New Contributions to the Systematic Classification of Hemiptera-Heteroptera.

By

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Introduction.

In the course of the morphological and biological studies of the Swedish families of the *Hemiptera-Heteroptera,* on which I have been engaged during the last few years, it has repeatedly struck me that an examination of the anatomical structure of the internal organs was a useful guide in determining the relationship between the families examined.

An examination of the external chitinous skeleton has often yielded valuable information and has thrown a good deal of light on the classification of the *Hemiptera.* But a study of the external structure alone will not in all cases suffice to cope with the numerous difficulties encountered. It will then be necessary to have recourse to an examination of the internal anatomy, and, in some cases, also to embryological and biological investigations.

In this paper, after a brief resumé of some of the principal anatomical and biological studies of these insects, I shall set forth some views which I may venture to call new. I desire to point out, however, that these views, which are based on studies along the various lines of approach indicated above, go to confirm the correctness, in the main, of the classification suggested long ago, with intuitive insight, by DUFOUR (1833, 1834).

I must admit that I have not made a thorough study of the important group *Hydrocorisae.* But thanks to R. HEYMON'S excellent investigations, which will be summarized in this paper, this group is already rather well known.

I should add that this little study is based on two papers previously published by me (1926 and 1928), to which the reader is referred for more detailed studies of the problems discussed here.

Historical review of classifications of the Hemiptera, especially those of recent years.

»Le désir de simplifier, par les réductions, la classification des animaux, entraîne souvent à violer les rapports naturels, en cumulant dans une même enceinte des genres fort étonnés de leur rencontre. M. Latrielle me paraît avoir encouru ce reproche dans la formation de la famille des Géocorises, telle qu'il l'a établie dans son dernier ouvrage (1); il était blen plus rapproché des vrais principes d'une généalogie naturelle des Hémiptères dans son *Genera,* publié plus de vingt ans auparavant (2). Sans m'engager ici dans des discussions qui seraient hors de mon sujet, je pense que les familles établies dans les *Hétéroptères* par mon respectable et savant ami doivent être converties en tribus, lesquelles se subdiviseraient en groupes naturels qui fonderaient à juste titre des familles. Je n'entreprendrai point cette réforme, qui, je le répète, n'est pas de ma competance actuelle, et je suivrai le cadre déjà adopté. Toutefois je crois qu'une troisième famille (ou tribu, suivant moi) doit être comprise dans la section des Hétéroptères, et trouver sa place naturelle entre celles qui existent déjà. Cette nouvelle famille, dont j'indiquerai plus bas les caractères, s'apellera, en adoptant pour la dénomination les mêmes bases que pour les autres, les Amphibicorises.»

With these words DUFOUR (1833) opposes LATREILLE'S attempt to divide the *Hemiptera-Heteroptera* into merely two groups, »Géocorises» and »Hydrocorises», a classification which has survived down to the present day.[1] He points out that the *Hydrometridae, Veliidae* and *Gerridae* (*Mesoveliidae* were not then known) constitute a separate group, »les Amphibicorises», quite as distinct as »Géocorises» and »Hydrocorises». In the last-mentioned group, however, he includes also the Corixids.

Since DUFOUR'S days a number of more or less complicated systems for the classification of *Hemiptera* have been set up.[2] But, setting aside the works of DUFOUR and in more recent times those of VERHOEFF (1882) and HEM SINGH-PRUTHI (1925), all the studies of these insects hitherto published deal solely, or almost solely, with the outer chitinous structure. The external chitinous structure is indeed of considerable importance, but it cannot be taken as a basis for the final determination of a system of classification.

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[1] It has been adopted, for example, by SAHLBERG (1920).

[2] An excellent review of these classifications is given by REUTER in »Neue Beiträge zur Phylogenie und Systematik der Miriden» (1910) and in »Bemerkungen über mein neues Heteroptersystem» (1912), to which the reader is referred.

