New contributions to the phylogeny and systematics of the Miridae with introductory remarks on the phylogeny of the families of Heteroptera.

By O. M. Reuter.

[Pp.23-79 only translated].

(Acta Soc. Sci. Fennicae t.XXXVII,n.3(1910):1-172)

II. The parts of the body of Heteroptera in phylogenetic and systematic respects.

Before going over to a thorough discussion of the phylogeny of Heteroptera families and to a presentation of my views which deviate from those of previous authors, I find it necessary first of all to examine the characters which the different body parts of Heteroptera have offered the authors as a basis for their systematic presentations with reference to their importance in respect to this matter as well as to point out some such characters which have not yet been used for systematics.

First, as for the head, its structure is so extraordinarily varying that the differences in this — if we disregard the remarkable structure of the Pantatomoideae— at most can serve as characters for separation of individual families. Perhaps it deserves to be noted here that one fact, namely the position of the oral opening, possibly is not without phylogenetic significance in certain cases. As is well-known, Zetterstedt had already (1828) divided the Hemiptera into two great phalanges, Frontirostria and Gulaerostria of which the latter (= Homoptera) is characterized by "rostrum gular or pectoral and rising from the lower part of the head (sub-gula)", the former (=Heteroptera) by "rostrum frontal and rising before the apex of the head". Blanchard in 1852 had also used the position of the oral opening as the basis for his division of the Heteroptera into Prostomophora and Hipostomophora, but differed from Zetterstedt in that he referred to the latter not only the Homoptera but also a few Heteroptera (the Ochteridae, Nerthridae, Notonectidae, and Corixidae). Such an artificial division will certainly find no supporters. Schioedte had emphasized the fact (Some new principal propositions on the morphology and systematics of Rhynchota, 1869;242) that from the Reduviidae, whose rostrum proved to be a direct prolongation of the head, to the Cicadaria, in which it lies close to the prosternum, a whole series of gradual transitions is to be found by way of the water bugs and a few land bugs, and that the position of the rostrum depends entirely on whether the front is more or less recurved ventrad. As the real basic difference between Heteroptera and Homoptera, on the other hand, he mentioned the circumstance that in the former the genae are free from the front coxae, in the latter they are hollowed out for reception of these. These statements of Schioedte's are certainly correct. However it still is not impossible that just the type of head with ventral directed front, reminiscent of the type of head in Homoptera, was characteristic of the original Heteroptera. The Schizopteridae in many respects, doubtless represent very primitive forms and the head with its front bent in ventrad is pressed so tightly not against the front coxae but against the acetabulum of the front coxae that the cheeks have become somewhat hollowed out thereby. This construction of the head is what obtained the name of Cicadina Fieb. for a species of the genus Schizoptera Fieb. Now since it is known that at least a few Schisopterids (Glyptocombus Heidem.) jump just like the Cicadina, the similarity thereto becomes still more striking. The structure of the head of the Ochteridae which are also, judging from many circumstances, very certainly Heteroptera that stand very low and which were referred by Blanchard to the Hipostomorpha, seems to me to be Less reminiscent of the Cicadina type than that of the Schizopteridae. But one genus which probably is very close to the Ochteridae and was even referred to this family by Kirkaldy (List of the pagiopodous Hemiptera 1906;149), namely the genus Peloridium Bredd., behaves differently. Breddin wrote about this; "The formation of the head is most striking in this odd animal. The horizontal plane which forms the under side of the head is continued caudad in a nearly level triangular plate which rests solidly on the prosternum and has become fused with it. The beak is attached at the apex of this plate, that is, at the base of the gula, the same as in Homoptera, say, of the family of fulgorids. In view of the significance which the position of the mouth opening has for classification of the higher Hemiptera, an attempt might have been made to refer the species to the Homoptera; on the other hand the animal still shows such close relationwhip with the Heteroptera in most other essental characters (arcuation of the venter, form of the legs, segmentation of the tarsi, form and seg-insertion of the antennae) that there is no doubt as to the fact of its belonging to this group. Therefore in the striking development of the head in Peloridium we still have to see only one modification of the type of Heteroptera head, in which we must imagine the anterior part of the head bearing the oral opening as recurved and turned down on the pectus [i.e., thorax or prosternum], so that cheeks and clypeus come to lie on the same plane". Now it must be noted here that it is not at all settled that this head is a "modification" of the Heteroptera head. It is just as possible that here as in Schizopteridae we have a primitive type from which the Ochteridae head and other types of heads of related Heteroptera have gradually come. It might be mentioned that the clypeus is turned caudad not only in Ochteridae but also in Acanthiadae. Nor is it excluded that the peculiar development of the Peloridium head was acquired later, for even among Miridae we now know a genus, the peculiar Hyporrhinocoris Reut., the anterior part of whose head bearing the oral opening is bent completely under and turned backwards, a modification which is doubtlessof secondary kind. It is indeed very hard to say what is the actual condition of the head of Corixidae which is "recurved backwards in the same way and turned down on the pectus", these also having been referred to the Hipostomophora in addition to the Notonectidae by Blanchard. There may be a primitive phenomenon here, and Börner ("Zur Syxtematics der Hexapoden" Zool.Anzeig.1904:511 et seq.) is right in separating these families out as a separate Suborder of the Heteroptera. But on the other hand, the Corixidae are so highly specialized in so many respects that even this development of the head can very easily be a modification that showed up later.

Compound eyes occur in all Heteroptera, with the exception of the parasitic family Polyctenidae which has probably been incorrectly placed in this Order. It is hardly necessary to say that the disappearance thereof, which is dependent on the parasitic way of life of these insects, is not a primitive but rather is a later-appearing character.

Like the occurrence of compound eyes, the appearance of ocelli is also a character specific to the Heteroptera type from the beginning. But these may be absent far more frequently than the compound eyes. When this is the case, here there is certainly a phenomenon which indicates a specialization of the original Heteroptera type that showed up later. In some cases, the disappearance of the ocelli is connected with the brachypterism of the spp. concerned. Hence in several spp., the ocelli of the brachypterous form are distinctly smaller than the ocelli of the macropterous form which is certainly to be expected also since the ocelli are adapted to far-sightedness and are highly developed especially in air-inhabiting insects. One subgenus of the nabid genus Reduviolus is known — Nesotyphlias (Kirk.) — whose spp. do without ocelli and have only a reduced membrane. As is known, in the Microphysidae the ♂♂ are macropterous and provided with large ocelli while the ♀♀ have only very short elytra and, with the exception of Nabidomorpha Popp., hardly a trace of ocelli. In other cases, the disappearance of ocelli, as in the Cimicidae, is to be considered together with the high-grade brachypterism present in them, as a definite result of parasitic adaptation. Furthermore the ocelli in all bugs living in water have disappeared and this has been stated as a character for the Subsection Aquatila Fieb. of the Cryptocerata. That this absence of the ocelli even in the last-mentioned Hemiptera is an adaptive character and that great phylogenetic importance is to be ascribed to it only when acquired early, is evident from the fact that the unique family Aepophilidae of the Gymnocerata, whose sole representative lives under water, likewise does without ocelli. It is more difficult to understand the absence of ocelli in some

Urolabididae, in 3 very large families - Pyrrhocoridae, Aradidae, and Miridae, as well as in most Tingididae (except the subfamily Piesmina), than the above named. But it is self-evident that the disappearance of ocelli in the said Urolabididae can be conceived of only as a character that showed up later, since not only the majority of Urolabididae but also the rest of the Pentatomoidea are typically provided with ocelli. I will show in detail, in Chapter VI that the ancestors of Miridae were also provided with ocelli. It is probable that the members of this and of the other aforesaid families, as well as perhaps the above mentioned Urolabididae fly principally only in the night and then have no use for ocelli. It is well-known that many Miridae can be taken at night with lights. The disappearance of the ocelli, as already stated, is likewise an adaptive character which can be used at most for the characterization of separate families.

