

MALLOPHAGA INDICA IV.
TRENDS IN EVOLUTION IN THE *LAEMOBOTHRION*-
COMPLEX (PHTHIRAPTERA : MALLOPHAGA), WITH
DESCRIPTION OF A NEW GENUS

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ABSTRACT. From a comparative study of the *Laemobothrion*-complex occurring on Gruiformes, Falconiformes, Ciconiiformes, and the hoatzin (Galliformes) the trends in the evolution of male genitalia, sitophore sclerite and peg-like setae are discussed. Taking these characters into consideration, the species are grouped into four distinct genera. A hypothetical evolutionary tree from an *archetype* based on the male genitalia, and a key for the separation of the four genera are presented.

Hopkins and Clay (1952) included in Laemobothriidae the genus *Laemobothrion* Nitzsch with two subgenera *Laemobothrion* sens. str. and *Eulaemobothrion* Ewing. Ewing (1929) erected *Eulaemobothrion* for species found on water birds, which differs from the typical *Laemobothrion* in having stout porrect peg-like setae on anterior margin of head. Hopkins and Clay (1952) and Clay and Hopkins (1960) included in the subgenus *Eulaemobothrion*, species found on Gruiformes, Ciconiiformes and *Opisthocomus* (Galliformes). The two authors also considered *Ornithopeplechthos* Eichler, *Pterophagus* Eichler and *Plegadilymantikos* Eichler, as inseparable from *Eulaemobothrion*. A key to species of *Eulaemobothrion* is found in Clay and Hopkins (1960), which excludes *L. pallescens* Kellogg, *L. emarginatum* Piaget and *L. (E.) plegadilymanticum* Eichler. Carriker (1963) described a female of *E. jabiruensis* and *E. eurypygae* and Tendeiro (1963) described *L. (E.) blagoveshtchenskyi*. Nelson and Price (1965), from a thorough study of the species found on Falconiformes, concluded that species belonging to *Laemobothrion* sens. str., found on birds of prey, are only four. Lakshminarayana (1968), while describing *E. biswasi* off *Porphyrio poliocephalus poliocephalus* (Latham), suggested that *Eulaemobothrion* merits a generic rank, since *L. (E.) atrum*, *L. (E.) blagoveshtchenskyi*, and *E. biswasi* show a remarkable similarity in having free parameres, long, slender more or less hockey-stick-like endomeres as against the robust, curved, more or less fused parameres and normal endomeres in *Laemobothrion* sens. str. On the basis of these characters, along with the frontal peg-like setae, the genus *Eulaemobothrion* was resurrected and redefined. It was also suggested that since

the male genitalia of *E. opisthocomi* Cummings, as figured* by Guimares (1940) are so different from those of species occurring on Gruiformes, its inclusion under *Eulaemobothrion* proper as debatable.

Nelson and Price (1965) figured the male genitalia in the four valid species *L. maximum* (Scopoli), *L. tinnunculi* (Linn.), *L. vulturis* (Fabricius) and *L. glutinans* Nitzsch from Falconiformes. These two authors also figured the sitophore sclerite of the hypopharynx and used it as the basis for the separation of the four species. The present author had the opportunity to examine three of the aforesaid species excluding *L. glutinans*, and realized that there seems to be a remarkable evolutionary pattern in the sitophore sclerite development, male genitalia, and the distribution of the four species. It was also thought worthwhile to examine these characters in *L. (E.) opisthocomi* and species occurring on Ciconiiformes. Material of *opisthocomi* and *L. (E.) kelloggi* (Bedford) occurring on *Hagedashia hagedash nilotica* Newmann (Ciconiiformes) from the British Museum was examined.

On the basis of comparative studies of male genitalia, sitophore sclerite and peg-like setae on the front of head, the following evolutionary trends in the *Laemobothrion*-complex may be traced :

Male genitalia : The male genitalia in *L. (E.) opisthocomi* (Fig. 1a) may be considered as of rather primitive type, wherein all the parts are clearly distinguishable, with free, straight and moderate-sized parameres. The sclerotization is not uniform, for some parts like endomeres are weakly sclerotized. Perhaps, the ancestral form (archetype) also may have had this kind, where all the individual components are free, but uniformly sclerotized.

