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MOULT OF WING AND TAIL-FEATHERS IN THE OSTRICH, *STRUTHIO CAMELUS*

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ABSTRACT

Structure and moult of wing and tail of a full-grown Ostrich, *Struthio camelus*, are described. In the wing, at least three feather generations could be recognized. The pattern of moult is more or less symmetrical in both wings and the sequence of feather replacement is not random. The tail consisted of 93 feathers of two different generations. Moult in the tail proceeds asymmetrically and seems to be fully irregular. The phylogenetic significance of these findings is discussed.

INTRODUCTION

Differences in patterns of wing and tail moult in different avian taxa have received much attention (Stresemann, 1963, 1967; Stresemann & Stresemann, 1966, and references therein), and already from the early observations by Heinroth (1898) and Beebe (1914) there is consensus among systematists that a phylogenetic component must be involved. However, the phylogenetic interpretation of the phenetic clusters in which these studies have resulted, remains unclear. Most studies on the moult of flight-feathers have been purely descriptive and the significance of different patterns has been assessed in functional and ecological terms only (e.g. Wattel, 1985; Noordhuis, 1989).

Moult in ratite birds has hardly been studied. With respect to species with a small number of remiges (Kiwi, *Apteryx*; Cassowary, *Casuaris*),

the reason is obvious, but Emu, *Dromaius*, and especially Rhea, *Rhea*, and Ostrich, *Struthio*, possess sufficient wing feathers to allow for a study on their moult patterns. Although many characters in ratite birds may be linked with the secondary loss of the ability of flight, there is no reason to assume beforehand that they have also lost the ancestral pattern of wing moult.

Little information for wild ostrich is available (e.g. Cramp & Simmons, 1977:41). Duerden (1911) observed that "in a wild ostrich only a few of the wing plumes are growing at any one time instead of the full number as in the domesticated bird, where the growth is regulated artificially" and although "the natural order according to which the various plumes appear has not yet been determined, it is well established that the feathers towards both ends of the wing develop in advance of those in the middle." Noordhuis (1989), however,