In my opinion, the antennae of primitive Heteroptera ~~have been~~ were 4-segmented. This number still occurs in most Heteroptera families ~~still~~ today. Even if the antennae of the adults have several segments, only 4 segments occur in the larvae. Kirkaldy also did not "entgangen" [?misprint for "entgegen" which = encounter instead of avoid or escape] this circumstance since he designated the Pentatomidae which were provided with typically 5-segmented antennae as the most primitive type of Heteroptera,* although the same was dismissed by him as "a matter of little consequence". When the number of antennal segments in the adults is more than 4, this is certainly a specialization that showed up later which either arose from the fact that the last antennal segments have been constricted off into several ~~from the fact that~~ as in the case of some Reduviidae and in the Nabidae subfamily Pachynomina; or even from the fact that, as in several Nabinae and in the Hebridae, a short supplemental segment has been shoved in at the base of the 2nd antennal segment. Very rarely there are only 3 antennal segments, as in the Nepidae, some Corixidae (Micronecta), and in the peculiar family Peloridiidae. But the first two families are highly specialized in many respects and microscopic examination of the last antennal segment of the Peloridiidae shows us a wart-like protuberance on the apex of the 3rd antennal segment which is certainly to be interpreted as the last remnants of the 4th antennal segment which has been fused with the 3rd. [*. Canad.Ent.1908:358].

The length and position of the antennae, as is well-known, has played a great role in systematics of Heteroptera and has even served as the chief basis for dividing these insects into two great Sections (Geocorisae and Hydrocorisae of Latreille or Gymnocerata and Cryptocerata of Fieber). In the former they are free and projecting, always longer than the head; in the 2nd, on the contrary, they are at most as long as the head and for the most part concealed. In fact, with respect to the above, there are 3 basic types of Hemiptera antennae: freely projecting antennae longer than the head; freely projecting very short antennae; and short, more or less concealed antennae. A very original [or primitive] form of the first type is the antennae of Dipsocoroidea whose first 2 segments are thickened and very short, but the last two are long and shaped like very slender setae. These antennae are not a little reminiscent of those of the Cicadaria. The middle type is peculiar to the genus Ochterus (Pelogonus) which has been referred to the first Section by some authors, to the second Section by others. The value of these different types to systematics has, however, not been recognized by all authors. As early as in 1869, Schioedte pointed out that the above difference in development of the antennae is a character which has been brought about by different conditions of life. Also as the names given by Latreille to the two sections indicate, the free antennae, whether long or short, characterize the land-inhabitants ** among Heteroptera; while the water bugs have short, concealed antennae. This latter type is doubtless to be looked upon as an adaptation to life in the water that was acquired later and it might not be at all excluded that it represents a heterophyletic homomorphism unless other conditions were at hand which made it probable that at least most of the so-called Cryptocerata were homophyletic. I will come back to this question hereafter (Chapter III). As for the form of the antennal segments in the so-called Gymnocerata, as Dumeril (1806) has already noted, this is not without significance to systematics. Doubtless the filiform or apically setiform antennae mean an older stage of development. Such [antennae] belong to the superfamilies Dipsocoroideae, Achanthioideae, Cimicoideae, Gerroideae, and Pentatomoideae (see Chap. IV). The last two antennal segments are fusiformly thickened only in a few more specialized forms of Acanthiadae (Chartoscirta Stål), Anthocoridae (Anthocoris), and Miridae (Eustictus Reut., Sahlbergiella Hagl., Ropalisesohatus Reut., Volkelius Dist., Physophoroptera Popp., Ceratocapsus Reut., Glaphyrocoris Reut.); extremely rarely (Macrocephalidae) only the last segment is clavate or cylindrical; but this last family is already highly specialized in many respects. Only the 4th antennal segment is fusiformly thickened in most Coreidae, Pyrrhocoridae, and Myodochidae as well as in the Neididae, Tingididae, and Aradidae a type which certainly points to a later differentiation.

Also the structure of the rostral sheath has been used by authors for systematics of the Heteroptera, in that the Geocorisae have been divided into two great groups, Tessaracondylae and Tricondylae, with reference to the number of rostral segments. But if the structure of antennae has been dependent on ecological circumstances, this is the case with the rostrum — which negotiates ingestion of food for the animal — in still higher degree and a basic division which rests only on such adaptive material must be more or less unnatural. The weakness thereof is already apparent from the fact that authors who have accepted this division, in order not to have to remove related forms too far from one another, have been compelled, for example, to place the Anthocoridae provided with 3-segmented rostrum under the Tessaracondylae, and the Nabidae, which have a 4-segmented rostral sheath, under the Tricondylae. In fact, as I have already pointed out, the structure of the rostrum has been strongly dependent on the manner of feeding of the animal. A long, 4-segmented, slender rostrum belongs especially to the phytophaga (for instance, the Miridae). In the Carnivora the rostrum is generally shorter and more powerful and the 1st segment is frequently greatly abbreviated (Nabidae, Microphysidae, Termatophylidae), until this finally becomes completely invisible (Anthocoridae, Cimicidae, Reduviidae, and Macrocephalidae). But the fact that phytophagous families like the Miridae, especially when, like these, they are not exclusively phytophagous, and carnivorous families often stand close to one another phylogenetically is a a phenomenon which is not at all rare among insects, and as I will try to demonstrate in Chap. III, in my opinion all the above cited families now belong to the same circle of relationships. The nabid genus Scotomedes Stål and the microphysid genus Nabidomorpha Popp. may be cited here as very instructive examples of the development of a 3-segmented rostral sheath from a 4-segmented one; these two genera have only a 3-segmented rostral sheath whereas in all other typical Nabidae and Microphysidae the rostral sheath is provided with another distinct but short basal segment. Therefore it is evident from the above presentation that the rostral sheath of Heteroptera was originally [or primitively]4-segmented and that the trisegmentation of the rostrum of all Gerroideae, Acanthioideae, Dipsocoroideae and Notonectoideae has been acquired only later. As is known, the rostrum of Corixidae is wholly without segments and also shows a remarkable structure in other respects, which can be deduced with difficulty from that of other Hydrocorisae. Therefore Börner set it up (see page 2) as a Suborder of its own, Sandaliorrhyncha.

Also the structure of the pronotum has in the Heteroptera been subjected to the most varied transformations and provides characters useful for erection of families only by way of exception. I would also have passed over it here if an attempt

---

**. The fact that the antennae of Ochteridae are so short is perhaps dependent on the further fact that these insects dig tunnels in moist sand, as larvae and nymphs, in which action long antennae would be a hindrance.

had not been made by one author, Fallen (1814) to use it as an essential principle of classification [or division]. That this could lead to no natural results hardly needs to be emphasized here.

Also the scutellum is generally of little importance to systematics. The size thereof is significant only in the families which we have united (Chap. IV) in the superfamily of the Pentatomoideae, in that it usually reaches at least the middle of the abdomen and the apex of clavus. In addition to the type with a short scutellum which is represented by most of the other families, the former already occurred early and is certainly to be considered as a basic type of the Heteroptera. The scutellum covering the whole abdomen, which is characteristic for the Pentatomid subfamilies Coptosomina, Cyrtocorina, and Scutellerina as well as for the Graphosomaria division of Pentatominae, must certainly be conceived in any case as a character that was acquired later,* The Coptosomina are, for the rest, certainly a highly specialized group, for example in the wing structure. The large scutellum of the likewise strongly specialized Macrocephalidae which are closely related to the Reduviidae, signifies a later stage of development. On the other hand, the disappearance, or concealment, of the scutellum beneath a posterior process of the pronotum is to be considered as secondary.
*insert: by all these groups, independently.

The hemelytra of most Heteroptera, as is well-known, consists of 3 different parts which have been named Clavus Corium, and Membrane. These 3 parts were doubtless present in primitive forms. What Fieber called Embolium is not, like the other parts, separated off but always lies in the same plane with the corium. Properly speaking, it is only the posterior (apicad) marginal field of the corium between costa and subcosta which is delimited by a transverse furrow and here has not been reduced, as is frequently the case. Therefore only the apical transverse furrow is to be considered as having arisen later. The embolium in any case already occurred in this form so primitive a family as the Ochteridae as well as in the families Nerthridae, Naucoridae, Belostomatidae, and Notonectidae. Furthermore in several Nabidae and typically in the Termatophylidae and Anthocoridae, all of which certainly are to be considered as "low-standing" families. A later specialization of the hem-elytra has entered through separation of the Cuneus (Miridae). The varied structure of the hemelytra in the Tingididae, as well as in the Hebridae, Gerridae, and Henicocephalidae is doubtless to be conceived of in all these as a later-acquired character, as Kirkaldy (1908) has already noted with respect to the last two families.

