AN INTRODUCTION TO A CLASSIFICATION OF THE AVIAN ISCHNOCERA (MALLOPHAGA): PART I.

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With 1 Plate and 26 Text-figures.

INTRODUCTION.

AN attempt to make a key for the genera of the Ischnocera on the lines of that made for the Amblycera (Clay, 1947) has presented many difficulties. These are mainly caused by the amount of convergent and parallel evolution which has taken place in this superfamily, resulting in those characters which could be used in such a key being found in unrelated genera. It is necessary, therefore, to make a more thorough study of both the external and internal anatomy with a view to finding reliable characters on which to base a classification, and to review the distribution and variability of those characters on which the genera have previously been based. The basic characters of the internal and external morphology are, in general, remarkably uniform throughout the Ischnocera, but superficially there are considerable differences in the proportions of the body and the development of sutures and of secondary lines of thickening. These differences are reflected in the large number of genera (over 130) which have been described, many of which grade into each other, or can hardly be regarded as more than well-marked species groups. Elsewhere (Clay, 1949) it has been suggested that the Ischnocera acquired these basic characters early in their evolution, possibly while the birds had a more uniform feather covering and before their divergence into different groups with the ensuing modifications of the feather structure. The more superficial characters on which the genera of the Ischnocera are based are mainly those which are adaptive to the different ecological niches on the body of the bird, and possibly to the different feather structure characterizing the particular group of hosts. During this evolution there was much convergence and parallelism, resulting in the original relationship between the genera being in many cases obscured. Thus an attempt to arrange these genera in families on the characters usually employed gives groups containing a heterogeneous collection of genera and obviously of polyphyletic origin.

The genus.—Since there will be frequent references to characters being of generic importance and as the generic concept is mainly a subjective one, it is necessary to state the principles on which genera have been recognized or discarded in this series of papers. The generic category is used for a convenient grouping of similar species of common phylogenetic origin. It is inherent in the generally accepted theory of the evolution of the Mallophaga that similar species from related hosts are themselves related. Throughout the great majority of the Ischnocera this fact is so obvious that it needs no emphasis— the exceptions to this general principle have been summarized and discussed elsewhere (Clay, 1949). This secondary check on the relationships of species

of Mallophaga based on the relationships of their hosts is naturally of the greatest value, but where the principle is applied indiscriminately it may lead to considerable errors in classification. Thus, genera are now being erected for groups of species morphologically indistinguishable from the remaining species in the genus merely because they parasitize a distinct group of hosts.

Two types of genera based on their origins can be distinguished in the Ischnocera. These are the end-products of the processes of speciation which brought about one, the allopatric species, and the other, the sympatric species ; the origin and evolution of these have been discussed elsewhere (Clay, 1949).

The allopatric genus comprises a number of species formed as a result of the isolation and divergence of their hosts (Clay, 1949 : 288) ; this has resulted in the parasites of an order, family or genus of hosts resembling each other more closely than the corresponding species of a different order, family or genus of hosts. It is, therefore, a matter of opinion whether the genus should include the small group of similar forms from the genus of hosts (frequently a polytypic species), or the larger group of less similar forms from the host family (superspecies or sometimes polytypic species), or the still larger and more diverse group of species from the host order. Naturally the cases of all parasitic groups and all host divisions are not analogous. Parasitic groups, which seem either to be more plastic or to parasitize ancient orders of birds where the hosts have been longer isolated and are more divergent, tend to show a greater amount of divergence between the species, or to contain aberrant species, or species with exaggerated dimorphism of the secondary sexual characters. Such groups of species encourage the erection of a large number of small genera, many of which are monotypic ; and although these genera come within the definition of a group of similar species of common phylogenetic origin, they cannot be considered as convenient groupings. This erection of genera for polytypic or superspecies merely burdens the memory with names which give no clue to relationships, in many cases makes it impossible to place a species if only one sex is known, and probably means the future erection of further monotypic genera for the inclusion of new species.

The present writer agrees with Mayr and Delacour (1945 : 5) : " We believe in large genera, since it is the function of a generic name to express relationship (as an aid to memory), not distinctness, which is expressed by the species." Unfortunately many workers on Mallophaga seem to be concentrating on obscuring as many natural relationships as possible, super-species, polytypic species and even aberrant members of a superspecies being made into genera. This results in the subspecies being called a species, a polytypic species a genus, a genus a family, with the ensuing multiplication· of the higher categories. There would seem to be no advantage, for instance, in dividing *Degeeriella* from the Falconiformes into two genera as has been done, nor in separating the *Philopterus* species found on the HIRUNDINIDAE (a family of the Passeres) from those parasitizing the remainder of the Passeres. *Goniodes* from the Galli contains a number of species groups, and these have been used as a basis for erecting unnecessary genera (Kéler, 1940). On the other hand, *Anatoecus*, from the Anseriformes, possibly a less plastic group of parasites, shows little divergence throughout the genus. It is only by realizing that both these groups comprise forms which (with the exception of the sympatric species) are geographical (or host) replacements of each other, and in the case of some groups could be included in one polytypic species or a

superspecies, that one can get a satisfactory generic concept in the Mallophaga.

Host distribution is of importance as a secondary check on the relationship between species and on the delimitation of genera. If, for instance, a genus is erected for species from a certain host group, but is based on characters which means the inclusion also of some of the species parasitizing not closely related hosts, then such a group does not contain a natural association of related species and does not come within the above definition of a genus. Such a case is illustrated graphically in fig. 1 : z is one host group ; A, B, C and D are four host groups related to each other. The species on all groups are similar, but those on z, B and D can be separated from those on A and C by certain characters (x and y). It is not permissible to use these characters to erect a genus to include the species found on z, B and D because the species on the A–C group of hosts must be more closely related to each other than any of them are to those on z (it is assumed that secondary infestations from z to B and D have not taken place). All the species on the five host groups must be included in one genus. The separation of *Clayiella* from *Philopterus* and some of the genera based on colour pattern (*Koeniginirmus* and *Docophorulus*) are such cases. The host distribution of the only two species included in *Kodocephalon* by Kéler (1940), namely *Goniodes suborbiculatus* from a species of COLUMBIDAE and *Goniocotes discogaster* from a species of the MEGAPODIDAE (Galliformes), suggests that this is not a natural association and is not, in fact, supported on morphological grounds.

On the other hand, a consideration of the host distribution of species alone, ignoring morphological characters, also results in the erection of untenable genera. An example of such a case is illustrated in fig. 2 : three unrelated host groups A, B and C are parasitized by similar species of Mallophaga. The species on A show a certain character x, and those on B a character Y, and of those on C (a much larger group of hosts with a greater number and diversity of species) some show character X, some Y, and some neither of these characters. It is not permissible to use characters X and Y as a basis for separating generically those species found on host groups A and B even though all three host groups are unrelated to each other. The separation of *Furnaricola* from *Rallicola* is such a case.

ALLOPATRIC GENERA.

In the majority of allopatric genera the host order or suborder forms a clear-cut line between groups of species and gives the limits of the genera— for example *Anaticola* on the Anseriformes, *Ardeicola* on the Ciconiiformes, *Falcolipeurus* on the Falconiformes. Where a genus is found on more than one host order (*Saemundssonia*, for instance, on the Charadriiformes, the Procellariiformes and the Gruidae) the species found on each host order cannot be segregated into genera unless there is a morphological basis for this. However, there are some cases of such groups of related species with a wide host distribution which raise the most difficult problem in the classification of the Ischnocera. It seems possible that in these—the *Degeeriella* complex may be used as an example—the immediate ancestor of the species groups on each host order gave rise not only to the *Degeeriella* type of species, but to others which occupied different ecological niches, and have now evolved into groups of species very different from the *Degeeriella* type to which they are most nearly related. Therefore, to include the whole *Degeeriella* complex,

comprising *Lagopoecus, Cuculicola, Picicola, Upupicola, Capraiella, Trogoni-nirmus, Acutifrons*, and another group from the BUCEROTIDAE, in one genus would be correct on morphological grounds, but there is a possibility that *Picicola* for instance is more closely related to another genus (*Penenirmus*) on the Passeres than to *Degeeriella*. In all cases where the distribution of a genus covers more than one host group there is the possibility that the species on one of the host groups are more closely related to another genus on that host group, although generically inseparable on morphological grounds from the species on the other host groups. This has been discussed elsewhere (Clay, 1949 : 295), and has been raised by Wood (1950 : 96) with reference to the geographical distribution of a group of rodents. It must be admitted that the present system of classification cannot satisfactorily represent such relation-
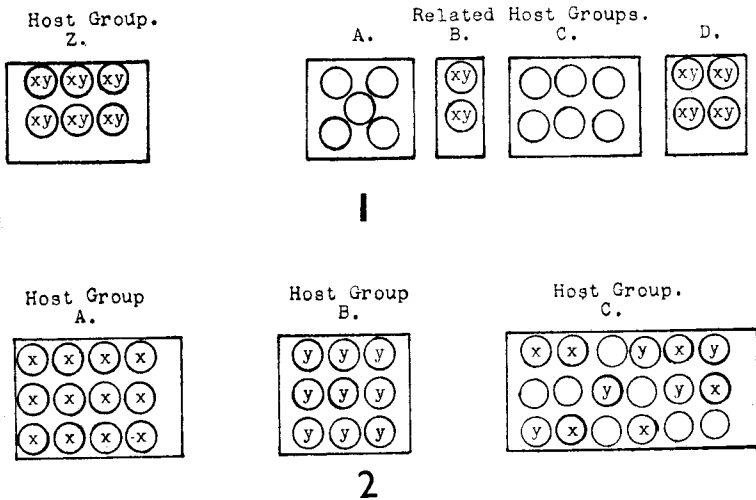
FIGS. 1, 2.—Distribution of species of Mallophaga on unrelated host groups. Explanation in text. Circles denote species of Mallophaga.

ships. However, unless there is good evidence to the contrary, genera must be based on morphological criteria and not on hypothetical speculations of their evolution based on distribution. Each of such cases must, of course, be judged individually—the wide distribution of *Saemundssoni* is most probably due to secondary infestations, whereas that of the *Degeeriella*-complex may be due to the discontinuous distribution of a once universally distributed genus.