Even the eggs have been taken as a basis for classification. REUTER, for example, comes to the conclusion that, in view of the similar shape of the eggs, the *Nabidae* and *Mesoveliidae* must be closely related to one another. This is certainly wrong. As I have shown in my previous papers, the shape of the egg is closely connected with the method of egg-laying and the structure of the ovipositor. Moreover the shape varies considerably even within the same group.

The only important contribution to the classification of the *Hemiptera* since the days of DUFOUR was that made by BÖRNER (1904), viz. the separation of the Corixids from the »Hydrocorises» into a distinct group: *Sandaliorrhyncha.*

Since the publication of REUTER'S treatises, but few authors have attempted the classification of the *Hemiptera-Heteroptera* on any large scale. OSHANIN, for example, in his »Katalog der paläarktischen Hemiptera» adopts REUTER'S system. He divides the *Hemiptera-Heteroptera* into the following seven series:

Series I. *Sandaliorrhyncha.*
» II. *Hydrobiotica.*
» III. *Trichotelocera.*
» IV. *Anonychia.*
» V. *Onychiophora.*
» VI. *Phloeobiotica.*
» VII. *Polyneuria.*

In series II he groups together such heterogeneous families as »Hydrocorises», on the one hand, and the *Saldidae, Gerridae* and *Veliidae* families, on the other hand. Series IV includes the *Capsidae, Reduviidae, Nabidae, Hebridae, Mesoveliidae, Piesmidae* and *Tingididae;* series V the families *Pyrrhocoridae, Lygaeidae* and *Neididae;* series VI the *Corizidae* and *Pentatomidae.*

TULLGREN (1918) points out that certain families have trichobothriae on the ventral side. These families he terms *Heteroptera trichophora;* under this designation he comprises the *Pentatomidae, Scutelleridae, Thyreocoridae, Coreidae, Pyrrhocoridae, Lygaeidae, Berytidae* and *Piesmidae.*

BUTLER (1923), following LATREILLE, groups the *Hemiptera-Heteroptera* into two main »*sections*», *Gymnocerata* and *Cryptocerata.* Among the *Gymnocerata* he includes »Hydrocorises», using that appellation in the sense attached to it by DUFOUR, that is so as to comprise the *Corixidae.* To the *Cryptocerata* he assigns the remaining families of the *Heteroptera.* JACZEWSKI (1922) points out the resemblance of the abdominal segment in the *Mesoveliidae* and *Gerridae.*

HEM SINGH-PRUTHI (1925), after thorough studies of the male genitalia of the *Hemiptera-Heteroptera,* classifies the *Heteroptera* on this basis into two groups, according as the genitalia are of the Pentatomid type or the Reduviid type. He says with regard to these two groups: »the first three: *Polyneuria, Phloebiotica* and *Onychiophora,* including the super-families *Pentatomoidae, Coreoidae, Aradoidae, Lygaeoidae,* have one type of genitalia, and the next four: *Anonychia, Trichotelocera, Hydrobiotica* (with the exception of the family *Acanthiidae*) and *Sandaliorrhyncha,* including the rest of the families, another type».[1] He points out, however, that these two groups »do not correspond to the divisions »*Gymnocerata*» and »*Cryptocerata*» of FIEBER.

Importance of the structure of the mouth parts for the classification of Hemiptera-Heteroptera.

In the course of my own studies of the *Hemiptera-Heteroptera,* I have, as already indicated, been forced to the conclusion that for purposes of classification, the structure of the mouth parts is far and away more important than that of any other organ.