The venation of the membrane seems to me to be of no less systematic importance, in that a dense venation is peculiar to the primitive types and is mostly more or less reduced in the derived forms. Such a dense venation belongs to the Pentatomidae (sensu latissimo) and Coreidae and here consists, as is well-known, of numerous veins mostly free from each other and running along close together. The membrane of the Pyrrhocoridae also has numerous (at least 8) veins which are often joined into cells. A primitive membrane also occurs in the Ochteridae, Velocipedidae, and Nabidae and, in the case of these, has oblong discoidal cells from which more or less numerous veins radiate toward the margins, a type in common which seems to point to an original [or primitive] relationship between these families. Likewise a primitive phenomenon is probably the net-veined membrane of Belostomatidae and Nepidae, in contrast to which the membrane of the Naucoridae, Notonectidae, and Corixidae which does without all veins — although these families are also of ancient origin — is still to be considered as a "higher" modification. The family Anthocoridae, through a whole row of genera and spp., offers us a shining example of how the veins of the membrane gradually disappear from the inside outwards until only the outermost vein remains behind, or even this one too is hardly perceptible.

The wing venation frequently offers very good characters, especially for separation of families and subfamilies. Here too, a reduction of the venation indicates a later development. Unfortunately we still do not have any comparative phylogenetic investigation of the wing venation.

The structure of the meso- and meta-sternum in the Heteroptera offers two different types. Either they consist of a single piece for their whole width, or they are composed of several pieces, as in all Hydrocorisae, the lateral pieces (Pleura) are separated from the sternum by distinct sutures (*), and the pleura can still be divided into a dorsal and a ventral piece by a suture (Ochteridae, Miridae, Isometopidae, Anthororidae and their hearest relatives, as well as the Corixidae so far as concerns the metasternum.) In and for itself a composite sternum in Hemiptera as in insects in general is to be designated as a more primitive character. But here the sutures are not open but they project inwards as raised elevations of the cuticle, as Schioedte (l.c.;251) has already stated, and these ridges have been used by most pagiopods, (**) i.e., the running, jumping, and swimming forms, as starting points for muscles. The sutures have therefore entered into the service of the biology of the animals concerned and this circumstance explains why they have persisted so long in separate families. Therefore the occurrence of a "composite" sternum among the Heteroptera is not always a primitive character but it can also characterize relatively highly specialized families such as Miridae and several Hydrocorisae.

The adult stink-glands which are situated on the metasternum probably developed very early in the Heteroptera. Absence of the orifice is certainly a character that was acquired later. The orificies are mostly very distinct among Miridae and Tingididae, for example. But there are individual genera in which they have completely disappeared and transitions between these two types are not rare. Bugs living in water can of course have no use for stink glands and no trace of orifices is found in them. This is so in all Hydrocorisae and also in the Aepophilidae whose single hitherto known member likewise lives under the water surface. Probably the families living on the water, Mesoveliadae, Gerridae, Veliadae, and Hydrometridae also do without the stink-gland openings for the same reason. Kirkaldy frankly maintained (1908;360 and 1909;XXIII) that the adults of these families had a median orifice on the fused metasternum and first ventral segment. But it is impossible to understand what use such an orifice, which is turned toward the water surface, could have for the animal and Dr. Poppius who examined several spp. of Gerris with respect to this character, has informed me that he could find no trace thereof. He found only a little tubercle or a deep black little roundish spot on the said spot. Life in damp places and on the banks of bodies of water seems to have brought a disappearance of the stink-gland orifices with it. That is, they are also lacking in the Dipsocoridae and the shore bugs, the Ochteridae and Acanthiadae, as well as the Leptopodidae which are related to them and which now to be sure live in dry places for the most part but have not developed orifices again, although the absence of such orifices was once characteristic of the Phylum to which they belong. It is distinctly evident from what was said above, that the absence of adult stink-gland openings is a character of adaptive nature which can be of greater systematic value only when it was acquired early and has been passed on for a long time.

The structure of the legs and especially of the hind coxae has played a role in systematics of Heteroptera that is not small. When Schioedte (l.c.;1869) took a stand against the bi-partition of Heteroptera into Gymnocerata and Cryptocerata and labelled it artificial, he made a new bi-partition of Heteroptera into Trochalopoda and Pagiopoda which he based on the structure of the hind coxae and the adjacent part of the metasternum (see page 13 [of the text]). But with that he forgot that, as I had already brought out in 1908 in my "Remarks on Nabidae" l.c.;89, the difference in structure of the hind coxae has been dependent upon the way of life of the animals no less than the difference in structure of the antennae (in the Gymnocerata and Cryptocerata) and that the former, just as well as the latter, is adaptive in nature. Its decisive significance to systematics could therefore be questioned a priori. Through the investigations which Dr. Poppius undertook at my suggestion, it has now been demonstrated also that even in thesame family occur both trochalopodous

[Foot-notes for the preceding page, paragraph 1]:

(*). It must be mentioned that in several reduviids a ridge delimits the middle part of the metasternum from the sides. But this ridge must not be confused with the above-named concave suture which runs out like a ledge toward the inside.

(**). The three thoracic segments are simple in the Velocipedidae, Acanthiadae, Leptopodidae, and Aepophilidae.

and pagiopodous genera. That is, he found that several genera of the Miridae family Bricocorina (Monalonion, Pachypeltis, Helopeltis, Physophoroptera, Odonie etc.) are trochalopods and that their short rotatory hind coxae, as well as the tiguous part of the metasternum, are formed almost exactly as in the Nabidae, a stance which probably depends on the fact that these spp. walk and do not run In similar manner, the rest of the trochalopodous forms of Heteroptera have cer developed from originally pagiopodous forms as a consequence of changed conditi life. Only one trochalopous family, the Nepidae, is found among Hydrocorisae. the representatives of the remaining families all swim and are therefore pagiop the spp. of the former are adapted to living and creeping on the ground and acc ingly the structure of the coxae and the adjacent part of the sternum [or thorax have changed appropriately. In contrast to Kirkaldy, I am assuming that the hin coxae of the original Heteroptera were the so-called "Coxae cardinatae". This as tion is supported by the fact that the coxae of Homoptera likewise belong to the type. As for the above-mentioned Nepidae in particular it is not possible to co sider them, as did Schioedte, Kirkaldy, etc., as nearest the Reduviidae, Gerridae, for the reason that their meso- and meta-sterna are joined and such a thing certai can no longer be again derived from a simple [structure]. Moreover, in a discussi (see page 17 [of the text]) Schmidt presented the new relationship of the Nepidae w the pagiopodous Belostomatidae in detail. Therefore the genuinely related families were again separated from each other by the classification based on structure of the hind coxae. Thus it is, for example, on the one hand with the Anthocoridae and Miridae, and on the other hand the Nabidae which show such great agreement not only in the structure of the ♀ genital segments but also in the striking structure of the egg chorion.

The structure of the front legs has often been greatly influenced by living conditions. This was especially the case with such families as those whole members are predatory (Nerthridae, Naucoridae, Nepidae, Macrocephalidae) in which appropriate and, not seldom - as in some Macrocephalidae, - very strange alterations both of the femur and of the tibia, have occurred. We find an entirely different and most remarkable transformation of the forelegs and especially of the forefeet — likewise adapted for taking up food — in most of the Corixidae living on small algae. Of course it is not necessary to point out that all such transformations represent a later stage of development. A singular specialization of the original type, likewise of ecological nature, began [or took place] with the hind legs of swimming Hydrocorisae families. Finally, in this connection. we may mention the fossorial legs of Thyreocoridae; this family is certainly to be considered as more highly specialized than most of the remaining Pentatomoidea.