SYMPATRIC GENERA.

The genus which is the end-product of the sympatric species presents a more difficult problem. Sympatric species are found in every stage of divergence, from those which differ only in the details of the male genitalia (the females being very similar or indistinguishable) to those which can be separated generically on well-marked characters. The degree of divergence will depend mainly on the age of the two sympatric species and whether they have taken up different habitats on the host—in the latter case such forms may now be placed in different families. Where the two species have been

subjected to the same environmental factors degree of divergence is presumably dependent on the length of time they have been separated. The question of good generic divisions in these cases is an extremely difficult one. All these sympatric species groups will come within part of the generic definition given above, that is, a group of related species, so that the question to be decided is that of convenience. Other factors being equal it is convenient to have two distinct species on one host contained in different genera, but it is not convenient to have a position where species cannot be placed if only one sex is known, nor is it convenient if the two genera grade into each other to such an extent that there are no criteria for placing some of the species in one genus rather than another. The original species of *Soricella* were so distinct from *Columbicola* that a generic division seemed justified, but a large series of species from the COLUMBIDAE shows that these two groups grade into each other to such an extent that a generic division is now impossible. If the *Goniodes-Goniocotes* complex of species are examined from a large number of host species, even the apparently well-defined genera *Goniodes* and *Goniocotes* seem to grade into each other. On the TINAMIDAE, where there is a wealth of sympatric species and genera, generic separation becomes an almost insoluble problem.

The complexity and difficulty of generic separation in these sympatric forms has led to the erection of a multiplicity of genera, either owing to the small amount of material examined, or to the fact that the alternative to a great number of small genera seems to be the inclusion of a large number of species (for example all *Goniodes* and *Goniocotes*) in one genus.

While a correct evaluation of such genera is probably not possible without a more complete series of species than is usually available, it would seem to be more satisfactory to keep the generic divisions fairly wide to include as many related forms within the same genus as possible.

MATERIAL AND METHODS.

Whole specimens have been examined after treatment by caustic potash and mounting in Canada balsam, by mounting in polyvinyl lactophenol and by staining with lignin pink or mercurochrome. Both the internal and external anatomy has been studied by dissections, and sections of examples of a small number of genera have been examined.

Although it has been possible to examine specimens of practically all the known genera, the amount of suitable material available has limited the dissection of examples of all these genera, and time has limited the number of different species of each genus dissected. However, any such attempt at the classification of the Ischnocera must be considered as tentative due to the great amount of work still necessary, not only on the morphology but also on the biology of this group, together with the limitations involved by the number of genera and species still unknown.

ACKNOWLEDGMENTS.

A. THE HEAD.
Terminology.

Scornful references (Cope, 1941 : 72) have been made to the terminology

used to designate parts of the head in the Mallophaga, and a suggestion made that these should be replaced by terms with a morphological significance. This criticism would be more impressive if those working on the morphology of the Mallophagan head could agree on the homologies of the various sutures and lines of thickening which are used in the classification of the group.   Until this has been achieved it seems more satisfactory to retain the names which can be understood by all workers than to follow the various ideas and theories of the homologies of different parts of the head put forward by recent morphologists.   Even in the terms now in use there is little conformity, however, and it has been necessary to adopt some new names and to define and restrict those already in use.   Two terms as used here must first be defined :
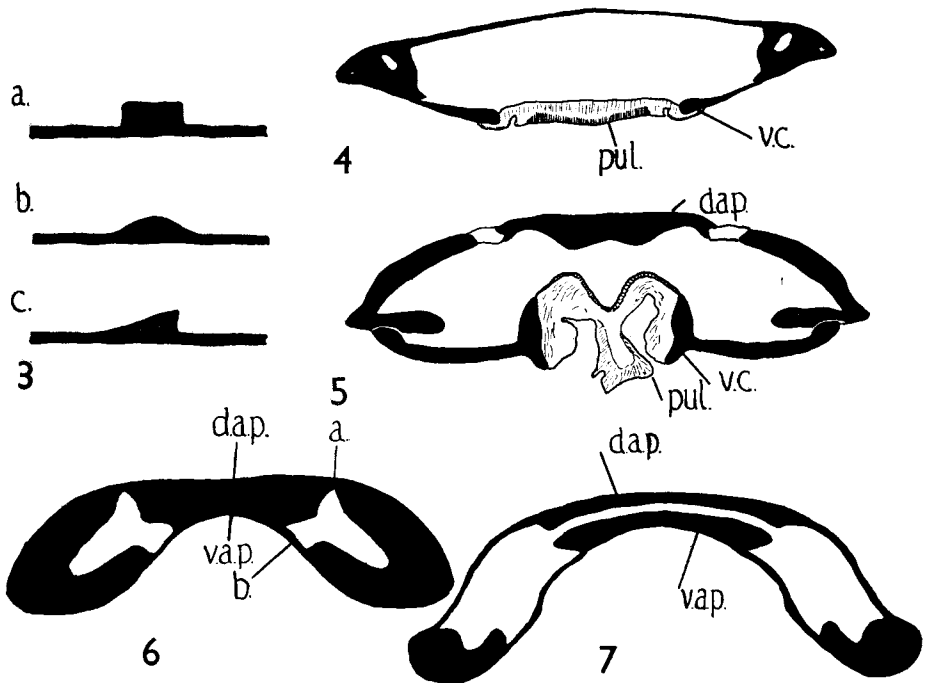
FIGS. 3–7.—Transverse sections of preantennal region of head.   (3) Endocarinae (diagrammatic).   (4) *Coloceras* sp., at level of pulvinus.   (5) *Philopterus* sp., at level of pulvinus.   (6) *Brüelia* sp., at level of anterior plate.   (7) *Philopterus* sp., at level of anterior plate.   Explanation of lettering as in figs. 10, 11.

Endocarina.—One of the most characteristic features of the Ischnocera is the presence of various dark bands running across the head.   These so-called bands are internal ridge-like thickenings of the cuticula.   The conspicuousness of the band is due to the thickness of the cuticula, and, as the " edges " of the band as seen in the surface view of the mounted insect are the lateral sides of the internal thickening, the definition of the band is dependent on the angle the thickening makes with the normal inner surface of the body wall.   Thus a ridge which in transverse section shows these angles as right angles (fig. 3A) will appear as a very distinct band, but one in which the sides slope gently into the inner surface of the rest of the body wall (fig. 3B) will appear externally as an indistinct band.   In some cases one side of the ridge may be at right

angles, and the other merge imperceptibly into the general surface (fig. 3c) so
that the band is only delineated on one side. Sometimes this thickening may
become less in certain areas so that portions of the bands become indistinct
or apparently absent. All these types of internal thickenings are here called
endocarinae or carinae. In many instances the form of some of the endo-
carinae are useful generic characters, but their apparent absence in other cases
may have no significance—the presence or absence of the whole or part of the
temporal carinae is a case in point. In some heads there may be dorsal and
ventral endocarinae as well as those projecting from the lateral walls. It is
not surprising, therefore, that considerable difficulty is experienced in tracing
these carinae in mounted specimens, and that so many figures of Ischnoceran
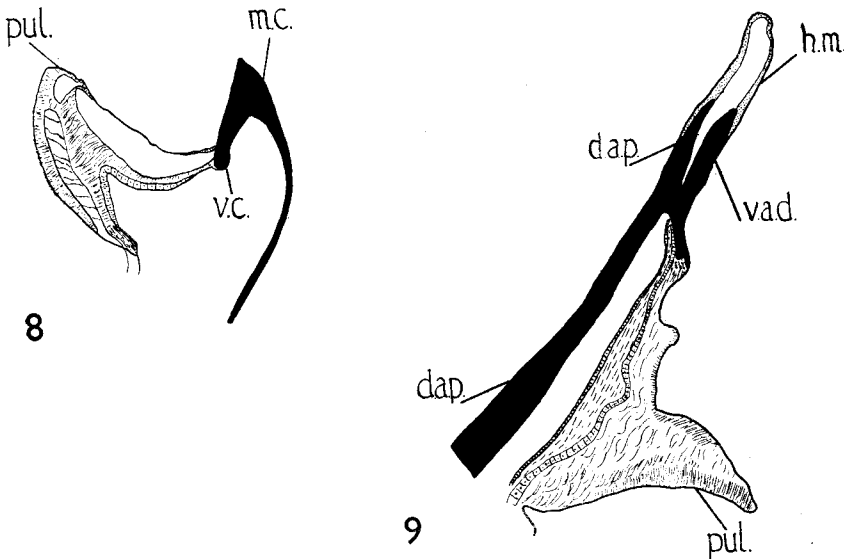
FIGS. 8, 9.—Longitudinal sections of preantennal region of head. (8) *Lipeurus* sp.
(9) *Philopterus* sp. Explanation of lettering as in figs. 10, 11.

heads give a composite picture partly dorsal and partly ventral. The section
of a head of a species of *Philopterus* a little way anterior to the origin of the
mandibles (fig. 5) illustrates the complexity of the endocarine in the more
specialized forms.

