WOOD OWLS OF THE GENERA STRIX AND CICCABA

by

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> "... speaking here as a taxonomist to taxonomists, I am certainly no less than respectful toward the noble art of classification"
> (Léon Croizat, 1958, p. 119).

In considering a thorough systematic study a necessity before entering into zoogeographical theories, the author feels he may expect the full and sympathetic approval of Professor H. Boschma, to whom this paper is dedicated. Indeed, taxonomy or systematic zoology is one of the corner-stones of a sound building of zoogeography. The present paper, therefore, dealing with the taxonomy of wood owls and subsequent zoogeographical inferences probably is in line with the way of thinking of Boschma as a systematist. The author will add a further perspective of systematic zoology by proposing a way leading to deeper understanding of owl taxonomy through laboratory experiments, which, however, he has not yet been able to carry out himself.

James Lee Peters (1940), the latest reviewer of the owls in his "Check-list of birds of the world", volume 4, was confronted with the problem of designing a systematic arrangement of the group of "wood owls", medium-large owls with big round heads without ear-tufts and usually dark eyes. In a preliminary paper Peters (1938) turned back to a classification of owls proposed by Sharpe (1875) and more or less strictly followed by Ridgway (1914), using the size and shape of the external ear as a character distinguishing between a "bubonine" and a "strigine" group of owls, ultimately giving these groups subfamily rank.

In the "bubonine" owls the ear opening is a relatively small, oval opening in the skin with only a slight asymmetry on the left and right sides. There is no conspicuous dermal ear flap. In this group of owls the huge eagle-owls (*Bubo*) and tiny scops owls (*Otus*) are united among others.

In the "strigine" (sive syrniine) owls the ear opening is extremely large and there is a wide dermal flap, at least on the anterior margin, on the sharp

edge of which a line of feathers of the facial disc is implanted. In general the shape of the outward ear is very complicated and there is generally a conspicuous asymmetry of the left and right sides. Usually the right ear opening is larger than the left, but, in some individuals I found this condition reversed. In this group belong the wood owls (*Strix*) and long-eared owls (*Asio*), for example.

In accepting the structure of the outward ear as a character leading dichotomously to separate taxonomic groups, Peters (1938) found himself in a position to divide the group of wood owls, in spite of great similarity in outward appearance, into a "strigine" group, more properly known as the genus *Strix*, and a "bubonine" group, for which the generic name *Ciccaba* was available. They were assigned to different subfamilies (Peters, 1940) and therefore, were considered to be only distantly related.

The geographic distribution of the twelve species of *Strix* sensu Peters (1940) is almost world wide; these owls being absent from Africa south of the Sahara and from the Australian region only. In contrast to this, the genus *Ciccaba*, with five species, has a considerably more limited distribution, its members occurring only in Central and South America (four species) and Africa south of the Sahara (one species).

As a matter of fact no serious objection can be raised against using the structure of the outer ear as a primary taxonomic character. One may ask, however, whether the resulting systematic arrangement reflects the affinity of the species from the point of view of their history of origin. In other words, does this taxonomic arrangement, justified though it is, serve as a sound basis for zoogeographic studies?

> "It may very well be that my own efforts are not to succeed any better than those of the authors I have quoted..."
> (Léon Croizat, 1958, p. 19).

Referring to Peters (1940) as systematic authority, Croizat (1958, 1958a) has used the distribution pattern of the *Ciccaba* owls as a basic example of his "across the Atlantic" type of distribution. The index to his voluminous work "Panbiogeography" (1958) refers to 33 entries concerning the *Ciccaba* case. In spite of the 2612 pages of text (not counting bibliography and indices) it is not easy to understand what Croizat really wants to say. But in this connection this is not a relevant point. It will be the subject of the next few lines to examine only whether the arrangement of wood owls into

two genera of widely different systematic places can be recommended as a basis for zoogeographic studies.

In the list of species, ears of which were examined and measured by Peters (1938, pp. 185-186), all of the four South American species of *Ciccaba* occur beside the sole African representative of the genus, *Ciccaba woodfordii* (A. Smith). However, only three of the currently recognized nine species of *Strix* are listed, two American (*S. hylophila* Temminck, and *S.* (*varia*) *fulvescens* (Sclater & Salvin)) and one palaearctic (*S. aluco* L.). The average length of the left and right ear slits of these owls measured by Peters (1938) in study-skins have been computed and summarized in Table I.