As is known, the tarsi of Heteroptera are 2-segmented in the earlier stages of life (in the larva and the nymph) while for the most part they consist of 3 segments in the adults. Still it might be wrong to consider the families whose members also have only 2-segmented tarsi as adults as more primitive than the others. Such families are the followins: Aradidae, Tingididae, Macrocephalidae, Microphysidae, Hebridae, and Hydrometridae. Furthermore, 2-segmented tarsi occur in some Hydrocorisae and in the Pentatomidae Subfamilies Coptosomina, Cyrtocorina, and Acanthosomina. (Sometimes only the front tarsi are 2-segmented, as for instance, in the reduviid subfamily, Salyavatine.) It cannot be denied that most of all the foregoing families must be considered as very highly specialized for several reasons. In them, even the two-segmentedness of the tarsi is not to be considered as a primitive characters, but it has rather arisen from the fact that the first segment has been greatly reduced, as Handlirsch (1897) expressly pointed with respect to the Macrocephalidae (Phymatidae): "In the reduction of segment number the first segment has also become rudimentary, the apparent first [being] actually the second". Meanwhile this reduction has arisen quite independently in the different families and therefore it is certainly not right to put otherwise far different families together on the basis of such a heterophyletic homomorphism/ inother respects When Fieber (Eur. Hem.:21) was in fact compelled to select characters for his key which permitted him to put related families together in a series, it is certain that the selection of the structure of the tarsi, as a consequence of which he put the families Phymatidae, Aradidae, Tingididae, and Microphysae after each other, was a mistake. The family Polyctenidae is the only one whose tarsi (although only the 4 posterior ones) are 4-segmented. Speiser (1904;378) explains this by the fact that the 2nd segment appears to be separated into 2 parts by a light annulation and refers to the similar annulation which also characterizes the tibiae of these remarkable animals.

The construction of the claws is not without significance for systematics of Heteroptera. In general, the occurrence of pulvillae (Arolia) characterizes only the families which belong to the pentatomid or coreid stems, according to Handlirsch; while the absence of the same is almost characteristic for all the other families. Only the family of the Hebridae is an exception to this; their systematic position has meanwhile been considered as doubtful by Handlirsch, as well as that of the Miridae. As concerns the latter, however, it may be stated that the arolia are still entirely absent in a great many lower genera thereof today, a fact which has not been sufficiently considered hitherto. The structure of the claws, therefore, actually does not prevent us from recognizing the relationship of Miridae with Reduviidae, as Brullé thought (1835;406). The fact that the arolia are always absent in Hydrocorisae is, of course, dependent upon the way of life but is not for that reason to be considered as an adaptation since these animals probably branched off from primitive forms which had not yet developed arolia. For the rest, it seems as if development of the arolia of the claws began first with life on plants. It is always absent in families living on prey, except only the pentatomid subfamily Asopina which probably developed later from the phytophagous pentatomoid Phylum in a predatory direction.

The construction of the abdomen shows manifold modifications in different families of Heteroptera which particularly concern the apical segments. As is known, the first segment is frequently incomplete and fused with the metathorax so that frequently the 2nd segment is described as the first. The structure of the anterior ventral segments has not been much considered by the authors for systematic purposes. Meanwhile, Schioedte (l.c.;249) demonstrated that the manner in which these segments rest on one another is varied in that the apical margin of the preceding segment either covers the basal margin of the following segment like a roof, or only very simply rests upon it, in which case the segments may even be fused in the middle. Perhaps this fact deserves to be emphasized for future systematists. In my opinion, this difference is a desirable contribution to determination of the differences between the Miridae and the Anthocoridae.

As stated above, the apical segments of the abdomen especially, which are in the closest connection with the genital apparatus, have been subjected to numerous modifications. Comparative morphology of these segments would doubtless be of no little importance in genetic and systematic respects. As for the ♀ genital segments, Verhoef (see page 17 [of the text]) has already attempted to do such a thing. Unfortunately the investigations of this author are still very faulty [i.e., full of gaps]. On the other hand, the results which he based on them are very one-sided which must naturally be the case when one wishes to construct a System on the modifications of practically only a single part of the body. Moreover it seems that the ♀ genital segments might present a much more plastic material for modifications than is compatible with their usefulness for the characterization of the higher systematic units. Only the different types of ♀ genital segments which sometimes show up even in the same family, as for instance in Aradidae (Aradus, Aneurus) and Phrrhocoridae (Pyrrhocorina and Largina) may be recalled. It is certainly not to be denied that, for instance, the Nabidae and Reduviidae are closely related in many respect and definitely belong to the same phylogenetic branch; nevertheless the ♀ genital segments of the two families developed very differently in that the former whose spp. sink their eggs into the plant tissues is provided with a saw-case; but the latter,.whose spp. oviposit in the open, do without such a thing entirely. Other examples could be cited which teach us not to lay too great weight, systematically, on construction of the ♀ genital segments. Still it seems to me that some facts deserve to be considered. Such a one is just the occurrence of a saw-case in a few families. Brullé (1835) pointed out that the structure of the ♀ genital segments of Miridae seemed to form a transition to the Homoptera and for this reason referred the said family to the undermost end of the series of families of the Heteroptera in which view the author has joined him (Rev.Crit.Caps.,:63). Whether the occurrence of the saw-case in Miridae can in fact be interpreted as an inheritance from ancestors had in common with the Cicadaria, can still be questioned. But in the meantime it must be considered that even low types of other phylogenetic branches, such as Nabidae and Veolcipedidae, have a similarly developed saw-case. It seems therefore as if this type of ♀ genital segment were the original one at least in some systematic complexes. Perhaps this is also true of the sawcase of Myodochidae, for it is certainly not impossible that such a thing, which was characteristic for the hypothetical common ancestor of the same and the Pyrrhocoridae and has been retained by them, has been lose in these.

Morphology of the ♂ genital segments has been studied still less than that of the ♀ (*), but it could perhaps present interesting points of view even for phylogeny. Here I will only note in passing that the construction of the structures known by the names of Styli genitalés, Forcipes or Hami copulatorii, probably deserve to be considered in systematic and phylogenetic respects. Investigation of these has just convinced me that the Dipsocoridae and Anthocoridae must be considered heterophyletic and that the Aepophilidae belong not to the circle of relationship of the Cimicoidea nor to that of the Gerroidea, but rather to that of the Acanthioidea (concerning these superfamilies, see Chap.IV). The two Styli (Forcipes) are either homomorphous or heteromorphous. The later type occurs in the Miridae, for instance and seems to me to represent a higher differentiation without question.

The position of the spiracles was discussed by Handlirsch in "How many spiracles do the Rhynchota have?" (1899). Although the material examined was only a limited one, his results are not without value to phylogeny and systematics. It is desirable only that their generality could have been established by new and broadened studies. The position of the abdominal spiracles seems to be especially significant to systematics. The fact that 2-7 pairs are situated ventrally in the so-called Gymnoceratae is a general rule. Where they occupy a different position, we have a later acquirement. In this respect, the Lygaeidae (=Myodochidae), Tingididae, Aradidae, and Berytidae (=Neididae) are to be called specialized families in that the said spiracles of the first 3 families, always in different subfamilies and even genera, occupy a varying position; and in the latter all are dorsal, at least in the only genus that has been investigated. The fact that on the other hand the spiracles of Phrrhocoridae belong to the primitive type with respect to position, is of no less importance to a correct concept of the phylogeny of this family (see Chap.III). Also the last 7 pairs of abdominal spiracles of the so-called Cryptoceratae living in water, whose respiratory processes are not so simple as those of the Gymnoceratae, proved to be originally ventral and always occupy that position in the larvae. Still significant modifications with respect to the spiracles occur in many water bugs with the last molt which leads

---

(*). Sharp's discussion "On the structure of the terminal segments in some ♂ Hemiptera" (1890:399 et seq.) is to be taken into account. However the author discusses only the pentatomids (sensu latissimu) hence his paper is of less significance for systematics of all the Heteroptera families.

to the imaginal stage; for instance in the Belostoma all abdominal spiracles, except the first and the last pairs, atrophy while they continue to function in very closely related forms (Hydrocyrius etc.) or only those of the 2nd, 3rd, and 7th segments atrophy whereas the others (4, 5, 6) develop in a very peculiar manner, (Nepa, Ranatra). On the other hand the primitive type still appears in Naucoris, Notonecta, and Corixa.