Sutures.—The term suture is used here in the sense of the second definition
given by Snodgrass (1935 : 53), that is, " Lines where the sclerotization of the
cuticula has become secondarily discontinuous in order to give flexibility."
These thinner areas are again a characteristic feature of the Ischnoceran head,
and are frequently constant throughout groups of related species and may
form reliable generic characters. The term is used for all such areas which
appear unsclerotized in the whole insect, although in some cases (only dis-
cernible in sections) the sclerotization is thin, not actually interrupted ; in
mounted specimens the points (*a*) and (*b*) on fig. 6, for instance, will appear
as sutures.

The General Structure of the Primitive Head and its Modifications.

It is generally assumed that the primitive Ischnoceran head had the
marginal carina complete—the so-called circumfasciate type of head now

found in such genera as *Goniodes* (fig. 10), and that the sutures and form of endocarinae found in such genera as *Saemundssonia* (fig. 11) are secondary. This view is supported by the fact that in some genera in which the adults show the anterior sutures, the nymphal stages have the circumfasciate head. The more primitive type of head capsule[1] has the following general characters : The preantennal region is enclosed by a thickened rim which turns inwards immediately anterior to the antennae to form a thickening dorsally, and to fuse with the framework supporting the mandibles ventrally. Passing anteriorly from this framework each side is an endocarina which forms a semicircle in front of the prestomum and to which is attached the pulvinus, (*sensu* Cope). The pulvinus, which is a membranous lobe of characteristic structure, is present in all the Ischnocera, and seems to have an important function in grasping the feather and directing it towards the mandibles for attachment and feeding. Posteriorly the mandibular framework is prolonged backwards and may or may not reach the occipital margin. The various modifications which have taken place in this primitive type of head together with a terminology for those parts of importance in classification follows :

Preantennal Region.

Marginal carina (epistoma, Kéler, 1938 ; frontal band, Harrison, 1937).— In the primitive forms, as already shown, this band forms the rim of the preantennal region (fig. 10) ; in some genera (*Episbates*) there may be no definite thickening round the anterior margin of the head. This carina turns inwards immediately anterior to the antenna each side to form the thickened preantennal nodus dorsally, and to fuse with the articulation of the mandibles ventrally. Dorsally the thickening may pass inwards from the nodus to form the transverse carina, either interrupted medianly (*Saemundssonia*, fig. 11) or continuous across the head (*Columbicola*). The primitive form of the marginal carina may become modified in the following ways :

1. In the mid-part of the anterior margin the carina may become depressed to a greater or less extent ; at the place of this depression the anterior margin of the head is hyaline (the hyaline margin). Example : *Brüelia brachythorax* fig. 19.

2. The marginal carina may be divided into two or more parts by interruptions of its sclerotization as follows :

A median interruption in the anterior part of the carina giving a marginal carina each side of the head. Example : *Aptericola* (fig. 12, *m. c.*).

A lateral interruption each side giving a postmarginal carina (antennal band Piaget, 1885) running from the preantennal nodus to the interruption, and the premarginal carina (clypeal band, Piaget, 1885) running from the lateral interruption to the median anterior interruption (fig. 11, *pom.c.* and *prm.c.*).

In some species the marginal carina may be interrupted medianly and continued forward as the hyaline margin dorsally, but ventrally shows a further pigmented and sclerotized portion which fuses with the prolonged ventral carina. Example : *Meropoecus, Rallicola* species.
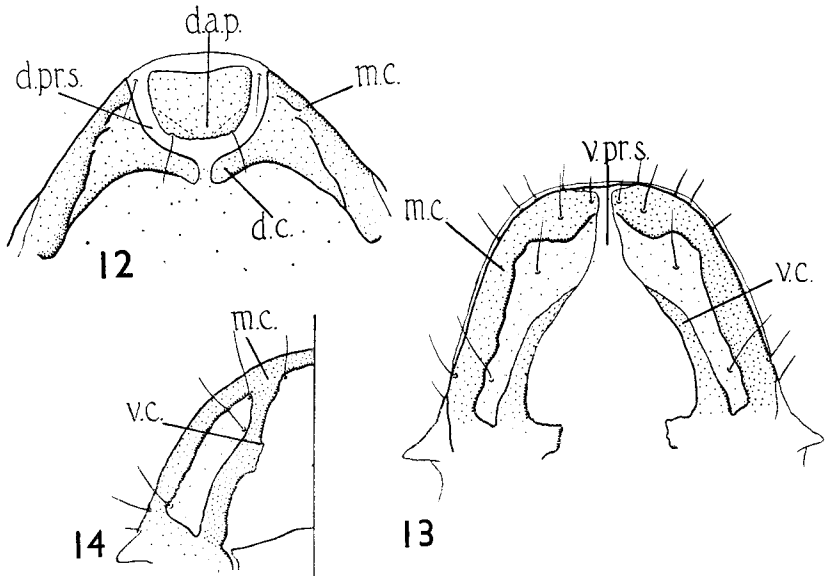
The dorsal preantennal suture and the anterior plate (clypeal signature, *auctorum*).—The dorsal surface of the preantennal region may have a suture

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[1] Kéler has given a full account of the morphology of two Ischnoceran heads (1938 and 1939), so that details of the structures need not be repeated.
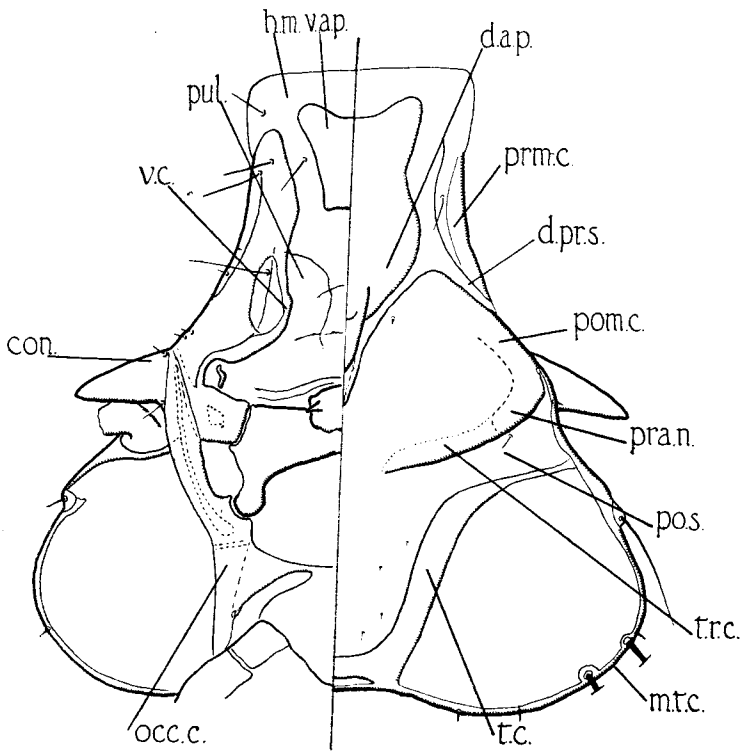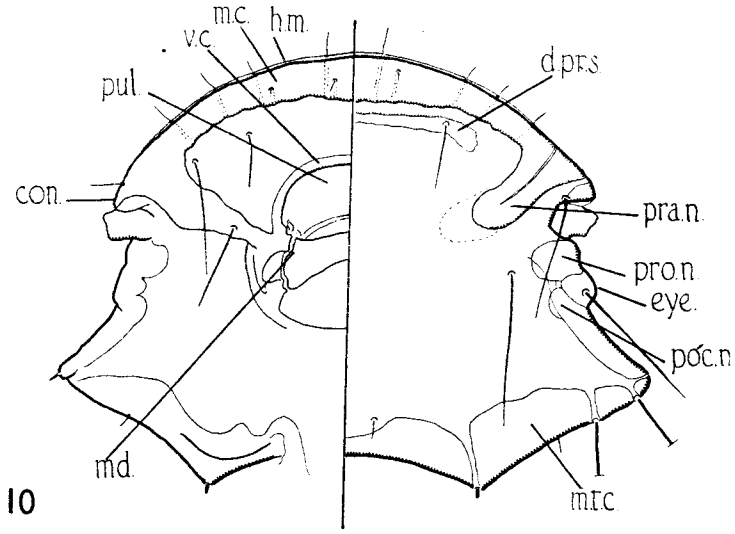
FIGS. 10, 11.—(10) *Goniodes* sp., head. (11) *Saemundssonia* sp., head. *con*, Conus; *d.a.p.*, dorsal anterior plate ; *d.pr.s.*, dorsal preantennal suture ; *h.m.*, hyaline margin ; *m.c.*, marginal carina ; *md.*, mandible ; *m.t.c.*, marginal temporal carina ; *occ.c.*, occipital carina ; *poc.n.*, postocular nodus ; *pom.c.*, postmarginal carina ; *po.s.*, postantennal suture ; *pra.n.*, preantennal nodus ; *prm.c.*, premarginal carina ; *pro.n.*, preocular nodus ; *pul.*, pulvinus ; *t.c.*, temporal carina ; *tr.c.*, transverse carina; *v.a.p.*, ventral anterior plate ; *v.c.*, ventral carina.

which either does not reach the marginal carina (some species of *Goniodes*, fig. 10, *d.pr.s.*), or reaches but does not interrupt it. A suture such as is found in *Lagopoecus* cuts off a semicircular area of the dorsal surface; if the marginal carina is now interrupted medianly a distinct area of the dorsal surface will be cut off, forming the so-called "clypeal signature" (here called the dorsal anterior plate), a characteristic feature of many Ischnoceran heads. The anterior plate also has a ventral component (ventral anterior plate, fig. 11, *v.a.p.*) which may be fused to the dorsal plate throughout its length, and thus forms a solid block of sclerotization throughout the depth of the head as in *Brüelia marginalis* (fig. 6), or it may be fused only at its proximal end as in *Philopterus* (figs. 7 and 9). The ventral plate may be a narrow rim across the anterior part of the anterior plate as in *Haliperus*, where it is striated, or it

FIGS. 12–14.—Preantennal region of heads. (12) *Aptericola* sp., dorsal. (13) *Degeeriella* sp., ventral. (14) *Tinamotaecola* sp., ventral. *d.c.*, Dorsal carina; *v.pr.s.*, ventral preantennal suture; explanation of other letters as in figs. 10, 11.

may be longer, narrowing proximally, and with a flattened, rounded or pointed proximal margin (fig. 11). It seems possible that the ventral plate in some genera represents the median portion of the marginal carina which has been cut off by sutures from the lateral part of the carina each side. In its simplest form the dorsal anterior plate is merely an area of the dorsal surface of the head cut off by a suture (*Rallicola*, *Brüelia*), but it may become modified by internal thickening, and in some genera has a single (*Saemundssonia*, *Philopterus*) or double (*Ibidoecus*) heavily sclerotized backwardly directed point.