Lakshminarayana (1968) found the genitalia in *atrum*-group of species harbouring on Rallidae (Gruiformes) as simple, with free parameres, long, slender, and hockey-stick-like endomeres. Probably, some of the components seen in the archetype and *opisthocomi* might have atrophied (?). This condition is also found in *E. eurypygae* Carriker occurring on Eurypygidae (Carriker, 1963), and *L. cubense* Kellogg and Ferris found on *Aramus* (Aramidae) and figured by Timmermann (1954) ; both the host families belonging to Gruiformes. The other species, *L. gracile* Giebel (*L. gracilentum* Harrison and the type species of *Pterophagus* Eichler) found on *Psophia crepitans* Linn. (Psophiidae : Gruiformes) has not been examined, but believed to be similar to that of *atrum*-type found in species occurring on other Gruiform families. The *atrum*-type of genitalia is regarded as highly advanced over *opisthocomi*-type and the archetype (Figs. 1a and b).

In *L. (E.) kelloggi* off *Hagedashia* (Ciconiiformes) some of the components found in the archetype seem to have atrophied, sclerotization not uniform, parameres nearly straight, showing a tendency to fuse, and the endomeres normal

* Carriker (1957) claims, however, that "A figure of the male genitalia of this interesting species is here presented, since I do not believe it has been illustrated".

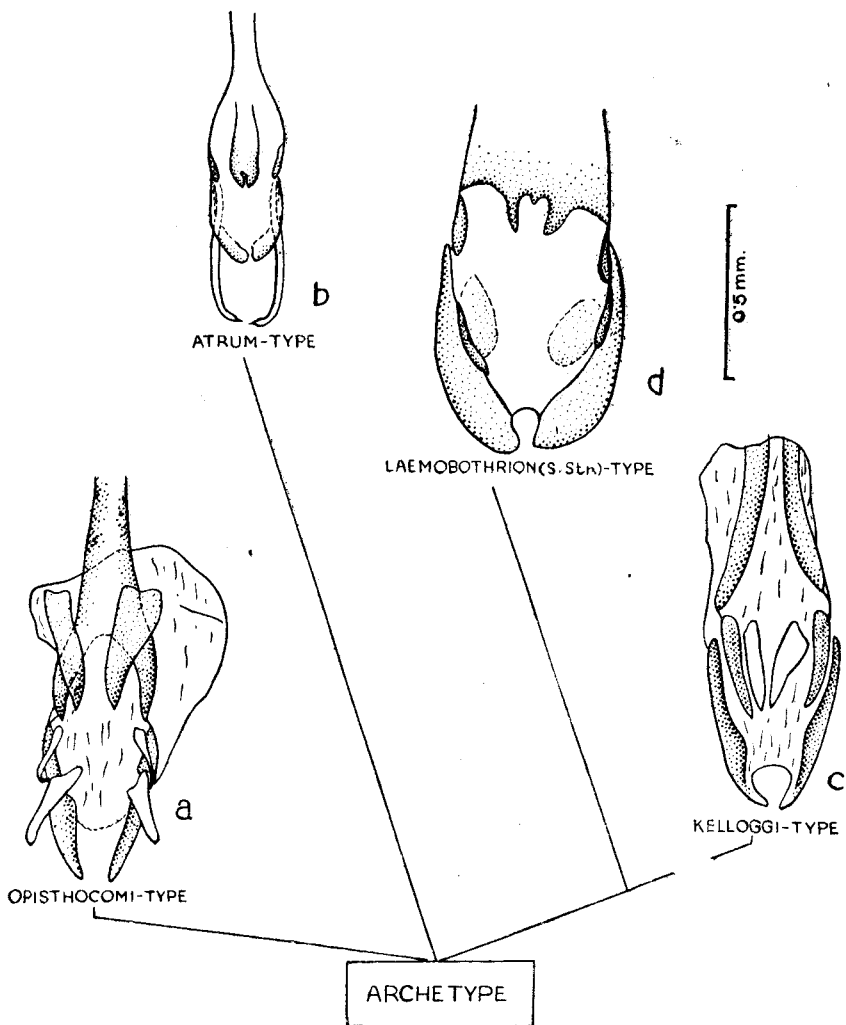


Fig. 1. Pattern of male genitalia : a, *Ornithopeplechthos opisthocomi*; b, *Eulaemobothrion biswasi*; c, *Ciconiicola kelloggi* and d, *Laemobothrion vulturis*.