When I compared representatives of the groups *Geocorisae* and *Sandaliorrhyncha,* on the one hand, and DUFOUR'S group *Amphibicorisae* (inclusive of the *Mesoveliidae* family), on the other, I found that the structure of the mouth parts afforded a good basis for the retention of these divisions. I discovered in my investigations of *Geocorisae* that the *Saldidae, Nabidae, Lygaeidae* and *Corizidae* families, and moreover (as shown by subsequent researches) also the *Pentatomidae, Aradidae, Neididae, Cimicidae* and *Capsidae* families, all have in common a characteristic type of lever mechanism for the mandible (Fig. 1). The mandible (*m*), like the maxilla, assumes the form of a seta and is projected forwards by a muscle (*pman*) which is not attached directly to the seta but to a lever (*h*). This lever has the form of a triangular plate with a forwardly directed corner attached to the inner side of the head-capsule, a backwardly directed corner to which the muscle is fixed, and an inwardly directed corner which is attached to the mandibular seta by a tendon. The maxillary seta (*max*) is provided with a guide-rod.

In the *Sandaliorrhyncha* group the lever of the mandible has likewise the form of a triangular plate; that plate, however, is much more elongated at the rear, besides which it is folded an-

[1] The terms are according to OSHANIN'S »Katalog der paläarktischen Hemipteren».

teriorly. Moreover the lever at its inwardly directed corner is attached directly to the mandibular seta (Fig. 2). In this group the maxilla is devoid of a guide-rod.

The *Amphibicorisae* group, on the other hand, have a quadrangular lever plate, provided with double walls (Fig. 3, 4). The front part of the plate is attached to the head. The muscles are fixed to the upper and posterior part of the plate, and the mandibular seta is merely attached to, but not firmly united with the lever. The maxilla is devoid of a guide-rod.

The other organs show such a great variety of structure that to enter into particulars would be beyond the scope of this paper. I shall therefore refer the reader to my previously published studies. Here I merely desire to point out that the structure of these organs is of far less value for wider classification. The different varieties should be regarded as distinctive characters of species or families. It should be noted, however, that the *Saldidae* have the most primitive structure of all the families investigated. The female still retains the parts of the eighth segment to which the anterior shanks of the ovipositor are attached, and the chitinous plates have not been merged into one another to any extent (c. f. EKBLOM 1926).

Before proceeding further, I must touch on the fourth group, the *Hydrocorisae,* which includes the Swedish families, *Nepidae, Notonectidae* and *Naucoridae.* Good studies of these families have been published by GEISE (1883) and HEYMONS (1899). WEDDE (1885) gives a cross section through the setae of *Notonecta.*

Let us glance at the motor mechanism of the mandibles and maxillae in this group. GEISE points out the existence of a lever in *Notonecta*, but he believes that it is mounted on the maxilla, and is otherwise hazy about its structure. HEYMONS, on the other hand, gives a good description of the lever. He says (p. 369): »Der mandibulare Protractor heftet sich vielmehr an eine grosse gabelförmige Chitinsehne an, von welcher ein Ast sich mit der Mandibulartasche verbindet». This statement is illustrated by a figure (Fig. 5).

A similar lever mechanism was observed by HEYMONS likewise in *Nepa* and *Naucoris,* and by myself also in *Aphelocheirus.* This lever mechanism thus appears to be common to all the *Hydrocorisae.* I myself have found by dissection that the mandibular lever in *Nepa* is thicker and more triangular than in *Notonecta* (Fig. 6). The protractor is attached not merely to the posterior corner, but also on the outer side of the lever. It thus somewhat resembles, in shape and structure, the type of lever found in the *Geocorisae,* especially in *Salda* and *Nabis.* In contradistinction, however, from the said group, it is attached, as in other *Hydro-*