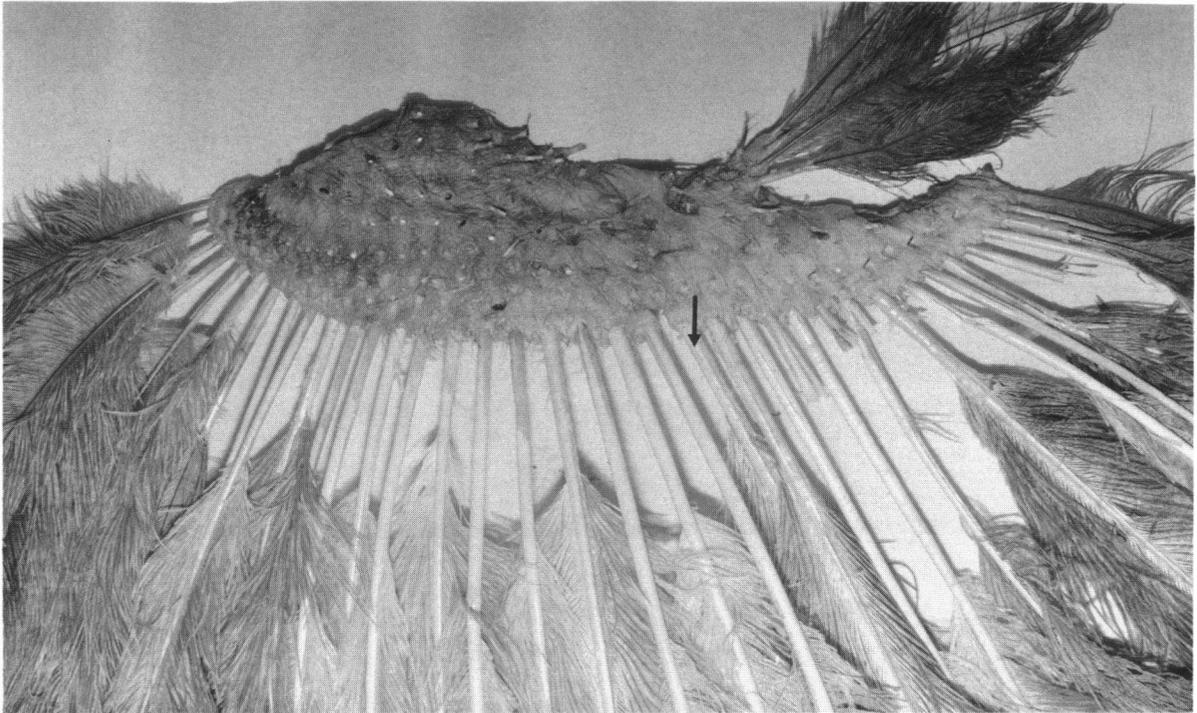


Fig. 1. Left wing, showing remiges (seen from above; all coverts have been removed). P1 indicated by arrow.

assumed an irregular pattern of primary moult for *Struthio*. In Kiwi, Cassowary, Emu, and Rhea no tail-feathers can be distinguished among the general feathering of the hinder parts, only *Struthio* has a tail consisting of long, curled and loose-vaned feathers. Apparently, neither the structure nor its moult pattern has been examined so far.

In this study, the structure and moult of wing and tail-feathers in a freshly dead specimen of the Ostrich, *Struthio camelus* L., 1758, are described. Study skins or stuffed specimens of the Ostrich are not suitable for an accurate recognition of individual wing feathers, while living birds cannot easily be handled for this purpose. For an exact investigation of moult patterns, one is therefore compelled to turn to freshly dead birds. Since it is clear that large series of this kind are not available, this report, based on the investigation of a single specimen, is published as a starting point for further studies.

MATERIAL AND METHODS

All data refer to a full-grown female Ostrich. The bird had been captured in the wild, was confiscated at Amsterdam Airport in September 1988 and died eight months later in the Amsterdam Zoo (Natura Artis Magistra).

Primaries are counted from the innermost (p1) outward, secondaries from the outermost (s1) inward, and tail-feathers from the centre (t1) outward. Remiges and their adjacent coverts were examined after removal of all other upper wing-coverts.

RESULTS

Structure and moult of the wing

In the wing, 16 primaries were present (Figs. 1 & 2): eight metacarpals (p1-p8), one addigital (p9), four middigitals (p10-p13) and three