The dorsal preantennal suture, which cuts off the anterior plate posteriorly, arises in the more modified forms either at the distal ends of the interrupted marginal carinae (*Aptericola*, fig. 12, *Meropoecus*), or at the distal ends of the postmarginal carinae (*Saemundssonia*, fig. 11, *Philopterus*, *Quadraceps*). In some genera the dorsal suture is not continued across the head and is represented by two lateral sutures each side of the dorsal plate, the posterior part of this plate thus being continuous with the rest of the dorsal surface

of the head (*Brüelia* species and *Craspedonirmus*). Some adults which show no dorsal suture have nymphs in which a dorsal suture is present (with which the anterior dorsal setae (see below) are associated). It is possible, therefore, that the adult suture represents part of this nymphal suture and that its absence in some adults is secondary. This also applies to the postantennal suture.

The proximal edge of the dorsal suture may have a line of thickening (fig. 12, *d.c.*)—the dorsal carina (internal bands, Harrison, 1937). This thickening may be continuous across the head (*Pseudonirmus*), or turned posteriorly in the midline and prolonged as two parallel bands. In *Halipeurus* the ends of these two bands actually lie free in the head cavity. Other parts of the dorsal surface of the preantennal region may have various areas of thickening, either proximal to the dorsal suture (some species of *Columbicola*), or anteriorly where there is no dorsal suture.

The pulvinus and ventral carina (Zygoma, Kéler, 1938; ventral bands, Harrison, 1937; internal bands, Piaget, 1885).—The ventral carina is continuous with the marginal carina and the mandibular framework, and is the thickening to which the pulvinus is attached. This latter structure, as already mentioned, is of importance in feeding and attachment, and the form of the ventral carina seems to be closely correlated with that of the pulvinus. In *Lipeurus* the pulvinus is a simple lobe attached to the complete semicircular ventral carina (fig. 8), and similarly in *Perineus* (Plate I, fig. 1), although in this genus there is no definite carina medially. In *Coloceras* (Plate I, fig. 2), in which the ventral carina is complete, the pulvinus has a lateral lobe each side, giving a broad median groove (the mouth-channel, Kéler, 1938 : 403). In the most highly modified forms, where the ventral carina is interrupted medianly and each carina has a thickened flattened surface lying parallel to the one on the other side, the pulvinus has a well-developed lateral lobe each side attached to this parallel part of the ventral carina (Plate I, fig. 4). In these forms the piece of feather being eaten lies in a central groove, held in position by the lateral lobes, and the pulvinus thus forms an efficient holding organ. The central portion of the pulvinus is also extrusible, and may be blown out as a lobe like structure (fig. 5, *pul.*). In such forms as *Philoceanus becki* and *Trabeculus* the pulvinus reaches its greatest development and has caused distortion of the preantennal region : in the latter genus the ventral carinae are pushed outwards proximally, where they fuse with the marginal carina. The surface of the pulvinus may be smooth or slightly sculptured and in some genera (*Austrogoniodes, Anaticola,* Plate I, fig. 3) the central groove has a median line of sclerotization.

The ventral carina, which in the more primitive forms passes forward from the mandibular framework each side to form a complete semicircle (Plate I, fig. 2 and fig. 10), may be modified in the following ways :

It may be interrupted medianly so that the thickening is only visible laterally, the pulvinus being attched to the edge of the sclerotized surface of the mid preantennal region. Example : *Episbates.*

It may be interrupted medianly with a suture—the ventral preantennal suture—running forwards from the two ends of the carina to, or nearly to, the complete marginal carina. Example : *Degeeriella* (fig. 13).

The edge of the ventral preantennal suture may be thickened each side (thus becoming a continuation of the ventral carina), and fused distally with the complete marginal carina. Example : *Tinamotaecola* (fig. 14).
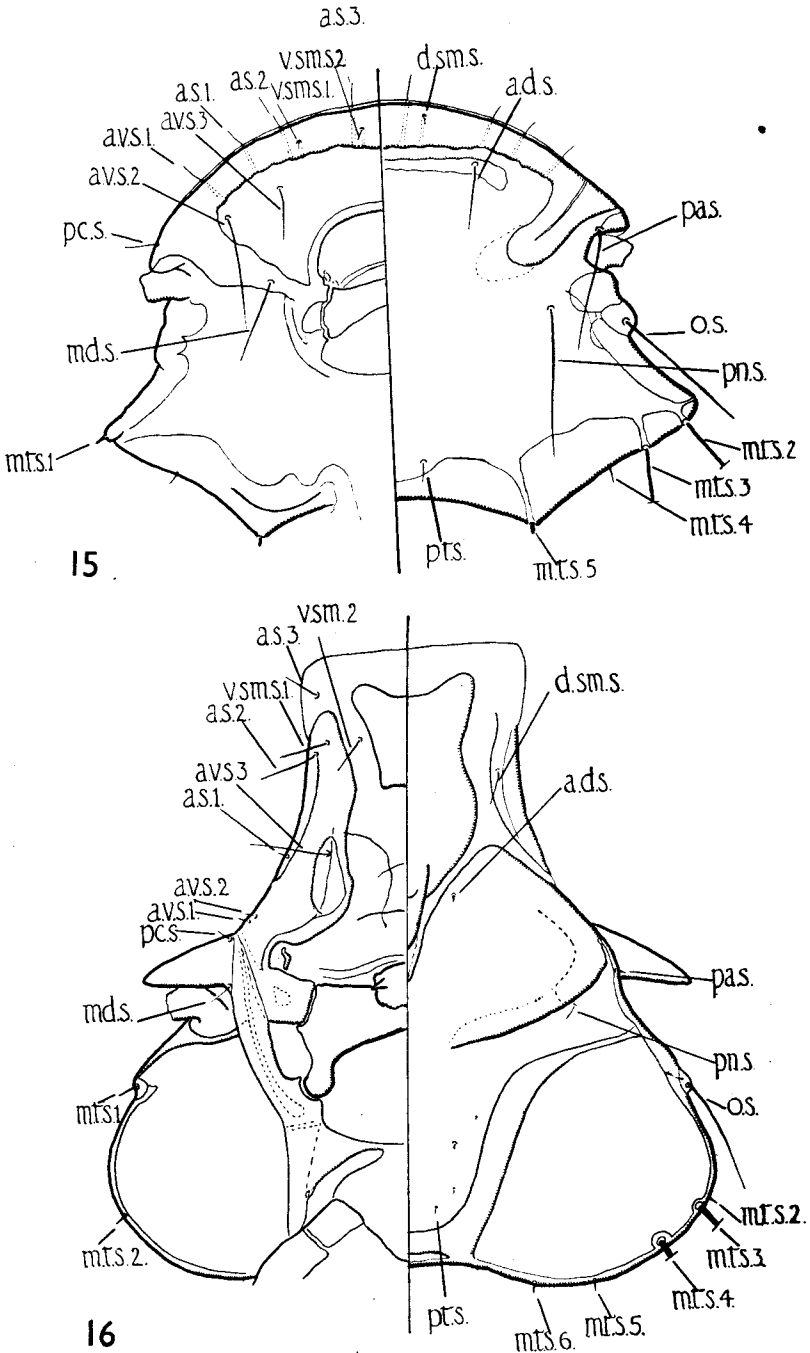
FIGS. 15, 16.—Heads to show setae. (15) *Goniodes* sp. (16) *Saemundssonia* sp. *a.d.s.*, anterior dorsal seta ; *a.s.*, anterior seta ; *a.v.s.*, anterior ventral seta ; *d.sm.s.*, dorsal submarginal seta ; *md.s.*, mandibular seta ; *m.t.s.*, marginal temporal seta ; *o.s.*, ocular seta ; *pa.s.*, preantennal seta ; *pc.s.*, preconal seta ; *pn.s.*, postnodal seta ; *pt.s.*, postemporal seta ; *v.sm.s.*, ventral submarginal seta.

Part of the ventral carina each side may form a thickened flattened surface, lying parallel to that of the opposite side, to which the lobes of the pulvinus are attached. The ventral carinae may or may not reach the complete marginal carina, or the marginal carina may be interrupted medianly and the ventral carina fused to its edge each side (Plate I, fig. 4). In many genera the ventral carina does not form a distinct band anteriorly as in *Tinamotaecola* (fig. 14), but has a thickened inner edge only. Example : *Saemundssonia* (fig. 11).