(Fig. 1c). The genitalia in this species closely approach those present in *Laemobothrion*-type present in species off Falconiformes, and conspicuously differ from those of *opisthocomi* and *atrum* types. *E. jabiruensis* Carriker occurring on *Jabiru mycteria* Linn. (Ciconiiformes) was described by Carriker (1963) based on a female. It is not possible to place this species with certainty until the male is discovered, but on the basis of the frontal peg-like setae on head, it is probable the species might belong to *kelloggi*-type.

The genitalia in *L. maximum* (identical in *L. vulturis*), *L. glutinans*, and *L. tinnunculi* are excellently figured by Nelson and Price (1965). Here the parameres approach each other, a little curved, not freely movable and fused. Blagoveshtchensky (1956, 1964) however, believed that parameres are absent in *Laemobothrion*. Timmerman (1954) supposed them to be in the process of disappearance. The genitalia in *Laemobothrion* sens. str., may be considered a little advanced over *kelloggi*-type (Fig. 1d). Further, there seems to be a tendency in the gradual reduction in the size of components numbered 1 and 2 (Fig. 2) in the four species within *Laemobothrion* sens. str. Taking this character into consideration, one may place *maximum* (also *vulturis*) at the base of the evolutionary tree, wherein the parts are long, *glutinans* a little higher (perhaps not in direct line), and finally *tinnunculi*, where the reduction is profound. This arrangement corresponds with the probable evolution of the species on different falconiform hosts (*vide infra*).

Sitophore sclerite

Nelson and Price (*op. cit.*) were probably first to use this character for separating species within *Laemobothrion* sens. str., though no evolutionary importance was attached to it by them. In *maximum* a reduced U-shaped structure, and two large holes are evident, in *vulturis* (also *glutinans*) a conspicuous and large U-shaped structure and two large holes are present, and in *tinnunculi*, the U-shaped structure is lost and the two holes are very small (Fig. 3b, 4a-d). It is apparent that in the course of evolution either of the structures are reduced or absent.

The sitophore sclerite in other species of the *Laemobothrion*-complex has also been examined. In *opisthocomi* (Fig. 3a), both the U-shaped structure and two holes are present (may be a primitive condition); in *atrum*, *blagoveshtchenskyi* and *biswasi* (Fig. 3d) only the holes are noticed; whereas in *kelloggi* (Fig. 3c) both the structures are apparently absent*.

Carriker (1963) figured a U-shaped structure in *E. jabiruensis*, but this or the holes are not shown in *E. eurypygae*. Dr. Emerson kindly checked up the type material and informed that the specimens agree with Carriker's illustrations.

The probable evolutionary trend may be summarized as follows: the primitive forms may have had a sitophore sclerite with both U-shaped structure and holes as in *opisthocomi*, *vulturis*, and *glutinans*; the U-shaped structure may be reduced as in *maximum*, or totally absent as in *tinnunculi* and some members of *atrum* group; or both the structures lost as in *kelloggi* and *eurypygae*. The

*Dr. (Miss) Theresa Clay (in litt.) informs me that in *gracile* found on *Psophia crepitans* (Gruiformes) a U-shaped structure is present and in *setigerum* found on *Mesembrinibis cayennensis* (Ciconiiformes) only the holes are present.

reduction of holes in *tinnunculi*, where the U-shaped structure was lost altogether, is also interesting.