The internal structure of the heteropterous body has still, as already indicated, been very incompletely presented. Except for a few smaller discussions [cf. bottom of page 33 of the text, foot-note for references] we have our knowledge on this from Dufour's "Anatomical and physiological research on Hemiptera" (1833) and Heymons' "Contributions to the morphology and history of development of the Rhynchota" (1899) only. Unfortunately the results in the first-named work were based on investigation of a very limited material on account of which no generality can be ascribed to them this being a necessary pre-requisite to their use for phylogeny and systematics. I will [come back to this] in Chap. III and again mention some details which seem to me to be of special importance. As I have already emphasized in beginning Chap. I there is no doubt that comparative morphological investigation of the internal anatomy of Heteroptera, . which must embrace representatives of all the subfamilies at least, would be of the greatest importance for correct conception of the the opposed conditions of relationship of these animals. In this respect, even Heymons' significant paper furnishes us with but little information.

One discussion especially deserves to be emphasized among the papers concerning Heteroptera larvae and nymphs, namely, Gulde's "The dorsal glands of larvae of the Hemiptera-Heteroptera" (1902; 85 et seq.) the results of which have already been used by Kirkaldy for the characterization of individual families. Provided these are generally valid — which however can be questioned since the material examined was very limited — they still are certainly of not a little significance to systematics and phylogeny. The most primitive condition is found in the Thyreocoridae, Scutelleridae, Pentatomidae, Pyrrhocoridae, Aradidae, Reduviidae, Nabidae, Cimicidae, Anthocoridae and even, except for a few genera, the Myodochidae, the dorsal glands of which are siutated at the anterior margins of the 4th, 5th, and 6th segments. The disappearance of the dorsal ~~[illegible]~~ glands of the 4th (Coreidae, Neididae, Macrocephalidae, and a few myodochid genera) or of the 6th (Tingididae) segments is to be considered as a specialization that showed up later. According to Gulde, in the Acanthiadae and Miridae only one gland is found at the anterior margin of the 4th segment; and the Gerridae, Veliadae, and Hydrometridae as well as all Hydrocorisae lack the dorsal glands entirely. In the last named families, however, this lack obviously depends on ecological conditions and is therefore of little importance. Certainly the stink glands have no purpose for insects living on or in the water and therefore are always absent both in the adults and in the larvae and nymphs. (As is known, the imaginal and nymphal stink glands of the Heteroptera are not homologous at all; the former are found on the metathorax, the latter on the abdomen. The fact that none have reached development in the water bugs must certainly serve as proof that this lack in the former and in the latter is dependent on the same fact, i.e., here by reason of life in the water.) This lack is therefore not a phenomenon of relationship for as soon as a hemipteron of either type adapts itself to living in the water, the stink glands of course disappear. This is also true of the family Aepophilidae that was unknown to Gulde. Such a modificati dependent on biological circumstances, can moreover show up very early and in relatively lower types, as in several Hydrocorisae. Also the reduction of the dorsal glands in Acanthiadae nymphs has certainly been dependent on life in moist places and can by no means be interpreted as a proof of relationship with the Miridae whose nymphs likewise have only one dorsal gland. In these a similar phenomenon has happened, but probably for quite different reasons. If, therefore, sometimes there is a heterophyletic homomorphism in the construction of nymphal dorsal glands, which offers nothing to phylogenetic deduction, on the other hand, however, its structure seems to be able to fupply important information in other cases, which concerns derivation of individual families. Thus for example, Handlirsch (The fossil insects;1248) among other things, derives the Myodochidae, Pyrrhocoridae, and Aradidae from the Coreidae. Now the fact that the dorsal glands of coreid nymphs represent a reduction of the primitive type which is still apparent in the first 3 families, is evidence against such a concept. Just as little could the Tingididae, as Handlirsch likewise assumed, come from the Coreidae since these, like those, never have dorsal glands on the 4th, but rather on the 5th and 6th segments. It might still be mentioned here that too much weight has been placed by Kirkaldy (The phylogeny l.c.;362) on Gulde's observation that the dorsal gland of the 4th segment in the Pentatomidae and a few Scutelleridae is paired and has a paired orificium since for this reason, he is willing to consider the pentatomids as the most primitive type of Heteroptera. Schumacher recently found (Beiträge der Verbreitung u.Biologie der einheimischen Poeciloscytus-Arten. 1909;387) that paired excretory pores can sometimes occur even in mirid nymphs and still the dorsal gland apparatus in these is so highly modified that it has disappeared in the 5th and 6th segments and persists still only in the 4th.(*)

(*). According to Schumacher the glands belong to the 3rd segment and extend between the 3rd and 4th tergites. Unfortunately I cannot determine how the contradiction between Gulde's and Schumacher's data is to be interpreted since investigations of my own are not possible at present.

Finally it is to be said that the structure of the Hemiptera eggs and especially of the micropilary apparatus ought to be of no less value to the knowledge of the true conditions of relationship of these animals. Unfortunately investigations hereon are still very defective. However, Leuckart's discussion "On the micropyle and the finer structure of the chorion in insect eggs" in Muller's Archives for Anatomy 1855; 137 et seq., in which he described 5 distinct types of the micropylary apparatus in Heteroptera is of great value. The first appears in Pyrrhocoris and consists of five short cup-shaped attachments, centrally at the anterior pole; no operculum. On the other hand the short compact eggs of the Pentatomidae and Scutelleridae investigated have an operculum whose margin is surrounded by a larger or smaller number (13-26) of slender elongated cup-shaped micropyles. An entirely different formation shows up in the Reduviidae and is common in this family as well as in the Nabidae, Miridae, and Cimicidae. The arrangement of the micropyle here is a parietal one; that is here it runs in the form of a canal to the inner surface of an umbrella-shaped prolongation which embraces [or includes, spans, etc.] the operculum and in a certain sense represents a prolongation of the external ridge of the operculum fold. The eggs of Coreidae present an entirely deviating type (unfortunately the author investigated only the eggs of Chorosoma schillingii). The micropyles are only 2 in number and both of these are in the median line of the egg, the one on the operculum and brought close to the anterior margin thereof, the other above this operculum and placed on the anterior tip of the egg. To the author the conditions in Chrosoma seem to form a transition to the "water-bugs". That is, by "water-bugs" the author means not only the Hydrocorisae of which he examined the eggs of the genera Corixa, Notonecta, and Nepa, but also the Hydrometridae, Gerridae, and Veliadae. In all these he finds a perfectly corresponding type. (Leuckart notes that the eggs of Naucoris cimicoides, according to Dufour's data, were developed according to a different type in that they had parietal micropyles. Probably this observation is not sound since the eggs of N.maculatus F.(apterus Duf.) were described as developed in the other water bugs.) The eggs lack an operculum and are provided with a single micropyle, or at most 2 micropyles, centrally at the anterior pole. Finally, it is of great interest that the author found that the Homoptera and especially the Cicadaria join immediately onto the water bugs by reason of the formation of the micropyle. Unfortunately the exact and detailed investigations by Leuckart embrace only a limited number of Heteroptera families and still at the present time the eggs of the following families have not been more thoroughly investigated; Thyreocoridae, Urolabididae, Neididae, Myodochidae, Tingididae, Aradidae, Hebridae, Henicocephalidae, Microphysidae, Termatophylidae, Anthocoridae, Polyctenidae, Mesoveliadae, Aepophilidae, Leptopodidae, Velocipedidae, Dipsocoridae, Schizopteridae, Ochteridae, Nerthridae. In several cases in which the systematic position of a family is questionable, very certainly an investigation of the eggs will be able to furnish decisive information. Doubtless this is a fertile field for study. Investigation of the myodochid, tingidid, and aradid eggs would be of particular importance in explaining the closest kindred relationships of these great families, as well as examination of the eggs of Hebridae, Mesoveliadae, Aepophilidae, Dipsocoridae, and Ochteridae.* Since Leuckart designated the structure of coreid eggs as a transition to that of the "water-bug" eggs, he was probably led astray if he had intended to deduce the latter type from the former. Investigations made by my brother, Dr. Enzio Reuter, on eggs of Acanthiadae showed that the structure of the eggs of these animals can serve just as well or even better as basic type for eggs of water bugs than that of the coreids. Therefore even the structure of the eggs seems to support the hypothesis that the water bugs came from ancestors similar to Acanthiaden. An investigation of Ochteridae eggs would be of great significance to this question.