In the more specialized heads the area between the proximal part of the ventral carina and the marginal carina has various modifications which may form useful generic characters.

In some of the genera (e.g., *Halipeurus*) parasitizing the Procellariiformes there is a line of demarcation running anteriorly from the interrupted ventral carinae each side, giving a similar appearance to a ventral preantennal suture, but the surface of this area is sclerotized and sculptured (possibly secondarily). In *Halipeurus* and other genera from the Procellariiformes the ventral carinae merge with the inner ventral surface of the head shortly after their proximal point of origin, but distally there is an isolated band of thickening along each side of the line of demarcation, which may be called the ventral carina. Another modification found in one of the genera (*Naubates*) from the Procellariiformes is the presence of a more dorsal posterior prolongation of the ventral carina, which probably gives some extra support to the pulvinus.

As the preantennal region becomes more modified the ventral carinae become thicker and the attachment of the pulvinus more specialized. A comparison of fig. 4 (*Coloceras*) and fig. 5 (*Philopterus*) demonstrates this increase in complexity of the pulvinus and ventral carinae.

Postantennal Region.

Temporal carina (temple band, of some authors; occipital band, Piaget, 1885; zugel, Kéler, 1938).—This endocarina, when present, runs from the occipital margin of the head across the temples, and becomes continuous either with the preantennal nodus (*Philopterus, Cummingsiella*), or with the temple margin just above the eye (*Saemundssonia*, fig. 11, *t.c.*). In many species it merges with the inner surface of the dorsal sclerotization, and is only apparent near its point of origin at the occipital margin.

Marginal temporal carina.—The temples are usually enclosed by a thickened rim—the marginal temporal carina, which may be enlarged into irregularly shaped patches of thickening round the eye—the preocular nodus and the postocular nodus—and on the occipital margin—the occipital nodus.

The postantennal suture.—This suture either passes across the temples (*Lagopoecus*) or appears as two lateral sutures (*Quadraceps*).

The occipital carina (tremse, Kéler, 1948).—This runs backwards each side from the mandibular framework and may or may not fuse with the occipital margin ; the posterior tentorial pits are always associated with this occipital thickening.

The chaetotaxy.

The setae of the head are remarkably constant in position and number throughout the Ischnocera, and can frequently be used as guides to certain parts of the head. There are five pairs of setae which are always present and approximately in the same position throughout the superfamily ; these are :

A ventral seta arising just anterior to the conus—the preconal seta (*pc.s.*, figs. 15 and 16).

A ventral seta, on, or near the outer surface of the mandibular framework, the mandibular seta (*md.s.*). In some species (e.g., *Pectinopygus* sp.) this seta has become pushed out laterally and actually arises on the lower margin of the conus.

A seta on the dorsal, usually anterior, edge of the antennal socket, the preantennal seta (*pa.s.*).

A dorsal seta posterior to the preantennal nodus, the postnodal seta (*pn.s.*). Where there is a postantennal dorsal suture this seta lies in or near the suture (fig. 16, *pn.s.*).

A seta arising on the dorsal surface of the lens of the eye, the ocular seta (*o.s.*).

The remaining setae are also found throughout the superfamily, but their position, and sometimes number, is not so constant. In the primitive type of head (e.g., *Goniodes*, fig. 15) there are four or five setae arising on the anterior margin each side of the midline ; in other genera (e.g., *Trogoninirmus*), also with a complete marginal carina (or circumfasciate head), they may originate submarginally on the dorsal surface. In the modified type of head (fig. 16) the outer of these marginal setae is associated with one of the anterior ventral setae (see below), and is here called the first anterior ventral setae (*a.v.s.* 1). As the remaining three or four may be marginal or submarginal on the dorsal or ventral surface they are called the anterior setae (*a.s.* 1–3).[2]

Where the dorsal preantennal suture interrupts the marginal carina the first anterior seta is often (but not invariably) associated with the point of interruption, either marginally or submarginally on the dorsal or more rarely on the ventral surface. In those species where the dorsal suture does not interrupt the marginal carina though they belong to a genus in which the majority of species show the interruption, as in *Philopterus*, then the first anterior seta will be found at the lateral edge of the dorsal suture, that is, near the point where the interruption of the marginal carina usually occurs in species of *Philopterus*.

Arising on the ventral surface of the marginal carina in the primitive type of head, each side of and near the midline is a pair of setae—the ventral submarginal setae (*v.sm.s.* 1–2). In other genera (e.g., *Lipeurus*, *Degeeriella*, *Labicotes*, *Otidoecus*) these may arise on the ventral surface below the marginal carina. In the most specialized type of head (fig. 16) the outer of this pair (*v.sm.s.* 1) usually lies on the marginal carina and the inner (*v.sm.s.* 2) just lateral to the ventral anterior plate. In *Anatoecus* this latter seta is minute and difficult to see. ·

Lateral and posterior to the ventral submarginal setae are two ventral setae each side—the anterior ventral setae (*a.v.s.* 2–3). In specialized forms where the ventral carina is modified these two setae, together with the first of the marginal setae (*a.v.s.* 1), often form a characteristic group associated with the ventral carina and the area between it and the lateral margin of the head— these three setae are called the anterior ventral setae (*a.v.s.* 1–3). In some genera (e.g., *Philopterus*, *Saemundssonia*, *Degeeriella*) the outer two (*a.v.s.* 1–2) are close together and arise just anterior to the preconal seta ; in others (e.g., *Naubates*, *Halipeurus*, *Anaticola*, some species of *Pectinopygus*) all the

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[2] All setae are counted from the lateral margins of the head towards the midline, and those on each half of the head are counted separately.

anterior ventral setae may be grouped much nearer the front of the head, or (e.g., *Degeeriella, Rhynonirmus*) *a.v.s.* 1–2 may arise near the conus and *a.v.s.* 3 near the anterior margin of the head. Their position seems to be mainly dependent on the shape of the head.

On the dorsal surface of the preantennal region there is a single submarginal seta lying each side of the midline, either on the marginal carina or just below it—the dorsal submarginal seta (*d.sm.s*). In the specialized forms this is usually found on the premarginal carina (fig. 16, *d.sm.s.*). Posterior to this seta is a single seta—the anterior dorsal seta (*a.d.s.*), which is commonly associated with the dorsal preantennal suture when this is present. In the great majority of species with modified heads this seta arises either in the suture or on its posterior margin. However, in some genera (e.g., *Haliperus*) it may arise some distance posterior to the suture, or its position in relation to the suture may vary in different species of one genus (e.g., *Ardeicola*). In *Columbicola* the anterior dorsal setae are never associated with the suture (which in any case may not be homologous with the dorsal suture of other genera), and there is a second pair of setae posterior to these, about the level of the conus.

The margins of the temple always have a number of setae, some arising dorsally and some ventrally, but for the purposes of terminology they are all called the marginal temporal setae (*m.t.s.* 1, 2, 3 . . . .). The first seta on the temple (*m.t.s.* 1) usually arises on the ventral surface just behind the eye ; in a few genera (e.g., *Saemundssonia*) it is actually on the ventral surface of the lens, and in others (e.g., species of *Goniodes*) it may arise some considerable distance behind the eye. Its position on the eye is apparently of generic value in *Saemundssonia*. Specimens of this genus have been examined from 52 species belonging to 24 genera of the Charadrii, 39 species belonging to 11 genera of the Lari, 8 species of 5 genera of Alcae, 8 species of 8 genera of Procellariformes and 1 species of GRUIDAE. In all these the first marginal temporal seta is on the lens. In *Quadraceps*, probably a related genus, this seta may be either on the lens or just below it, and where it is close to the lens it arises on it in some specimens of a species and below it in others. The remaining temporal setae usually comprise a small ventral seta (*m.t.s.* 2), two dorsal macrochaetae, and two smaller setae on the occipital margin (fig. 16). But there is considerable variation in the number and size of the temporal setae even within one genus : in *Goniodes* many of the species have the number as shown in fig. 15, but *G. wilsoni* and *G. perlatus* have eight or more elongated setae each side.

Near the midline on each side there is a single seta above the occipital margin, the post-temporal seta (*pt.s.*).

All or any of the head setae may become greatly elongate (e.g., *Meinertzhageniella*) or reduced to stout spines (e.g., *Austrophilopterus, Anatoecus*), or reduced to microchaeta so that they are often difficult to find. Some species may have additional setae on the dorsal surface of the head (e.g., *Austrogoniodes*), arranged in such a way that it is no longer possible to identify the primitive ones to which names have been given. Abnormally any of the setae may be duplicated in a specimen, often on one side of the head only.

The Phylogenetic Importance of the Characters of the Head.