corisae, to the mandible (more strictly, the surrounding membrane) without a tendon. HEYMONS has observed the existence of a guide-rod in *Nepa* and *Naucoris,* and thinks it may possibly occur also in *Notonecta.* He says: »Ich bemerke der Vollständigkeit wegen, dass ich an der Maxillartasche von *Naucoris* einen Chitinbalken angetroffen habe, der von der hinteren seitlichen Kopfwandung ausgeht und den Grund der Tasche umgreift. Dieser Chitinbalken dient indessen keineswegs zur Anheftung des Protractor, sondern hat offenbar nur den Zweck, eine laterale Verschiebung der Kiefertasche innerhalb des Kopfes unmöglich zu machen. Ob eine solche Sicherung auch bei *Notonecta* vorkommt, vermag ich nicht bestimmt zu sagen, bei *Nepa* ist jedenfalls eine ähnliche Einrichtung vorhanden.» In dissecting *Notonecta* I did not discover any guide-rod, whence I am convinced that it is missing in this species. Another point of resemblance with *Salda,* but also with the *Amphibicorisae,* is that the head at the rear is produced into two chitinous rods (Fig. 7).

The internal structure of the setae (figs. 7—10) in the *Hydrocorisae* has been well described by GEISE. He shows, with respect to *Notonecta,* that the labrum, in cross section through the base, is merely grooved by its lateral edges to the labium (Fig. 8). The mouth parts of *Notonecta* thus present a striking resemblance to those of *Salda* and *Nabis* (Fig. 9). He points out that in *Nepa,* on the other hand, the labrum is enclosed in the labium and entirely encircling the setae (Fig. 10). In other respects he finds a close correspondence between the two genera *Notonecta* and *Nepa.*

The setae in *Nepa* show, as I have found, in cross section (fig. 11) a very near resemblance to those of *Salda* (Fig. 12) and also of *Nabis,* the sole difference being that at the base both maxillae participate almost equally in the development of the salivary tube. Further towards the extremity the salivary tube, as in *Nepa,* is formed chiefly by the left maxilla (Figs. 13, 14).

A characteristic feature in *Nepa, Naucoris* and *Notonecta* is the development of the lamen maxillaris (Fig. 5); in the first-mentioned genus it is covered from outside by the processus maxillaris, in the two latter, according to HEYMONS, by a »Hautduplicatur».

The female genitalia of *Naucoris* are illustrated by HEYMONS (Fig. 15). We see from his illustration that the ovipositor is well developed and provided with barbs, thus being of an original type.

Classification.

The investigations reported above show that the *Hemiptera-Heteroptera* can be divided into four distinct main groups, viz.:

I. *Geocorisae* characterized by a triangular mandibular lever, attached by a tendon to the membrane surrounding the mandible. They have a maxillary guide-rod.

II. *Hydrocorisae* characterized by a three-branched mandibular lever whose inwardly directed branch is attached direct to the mandible. Some of the families have a maxillary guide-rod.

III. *Sandaliorrhyncha* characterized by a triangular mandibular lever, which is united with the mandible, and is folded anteriorly and provided with double attachments to the head-capsule. The maxillary guide-rod is missing.

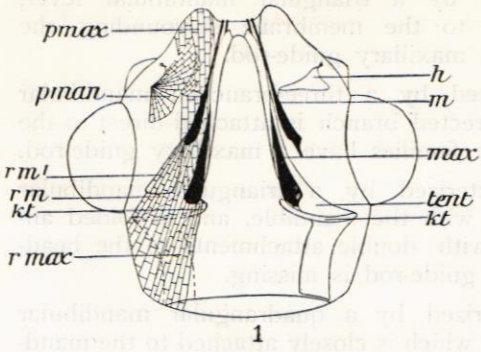
IV. *Amphibicorisae* characterized by a quadrangular mandibular lever with double walls, which is closely attached to the mandible, but not firmly united with it. The maxillary guide-rod is missing.

Do the investigations reported above enable us to draw any conclusions in regard to the relationship of these groups to one another? Which of the groups is to be regarded as the most primitive?