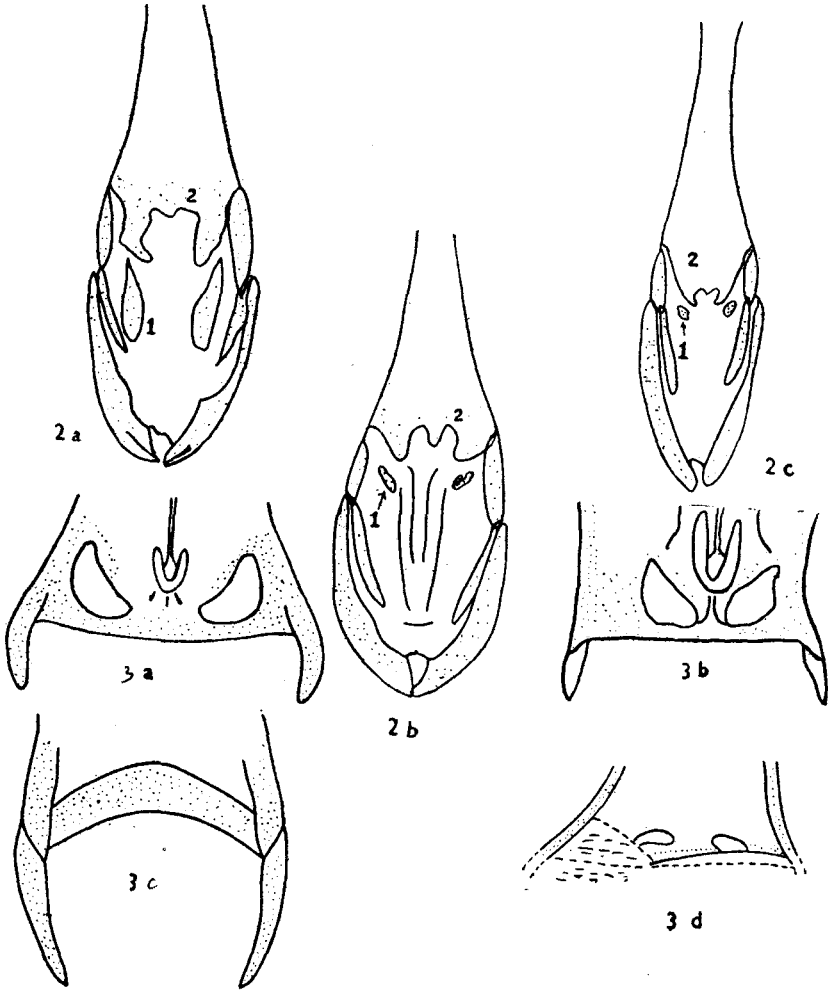


Fig. 2. Male genitalia : a, *L. maximum* ; b, *L. glutinans* ; c, *L. tinnunculi* (after Nelson and Price, 1965).

Fig. 3. Sitophore sclerite of the hypopharynx : a, *O. opisthocomi* ; b, *L. vulturis* ; c, *C. kelloggi* ; and d, *E. biswasi*.

Peg-like setae : Lakshminarayana (1968) has shown that though the peg-like setae on the front of head was mainly used to separate the two subgenera *Eulaemobothrion* and *Laemobothrion*, there seems to be a variation between species and individuals, as well as the right and left sides of an individual in *Eulaemobothrion* sens. str. as redefined.

This character has been examined in other members. The peg-like setae in *kelloggi* and *opisthocomi* are broad and long, whereas in *atrum* group, they are short and more or less pointed (Fig. 5 a-c) and in *Laemobothrion* sens. str., they are altogether absent. Further, in *opisthocomi*, they are present not only in the front but also laterally. Perhaps, the ancestral form might have had peg-like setae uniformly distributed on the head.

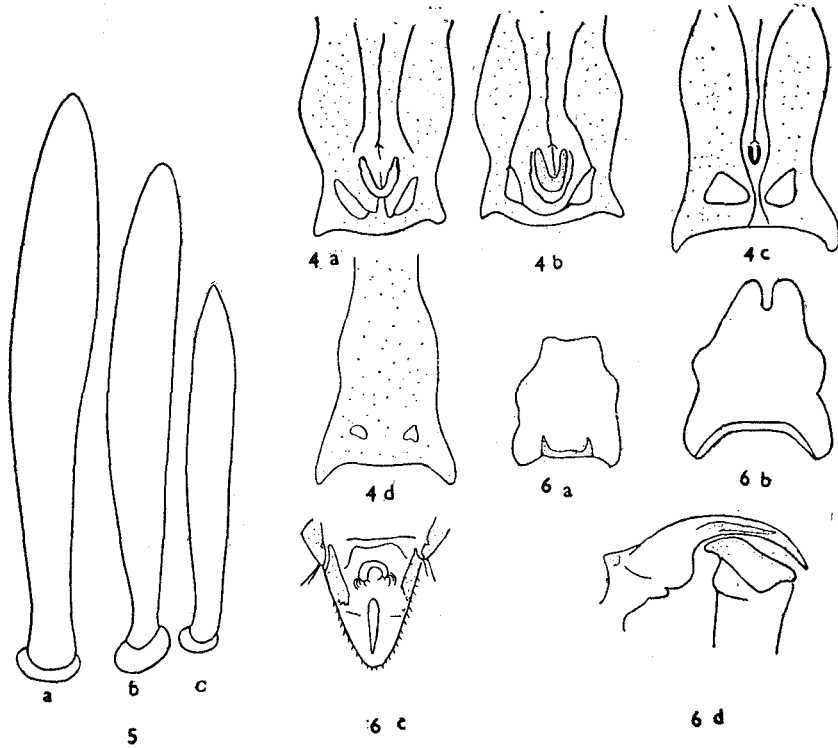


Fig. 4. Sitophore sclerite of the hypopharynx : a, *L. vulturis* ; b, *L. glutinans* ; c, *L. maximum* ; and d, *L. tinnunculi* (after Nelson and Price, 1965).