In the superfamily Amblycera (which is the more primitive) the mandibles are near the anterior margin of the head ; in the Ischnocera the region of the

head in front of the mandibles has become elongated, sometimes to a consider-
able extent in the more specialized genera such as *Craspedorrhynchus* and
Echinophilopterus. With the elongation of the preantennal region is found
the tendency for the breakdown of its rigidity by the formation of sutures
and by the interruptions of the endocarinae. The most important line of
evolution seems to have been that which increased the efficiency of the pulvinus
as a holding groove for pieces of feathers. This was achieved by the inter-
ruption of the primitive semicircular ventral carina, thus increasing the
mobility of the pulvinus and giving better attachment for its lateral lobes.
This interruption of the ventral carina has certainly taken place more than
once—the HEPTAPSOGASTRIDAE have genera both with and without the complete
carina. The prolongation of the ventral carina each side and its fusion with
the interrupted marginal carinae gives additional support to the pulvinus,
and strengthens that form of head in which the presence of both dorsal and
ventral membranous areas allows a limited mobility. Although the inter-
ruption of the endocarinae and the formation of sutures have probably taken
place on the same general lines in unrelated stocks, their present arrangement
differs in detail to a greater or less extent. These differences may have been
caused by the differences in the minute feather structure of the host. There
are only four host groups—the Sphenisciformes, Tinamiformes, the Galli and
the COLUMBAE on which the parasite genera with unmodified heads are
dominant ; the last three groups also have parasite genera with modified heads.
On the Tinamiformes are found *Pseudolipeurus, Pseudophilopterus*, and *Tinamo-
taecola*, all with modified heads, and even within the family HEPTAPSOGASTRI-
DAE the ventral carina is interrupted in some genera (e.g., *Megapeostus*) and the
marginal carina modified (e.g., *Discocorpus*). In the genera from the Galli,
apart from *Lagopoecus* and *Cuclotogaster* in which the ventral carina is inter-
rupted, *Oxylipeurus* shows a tendency towards the formation of anterior
sutures and the modifications of the marginal carina. In *Columbicola* from
the COLUMBAE the ventral carina is interrupted and the anterior region of the
head shows considerable modification. One genus (*Episbates*) on the Pro-
cellariiformes has the head unmodified, but all the other genera from this
Order and the rest of the Aves have the head modified in some way even if it
is only the median interruption of the ventral carina. It would seem, therefore,
that the modifications of the preantennal region of the head are advantageous
to the parasites on the majority of bird orders. Elsewhere (Clay, *in press*)
tentative suggestions have been made on the possible role played by the
minute structure of the feathers in the retention of the primitive features
of the head.

Brüelia, a genus which parasitizes the Passeriformes and some related
orders, comprises a large number of species, amongst which can be traced a
series from those with an entire marginal carina and no anterior plate, to
those with the marginal carina interrupted medianly and laterally, and with
the anterior plate well developed. Thus, the species from *Podoces* (fig. 17)
shows the complete marginal carina although medianly less heavily sclerotized,
that from *Nucifraga* (fig. 18) shows a greater median modification, that from
Bombycilla (fig. 19), the types species of *Brüelia*, has the marginal carina
indented medianly and the anterior margin of the head at this point hyaline.
In this and other species there is a triangular-shaped area of sclerotization in
the indented part of the marginal carina. In the species (fig. 20) from
Harpactes erythrocephalus (Trogoniformes) the marginal carina is entire, but

there is a dorsal suture which cuts off a simple anterior plate. In that from *Turdus pilaris* (fig. 21) the marginal carina is interrupted medianly and there is an incomplete interruption laterally ; the dorsal suture does not pass across the head, and leaves the posterior part of the anterior plate continuous with the dorsal sclerotization of the head. In the species from *Turdus merula, Brüelia merulensis* (fig. 22), the marginal carina is interrupted medianly and laterally and there is a well-marked dorsal suture and anterior plate. The nymph of this latter species (fig. 23) has the marginal carina entire, and similar to that of the adults of other species of *Brüelia*.

Ventrally all species of *Brüelia* have the ventral carina interrupted. In some the ventral carina may be sclerotized only proximally each side (species from *Podoces*, fig. 24), giving a situation similar to that in *Degeeriella* (fig. 13). In those species in which the marginal carina is complete (but indented) dorsally and interrupted ventrally, the sclerotization of the inner edge of the ventral carina is carried forward each side to fuse with the interrupted marginal carina ; in *Brüelia merulensis*, where the marginal carina is divided laterally into a pre- and postmarginal portion, this sclerotization is fused to the distal ends of the premarginal carinae (fig. 25). *Sturnidoecus*, obviously nearly related to *Brüelia*, owes its distinctive appearance to the elongation of this ventral thickening beyond the dorsal marginal carina, and to its broader head, which has those characters associated with increased size (see below). Thus, the species of *Brüelia*, which by the characters of the abdomen form a compact group, show considerable diversity in the characters of the head. Any attempt to separate them into genera on these head characters would mean the erection of five or six genera, which would not only grade into each other but completely obscure their relationships, and in some cases would mean the association of a number of species not forming a natural group. The characters on which *Guimaraesiella* Eichler, 1949, for instance, was separated from *Brüelia* are found not only in the type-species, *Docophorus subalbicans* from the PARADISEIDAE, but in species from the TURDIDAE, GEOSPIZIDAE and others. There seems no reason, therefore, to recognize the following genera : *Corvonirmus* Eichler, *Guimaraesiella* Eichler, *Xobugirado* Eichler, *Meropsiella* Conci, *Painjunirmus* Ansari and *Traihoriella* Ansari. The genera *Sturnidoecus* and *Bizarrifrons* and species from the CORACIIDAE (" *Docophorus* " *longipes* Piaget) are also closely related to *Brüelia*, as shown by the characters of the abdomen, but have probably diverged far enough from their original *Brüelia*-like ancestor to be recognized generically.

The most specialized species of *Brüelia* (for example, *B. merulensis* or *B. galapagensis*) have a form of head which, with various minor modifications, is found in a great number of related or not closely related forms. The characters of this head are as follows :

> Part of the median anterior margin of the head hyaline.
> Marginal carina interrupted anteriorly and laterally.
> Dorsal preantennal suture and dorsal and ventral anterior plate present.
> Ventral carina interrupted and fused to the ends of the premarginal carina.
> Pulvinus with lobes attached to the flattened parallel surfaces of the ventral carina.

In those species with heads modified on the above lines some show the complete marginal carina (at least dorsally) in the nymph, for example

Brüelia merulensis (fig. 23), *Strigiphilus oculatus* (fig. 26), *Aptericola novae-zealandiae ;* in others such as *Philopterus* even the first stage nymphs are little different from the adult. This may mean that either the latter have been established for a longer period of time, or (which is more likely) they have assumed a mode of life which necessitates the modification of the head and without which the nymphs could not survive. It is probable that this type of head has been evolved more than once in both related and unrelated
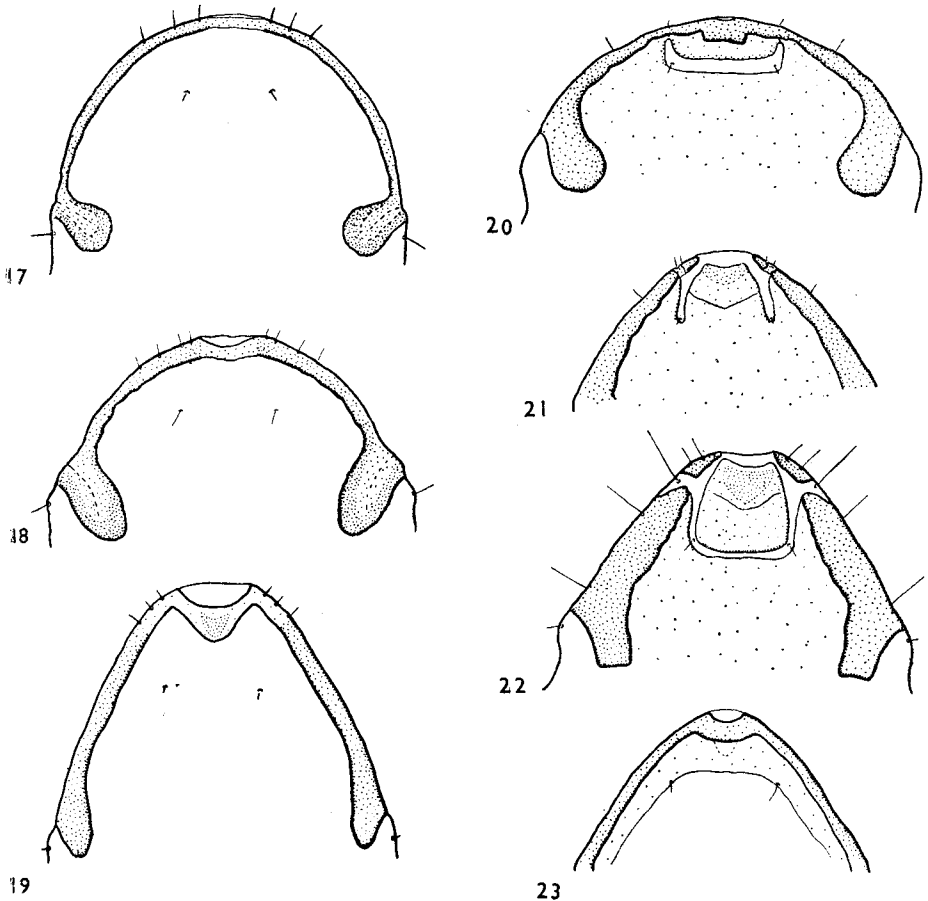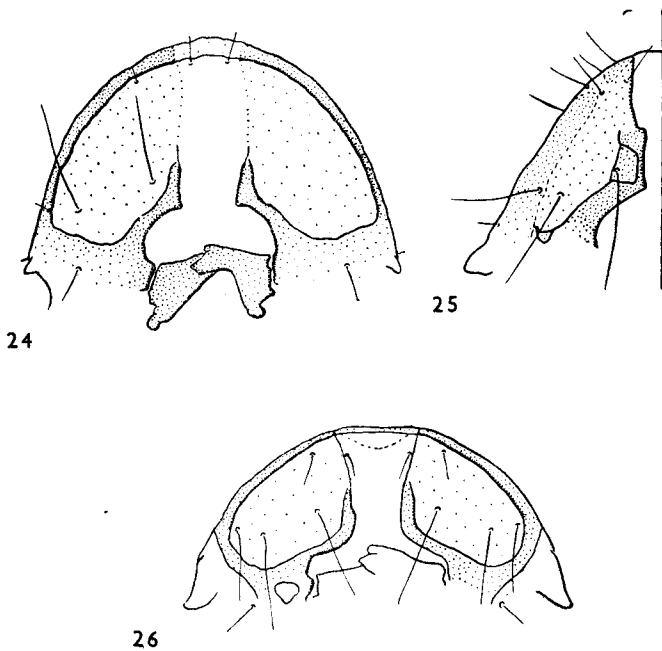