As I have previously indicated, I consider that *Salda* most closely approaches the ancestors of the *Heteroptera* in structure and habits, though also the *Hydrocorisae* have many primitive characters. Those ancestors appear to have lived in damp places, a mode of life which has survived in *Salda's* primitive method of egg-laying (among wet algae, moist sand etc.). Moreover their habit of feeding on creatures, such as fly larvae, which tenant damp soil and on animals found in a dead or half-dead condition, is, I believe, a primeval mode of existence. Attention has previously been drawn to the primitive features in their body structure. From these *Salda*-like ancestors, which I may term *Protosaldidae*, the *Geocorisae* group (inclusive of the now surviving *Saldidae*) derived its origin and became land animals. Among this group the *Nabidae* still closely resemble the *Saldidae* in structure and habits. It is noteworthy that *Nabis ferus* still lays its eggs in the stems of plants (*Scirpus*) found by the shores of lakes, which is doubtless a primeval characteristic. Otherwise, like many other *Nabis* species, it lives among dry fields, meadows, etc.

Another group, namely the *Hydrocorisae*, has adapted itself to life under water. This mode of existence has been completely adopted by *Aphelocheirus*, whilst the other branches, especially the *Nepidae* family, still largely maintain contact with the atmosphere.

The three-branched lever in *Hydrocorisae* is, of course, merely a modification of the triangular lever. In *Salda* and *Nabis* the posterior



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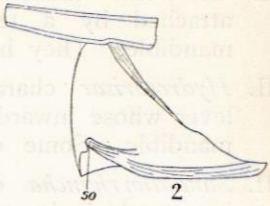

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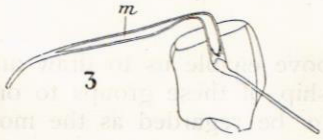

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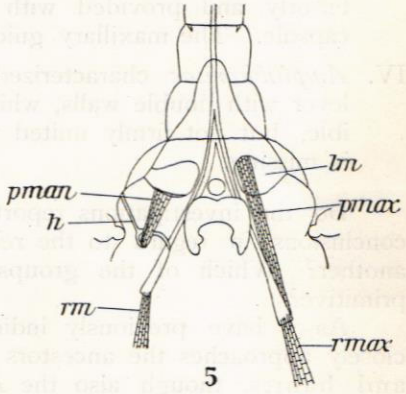

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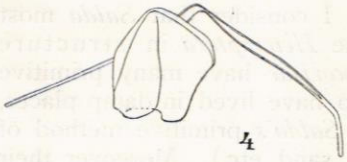

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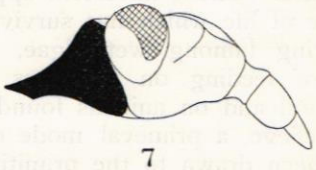

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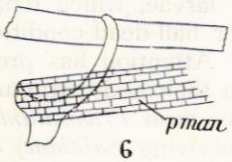

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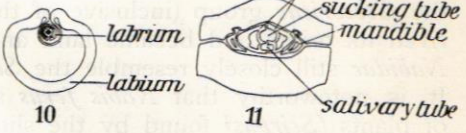

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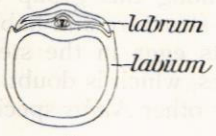

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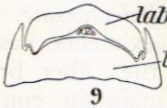

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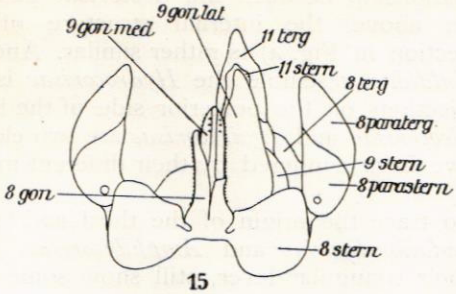

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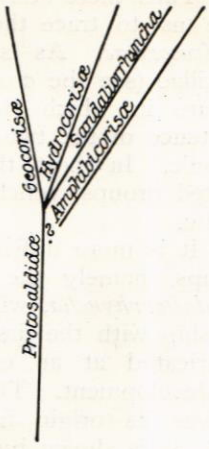

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Fig. 1. The inner mechanism of the mouth parts of *Aphanus pini*, *m* mandible seta; *max* maxillary seta; *h* lever for the mandible; *kt* guide rod for the maxilla; *pman* protractor mandibularis; *pmax* protractor maxillaris; *rm*, rm_1 retractor mand., *rmax* retractor max., *tent* tentorium. On the right side are the muscles removed. × 50.

