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REDUCTION OF THE CLAVICLES IN THE MESOENATIDAE, WITH SOME REMARKS CONCERNING THE RELATION- SHIP OF THE CLAVICLE TO FLIGHT-FUNCTION IN BIRDS

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During recent studies on the arteries in the neck and thorax of the Meso-enatidae, it was observed that the clavicles are reduced to a pair of extremely small bones which articulate with the clavicular face of the head of the coracoids.

In discussing the taxonomic position and some features of the anatomy of *Mesites*, Beddard (1898) stated, “. . . The furcula is quite degenerate.” Stressemann (1927-1934), apparently following Lowe (1928) stated, “Keine Spur einer Furcula.” Both statements are vague and open to interpretation. According to Lowe (1924, p. 1148), “There is not the faintest indication of a clavicle in *Mesites*.” This is not the true condition, however, and it is well to clarify this matter, and to give a brief account of the actual condition as found in single specimens of each of the two species of *Mesoenas* (*variegata* and *unicolor*) and in two examples of *Monias benschi*. A single alcohol-preserved specimen of each, and, in addition, a complete skeleton of *Monias*, were studied from the anatomical collections of the American Museum of Natural History and the U. S. National Museum. In each case the clavicles were carefully measured.

The clavicles, in each of the three species, are reduced to small rudimentary or vestigial bones which represent only the head of the clavicle or epicleidium.

TABLE 1
Measurements of the os claviculum in three species of Mesoenatidae

	<i>Mesoenas variegata</i>	<i>Mesoenas unicolor</i>	<i>Monias benschi</i>
Epicleidium:			
Depth	3 mm	3 mm	1.5 mm
Length	2.5 mm	2.5 mm	2.7 mm
Ligamentum			
Corpus claviculari:	broad and heavy	narrower and strong	thread-like or nearly absent

The body of the clavicle (*corpus claviculari*) is reduced or completely resorbed, although it remains as a strong ligament in *Mesoenas*—broader in *M. variegata* than in *M. unicolor*—and absent or so greatly reduced in *Monias benschi* as to make determination of its presence quite difficult. In *Monias*, it is reduced to a thin, thread-like cord which may be imbedded in the myofascia surrounding the coracoid muscles, and its identification as a *ligamentum corpus claviculari* is a matter of interpretation.

Dissection of a single specimen of *Apteryx australis mantelli* Bartlett (U.S.N.M.) revealed the complete absence of the *os claviculum*, nor was there satisfactory evidence to indicate a ligamentous vestige of this structure.

Glenny and Amadon (1954) found a similar reduction in the clavicles of *Otidiphaps nobilis* Gould, and, in addition, have listed several species of Barbets in which the furcula is incomplete except for a ligamentous pons between the separate clavicular elements, a condition similar to that found in a great many of the Old World Parrots. The amount of reduction in the body of the clavicle varies somewhat, but little exact information is readily available on this subject.

In Rand's account of the habits of the members of the Mesoenatidae (1936), he particularly stressed the point that these birds are typically terrestrial in habit. Flight appears to be absent in these birds and such escape attempts as were made were by foot and not by wing. In a more recent paper on the nests of *Mesoenas unicolor*, Rand (1951) pointed out that all of the three species of the Mesoenatidae are ground birds which either do not fly or fly poorly, and also stated that of two nests of *Mesoenas unicolor* which were found, both were located in the rain forest, and that they were located in a fork of a sloping tree and that in each case, the lower trunk of the tree had several low branches on it, thus making it possible for the bird to hop up to the nest.

Reduction in flight-function should not be construed to be directly correlated with and, in part, dependent upon the reduction in the clavicles, although instances of reduction or even deletion may be cited to substantiate this view (Kiwi, Ostrich, and other ratite birds).

In discussing the skeleton of the flightless Diatrymiformes, Lambrecht (1933) stated, "Claviculae verkümmert oder fehlend," and Matthew and Granger (1917) stated, that the clavicula may be fused to the tip of the acromial process, in *Diatryma steini*, and if not, it is wholly absent as there is no facet for a separate bone.