FIGS. 17–23.—Preantennal region of the head, dorsal. (17) *Brüelia koslovae.* (18) *B. multipunctata.* (19) *B. brachythorax.* (20) *Brüelia* species from *Harpactes erythro-cephalus.* (21) *B. marginata.* (22) *B. merulensis.* (23) *B. merulensis,* nymph.

forms, due no doubt to the similarity of the basic Ischnoceran type in which specialization would be forced to take place on similar lines (see Clay, 1949, for fuller discussion). Thus, *Philopterus, Quadraceps, Wilsoniella, Mulcticola, Penenirmus* and *Pectinopygus* all have this general type of head, but are in no way closely related. It is not supposed that all the genera with this similar type of head evolved on the same lines, nor that the development from nymph to adult is always the same—an examination of the nymphs of *Ibidoecus,* for instance, suggests that the anterior plate has been formed rather differently

from that of *Brüelia*. It is possible that the method of formation of the dorsal suture and anterior plate may give an indication of relationships between the genera, but a study of the embryology and nymphal development will have to be made before a supra-generic classification based on mode of development can be formulated.

Although this form of modification of the head (discussed above) appears to be the most widespread, examples being found on the majority of bird orders, there are cases where specialization has been achieved on other lines. The genera of Ischnocera found on the Galli have the primitive type of head with a complete marginal carina and uninterrupted ventral carina (fig. 10), or if interrupted the sclerotization is not carried forward. One genus, *Oxylipeurus*, however, shows a tendency for the anterior region of the head to become

Figs. 24–26.—Preantennal region of the head, ventral. (24) *Brüelia koslovae*. (25) *B. merulensis*. (26) *Strigiphilus oculatus*, nymph.

modified in various ways. The unmodified species (e.g., *O. mesopelios*) have a complete marginal carina with the dorsal preantennal suture not interrupting the marginal carina laterally; the dorsal suture may be indistinct (species from *Oreortyx*, *Epicolinus* Carriker), or absent (*O. himalayensis* from *Tragopan* and a species from *Crax*). In other species (e.g., *O. repandus*) the preantennal suture may partially interrupt the marginal carina laterally; in *O. inaequalis* the postero-lateral margin of the suture is sclerotized each side, giving short dorsal carinae. In *O. megalops* there is considerable modification of the anterior part of the head in a way which cannot be homologized with that discussed under *Brüelia*, and which is unlikely to lead to a form of head found in the most specialized species of that genus, although it is a type which could have led to the modifications found in *Columbicola*. The

temporal carinae are never fully developed, and may be absent. The pulvinus is either of the primitive lobe-like type, or has lateral lobes as in *Coloceras*, or internal sclerotization (*O. ischnocephalus*). The ventral carina usually merges each side with the ventral sclerotization of the head, and does not join with that of the other side to form a definite semicircular band as in *Goniodes* (fig. 10). The sclerotization may be interrupted by a ventral suture which runs anteriorly (as in *Degeeriella*), reaching nearly to the marginal carina (*O. megalops*); in *O. aepypodius* there is a thickening along the edges of part of this suture forming distally short ventral carinae similar to those found in *Pseudonirmus*.

Thus *Oxylipeurus*, parasitizing a single host order, comprises a related group of species (as shown by the characters of the abdomen) which show a tendency towards the modification of the anterior region of the head. This has probably taken place more than once, sometimes on parallel lines, in different groups of species restricted to particular families of birds. It seems unsatisfactory to use these head characters as criteria for the erection of genera —at least six of such genera would be needed, and in some cases would include species from unrelated host groups. The two genera already separated from *Oxylipeurus*, namely *Eiconolipeurus* and *Epicolinus*, should, therefore, not be recognized; *Splendoroffula*, found on the MUSOPHAGIDAE, is also doubtfully separable from *Oxylipeurus*.

Structural modifications in the Ischnocera have been caused by the adaptation of the parasite to the environment of the different ecological niches on the body of the bird. This factor has been discussed elsewhere (Clay, 1949), but in relation to the structure of the head it was the occupation of the head and neck niche which seems to have had the most important influence. The occupants of this niche have a broader head, correlated with the general shortening and broadening of the whole body. This enlargement of the head is usually associated with the prolongation of the head anteriorly and with the enlargement of the mandibles and the concomitant development of the mandibular framework. This type of head shows the greatest development of endocarinae, presumably for support of the larger mandibles and the larger size of the head in general. It also has the greatest development of sutures in the preantennal region, possibly to give a limited mobility to this flattened expansion of the head. In the postantennal region support is given to the mandibular framework by the prolongation of the occipital carinae to the occipital margin; and further support to this region is given by the development of the temporal carinae. Although well developed temporal carinae are found in narrow-headed forms, these lines of thickening are, in general, characteristic of the broad-headed forms, and are found in such unrelated genera as *Megaginus*, *Docophoroides*, *Trabeculus*, *Anatoecus*, *Philopterus* and *Sturnidoecus*. Moreover, where there are two related genera or species groups which differ mainly in shape, these endocarinae are usually present in the broad-headed forms and absent in the narrow-headed ones: thus *Sturnidoecus* has these carinae well developed, unlike *Brüelia*, in which the species have narrower heads; *Acutifrons* contains broad-headed species, which differ only from *Degeeriella* by the well-developed temporal carinae; *Cuculicola cheluria*, a broad-headed species, has well-developed temporal carinae, which are absent in the narrow-headed *Cuculicola latirostris*.

Thus, the apparent similarity between different genera is often caused by linked characters dependent on the environment in which the parasite lives;

this has resulted in many of the round-bodied, large-headed forms (head lice) being placed in one family and many of the long-bodied narrow forms (wing lice) in another. On the other hand, it has also led to the erection of genera for groups of species which, because they have changed their habitat or possibly because their host has a broader type of feather with the resulting broadening of the parasite, differ only in those superficial characters of the head (and sometimes abdomen) correlated with increased size. It is doubtful, for instance, whether *Acutifrons* is more than a species group of *Degeeriella*. Hopkins (1943), in a most instructive paper, has shown how the TRICHO-DECTIDAE from the antelopes have been separated into genera on adaptive, not phylogenetic characters, the environmental factor probably responsible being the texture of the coat of the host.

The value of the characters of the head in showing phylogenetic relation-ships can now be summarized. The variation is discussed in relation to characters of the abdomen which are constant throughout any group in question.

Marginal carina.—In many groups the form of this carina is a good generic character, but there are a number of exceptions : *Brüelia* and *Oxylipeurus* have already been discussed ; in *Philopterus* the marginal carina may have the well-marked lateral interruption characteristic of most of the genus, or there may be no interruption but a deep indentation (species from *Megarhynchus*, TYRANNIDAE), or the marginal carinae may be complete laterally (species from the PITTIDAE). Although the form of the marginal carina may sometimes be a generic character, there seems little doubt that it will not form a supra-generic character except in those cases where it is unmodified (GONIODIDAE) ; the majority of families will probably prove to have genera with the carinae both entire and specialized to a greater or less extent.

Hyaline margin.—This region is only appreciably developed in those forms with modified heads, although it seems to be homologous with the narrow hyaline rim of the head in *Goniodes* (fig. 10) called the "limbulus" by Kéler (1939 : 14). Its form is largely dependent on that of the marginal carina and, therefore, in a genus (e.g., *Brüelia*) where there is considerable variation of this carina there is also variation of the hyaline margin. In *Rallicola*, where it is always present, it may be extremely narrow (*R. fulicae*) or broad (*R. ortygometrae*). In those species with modified heads its point of origin each side gives a characteristic appearance. In *Anatoecus, Craspedonirmus* and *Carduiceps* it arises each side at the point of the lateral interruption of the marginal carina, and this point of origin appears to be constant and charac-teristic throughout these genera. In other genera its point of origin varies : in *Philopterus*, for instance, it may arise at the anterior ends of the marginal carinae (*P. cincli*), or some little way proximal to this (species from *Grauculus*) ; its breadth at the lateral sides of the head also varies in this genus : it may run forward as a narrow strip (*P. fringillae*), or be enlarged laterally (species from *Dicrurus*, MOMOTIDAE and others), giving a characteristic appearance to the head. The anterior edge of the hyaline margin may be medianly indented as a generic character (*Incidifrons*), or as a specific character (*Philop-terus*) ; the anterior edge may be more heavily sclerotized and pigmented, a character found in some species of *Philopterus* (those from the MOMOTIDAE, TYRANNIDAE, NECTARINIIDAE and others) and in the species of *Penenirmus* parasitizing the CAPITONIDAE (Barbets).

Dorsal carina.—The form of this carina (bordering the posterior edge of the preantennal suture) may be of generic value (*Pseudonirmus*), or vary

considerably in closely related forms : in the *Saemundssonia* species from *Alle alle* it is strongly developed and passes round the posterior end of the preantennal suture, while in the species from another of the ALCIDAE (*Fratercula arctica*) it is scarcely developed.

Transverse carina.—Where this is present as a complete band across the head it seems to be constant throughout the genus (e.g., *Columbicola*), but it is not of supra-generic importance, as in *Turturicola*, apparently related to *Columbicola*, it is absent.

