatr *Diomedea exulans*, and the crested guan *Penelope purpurascens* (Chandler 1916: 10e & 46a respectively), but regarding the taxonomic distribution of prongs, he did refer explicitly to these figures in the text.

Sick (1937: 329) depicted pronged hamuli in the rock pigeon *Columba livia*, whooper swan *Cygnus cygnus* and reported their occurrence in several other taxa (S 1937: 366).

MATERIAL AND METHODS

Feathers (mostly body-feathers) were plucked from study skins in the collection o Zoological Museum Amsterdam (ZMA). Pennaceous barbs were removed from rachis and the barbules were spread before mounting the barbs. For LM, the barbs mounted dry between object glass and cover slip, which were glued together along edges, examined with a Nikon Optiphot Biological Microscope, and photographed the Microflex AFX photomicrographic attachment (dark box FX-35WA/FX-35W, Kod MAX 100 film) using a green-yellow filter. For SEM, the barbs were mounted aluminium stubs using double-sided tape, coated with gold-palladium for 2-3 minu and examined with an ISI ds 130 scanning electron microscope (bottom st accelerating voltage 9 kV, working distance 20 mm.).

Feathers of the following species were examined (sequence follows classificatio given by Wetmore 1960):

Tinamiformes: Tinamidae: solitary tinamou *Tinamus solitarius*.

Pelecaniformes: Pelecanidae: brown pelican *Pelecanus occidentalis*.

Ciconiiformes: Ciconiidae: black-necked stork *Ephippiorhynchus asiaticus*.

Anseriformes: Anatidae: Cuban whistling duck *Dendrocygna arborea*, chestnut *Anas castanea*.

Falconiformes: Accipitridae: golden eagle *Aquila chrysaetos*.

Galliformes: Megapodiidae: Nicobar megapode *Megapodius nicobariensis*, du megapode *Megapodius freycinet*; Tetraonidae: ruffed grouse *Bonasa umbe* ptarmigan *Lagopus mutus*, Phasianidae: bobwhite *Colinus virginianus*, peacock-pheasant *Polyplectron bicalcaratum*, pheasant *Phasianus colchicus*.

Gruiformes: Rallidae: king rail *Rallus elegans*.

Charadriiformes: Haematopodidae: oystercatcher *Haematopus ostraleg* Scolopacidae: whimbrel *Numenius phaeopus*, bar-tailed godwit *Lim lapponica*; Laridae: brown-hooded gull *Larus maculipennis*, black-headed gu *ridibundus*, sandwich tern *Sterna sandvicensis*; Alcidae: razorbill *Alca torda*.

Columbiformes: Pteroclidae: black-bellied sandgrouse *Syrrhaptes orienta* Columbidae: turtle-dove *Streptopelia turtur*, rock pigeon *Columba livia*, w pigeon *C. palumbus*, blue-tailed imperial pigeon *Ducula concinna*, emerald-d *Chalcophaps indica*, crowned pigeon *Goura cristata*, tooth-billed pig *Didunculus strigirostris*.

Psittaciformes: Psittacidae: Amboina king-parrot *Alisterus amboinensis*, hyacinth mac *Anodorhynchus hyacinthinus*, Pennant's rosella *Platycercus elegans*.

Cuculiformes: Cuculidae: cuckoo *Cuculus canorus*, Klaas's cuckoo *Chrysococcyx kla* yellow-billed cuckoo *Coccyzus americanus*.

Strigiformes: Tytonidae: barn-owl *Tyto alba*.

Passeriformes: Corvidae: raven *Corvus corax*.

Our terminology of feather structures follows Chandler (1916) and Lucas & Stettenhe (1972).

SULTS

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RESULTS

In LM, the middle portion of hamuli may seem thickened (cf. Messinger 1965: fig. 14), but SEM observations clearly indicated that the widened or "thickened" appearance results from rotation or torsion of these tape-like structures (see Figs. 5-9). Pronged hamuli, in contrast, were found to be non-artifacts.