Fig. 5. Peg-like setae : a, *C. kelloggi* ; b, *O. opisthocomi* ; and c, *E. biswasi*.

Fig. 6. (a-b) Outline of the head: a, *C. kelloggi*; b, *O. opisthocomi*; c, terminal segments of the female abdomen in *O. opisthocomi* ; and d, mandibles in male *O. opisthocomi*.

Taking the male genitalia, sitophore sclerite, and peg-like setae together, the probable evolution of the members of the *Laemobothrion*-complex can be presented as follows : the hypothetical archetype can be deduced as a species with large peg-like setae distributed on the fronto-lateral aspect of the head, and probably body too, a sitophore sclerite with a large U-shaped structure and two large holes, and the male genitalia with component parts well sclerotized, having free parameres, and normal endomeres.

From this common ancestor may have descended a species very much similar to *opisthocomi*, which at present exists only on *Opisthocomus hoazin*. Though *opisthocomi* has the primitive characters like long, broad peg-like setae on the fronto-lateral margin of the head, sitophore sclerite with a large U-shaped structure and two large holes, genitalia with many component parts (some of which are less sclerotized than others), still it may not be the direct ancestor to the species found on other bird orders, due to its peculiar features like the deeply sunk front margin of the head (Fig.6b), sexually dimorphic mandibles (Fig.6d) against the other species where the head is little emarginated (Fig.6a) with sexually non-dimorphic mandibles. The terminal segments of the female *opisthocomi* (Fig.6c) are also different from others.

Directly from the archetype two other lines might have evolved. In one, some of the components of the male genitalia are atrophied, parameres still free, endomeres were long drawn into slender, hockey-stick-like structures, the frontal peg-like setae reduced in size, number and distribution restricted, U-shaped structure is lost (except in *gracile*)—a condition seen in the *atrum*-group of species occurring on Gruiformes—indeed a very advanced condition over the archetype and *opisthocomi*.

On the other side, a second line of evolution might have taken place, in which there is also a tendency for the atrophy of some of the components in the male genitalia, a tendency for the fusion of parameres as seen in *kelloggi* and *Laemobothrion* sens. str., harbouring on Ciconiiformes and Falconiformes respectively. In the former, the condition is not as advanced as in the latter. Still, *kelloggi* may not be the direct ancestor to *Laemobothrion* proper, for here we find a sitophore sclerite without a U-shaped structure and two holes. It is probable that *kelloggi* might have evolved together with species of *Laemobothrion*, but deviated from the latter line, by the retention of peg-like setae, and more advanced in the absence of U-shaped structure and holes to the sitophore sclerite. The probable evolutionary trend within the *Laemobothrion* sens.str. has already been discussed above. It may be stated that the ancestors of *kelloggi* and *Laemobothrion* sens. str. on the Ciconiiformes and Falconiformes appear to have evolved together.

Since the genitalia are so diverse, they effect a kind of morphological isolation. It is possible to arrange the species into four generic groups. Since *kelloggi* is now placed in a separate group from *Eulaemobothrion*, *opisthocomi*, and *Laemobothrion* sens.str., a new genus *Ciconiicola* is proposed to include *kelloggi*, and since Eichler (1941) has already made *opisthocomi* as the type species of his genus *Ornithopeplechthos* (not recognized as valid by Hopkins and Clay, 1952) it is resurrected and redefined in the key.

Ciconicola, gen.nov.

Type species : *Laemobothrion kelloggi* Bedford

This genus is erected for the present to accommodate *L. (E.) kelloggi* Bedford, from *Hagedashia hagedash nilotica* Newmann, from Fort Portal, Tero, Uganda, 31. vii.1945, Coll. G.H.E. Hopkins, in the British Museum (Natural History) collection.