---

*. With the assistance of my brother, Dr. Enzio Reuter, I have tried to undertake such an investigation but had to give it up since it was impossible to get mature eggs of the insects concerned.

III. Remarks on the phylogeny of families of Heteroptera.

The statements made in the preceding chapters may be summarized as follows:

The following are to be conceived as primitive characters of Heteroptera adults:

Occurrence of both compound eyes and ocelli;
4-segmented antennae;
4-segmented rostral sheath;
Hemelytra consisting of 3 well separated areas, clavus, corium, and membrane;
  a so-called embolium at the outer margin of the corium;
Membrane with many veins, which are free or partly united into cells;
**Composite [or combined] meso- and meta-sterna;
Metasternum probably with stink-gland orificia;
Hind coxae of the pagiopodous type;
Homomorphous pairs of legs;
3-segmented tarsi;
Claws without arolia;
Homomorphous ♂ genital forceps or genital claspers;
Probably the ♀ genital segments provided with a saw-case [or ovipositor sheath];
2-7 pairs of abdominal spiracles always ventral;

The occurrence of 3 dorsal glands is to be considered as a primitive character of
  nymphs and larvae.

In the adults, the following are to be considered as modifications acquired later:

Absence of ocelli or even the compound eyes also (Polyctenidae);
Antennae with more or lessthan 4 segments;
Reduction of the rostral segments to 3 or even to 1 (Corixidae);
Homogeneous hemelytra, reticulate elytra; cuneus separate;
Reduction of membrane venation;
** Simple meso- and meta-sterna;

[The German word translated composite literally means "put together"; it is not the same as the word for "fused".]

Reduction or absence of stink-gland orificia of the metasternum;
Hind coxae of the trochalopodous type;
Heteromorphous pairs of legs;
Reduction of number of tarsal segments; partition of the 2nd segment so that a 4-segmented tarsi results is rare (Polyctenidae);
Occurrence of claw-arolia;
Heteromorphous ♂ genital forceps;
Absence of a saw-case;
Abdominal pairs of spiracles lying partly or wholly dorsal.

Reduction or absence of the dorsal glands is to be considered as a modification that was acquired later in nymphs and larvae.

Among present Heteroptera families is found one which is characterized by nearly all the above-stated primitive characters, namely, the Family Ochteridae. Only the stink-gland orificia of the metasternum are absent in the adults of this family and the number of tarsal segments is reduced. How the dorsal glands of the nymphs act is not yet known. In any case it seems to me that this family, of all those now existing, comes nearest to the most primitive type of Heteroptera. Moreover, an insect which completely agrees with the above described hypothetical original type in all respects has certainly never been present in nature.

For one or another reason, the primitive structure of different parts of the body has already been modified earlier in the remaining families; this is especially so in case of the antennae, the rostral sheath, the thorax [or sternum], the stink glands, and the genital segments, also partly so for the legs. However, the families whose membrane has retained the primitive type and whose abdominal spiracles have kept the primitive position can be considered as primitive. Such primitive families are the Velocipedidae, Nabidae, Pyrrhocoridae, Coreidae, and Pentatomidae (sensu latissimo).

The task of this Chapter is supposed to be to find out how these families possibly behave to each other and how the other more specialized families are to be derived from them.

In the first place, we must investigate the systems of earlier authors in more detail. But of those systems which were referred to briefly in Chapter I the majority cannot be taken into account as soon as the question has been studied from phylogenetic points of view because the arrangement of those systems is linear and in such it has only been approximately possible to give the kindred relationships between the different families. As for these systems, the remarks that I have already made elsewhere, may suffice. After reading through this chapter one will be able to understand the meaning thereof better.

Really there are only 3 systems which, apart from a phylogenetic arrangement, deserve discussion here; that of Osborn (1895), that of Kirkaldy (1907, 1908, 1909) and that of Handlirsch (1908).

1. Osborn's system; [diagrammed, page 38 of text].

Kirkaldy (1908;358), in part correctly so, designated Osborn's system as "superficial, not phylogenetic". The concept that aquatic Hemiptera do not represent a more primitive step is already a noteworthy advance in Heteroptera systematics and it seems to me that Osborn is quite close to being right since he designates forms which are close to present-day Acanthiadae as those forms from which the present water-bugs, on the one hand, on the other the terrestrial and arboreal Heteroptera have developed. I may only remark that probably at the same time other basic types have also existed as I will set forth in more detail below. Yet Kirkaldy is right in his critique of Osborn's system insofar as this author frequently studied the kindred relationships of the separate families very superficially. Thus, for instance, as Kirkaldy remarked, he still considers the Aradidae and Cimicidae or the Pyrrhocoridae and Miridae related, following the example of older authors, but the first 2 families hardly have more than the gular groove in common, and the last two hardly more than the absence of ocelli. Therefore Osborn's diagrammatic presentation of the mutual kindred relationships of individual families, which are by no means motivated in more detail by the author, seem to me to be of little value. How little they agree with the results of present-day phylogeny is indicated by the derivation of the Parasita from the Cimicidae, among other things.

2. Kirkaldy's system. [Diagrammed, page 39 of the text].

Kirkaldy's system (see pages 20 and 22 [of the text]) stands or falls with acceptance or rejection of the essential significance which Schioedte ascribed to the structure of the hind coxae. That is, Kirkaldy also based the principal division of the Heteroptera on this. I have already stated (pages 6 and 7) my opinion on this question and in doing so emphasized the fact that such a division would separate related families from each other, without question, like the Nabidae on one hand and the Anthocoridae and Miridae on the other. It seems to me it would be just as wrong to remove the Nepidae from the other Hydrocorisae and to derive them from the Reduviidae because they are trochalopodous and not pagiopodous. Even the structure of the sternum [or thorax] of the Nepidae prevents such an interpretation, as I set forth on page 7. In 1891, Schmidt expressly detailed (see pages 17 [of the text] and 16) the relationship between the trochalopodous Nepidae and the pagiopodous Belostomatidae. Probably the above-mentioned basic discussion of Schmidt's has remained unknown to the authors who, like Bergroth (1887:146-149) and Kirkaldy (1903:357) ascribed such a great value to Schioedte's Systematics of Heteroptera. Perhaps if they had considered it more in detail they would not have accepted Schioedte's Classification so unconditionally and indeed, bi-partition of Heteroptera into Trochalopoda and Pagiopoda is no longer permissible after Poppius's new discoveries relative to the varying structure of the hind coxae in Miridae (see page 6).

My conception of the phylogeny of Heteroptera is also essentially different from that of Kirkaldy. While this author considers the trochalopodous forms as primitive, I believe, on the contrary, that the primitive Heteroptera, just like the Homoptera, were pagiopodous. Kirkaldy designates the Pentatomidae (Asopina) among present-day Heteroptera as the ones that come closest to the most primitive type. On the other hand, I find this type almost completely represented by the Ochteridae and in this respect I come closer to Osborn's concept, for in fact the Acanthiadae are certainly closely related to the Ochteridae.

Now if we briefly examine and judge Kirkaldy's diagrammatic presentation of Heteroptera phylogeny, we would have to raise several objections to the concept of the Cimicina (Asopina) as the most primitive Heteroptera. Neither the structure of the antennae (see page 3) nor that of the thorax [or sternum] (see page 6) is that of a primitive heteropteron and the paired pores of the nymphal dorsal gland of the 4th segment which, according to Kirkaldy, are supposed to indicate a primitive step in development, are of little importance in systematic respects (see page 11). Also the occurrence of claw-arolia seems to me to be a character that was acquired later, even though it was acquired early. Why just the Cimicina in particular are to be considered as the most primitive Cimicidae (Pentatomidae) also seems puzzling to me. On the contrary, I believe that the spp. of this Subfamily, which differ from all the others by a predatory way of life, have been secondarily adapted to it and have developed a more powerful beak.