TABLE I

Mean length of outer ear opening in seven species of wood owls; computed from Peters (1938, p. 185-186). Figures referring to *Ciccaba* are printed in italics. Number of specimens in parentheses. Measurements in mm.

Species	Left ear	Right ear
Tropical and sub-tropical America:		
Ciccaba huhula (Daudin) (1)	*12½*	*20*
C. nigrolineata Sclater (2)	*13*	*18*
C. virgata (Cassin) (7)	*12*	*17½*
C. (*virgata*) *borelliana* (Bertoni) (1)	*16*	*21*
Strix hylophila Temminck (1)	19	24½
Temperate South America (mountains):		
C. albitarsus Bonaparte (3)	*19*	*22*
Central America (mountains):		
S. (varia) fulvescens (Sclater & Salvin) (1)	25	27½
Tropical and sub-tropical Africa:		
C. woodfordii (A. Smith) (4)	*8½*	*12*

Although the structure of the outer ear may be distorted or damaged in dried study-skins, well-made skins allow a fair degree of exactness of measuring the length of the ear opening and the width of the dermal flap. My own measurements of ear opening length taken from four species of *Ciccaba* and nine of *Strix* therefore fortunately do not much differ from those of Peters (Tables II and III). Accepting the dividing principle of "bubonine" and "strigine" ears, the African Wood Owl (*C. woodfordii*) clearly belongs in the *Ciccaba* group. But so more or less do the Brown and Spotted Wood Owls from southern Asia, listed by Peters (1940) as *Strix leptogrammica* Temminck and *Strix seloputo* Horsfield, respectively. These species were not included in Peters' study (1938) preparatory to his "Check-

list". Provided the character of the outer ear is accepted as a way of distinguishing between separate groups of owls of almost or wholly subfamily rank, at least two more species have to be incorporated into *Ciccaba* than originally proposed by Peters. So far I know of no author who has expressed the slightest doubt about placing *S. leptogrammica* and *S. seloputo* in *Strix*. It need hardly be stated that a change of generic place for these owls is not without repercussions on Croizat's zoogeographical theories. The total range

TABLE II

Mean length of outer ear opening and width of dermal flap in 13 species of wood owl in relation to body size. Figures referring to *Ciccaba* are printed in italics. Number of specimens in parentheses. Measurements in mm.

Species	Wing (mean length)	Left ear (mean length)	Right ear (mean length)	Dermal flap (mean width)
Strix nebulosa J. R. Forster (8)	447	27	27	15
S. uralensis Pallas (6)	362	24	27	13
S. seloputo Horsfield (3)	360	12	12½	1
S. varia Barton (5)	339	25	27	12
S. occidentalis (Xantus) (1)	331	17½	22	13
S. leptogrammica Temminck (5)	327	17½	22	2
Ciccaba nigrolineata Sclater (3)	*289*	*11*	*12*	*0*
S. rufipes King (1)	272	17	11	5
S. aluco L. (7)	262	21	22½	9½
C. huhula (Daudin) (3)	*260*	*9½*	*14*	*1*
C. virgata Cassin (3) [1]	*258*	*13*	*20*	*2*
S. hylophila Temminck (1)	251	17	21	7
C. woodfordii (A. Smith) (5)	*245*	*10*	*13*	*1*

Individual lengths of left ear opening: *S. nebulosa* 25½, 26½, 26½, 27, 27, 28, 29, 29; *S. uralensis* 20, 23, 23½, 24, 25, 26; *S. seloputo* 11, 12, 12; *S. varia* 21½, 22, 24½, 26, 29; *S. leptogrammica* 16, 17, 17, 17½, 20; *C. nigrolineata* 10, 11, 13; *S. aluco* 19, 19½, 19½, 20, 20½, 23½, 24; *C. huhula* 7, 9½, 12; *C. virgata* 11, 13, 15½; *C. woodfordii* 9, 10, 10, 10, 11.

Individual lengths of right ear opening: *S. nebulosa* 24, 27, 28½, 24, 26½, 22+, 27, 31; *S. uralensis* 28, 26, 26½, 26½, 26½, 25½; *S. seloputo* 13, 12, 12½; *S. varia* 27, 24½, 24, 33, 27; *S. leptogrammica* 23½, 20, 27½, 19½, 20; *C. nigrolineata* 9½, 13, 13; *S. aluco* 25, 22, 25½, 23, 22½, 20, 21½; *C. huhula* 13, 12, 16; *C. virgata* 18, 19½, 22; *C. woodfordii* 15, 12, 12½, 12½, 14.

