THE AFFINITIES OF GRYLLOBLATTA INDICATED BY A STUDY OF THE HEAD AND ITS APPENDAGES

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Since specimens of *Grylloblatta* are extremely rare and valuable, I am deeply indebted to Mr. Eric Hearle and to Mr. H. S. Barber, for their kindness in supplying me with the material used in the preparation of this paper. The following discussion is based upon the study of *Grylloblatta campodeiformis* Walk., and *Grylloblatta barberi* Caud., with which I have been able to compare sketches of the parts of the only other known Grylloblattid, *Galloisiana nipponensis* Caud., through the kindness of Mr. A. N. Caudell.

The affinities of *Grylloblatta* indicated by the study of its terminal abdominal structures have been discussed by Walker 1919 and 1922; and the writer (Crampton 1915, 1917, 1923, 1924 and 1926) has discussed the evidence of its affinities indicated by a study of its antennæ, maxillæ, head, thorax and ovipositor. I believe that *Grylloblatta* is practically a living Protorthopteron very closely related to the common stock from which sprang the Tettigonioid and Grylloid Orthoptera, and the closest affinities of *Grylloblatta* are with the Tettigonioids. Outside of the true Orthoptera, the next of kin of the Grylloblattids are the Dermaptera, and the Phasmids are somewhat more remotely related to them. The Grylloblattids (with the rest of the Orthoptera) Dermaptera and Phasmids were descended from a common Protorthopteroid stock which also gave rise to the Embiids, whose line of descent parallels that of the Grylloblattids rather closely, but the nearest relatives of the Emblids are the Plecoptera. The Protorthopteroid ancestors of the Orthoptera (including Grylloblatta) Dermaptera and Phasmids were descended from Protoblattoid forms, from which the Blattids and Isoptera have departed but little. In the following

discussion I would point out the evidences for this view afforded by a study of the head and its appendages in *Grylloblatta*.

The head capsule of *Grylloblatta* as shown in Fig. 2, gives no support to the view of Imms, 1925, for example, who maintains that *Grylloblatta* is one of the Cursoria, since the head of Grylloblatta is very similar to that of the Orthopteron *Gryllotalpa* in its general outline, the position of the eyes the location of the antennæ, and numerous other features. *Gryllotalpa*, however, and the other Grylloid Orthoptera have ocelli, so that in acking these structures, the head of *Grylloblatta* resembles that of certain Tettigonioid Orthoptera such as *Ceuthophilus*, as is also true of other features of the head in these insects. On the other hand, the head of *Grylloblatta* is not like that of such Cursoria as the Blattids, Mantids, etc. and the evidence from this source would indicate that *Grylloblatta* is either a true Orthopteron, or possibly a relict of the extinct Protorthoptera-like ancestors of the Grylloids and Tettigonioids.

In tracing the type of head capsule exhibited by the Grylloblattids to its prototypes in the lower Orthopteroids clustered about the base of the line of descent of the Orthoptera, it at once becomes evident that the head capsule of *Grylloblatta* is so like that of the Dermaptera that the head of *Grylloblatta* should be referred to as Dermapteroid or Forficuloid. Thus, in a typical Dermapteran head, there is a pale anteclypeus, like the region labelled *ac* in Fig. 2; the antennæ are located near the bases of the mandibles, as in Fig. 2; the eyes are located far down the tempora (*tm* of Fig. 2); temporal sutures (*ts* of Fig. 2) demark the temporal regions *tm* from the parietal regions *pa*; the arms of the frontal suture *fs* are widespread as in Fig. 2; there are no ocelli present, and many other features of the Dermapteran head-capsule clearly indicate that the head of *Grylloblatta* (Fig. 2) is Dermapteroid. The evidence of the head-capsule would thus indicate that among the lower Orthopteroids, the Dermaptera are the next of kin of the Grylloblattids, and the correctness of this view is borne out by the evidence of the thoracic sclerites and many other features.

The head capsul of the Phasmids such as *Timema* approcahes the Grylloblattid and Dermapteran type in most of the features

mentioned above, but the Phasmid type although clearly derived from the same source, apparently follows a path of specialization leading to extreme development along the line of massing the parts in the anterior region of the head, thus leading away from the common ancestral type from which the Grylloblattids and Dermaptera arose. The relation of the eyes and antennæ, etc., to the bases of the mandibles is likewise very similar in the Embiids and the forms mentioned above; but the Embiid type is evidently leading away from these Orthopteroids—although it, also, was evidently derived from Protorthopteroid prototypes.