Still other species of birds have partial or almost complete reduction of the clavicles and yet are capable of maintaining a satisfactory, at times even strong, flight-function. Examples of this are to be found among the Old World, and especially the Austral-asian, parrots, in which the epicleidium and a ligamentum corpus claviculi alone remains, and in *Otidiphaps nobilis* Gould, the Pheasant Pigeon, of New Guinea, which, although it inhabits the forest floor most of the time, still possesses the capacity for strong, powerful flight when occasion demands. On the other hand, *Rhynochetos jubatus*, the Kagu, of New Caledonia, has a well developed furcula, but its powers of flight are greatly reduced (Glenny, 1947) and escape is chiefly by running although this bird will fly for short distances when pursued. The pectoral muscles seem to be weak and poorly developed in this species, and this may account in part for its reduced flight capacity.

Other instances of flightless birds, in which the clavicles are present and fused to form a furcula, are found in *Atlantisia rogersi* (Lowe, 1928) and in *Notornis mantelli* (Parker, 1881). In both of these species, the typical gruiform furcula is present. In *Opisthocomus hoazin*, the clavicles, coracoids, and sternum are fused into a single complex of bone elements which affords rigid support, but which does not appear to contribute greatly to the flight-function since in this species, the capacity for flight is greatly reduced.

It should not be inferred that reduction or even loss of the clavicles results in a comparable reduction or loss of flight but that the latter may be due to a complex of factors, both structural and mechanical in nature along with certain less tangible ecological and behavioral factors. The Penguins and the Great Auk, *Pinguinis impennis* (Linn.), which lack the capacity for aerial flight, have the clavicle very well developed, even, in some cases, including a sizeable hypocleidium. These birds, however, are flightless only with regard to air, their mode of progression in the water is such as to merit saying that they fly in that medium instead of in the air above it.

It may be of interest to note that the Mesoenatidae, Raphidae, *Otidiphaps*, *Rhynochetos*, and *Apteryx*, to mention but a few examples, are or were insular species.

Geographical isolation may have contributed measurably to survival of forms with reduced capacity for flight. At the same time, however, a small, geographically isolated population, of any highly specialized form, is less apt to become highly variable, and thereby to develop any appreciable number of distinct species, through the evolution of multiple factors or characters, than is the case of a central or more generalized form, which has a large and widely distributed population,

wherein many lines of specialized evolution may develop. The Fringillidae may be cited as an example of this latter case. In such an instance, factors of competition need not be considered to be of such great importance so much as the effect of hybridization in large populations. Since most structural innovations tend to be recessive for a population, at least during the early period of occurrence, incidental specializations such as addition of structures, elaboration of existing structures, reduction and even loss of an existing structure are less apt to be perpetuated in a large, hybridizing population than in a smaller or a highly concentrated, isolated, inbreeding population.

In general, among the higher and more highly specialized vertebrates, there is a marked tendency towards reduction of previously existing (ontogenetic) structures than in the evolving of new elements.

Ultimately, success of either a large or small population depends upon its general capacity to survive under conditions of competition within the limits of the habitat. That survival factors have not seriously impaired the success of the Mesoenatidae, despite a holoterrestrial habitat, is evident. Contributing to their success may be the factors of geographical isolation, in Madagascar, and adoption of highly specialized ecological niches and a rather singular ecological stratification.

Both species of *Mesoenas* typically inhabit the forest floor, while *Monias* inhabits the low brush forest, in flat sandy country covered with dense brush (Rand, 1936). This may well be an important factor contributing to their success, since a good cover is afforded by the canopy above and fairly clear floor affords better visibility and several directions for escape. As a result, flight is not to be construed as essential to survival in such a habitat, but survival may be facilitated by the ability to run and escape predators in this manner.

It is not clear how much pressure is brought to bear on these birds by natural predators. If this is not significant, then this becomes another factor which may have enhanced their opportunities for survival.

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