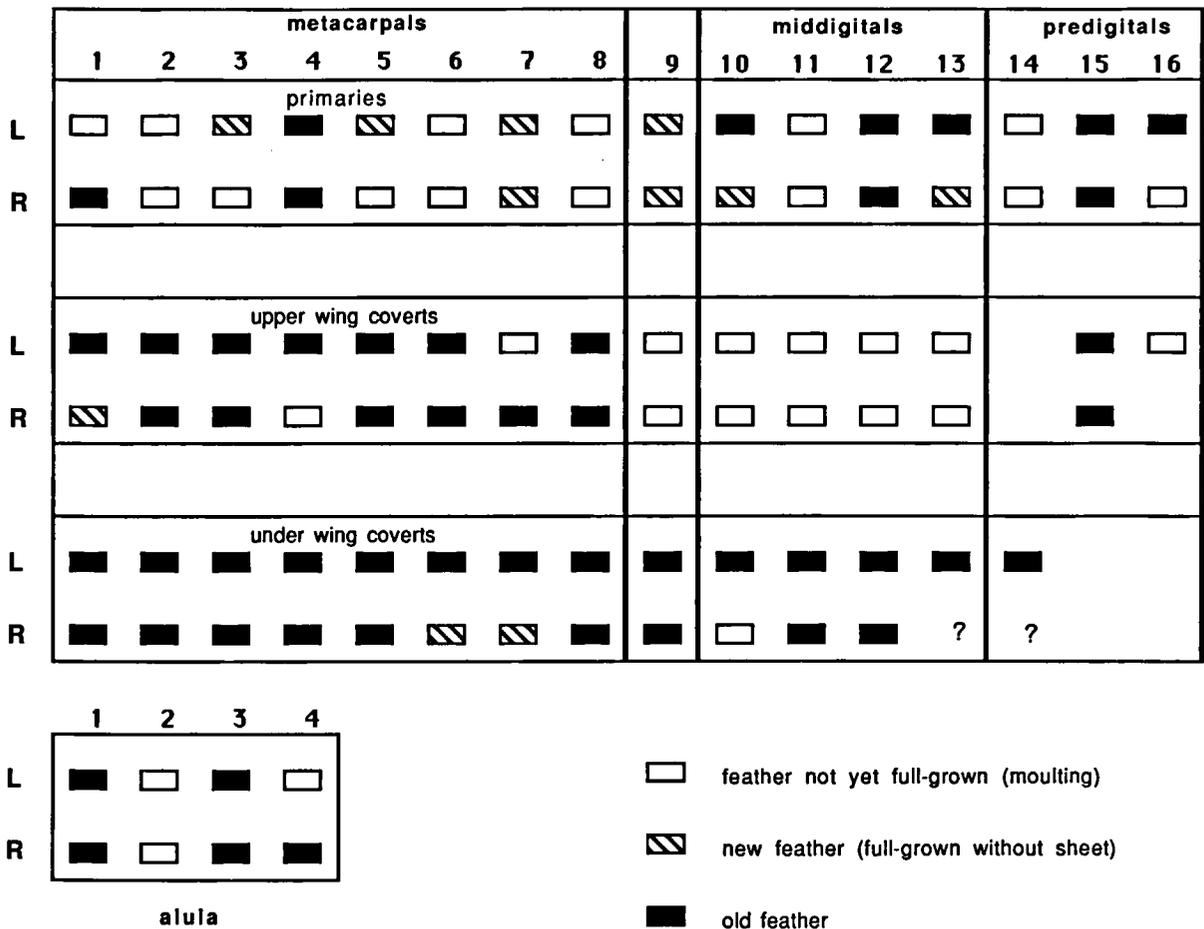


Fig. 2. Moults of primaries and their coverts. Nota bene — sheet must be sheath.

predigitals (p14-p16). The alula consisted of four small feathers.

The exact number of secondaries was more difficult to establish, but at least 20 were counted (Fig. 3). The under surface of the wing was bare except for a single row of under wing-coverts. Each primary was provided with one upper and one under wing-covert, which lay distally to the primary they belong to (oriented towards wing-tip). These series became interrupted towards the outer primaries: p14 in the left wing and p14 and p16 in the right wing had no upper wing-covert, and in both wings p15 and p16 had no under wing-covert. In both wings, the upper secondary-coverts formed a complete series of 20 feathers, but the under

secondary-coverts were structurally incomplete: in the left wing, the under wing-coverts of s10 and s15-s20 were lacking, in the right wing those of s17-s20.

In the left wing, 26 newly replaced feathers were growing (Figs. 2 & 3): six primaries, two feathers of the alula, seven secondaries, seven upper primary-coverts, three upper secondary-coverts, and one under secondary-covert. In the right wing, the total number was 30: eight primaries, one feather of the alula, nine secondaries, six upper primary-coverts, four upper secondary-coverts, one under primary-covert, and one under secondary-covert. In both wings, primaries of at least three different generations could be recognized.