Fig. 2. The right lever with a part of the mandible from *Corixa sahlbergi*. *So.* the anteriorally placed fold. Interior view. × 105.

Figs. 3, 4. The right lever with a part of the mandible of *Hydrometra stagnorum*, interior and exterior view. × 159.

Fig. 5. The inner mechanism of the mouth parts of *Notonecta*. *lm* lamen maxillaris (after HEYMONS).

Fig. 6. The right mandible with a part of the mandible from *Nepa cinerea*, exterior view. × 200.

Fig. 7. Head of *Nepa cinerea*, lateral view. × 35.

Fig. 8. Cross section through the base of rostrum of *Notonecta*. *l* labrum, *lab* labium (after GEISE).

Fig. 9. Cross section through the base of *Salda saltatoria*. × 143.

Fig. 10. Cross section through the base of rostrum of *Nepa cinerea* (after GEISE).

Fig. 11. Cross section near the base of rostrum of *Nepa cinerea* (after GEISE).

Fig. 12. Cross section near the base of rostrum of *Salda saltatoria*. × 1007.

Fig. 13. Cross section near the tip of rostrum of *Nepa cinerea* (after GEISE).

Fig. 14. Cross section near the tip of rostrum of *Salda saltatoria*. × 1007.

Fig. 15. The genital plates of *Notonecta*, *gon med* gonopophysis mediale; *gon lat* gonopophysis laterale; *stern* sternite; *parastern* parasternite; *paraterg* paratergite; *terg* tergite; *8 gon* gonopophysis of the 8th segment (after HEYMONS).

Fig. 16. Phylogeny of the four different groups of *Hemiptera-Heteroptera*.

corner of the lever is slightly elongated, so that it somewhat resembles the lever in the *Hydrocorisae*, especially in *Nepa*. The latter family appears to be rather closely related to the *Protosaldidae*.

Thus there still exist various points of resemblance which enable us to trace the relationship between the *Geocorisae* and the *Hydrocorisae*. As shown above, the internal structure of the maxillae (see the cross section in Fig. 4) is rather similar. Another feature in which the *Saldidae* resemble the *Hydrocorisae* is the existence of the two projections on the posterior side of the head-capsule. In short, the *Geocorisae* and *Hydrocorisae* are two closely related groups, which have been sundered by their different modes of life.

It is more difficult to trace the origin of the third and fourth groups, namely the *Sandaliorrhyncha* and *Amphibicorisae*. The *Sandaliorrhyncha,* with their triangular lever, still show some relationship with the first and second groups, but they seem to have divaricated at an early date and to have followed separate lines of development. The fourth group, the *Amphibicorisae,* evidently derives its origin from some group which separated at an early date, as is shown by their present isolated position. The characters described in Part I (p. 173), viz. the two projections at the rear of the head-capsule and the shape of the copulation hooks, both of which are found also in *Salda,* are indicative of descent from the *Protosaldidae*. We thus obtain the following phylogeny (Fig. 16).

It should be pointed out that somewhat similar views were advanced as far back as 1885 by OSBORN. But, as, in the words of REUTER, these views were based more »auf Bequemlichkeit als auf phylogenetischen Grund», and as the author does not back them up by scientific evidence, they are of no great value. On the basis of quite superficial investigations he suggests that the aquatic forms are not the most primitive, but are derived from littoral forms similar to the *Salda* species. Nevertheless, he supposes, the aquatic forms are not descended direct from the littoral, but with the semi-aquatic forms (= *Amphibicorisae*) as intermediaries. This, however, does not happen to accord with the actual facts. On the other hand, OSBORN is correct in stating that the *Geocorisae* are also descended from the *Saldidae*. His phylogeny, however, shows a somewhat peculiar classification of the *Hemiptera,* which does not require any further comment.