The genus is characterized by the presence of long, and broad peg-like setae (Fig.5a) on the frontal margin of the head; sitophore sclerite without U-shaped structure and holes (Fig.3c), and male genitalia with parameres showing a tendency to fuse (Fig.1c). Its place in the *Laemobothrion*-complex is shown in the following key :

1. Head always with frontal peg-like setae; parameres without any tendency to fuse. . . 2
 Head with or without frontal peg-like setae; parameres showing a tendency to fuse. 3
2. ♂ Genitalia with many component parts, parameres stout and free, endomeres normal (Fig.1a); head strongly emarginated or deeply sunk (Fig.6b) with long and broad peg-like setae (Fig.5b) on the fronto-lateral margin; sexually dimorphic mandibles (Fig.6d); sitophore sclerite with both U-shaped structure and two large holes (Fig.3a); terminal segments in female as in figure (Fig 6c) **Ornithopeplechthos** Eichler
 ♂ Genitalia reduced, parameres free, endomeres long, slender and more or less hockey-stick-like (Fig. 1b); frontal peg-like setae short and pointed (Fig. 5c); mandibles sexually non-dimorphic; sitophore sclerite usually without a U-shaped structure (Fig. 3d); hyaline area between sternites II and III of the abdomen present **Eulaemobothrion** Ewing
3. ♂ Genitalia with parameres short, straight, but with a tendency to fuse, endomeres normal (Fig. 1c); head with long, broad frontal peg-like setae (Fig. 5a); sitophore sclerite without a U-shaped structure or holes (Fig. 3 c) . . . **Ciconicola**, gen. nov.
 ♂ Genitalia with parameres short, robust, with a tendency to fuse (Fig. 1 d, 2 a-c); head without frontal peg-like setae; sitophore sclerite with or without a U-shaped structure, but with two holes (Fig. 3 b, 4 a-d) **Laemobothrion** Nitzsch

SOME REMARKS ON THE DISTRIBUTION OF THE *LAEMOBOTHRION*-COMPLEX

Hopkins (1942) found the occurrence of *Laemobothrion* and *Eulaemobothrion* on Falconiformes, Gruiformes, and Ciconiiformes anomalous and possibly "the relics of an unsuccessful family of Mallophaga which formerly had a very wide distribution on many orders of birds and has now become extinct on most of the groups on which it once occurred". Clay (1950) attributed some kind of straggling from Rallidae to Ciconiiformes.

The distribution of the *Laemobothrion*-complex is as follows :

1. *Ornithopeplechthos opisthocomi* (Cummings) is believed to be a primitive member of the whole complex with genitalia akin to that of an hypothetical ancestor, with peg-like setae not only in the front but laterally too on the head, a sitophore sclerite with two holes and a U-shaped structure. It has its own peculiarities like deeply sunk front margin of the head, sexually dimorphic mandibles, which isolate it from the other members of the complex. It is now restricted to *Opisthocomus*, an aberrant bird of Galliformes confined to America. It is interesting to find a corollary in its primitive structure and occurrence on a member of a phylogenetically old order of birds.

2. *Eulaemobothrion* as understood now is confined to the order Gruiformes, markedly differs from all others and evolved in its own fashion, in having a long, slender hockey-stick-like endomeres. The frontal peg-like setae are short, slender, fewer and variable. The sitophore sclerite may or may not be identical in all its members. It suggests that Rallidae, Aramidae, Psophiidae and Eurypygidae as related. The discovery of *E. eurypygae* by Carriker (1963) is very important. It clearly indicates the relationship of Eurypygidae with Gruiformes contrary to the view of Chandler (1916). Clay (1950) suggested that Lowe's Ralloidea should include Aramidae, Psophiidae, Heliornithidae, Rhynchochaetidae, Jacanidae and Rallidae ; they appear more nearly related to each other on the basis of Mallophagan relationship. To this Eurypygidae should also be added.

3. *Ciconiicola* at present includes a single species found on *Hagedashia* (Ciconiiformes). Its male genitalia approach very close to those of *Laemobothrion* found on Falconiformes. It retained apparently a primitive character like peg-like setae, with tendency to the fusion of parameres as in *Laemobothrion*. The sitophore sclerite, however, appears to be advanced over that of the latter. The closer resemblance in the male genitalia suggests that probably both *Ciconiicola* and *Laemobothrion* sens. str., might have evolved from a common stock. It is interesting to note that their respective host orders, viz., Ciconiiformes and Falconiformes were also believed to have evolved together from the same stock by ornithologists, and palaeontologists, (Chandler, 1916; Howard, 1950; Gregory, 1951 ; see also Mayr and Amadon, 1951).