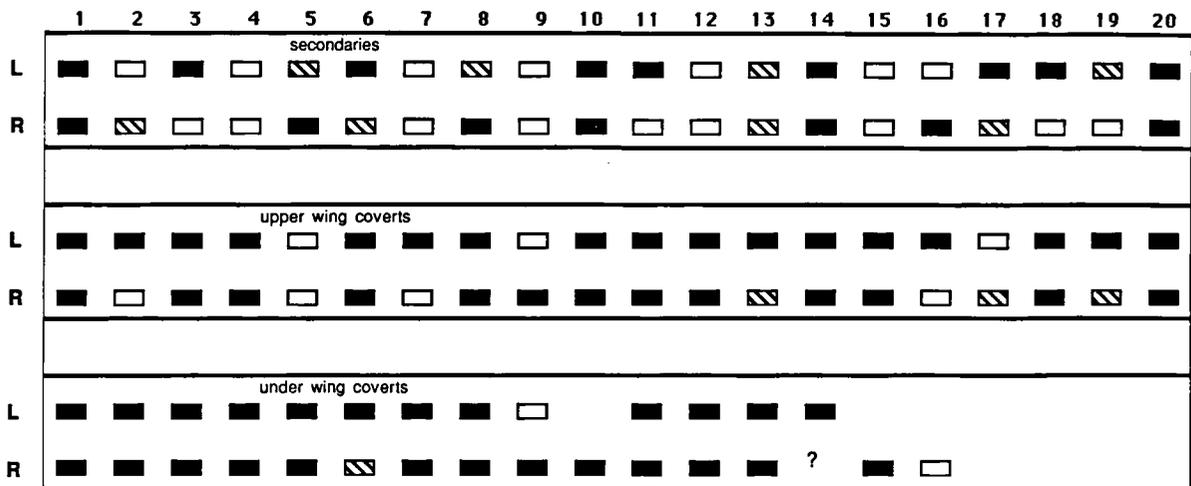


Fig. 3. Molt of secondaries and their coverts.

Structure and moult of the tail

The tail consisted of many loosely structured feathers, which graded into the body-feathers (Figs. 4 & 5). At both sides of the pygostyle, eight rows of seven feathers were present, but as some of these rows were structurally incomplete (not due to moult), the total number of feathers was 93; 45 in the left half and 48 in the right (Fig. 5). Unlike the condition in flying birds, only both central vertical rows were attached to the pygostyle, all others were loosely implanted in the skin, projecting into the subcutal fat layer. Two generations of feathers could be distinguished: 40 old and 53 new feathers. All freshly moulted ones still had (remnants of) sheaths, 33 of these were in growth (figs. 5).

CONCLUSIONS AND DISCUSSION

Structure and moult of the wing

Our observations on the structure of the wing fully agree with those of Wray (1887: fig. 2) and therefore we conclude that reports of a number of primaries other than 16 (Jeffries, 1881; Fürbringer, 1888) are erroneous. The number of secondaries (at least 20) corresponds with earlier reports (e.g., Wray, 1887).

Similar to the wings of neognathous birds, one upper and one under covert accompany

each remex. The regular implantation of the secondary coverts demonstrates that *Struthio* is eutaxic (cf. Steiner, 1918).

Structural asymmetry between left and right wing (Figs. 2 & 3) of one individual bird is not exceptional in this species, since Duerden (1920) not only reported similar differences in the wing-coverts, but even in the number of remiges.

The patterns of moult are more or less symmetrical in both wings. The suggestion that feather replacement proceeds at random can therefore be excluded. The primaries might be moulted from several foci, but a serially descendant moult cannot be excluded. Our observations do not support Duerden's (1920) statement that outer remiges are moulted prior to those in the centre of the wing. The replacement of the secondaries seems to start from several foci. The direction in which moult proceeds cannot be determined in a single specimen.

The upper wing-coverts seem to start moulting later than their corresponding remiges. The under wing-coverts start later than the upper coverts. Both rows of wing-coverts are not shed together with their remiges, but are more likely moulted in groups (see e.g., upper wing-coverts of p9-p13 in Fig. 2).



Fig. 4. Tail, seen from below.