Individual widths of dermal flap (only the larger of the left or right sides given): *S. nebulosa* 11½, 12, 15, 15, 16, 16, 16½, 17; *S. uralensis* 12, 12½, 13, 13½, 14, 14½; *S. seloputo* 1, 1, 1; *S. varia* 10, 11, 11½, 13, 13; *S. leptogrammica* 0, 0, 2½, 3, 4; *C. nigrolineata* 0, 0, 0; *S. aluco* 7, 8, 8, 9, 10½, 10½, 11; *C. huhula* 0, 0, 2; *C. virgata* 1½, 2, 3; *C. woodfordii* 0, 0, 0, 1, 3.

1) inclusive *C. borelliana* (Bertoni).

of members of the *Ciccaba* group could now even be considered as being pantropical, a distribution pattern which is among one of the most difficult for a zoogeographer to interpret.

It could also be stated, however, that the structure of the outward ear is too strictly an adaptive character for it to serve as a means of taxonomic distinction beyond genus level. Could it be possible that the length of the ear slit and the size of the dermal flap are directly adapted to the environment and the principal prey and therefore variable in closely related species? In view of this supposition I have tried to correlate the outward ear characters on a quantitative basis with body size (Table II) and with geographic distribution (Table III).

TABLE III

Width of ear opening and dermal ear flap in 13 species of wood owl in relation to climate. Figures referring to *Ciccaba* are printed in italics. Number of specimens in parentheses. Measurements in mm.

Species	Total of mean lengths of left and right ears	Mean percentage of asymmetry of ear lengths (left = 100%)	Mean width of ear flap
Tropical:			
C. huhula (3)	*23½*	*149*	*1*
C. nigrolineata (3)	*23*	*108*	*0*
S. leptogrammica (5)	39½	139	2
S. seloputo (3)	24½	107	1
Tropical and sub-tropical:			
C. woodfordii (5)	*23*	*133*	*1*
C. virgata (3)	*33*	*152*	*2*
Sub-tropical:			
S. hylophila (1)	38	124	7
Sub-tropical and temperate:			
S. rufipes (1)	28	65	5
Temperate and boreal:			
S. aluco (7)	43½	125	9½
S. occidentalis (1)	39½	126	13
S. varia (5)	52	111	12
Boreal:			
S. uralensis (6)	51	114	13
S. nebulosa (8)	54	99	15

While it is clear that in the species of *Strix* and *Ciccaba* combined the size of the external ear is not directly related to body-size, it is equally clear that this character does not provide a clear-cut means of distinguishing between a *Strix* group and a *Ciccaba* group; the species *S. rufipes* King (South America) being in between.

The same holds for the width of the dermal flap in front of the outward ear opening. This fold of skin is not only erectable and therefore apparently of great use in locating the noise made by prey animals; but, most curiously, it is definitely not correlated with the owls' body-size only; moreover, the species *S. rufipes* and *S. hylophila* (South America) occupy a position in between a strigine and a ciccabine condition. However, some conformity seems to exist between the variation of flap-width and geographical latitude: northern wood owls, living in boreal and temperate climatic zones, have a stronger developed dermal ear flap than sub-tropical and tropical wood owls. This differentiation does not lead to an acceptable distinction of a *Strix* group and a *Ciccaba* group either, as for instance the species *S. hylophila* and *S. rufipes* are again intermediate in this respect, and, although generally classed as members of the *Strix* group, they are somewhat nearer to *Ciccaba* than to *Strix*.

In view of these morphological data I am inclined to doubt the significance of a distinction between *Strix* and *Ciccaba* wood owls, on account of outward ear structure, let alone their assignment to different subfamilies. Probably the distinction of "strigine" and "bubonine" owls as different taxa, not only for the wood owls, but also for other groups of owls, is merely illusive. It is possible, however, that the tropical American species *C. huhula* (Daudin) and *C. nigrolineata* Sclater with their unique black-and-white-barred plumage colour pattern represent a distinct group of long geographic isolation and that, therefore, there is a practical reason of knowing these under a separate name (*Ciccaba* Wagler, 1832; type by monotypy, *Strix huhula* Daudin). This, however, would then be merely a matter of convenience. A classification of the wood owls different from that by Peters (1940) and provisionally accepted according to the above stipulated line, would lead to severe repercussions on Croizat's zoogeographic discussions, as is clearly seen in the distribution maps (figs. 1 and 2; see also Croizat, 1958a, p. 139, fig. 1). At the uncertain state of our present knowledge of the taxonomy and relationship of the wood owls any attempt at a zoogeographic interpretation of the distribution of these owls seems premature.