Temporal carina.—These carinae may be absent, partially developed or fully developed within one genus, but their distal point of termination when fully developed seems to be constant throughout a genus ; in *Philopterus*, for instance, they pass to the preantennal nodus, and in *Saemundssonia* to the preocular nodus.

Anterior plate.—In those genera containing species in which the dorsal anterior plate is a superficial area marked off from the rest of the preantennal surface of the head by the dorsal suture, there may also be species where it is absent altogether (e.g., *Brüelia*). Where the anterior plate is a thickened discrete structure its form is usually of generic value (e.g., *Ibidoecus*). There are, however, exceptions : in the *Philopterus* species from the PITTIDAE the posterior prolongation of the anterior plate is lightly sclerotized, and is not the heavily thickened point characteristic of most species of *Philopterus* ; in one species of *Quadraceps* (from *Limnodromas griseus*) the posterior part of the plate is prolonged into a thickened point, and is similar to that found in *Saemundssonia*.

Dorsal suture.—Where the marginal carina is complete the presence or absence of a dorsal suture (e.g., *Goniodes, Lagopoecus*) is rarely a generic character. Again in the same genus it may or may not be continued to the margin and interrupt the marginal carina (*Oxylipeurus, Brüelia*). In the forms with specialized heads where it is present throughout the genus, its point of origin is usually constant : in *Rallicola* (species examined from 23 genera of RALLIDAE) the marginal carina is never interrupted laterally, and the dorsal suture always arises at the anterior end of the marginal carina each side ; and in *Philopterus*, even in those species where the marginal carinae is not interrupted, the dorsal suture always arises near the middle of the preantennal region. In the species with modified heads the form of the dorsal suture also seems to be generically constant : either passing straight across the head (*Lunaceps*), passing posteriorly to a point (*Quadraceps*) or as two points (*Sturnidoecus*).

Ventral carina.—This endocarina shows great diversity throughout the Ischnocera, and its form is rarely (perhaps in the GONIODIDAE) a supra-generic character. It may be entire or interrupted in the same genus (*Heptapsogaster*), but its general form tends to be constant throughout a group of related species. In *Brüelia*, for instance, in which there is much diversity of head form, the ventral carina is always interrupted and the sclerotization carried forward as a flattened surface each side (fig. 24) ; in *Degeeriella* (fig. 13), in which the general form of the head resembles that of the simplest species of *Brüelia*, the ventral carina is always interrupted, but the sclerotization is not carried forward in the form found in *Brüelia*. The ventral carinae may or, may not be fused with the marginal band within one genus (*Brüelia*). The area between the proximal part of the ventral and marginal carinae may show generic characters in the specialized forms (e.g., *Saemundssonia*). The form

of the pulvinus is closely linked with that of the ventral carina, and its character seems to be constant through groups of related species.

Occipital carina.—These may or may not reach the occiput in the same genus (e.g., *Oxylipeurus*).

Gular plate.—A true gular plate seems to be absent in all the GONIODIDAE, *Austrogoniodes, Chelopistes,* some of the genera of the HEPTAPSOGASTRIDAE and in some of the genera parasitizing the Procellariformes. In *Oxyliperus* it may or may not be present. In *Colilipeurus* and *Turnicola* it is apparently absent, but may only lack pigmentation. It is also absent in *Hopkinsiella,* although in related genera it is present. The presence of a gular plate may, therefore, be a supra-generic, generic, or only a specific character.

Antennae and conus.—These structures have already been discussed (Clay, 1946 : 355) and it was suggested that the form of the conus was often correlated with the size of the antennae, and that sexual dimorphism in either of these structures was of little phylogenetic interest, the presence or absence of sexual dimorphism being found in closely related species. In *Philopterus* the conus may be well developed (species from CAMPEPHAGIDAE), reduced (species from TYRANNIDAE), or absent (species from PITTIDAE).

Chaetotaxy.—As already shown, the setae are, in general, constant throughout the Ischnocera and do not show supra-generic characters. The form of the setae may be of generic value : the spine-like dorsal setae of *Anatoecus,* the peculiar flattened third anterior setae of *Columbicola,* and the stout second anterior setae of *Anaticola.* Some large groups of species (*Goniodes*) show variation in number, size and position of the setae so that the chaetotaxy may give specific differences.

Mouthparts.—The form of the mouthparts may be constant throughout groups of unrelated genera, or may vary considerably in related species where the differences are merely of specific value. Cummings (1916 : 670) has shown, for instance, that the hypopharynx in *Ibidoecus* may be normally developed or greatly reduced.

In conclusion it can be said that the head is basically similar throughout the superfamily Ischnocera.[3] Superimposed on this basically similar structure are found many variations in the superficial characters of the head—this part of the body apparently being the most closely adapted to the environment. Much of this adaptation seems to have taken place on parallel lines. This has resulted in groups of species obviously closely related by the more stable characters of the abdomen showing very different head characters, and others probably not related having similar characters of the head. This, together with the fact that in most groups of related genera there are some which have retained the primitive head characters, makes it difficult to base a supra-generic classification on the characters of the head, although it may prove that the manner by which the specialization of the head is brought about during development will indicate relationships between some of the genera. Further, the many genera which have developed modifications of the head on similar lines (as discussed under *Brüelia*) may be descendants of a common ancestor in which this was the only modification of the head possible, whereas those in which specialization has taken place on different lines (e.g., *Anaticola, Columbicola, Oxylipeurus*) are not related to the genera with the "*Brüelia*"-like heads.

[3] Dr. S. Symmons (*in press*) has shown that the tentorium of the Ischnocera, unlike that of the Amblycera, is uniform in structure throughout the group ; species from a number of unrelated genera were examined.

At the present time groups of species inseparable on the characters of the abdomen should probably not be separated generically on small differences in head structure, especially where they do not parasitize a related group of hosts, and hence, where the characters they have in common may be adaptive, not phylogenetic.

SUMMARY

This paper is the first of a series dealing with a reassessment of the characters used in the generic separation of the Ischnocera. The generic concept as applied to the Mallophaga is discussed. The primitive head and its specializations are described and a terminology of the structures useful in classification given. The phylogenetic significance of the variation in the characters of the head is discussed.

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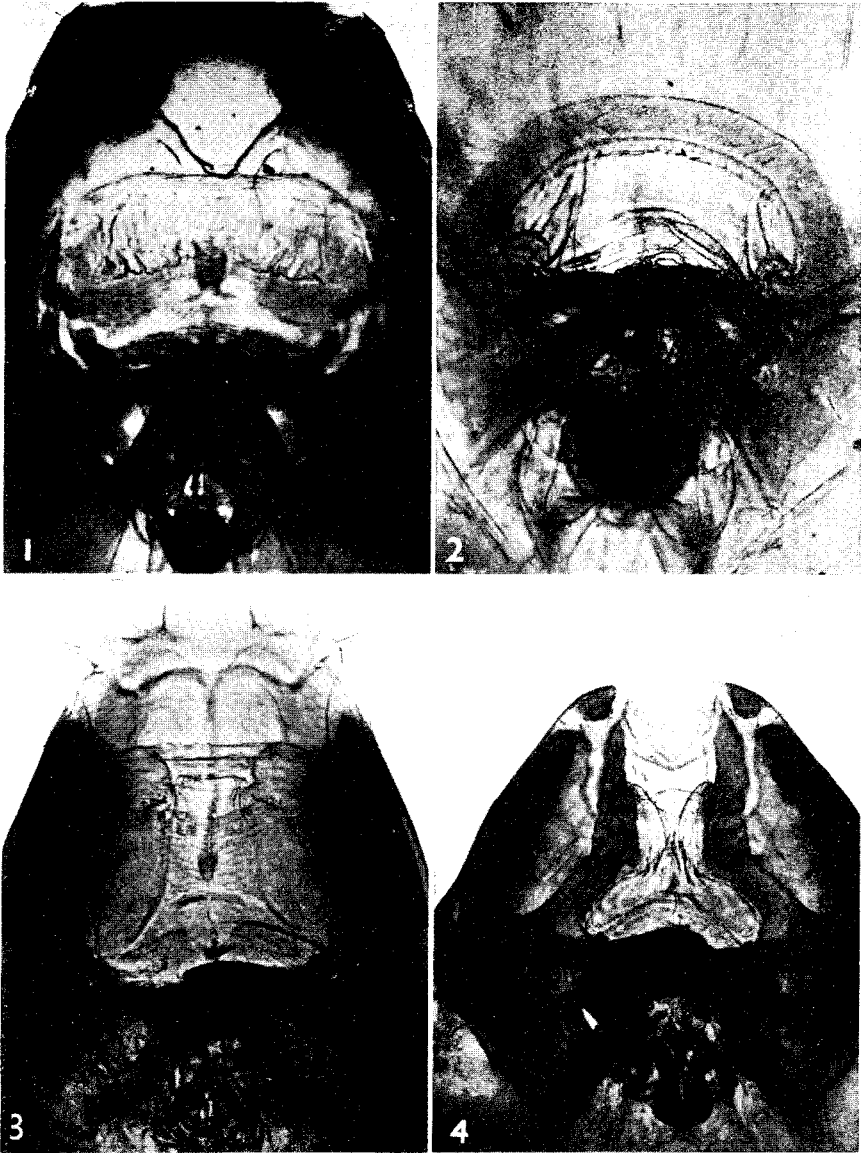
Heads of Mallophaga species to show pulvinus. Fig. 1. *Perineus* sp. Fig. 2. *Coloceras* sp. Fig. 3. *Anaticola* sp. Fig. 4. *Brüelia* sp.

(Specimens mounted in polyvinyl lactophenol and photographed by H. M. Malies.)