It is quite self-evident that the Urolabididae and Thyreocoridae were derived from the Cimicidae (or perhaps more correctly the Proto-Cimicidae). Hence the derivation of Aradidae and Tingididae from Cimicidae is much more apocryphal. Kirkaldy thinks that the Tessaratomina are supposed to supply the transition between Cimicidae and Aradidae and in fact there are some Tessaratomina genera which are very similar to the aradids in habitus. (One of them (Eumenotes Westw.) was even described by such a capable Aradidae specialist as Bergroth, as an aradid (Odonia)). But it is still to be ascertained whether this similarity is not conditioned by convergence of characters and not by actual blood-relationship. Among other things, it is to be noted that the Tessaratomina are provided with arolia, but not the Aradidae. Knowledge of the structure of aradid eggs would certainly be significant for solution of the aforesaid question. Furthermore as regards Tingididae, here too a similar investigation is needed. That is, these animals seem to have their nearest relatives in the Myodochidae and the "Subfamily" Piesmina to some extent occupies an intermediate position between the two families. (See Flor, Rynch.Liv.I:313. I now consider this Subfamily as an independent Family which was not mentioned in Chap. I.) But unfortunately the eggs of these 2 families have not been investigated and their internal anatomy is also very little known.

Kirkaldy likewise derives the Pyrrhocoridae from the Cimicina or forms related to them. The 4-segmented antennae, the venation of the membrane, the position of the abdominal spiracles, and the number of nymphal dorsal glands are evidence that the Pyrrhocoridae, although they no longer possess ocelli, still represent just as primitive a type as the Cimicidae (Pentatomidae). However, the veins in the membrane have quite a different course from that in Pentatomidae (and Coreidae). The head of the pyrrhocorids, furthermore, seems to be more primitively formed than that of the pentatomids with its sharpened lateral margins. Therefore closer relationship between Pyrrhocoridae and Pentatomidae already seems rather doubtful. Here there is also the very different structure of the eggs which, in Pyrrhocoridae, do without the operculum altogether and therefore probably are to be considered as belonging to a more primitive type.

According to Kirkaldy, Myodochidae and Coreidae issue from the pyrrhocorids. Surely it is not Kirkaldy's intention to derive these families provided with ocelli from the pyrrhocorids, which do without ocelli, but rather to derive them from the hypothetically ocelli-bearing ancestors thereof. ("... the Myodochidae seem to have been derived from ocellate Pyrrhocoridae" Kirkaldy 1909:XXI). In this case, I also agree with respect to the myodochids, with the addition that the aforesaid ancestors probably had a saw-case in the ♀. The pyrrhocorids and myodochids are doubtless closely related and it is to be assumed that investigation of the still unknown eggs of Myodochidae will confirm this assumption. The one family, however, cannot have been derived from the other because they both have branched off from the same stem in a distinctly diverging direction. Characters of the pyrrhocorids that were acquired later are the absence of ocelli and probably also the structure of the ♀ genital segments; those of the Myodochidae are the reduced venation of the membrane and the varying position of the abdominal spiracles (see page 9). Derivation of the coreids from the pyrrhocorids seems to me to be poorly motivated. Certainly the dense venation of the coreid membrane cannot possibly be derived from that of the pyrrhocorids. Furthermore, the eggs of Pyrrhocoridae and of Coreidae are quite differently constructed. I am therefore convinced that the former are not so closely related to the latter as Kirkaldy assumed.

The above-mentioned families form the first Superfamily of Kirkaldy, which he named Cimicoideae. The seonnd ~~family~~ superfamily, the Nepoideae, was derived from the former in that the author conceives of the Nabidae as "a development of some "Protomyodochidae" in the direction of greater rapacity and agility" (l.c.:362). Although Kirkaldy therefore designated the Nepoideae as "almost certainly derived from a myodochid stem" (Cat.of Hem.; XXI), I must still admit that such a derivation seems to me quite arbitrary. In my opinion the Nabidae must be considered as more primitive than the Myodochidae in many respects. Thus with reference to the structure of the antennae and the claws, to the always ventral position ofthe 2nd to the 7th abdominal spiracles, and especially to the abundant venation of the membrane, it is so. To be willing to derive such a striking low family from the relatively highly specialized Myodochidae is, in my opinion, to turn the system up-side-down.

The Nepoidea, beginning with the Nabidae, is therefore divided into 2 branches, according to Kirkaldy, the one represented by the Gerridae (*), the other by the Reduviidae from the last of which radiate the Nepidae, Enicocephalidae, and Macrocephalidae. As for the first branch, or the Gerridae, their relationship with the remaining families included in the same superfamily seems very questionable to me. Indeed the homogeneous nature of the hemelytra is a character which shows up in another one of the above named families, the Henicocephalidae and which could be conceived of as a specialization of the basic type. This fact would prevent uniting the Gerridae with the other families named just as little as the absence of stink glands in both adults and nymphs which is conditioned by life on the surface of the water, striking as this seems to be. Such a union, undertaken by several authors, has probably been caused by the somewhat similar structure of the short beak. But the structure of the beak is a character very dependent on way of life which certainly indicates a similar way of feeding but by no means necessarily a blood-relationship. There are, rather, several facts which seem to contradict such a thing. Thus, for instance, [it is true of] the internal anatomy of Gerridae which Leon Dufour found to be so different from that of the other families that he even considered them as representatives of a separate series (**). Furthermore I am ascribing no little significance to the quite different structure of gerrid and reduviid eggs. In this connection I recall that Leuckart on the whole found the same type of egg in the so-called Amphibicorisae and Hydrocorisae and that Leon Dufour also pointed out similarities in their internal anatomy. Unfortunately, the internal anatomy of Acanthiadae has not yet been investigated, which would be of the greatest importance just for knowledge of the phylogeny and kindred relationships of this family to the Amphibicorisae (Gerridae) on the one hand and to the Hydrocorisae on the other. Also the eggs of Acanthiadae have not been described up to now. Investigation of these, undertaken by my brother Dr. Enzio Reuter at my suggestion, meanwhile proved that the acanthiad eggs, like those of Amphibicorisae (and Hydrocorisae), have micropyles that are central and apical as well as few in number. Therefore it seems very probable to me that the gerrids are much more closely related to these families than with the reduviids (and nabids) which are characterized by a very peculiar type of egg. Osborn (l.c.; 1895) had already accepted such a relationship in that he derived the Limnobatidae and Hydrobatidae, that is Kirkaldy's Gerridae from the Saldidae (=Acanthiadae) in his phylogenetic diagram. A direct derivation of the one family from the other cannot be imagined as yet.

(*). The family Naeageidae (=Hebridae) has been left out of the diagram entirely.

(**). Here it might be stated that Brandt (1879) designated the Gerris-(Hydrometra) spp. as representatives of a very special type of Hemiptera nervous system. Whether the characterization of this type is valid for the whole family deserves to be further investigated.

According to Kirkaldy the families Enicocephalidae, Macrocephalidae and Nepidae sprang from the other branch of the Nepoidea, or the Reduviidae branch. As for the reduviids and the macrocephalids their close relationship is undeniable although probably the one family was not derived from the other, but ratherwas derived from a common basic type (see page 26). Doubtless the Henicocephalidae also belong to the family circle of the reduviids and nabids, but in any case they do not seem to me to come from the former since it is improbable that the stridulation grooves of the prothorax acquired by the reduviids (and macrocephalids) might have been lost again. Therefore the assumption that the Henicocephalidae may have issued independently from the Proto-Nabidae seems more natural to me. Finally, with respect to the Nepidae, I have already stated their, in my opinion, quite wrong position in the above-mentioned family complex (see pages 6,7 and 14). Schmidt (page 17 [of the text]) finds this family safely substantiated by the presence of the labial palpi, which are lacking in all other Heteroptera, by the lateral outgrowths of the antennae, by the structure of the forelegs and their similar insertion, by the wing formation which agrees in the smallest features, by the similar formation of the thorax [or sternum] and the abdomen with the spiracles, and finally by the close agreement in development of the ♂ genital apparatus. He only regrets that he had not had an opportunity to investigate the ♀ genital apparatus and, especially, the eggs. With regard to the latter, my brother Dr. Enzio Reuter at my suggestion again examined the eggs of Sphaerodema japonicum Vuilefr. and found they they likewise, the same as those of Nepidae, possess apical and central micropyles. Schmidt was therefore certainly right when he closed the presentation of his investigation as follows: "From the foregoing, I would like to state as assured the fact that the Nepidae and Belostomidae belong closer together — in spite of the difference in formation of the coxae and the swimming equipment [or adaptation] of the legs — than either of them with any other group and that therefore in this case the characters emphasized and used by Schioedte have been misleading."