The discussion above could be considered "bad taxonomy", since it makes use of characters that probably are highly adaptive and therefore unusually

plastic. It cannot be denied that this is perfectly true and, worse, that this blame can be put on owl taxonomy in general. Therefore it is urgently needed to add experimental work on the function of the auditory and visual

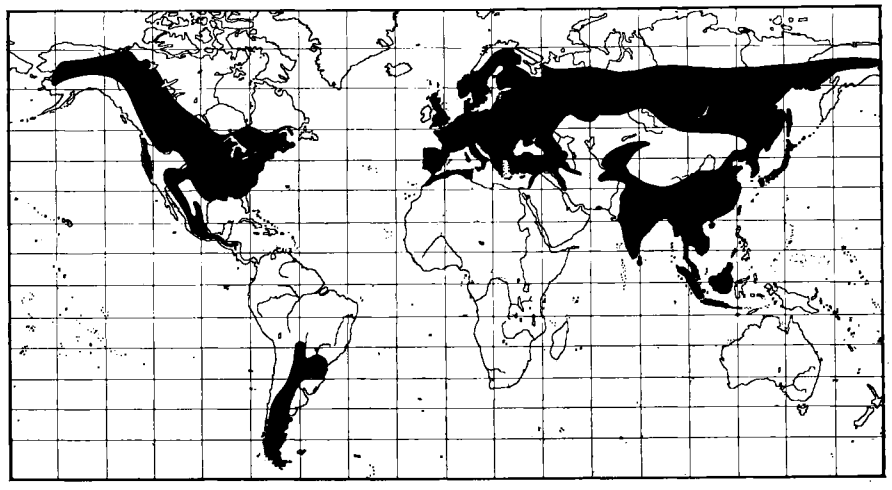

Fig. 1. Geographic distribution of the species of the genus *Strix* sensu Peters.

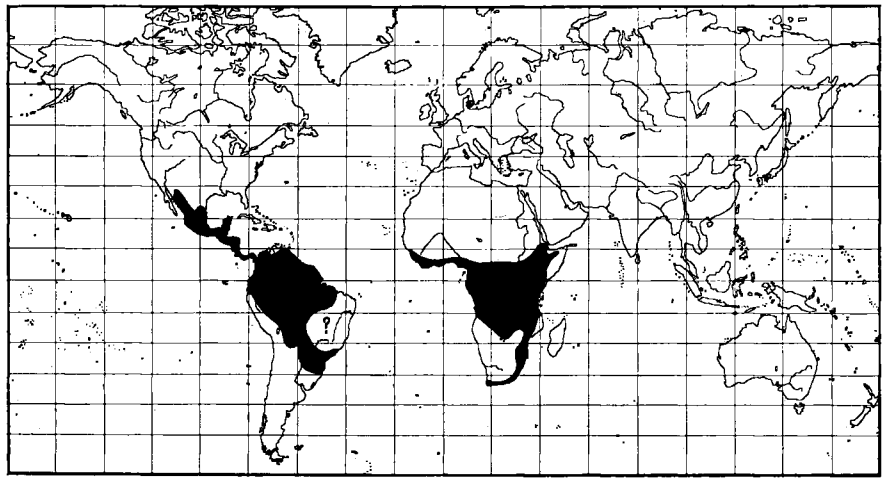

Fig. 2. Geographic distribution of the species of the genus *Ciccaba* sensu Peters.

powers of owls in relation to their environment, their hunting methods and their prey. Locating the high squeaks of mammalian prey in lonely and generally deadly silent, long sub-arctic and boreal nights by great powers of hearing helped by a movable, dermal ear flap may be as great a necessity

for the life of northern strigine owls, as it probably is misleading to the southern ciccabine owls in the chirping and creaking chorus of stridulent insects and peeping frogs that make the nights in many tropical areas at times ear-deafening. The theory therefore, that tropical surroundings transform strigine wood owls into ciccabine wood owls and vice versa is highly attractive, though, of course, equally premature. Experiments on sense-organ physiology seem to be necessary to provide a new basis for the systematic arrangement of the species of the whole group of owls. This is planned as one of the aims of an ornithological working group in the new Zoological Laboratory of the Free University in Amsterdam.

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