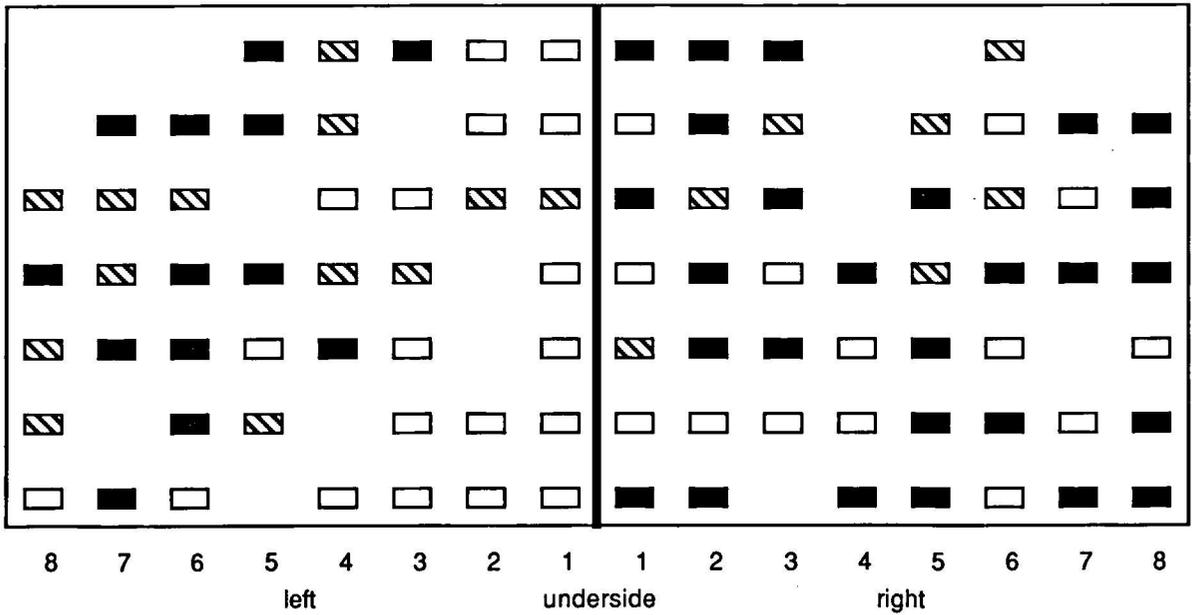


Fig. 5. Structure and moult of tail.

Structure and moult of the tail

The tail of the full-grown Ostrich consists of eight rows of seven feathers (Fig. 5). The total number of 93 rectrices is considerably higher than the 50 to 60 reported by Stresemann (1927-34:741).

It is difficult to ascertain which series of tail-feathers is homologous with the tail in flying birds. The number of rows at both sides of the pygostyle corresponds with the eight pairs of tail-feathers found in the chick of *Struthio* (Steiner, 1946). In the embryo a biserial arrangement of follicles is found, from which 16 rectrices with their upper coverts will grow, while the underside of the tail is bare (Steiner, 1946). This might indicate that the feathers in the most ventral row represent the homologues of normal tail-feathers and that the six dorsal rows consist of modified tail-coverts. Alternatively, one or both of the central vertical rows of tail-feathers, which are attached to the pygostyle, may be homologous with the tail-feathers in flying birds. This could be determined by marking the tail-feathers in newly hatched chicks and following their development into the adult tail.

Although tail moult was most active in the central rows of feathers, it seems most likely that the sequence of feather replacement is fully irregular. No symmetry exists between both tail-halves. The left side consists of considerably more newly replaced and growing feathers than the right side.

In case further studies will confirm that primary moult in the Ostrich is serially descendant, this will have phylogenetic implications. Since tinamous, galliforms, and anseriforms all show a descendant mode or a variation on this scheme ("Staffelmauser" in tinamous and some galliforms, nearly simultaneous in anseriforms), this pattern is the most probable character-state at the basal node of the avian tree (see Cracraft & Mindell, 1989). It can therefore be excluded that simultaneous moult is the plesiomorphic condition as was suggested by Verheyen (1958). Other patterns of

primary-moult (ascendant, transilient, from a focus at p4 or p6, etc., see Stresemann & Stresemann, 1966) can then be considered to be apomorphic and can be used to define monophyletic groups among extant birds.

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