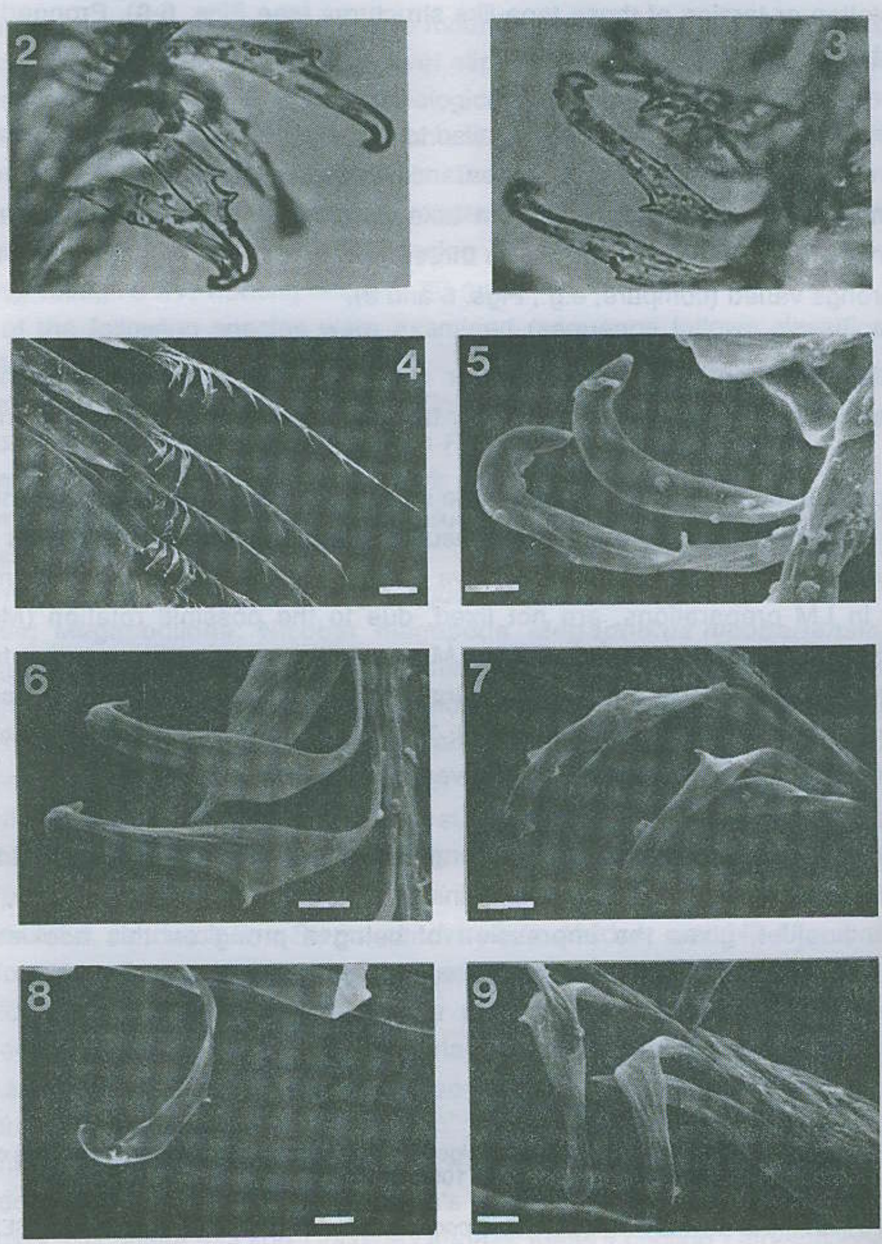
The number of prongs varied, but we failed to find any consistent differences with regard to their structure and frequency of appearance, both between hamuli of different feathers of a single bird and between different taxa. In one and the same barbule, both the number of prongs per hamulus (one to three, if present at all; Figs. 2-3) and the size of these prongs varied (compare, e.g., Figs. 6 and 8).

All variations mentioned above occur so irregularly, both interspecifically and intraspecifically, that neither functional nor taxonomic patterns could be discerned.

Actual prongs (non-artifacts) appear at one side of a hooklet, on the edge of the tape-like structure, look like a saw-tooth, and are usually orientated towards the hook's apex. The tape-like structure ensures that the relative positions of the hook and the prong, as they appear in LM preparations, are not fixed, due to the possible rotation (Messinger's "thickening") around the length axis. In LM preparations, prongs may seem to occur at both edges of the hamuli, but SEM examinations (e.g., Fig. 5) show that this condition is comparable to the "thickening" of hamuli: The direction of rotation determines whether the prong appears at the dorsal or at the ventral edge.

In LM, several artifacts may resemble prongs; SEM examination revealed that these may originate in different ways: It often happens, for instance, that a ventral tooth, which lies under a hooklet, gives the impression of being a prong on this hooklet (Fig. 9); conversely, actual prongs may look like a ventral tooth (Fig. 6).

FIGURE 2. Neck feather of blue-tailed imperial pigeon - *Ducula concinna*. Different numbers of prongs on hamuli of the same barbule (LM, appr. 1000 x).
FIGURE 3. Same feather (LM, appr. 1000 x).
FIGURE 4. Mantle feather of cuckoo - *Cuculus canorus*, distal barbules with pronged hamuli (SEM, scale bar = 28.0 µm).
FIGURE 5. Back feather of black-bellied sandgrouse - *Syrrhaptes orientalis*; due to rotation, prong appearing at ventral side of hamulus (SEM, scale bar = 4.4 µm).
FIGURE 6. Back feather of cuckoo - *C. canorus*; pronged hamuli of which upper prong seems to be underlying ventral tooth, but in fact is a true prong (SEM, scale bar = 4.6 µm).
FIGURE 7. Breast feather of pheasant - *Phasianus colchicus* (SEM, scale bar = 8.7 µm).
FIGURE 8. Back feather of raven - *Corvus corax* (SEM, scale bar = 6.0 µm).
FIGURE 9. Breast feather of oystercatcher - *Haematopus ostralegus*; true prong at the left, artifact - due to underlying ventral tooth - at the right (SEM, scale bar = 5.7 µm).



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[DIS]CUSSION

[Th]e occurrence of pronged hamuli corresponds well with Sick's (1937) findings. [Ho]wever, the sparse and irregular occurrence of pronged hamuli within a single barb [pu]ts their function of "fine-tuning" the distal and proximal barbules as was suggested by [Si]ck (1937: 330) in doubt. The observation of pronged hamuli in all taxa examined [im]plies that this characteristic has not the diagnostic significance as inferred by [M]essinger (1965). Prongs are widely but irregularly distributed among birds and it is [c]lear that historically many ad hoc observations have been made proposing that [t]hickened and/or pronged hamuli are of possible taxonomic significance. However, pronged hamuli apparently belong to the basic feather structure. These structures have a much wider taxonomic distribution than was reported by earlier workers and, therefore, prongs do not seem to be useful for identifying feather fragments. One may speculate that earlier in the evolutionary history of feathers they may have played a more prominent role and that they may have occurred in greater numbers, but that in extant birds these structures might be in the process of becoming reduced.

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