An interesting problem is to explain the development of the submarine forms. Presumably submarine life began with the hatching of the larvae under water, as is indicated by the larvae of the *Mesovelia* (EKBLOM 1928).[1] This problem, however, requires

[1] The larvae are often hatched under the surface of the water out of the eggs laid in the preceeding year in the sunken stalks of *Scirpus lacustris*.

further investigation, and I hope to be able to elucidate it in a subsequent paper.

In conclusion, I may point out that further studies are also necessary in order to clear up the relationships of the different groups and families with one another. It is desirable that this problem should be attacked along two different lines of approach: firstly, thorough anatomical investigations into other families, especially those of tropical origin, and secondly embryological examination of the mouth parts in particular.

Literature.

BÖRNER, C., Zur Systematik der Hexapoden. Zool. Anz. 27, 1904.

BUTLER, E., A biology of the british Hemiptera-Heteroptera. London 1923.

DUFOUR, LÉON, Recherches anatomiques et physiologiques sur les Hemiptères. Mém. présentés à l'Acad. d. Sc. Paris 1833.

——, Résumé des recherches anat. et physiol. sur les Hémiptères. Ann. d. Sc. nat. Zool. 2:e Sér., T. I. Paris 1834.

EKBLOM, T., Morphological and biological studies of the Swedish families of Hemiptera-Heteroptera, Part I and II. Zoolog. Bidrag från Uppsala 1926 and 1928.

GEISE, O., Mundtheile der Rhynchoten. Arch. f. Naturg., XLIX, 1883.

HEYMONS, RICHARD, Die Mundtheile der Rynchota. Entom. Nachr., Jahrg. XXII, Nr. 11, p. 173, vorläuf Mitteil. Berlin 1896.

——, Beiträge zur Morphologie u. Entwicklungsgeschichte der Rhynchoten. Abhandlungen der Kaiserlichen Leopoldinischen-Carolinischen Deutschen Akademie der Naturforscher. Vol. LXXIV. Halle 1899.

JACZEWSKI, T., Mesovelia furcata. Bulletin entomologique de la Pologne 1922.

OSBORN, The Phylogeny of Hemiptera. Proc. Ent. Soc. Wash. 1895.

OSHANIN, B., Katalog der paläarktischen Hemipteren. Berlin 1912.

REUTER, O. M., Neue Beiträge zur Phylogenie und Systematik der Miridien (Capsidae) nebst einleitenden Bemerkungen über die Phylogenie der Heteropteren-Familien. Acta Soc. Scient. Fennicae. Tom. XXXVII. 1910.

——, Bemerkungen über mein neues Heteropterensystem. Översikt av Finska Vet. Soc. Förh. I—IV 1912, 62 sid.

SAHLBERG, J., Enumeratio Hemipterorum-Heteropterorum faunae Fennicae. Helsingfors 1920.

SINGH-PRUTHI, HEM, The morphology of the male Genitalia in Rhynchota. Trans. Ent. Soc. 1925.

TULLGREN, A., Zur Morphologie und Systematik der Hemipteren I. Entomologisk Tidskrift. Årg. 39. Stockholm 1918.

VERHOEFF, C., Vergleichende Untersuchungen über die Abdominalsegmente der weiblichen Hemiptera-Heteroptera und -Homoptera, ein Beitrag zur Kenntniss der Phylogenie derselben. Verhandl. Naturwiss. Ver. preuss. Rheinlande, Westfalen Reg.-Bez. Osnabrück. Jahrg. 50. Bonn 1893.

WEDDE, HERMANN, Beiträge zur Kenntniss der Rynchotenrüssels. Archiv f. Naturg. 51. Jahrg. Vol. I. Berlin 1885.