The study of the head capsule thus bears out the evidence from other sources indicating that the Grylloblattids, Dermaptera and Phasmids are closely related, and sprang from a common Protorthopteroid ancestry; and these in turn were evidently derived from Protoblattoid ancestors. The Blattids, Mantids and Isoptera are the nearest living representatives of these Protoblattoid ancestors, and of these the Isoptera are in some respects the nearest living representatives of the Protoblattoid forms giving rise to the Protorthopteroid ancestors of the Grylloblattids, Dermaptera and Phasmids, so that we would expect to find among the Isoptera some types of head capsule suggesting the prototypes of the Dermapteroid head characteristic of the Grylloblattids, Dermaptera and Phasmids, and such is indeed the case. The resemblance, however, is more striking when one compares a Grylloid head, rather than the Grylloblattoid type, with a typical Isopterous head, since the head-contour, relation of the eyes, antennæ, bases of the mandibles, etc., are more nearly alike in the Grylloids and Isoptera, than is the case in the Grylloblattoids and most Isoptera. The thoracic sclerites of the Grylloblattoids and other Orthopteroids are very like those of the Isoptera, and the evidence from this source would lend support to that of the head capsule in indicating that the Isoptera are very like the Protoblattoid ancestors of the Orthopteroid group of insects.

While the head of such Blattids as *Cryptocercus* is rather suggestive of the precursor of the Orthopteran type of head, and the head capsule of such primitive Mantids as *Eremiaphila* exhibit certain features likewise suggestive of the starting point

of the evolution of the Orthopteran type, the head of a typical Blattid or Mantid does not resemble that of a typical Orthopteron as much as the head of a typical termite does, and the thoracic sclerites of the Blattids and Mantids are not as similar to those of the Orthoptera as the thoracic sclerites of the Isoptera are, so that in general, the Isoptera are nearer to the ancestors of the Orthopteroids than the Blattids and Mantids are, although in the character of their terminal abdominal structures, the Blattids and Mantids approach the Orthopteran type more closely.

In the slenderness of the lacinia and galea, the maxilla of *Grylloblatta* (Fig. 1) resembles that of *Gryllotalpa* and the Dermaptera, but the stipes of *Grylloblatta* is not divided into the

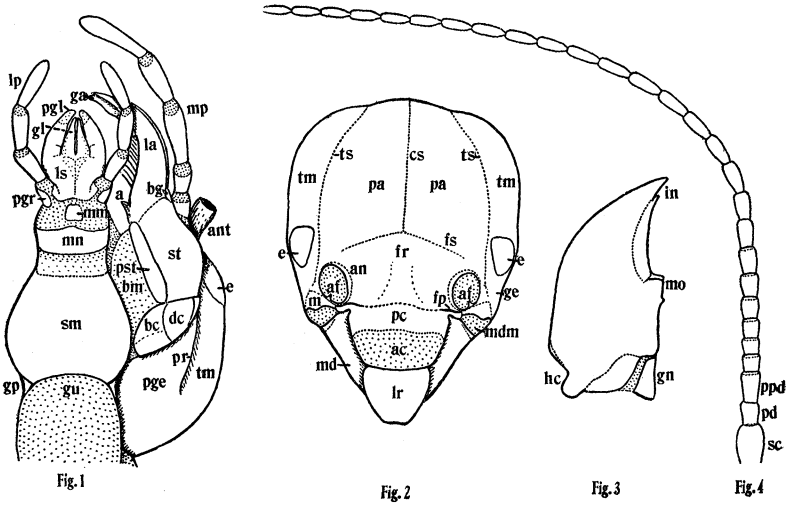

Fig. 1, Ventral (posterior) view of labium, maxilla, and sinistral half of head.
Fig. 2 Frontal view of head capsule.
Fig. 3, Ventral (posterior) view of dextral mandible.
Fig. 4, Antenna.

peculiar subdivisions present in these two Orthopteroids. The maxilla of a typical Isopteron or Blattid would readily serve as the starting point for evolving the types of maxillæ occurring in the Grylloblattids and Dermaptera; and the Isoptera seem to be

somewhat nearer than the Blattids are to the Orthopteroids, in the character of their maxillæ.

The character of the labium of *Grylloblatta* (Fig. 1) clearly shows that this insect is Orthopterous or Orthopteroid, since it is only in the Orthoptera that I have found a separate and distinct, well-chitinized mentum of the type shown in Fig. 1, *mn*. The labium of *Grylloblatta* lacks the transverse gular plate characteristic of all Dermaptera; and the type of labium exhibited by the Orthopterous insects might be derived more readily from Isopteroid or Blattoid precursors.

It is rather surprising that the maxillæ and labium of the Phasmids which I have examined are not as similar to these structures in *Grylloblatta* as the maxillæ and labium of the Embiids are. This, however, is doubtless due to the fact that my material is not as suitable as it might be to indicate the real relationships involved, and there are certain features of the submental region of the Phasmid labium, for example, that indicate a much closer relationship to the Orthoptera should be expected in the Phasmids than in the Embiids.