4. *Laemobothrion* sens. str., as believed now, is confined to the Falconiformes (Clay and Hopkins, 1960 ; Nelson and Price, 1965 ; Lakshminarayana, 1968). Following Nelson and Price (1965) the distribution of the four species of the genus is as follows :

PARASITE SPECIES	HOST GENERA
<i>L. maximum</i>	<i>Aviceda, Aquila, Buteo, Chondrohierax, Circaetus, Circus, Gymnogēns, Haliastur, Hieraaetus, Ictinia, Melicrax, Milvus, Pandion, Pernis, Polemaetus</i> and <i>Polyborus</i> (16 genera)
<i>L. vulturis</i>	<i>Aegyptius, Aquila, Gypaetus, Gyps</i> (incl. <i>Pseudogyps</i>), <i>Haliaeetus, Haliastur, Necrosyrtes, Neophron, Sagittarius, Torgos, Trigoiceps</i> and <i>Uroaetus</i> (12 or 13 with <i>Pseudogyps</i>)
<i>L. glutinans</i>	<i>Cathartes, Coragyps, Polyborus</i> (?), <i>Sarcoramphus</i> , and <i>Vultur</i> (4 or 5 genera)
<i>L. tinnunculi</i>	<i>Falco</i> (1 genus only)

Of these four species the genitalia in *vulturis* and *maximum* resemble each other, are a little advanced in *glutinans*, and more advanced in *tinnunculi*. The sitophore sclerites in *vulturis* and *glutinans* are identical and appear to be primitive, a little advanced in *maximum*, and very much advanced in *tinnunculi*. The distributional pattern indicates that *maximum* occurs on sixteen genera of Perninae, Milvinae, Accipitrinae, Buteoninae, Pandioninae, Circinae, and Circaetinae (Accipitridae) *Polyborus* (Polyborinae) and doubtful record on *Falco*; *vulturis* occurs on thirteen genera chiefly Aegyptiinae, Buteoninae and Milvinae in addition to Sagittaridae; *glutinans* occurs on four genera of Cathartidae and a doubtful record on *Polyborus*; and *tinnunculi* is confined to a single genus *Falco*. No records are available from Elaninae, (Accipitridae), Herpetotherinae and Polyhieracinae (Falconidae). On the basis of Eichler's Divergence and Fahrenheit Rules (Eichler, 1949), it appears that *maximum* being widely distributed is more primitive, though, its sitophore sclerite indicates a higher position than *vulturis*; the latter follows *maximum*, but its sitophore sclerite is less evolved; *glutinans* follows *vulturis*, their sitophore sclerites identical, but the male genitalia of *glutinans* are advanced over *vulturis*; *tinnunculi* on the basis of distribution, sitophore sclerite, and male genitalia is highly evolved over the other three species. The distributional ratio between *maximum* and *vulturis* thus appears misleading, but it is not really so: it appears that *vulturis* might have been replaced by *glutinans* in the New World, since their sitophore sclerites resemble each other, and with a little advanced type of genitalia in the latter species, together they occur on 17-18 genera of hosts, while *maximum* occurs only on 16 genera. This kind of relationship as suggested by the evolutionary trends in the morphological characters agree with the views expressed by some ornithologists, palaeontologists and parasitologists regarding the relationship of Old World and New World vultures (Chandler, 1916; Howard, 1950; Clay, 1950, see also Mayr and Amadon, 1951). The presence of other common genera like *Falco*-

peurus Bedford, *Kurodaia* Uchida (doubtful record), and *Cuculphilus* Uchida to both groups (in the light of Hopkins' principle*) strongly upholds that both Old and New World vultures are related.

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†* Hopkins (1942, 1949) suggested that one correspondance between the lice of two hosts, whose hypothetical relationship is under examination means very little ; two such correspondances establish a probability that it may be genuine ; and that three correspondances come very close to certainty. It seems applicable at species level while examining the relationship of two species of hosts in a genus (or genera within a family) and at generic-level while examining relationship of hosts of different families of an order or between orders. Hopkins' suggestion is now named as Hopkins' principle.

* Original not seen.

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