The mandible of *Grylloblatta* (Fig. 3) is very like that of such Orthoptera as *Gryllotalpa*, and resembles the type occurring in the Embiids quite closely. The mandible of *Grylloblatta* is not as much like that of the Phasmids and Dermaptera as one would expect, but it resembles the Dermapteran type as much as any. The resemblance to the Isopteran or Blattid type is not very marked, so that the evidence of the mandibles it not of great phylogenetic value.

The antenna of *Grylloblatta* (Fig. 4) is remarkably like that of *Embia* not only in the number of the segments composing it, but also in the relative sizes of the individual segments. The antenna of *Grylloblatta* is also very like that of such Phasmids as *Timema* and this type of antenna was apparently inherited from a common Protorthopteroid source. Among the true Orthoptera, the type of antenna found in the Acridids (Locustids) and their allies approaches the Grylloblattid type more closely than is the case with the antennæ of the Tettigonioids and Grylloids, which is rather surprising in view of the fact that *Grylloblatta* is more closely related to the Tettigonioid and Grylloid Orthoptera

than it is to the Acridids and their allies. The Grylloblattid type of antenna approaches that found in certain primitive Dermaptera and Isoptera more closely than it does the Blattid or Mantid type of antenna, and the antennæ of certain Grylloids and Tettigonioids are much more like the antennæ of the Blattids and Mantids than is the case with the antenna of *Grylloblatta*, although in a few Blattids, I have found a suggestion of the Grylloblattid type of antenna.

It is quite possible that there were two tendencies in the Protoblattoid ancestors of the Orthopteroid insects. One tendency was to retain the multiarticulate type of antenna with many annular segments in the basal region of the flagellum while the segments in the distal region of the flagellum tended to become more cylindrical. This tendency, exhibited by most Blattids and Mantids, affected the development of the Grylloid and Tettigonioid types of antennae. The second tendency among the Protoblattoid ancestors of the Orthopteroid insects was toward a reduction in the number of antennal segments, and to increase the proportion of cylindrical segments, while only a few segments in the basal region of the flagellum remain short, or approach the annular type to any degree. This tendency affected the Phasmid, Dermapteran, and Grylloblattid descendants of the Protorthopteroids more than any others.

In the main, the evidence of the head-capsule and its appendages is in harmony with that from other sources which supports the views as to the interrelationships of the Orthopteroid and Isopteroid insects proposed by Crampton, 1924; and according to these views the insects in question were grouped as follows:

Section Orthopteradelphia (Orthopteroid insects, sensu lato)
- Superorder Panisoptera (Isopteroid insects)
  - Orders Protodictyoptera (Protoblattids—fossil)
    - Dictyoptera (Blattids and Mantids)
    - Isoptera
- Superorder Panorthoptera (Orthopteroid insects, sensu stricto)
  - Orders Protorthoptera (Fossil)

Orthoptera (Saltatoria and Grylloblattids)
Dermaptera
Cheleutoptera (Phasmids)
Superorder Panplecoptera (Plecopteroid insects)
Orders Protoplatyptera Hadentomoidea—fossil)
Platyptera (Embiids)
Plecoptera

The Plecopteroid and Orthopteroid insects were descended from Protorthopteroid forebears which arose from the Protoblattoid ancestors of the Isopteroid insects, so that the ancestral types in the common Protorthopteran-Protoblattid stem gave rise to the lines of descent of the Isopteroid, Orthoptero d, and Plecopteroid insects which comprise the Orthopteroid nsects in the broad sense of the term The Palæorthoptera such as *Synarmoge*, serve to connect the common Protorthopteran-Protoblattid stem with the Palæodictyoptera, which are very like the ancestral-types giving rise to the winged insects in general.

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ABBREVIATIONS

a.. .Basal process of lacinia
ac..Anteclypeus
af..Antennifer
an..Antennale (basantenna)
ant.Antenna (basal segment)
bc..Basicardo
bg..Basigalea
bm..Basimaxillary membrane
cs..Coronal suture
dc..Disticardo
e...Compound eye
fr...Frons
fp..Frontal pits (frontocavæ)
fs...Frontal suture
ga..Galea
ge..Gena
gl. .Glossa
gn..Gnathite
gp..gular pit
gu..Gular region of membrane
hc..Hypocondyle (gnathocondyle
in..Incisors
la. .Lacinia
lp..Labial palpus
lr...Labrum
ls...Labiostipes
m...Mandibulare (basimandibula
md..Mandible
mdm.Mandibular membrane
mm.Medimentum
mn..Mentum
mo..Mola
mp..Maxillary palpus
pa..Parietals
pc..Postclypeus (epistoma)
pd. .Pedicel
pge.Postgena
pgl..Paraglossa
pgr..Palpiger
ppd.Postpedicel
pr...Postgenal ridge
pst..Parastipes
sc...Scape
sm..Submentum
st.....Stipes
tm..Tempora
ts...Temporal suture