Therefore if we eliminate the families Gerridae and Nepidae entirely from the Superfamily Nepoideae as certainly heterophyletic, we have left only the families Nabidae, Reduviidae, Macrocephalidae, and Henicocephalidae in that Superfamily, these certainly being related to each other. But Leon Dufour has already demonstrated the close relationship in the internal anatomy between the nabids, reduviids, and macrocephalids on the one hand, and the cimicids and mirids on the other* and Leuckart later set forth the fact (see page 11) that the eggs of Nabidae, Reduviidae, Cimicidae, and Miridae investigated by him all developed according to a common type which is quite different from that of the other Heteroptera eggs. Also the eggs of the Macrocephalidae (Phymatidae) judging from Handlirsch's short description, were similarly developed (**). The antennae of the above-mentioned families (with the exception of the Macrocephalidae) are likewise very similar on the whole and characteristically formed and the agreement in structure of the ♀ genital segments of nabids and mirids is indeed hardly only a phenomenon of convergence.

(*). Landois (1868) also emphasized the relationship between Cimex and Reduvius.
(**). "Monograph on Phymatidae" (1897:139, fig. 11).

Meanwhile the Miridae, Cimicidae, and the Anthocoridae which are closely related to these only because they are pagiopodous and not trochalopodous, were placed by Kirkaldy in a Superfamily very different from that of the 4 other families named. This Superfamily Miroidea was started with the Anthocoridae and this derived from the forms related to the Pyrrhocoridae, a derivation which, moreover, seems to be motivated by no facts. The old views on the relationship of Anthocoridae with the Myodochidae (and thereby with the Pyrrhocoridae) was long since given up as untenable (***). The right thing, unquestionably, would be to consider all of the above named families as homophyletic, without reference to the difference in formation of the hind coxae.

(***). The compound [or composite] sternum, the claws without arolia, the structure of the hind coxae, etc., in my opinion, are evidence that the Anthocoridae are more primitive than the Myodochidae.

According to Kirkaldy, the Dipsocoridae, Miridae, and Clinocoridae (=Cimicidae) radiate from the Anthocoridae, and Polyctenidae and Aepophilidae come from the Clinocoridae. As for the mutual relations of anthocorids, mirids, and cimicids, let me refer to the more detailed presentation on page 23). Here it may only be stated that I have become convinced by more careful research thereof that the Dipsocoridae are not homophyletic with the remaining above-mentioned families. By investigation of the genital segments, Poppius found that these developed in the dipsocorids according a very different type than in the other families, in that they seem to show a much greater agreement with the structure of the same thing in the Acanthiads. (Dr. Poppius will describe the genital segments of dipsocorids in more destil in another place.) Furthermore it has been impossible for us to discover the characteristic sutures of the meso- and meta-sternum for the composite sternum in the dipsocorids, but rather these seem, as in the Acanthiadae, to be simple. Also the orificia of the metasternum are absent, the same as in these. The venation of the hemelytra is likewise very different from that of the Anthocoridae and Miridae. Finally the formation of their antennae is quite peculiar and has its counterpart in no other family. For all these reasons, I find it correct to remove the Dipsocoridae from the branch of the Anthocoridae. It is really only the Subfamily Dipsocorina which shows a certain similarity in habitus with the anthocorids, whereas the forms belonging to the Schizopterina are mostly so different that even their Heteroptera nature is sometimes to be recognized only after careful investigation. Since, unfortunately, the eggs of these insects have not yet been examined, it is difficult to establish their true relationships. Doubtless, however, the wide-spread Dipsocoridae, represented by only very few spp., are very primitive forms. Not only does the formation of the antennae (2 very short basal segments and 2 long, seta-like apical segments the first of which is swollen at the base) seem to me to represent a primitive type; also the greatly varying venation of both hemelytra and wing, seem to be evidence of a low step in development in their inconstancy [or lack of permanency]. Finally I still recall the peculiar structure of the Schizopterina (see page 1). Therefore I find it best to consider it provisionally as an independent, primitive branch of the same value as Kirkaldy's other Superfamilies, which consists of 2 families, the Dipsocoridae and the Schizopteridae.

Also it now seems to me to be practically established that the Aepophilidae cannot be counted in the circle of forms of the Miroidea but they seem to be more closely related to the Acanthiadae. At least, they cannot be derived from the Cimicidae since the formation of the head is quite different from that of this family and of the anthocorids and furthermore since the ♀ genital segments have not developed according to the anthocorid and cimicid type but rather according to the mirid type. (If Signoret's description of Aepophilus in Tijdschr.voor Entom.,1880;l were right then the alleged 4-segmented beak must still be considered as a hindrance in the way of derivation from the Cimicidae. But in fact the beak is only 3-segmented (segment 1 shorter, 2 and 3 xxxxxxx about the same length). But they also show characters which are foreign to all other Miroidea. Some of these, such as the absence of metasternal stink-gland orificia in the adults and of dorsal glands in nymphs and larvae may however be considered as adaptive characters dependent upon the way of life (in water). But even the ♂ genital segment * has developed according to a very different type than in the other families belonging to the anthocorid branch, in that the genital pore is dorso-apical and provided with homomorphous styli reminiscent of those of the acanthiads. (*. This was interpreted by Signoret as ♀, remarkably enough.) Also the meso- and meta-sterna are simple as in the latter. (In the Cimicidae the contours of the different parts of these pieces of the sternum have been obliterated.) For the rest it is very hard to understand how insects living under stones covered by water might have arisen from parasitic forms like the cimicids. On the other hand, derivation from the acanthiads, xxxxxxxxxxxxxxx inhabiting the shore, or more correctly from their ancestors with, probably, similar habits, seems rather natural. The reduction of the eyes in size and the disappearance of the ocelli are characters resulting from life under the water and give the animal an appearance that deviates from the remaining acanthiads (Velocipedidae, Acanthiadae, and Leptopodidae). Certainly the ♀ genital segments have developed according to the same type [illegible] those of Miridae. But this is also the case with the genital segments of Velo

For the above reasons, therefore, I believe that the Aepophilidae are to be placed in Kirkaldy's system in his Superfamily Notonectoideae beside the Acanthiidae. Future investigation of the eggs will show whether this is so indeed.

We still have the family Polyctenidae to consider among Kirkaldy's Miroidea. Speiser (l.c.1904) has expressed the view that this represents a type adapted to a parasitic life and having been derived from the cimicoids and Kirkaldy followed him in that. I am passing over this family in my considerations, since it is unknown to me in nature.

Kirkaldy's last superfamily is the Notonectoideae which is joined to the Miroidea by the family Acanthiidae. This derivation also seems to me to be wholly arbitrary. On the other hand, it is not impossible that both the Notonectoidea and the Miroidea and Nepoidea once branched off from a common stem. The similar venation of the membrane in the Nabidae, Velocipedidae, and Ochteridae as well as the radiating veins of the membrane in some Miridae seem to support such an assumption.

However, with respect to the structure of the egg, so far as it is known, the families designated by Kirkaldy as Notonectoidea deviate very substantially from the Nepoidea (without Nepidae and Gerridae) and the Miroidea (without Dipsocoridae and Aepophilidae); while the different families forming the superfamily Notonectoidea, with the addition of Gerridae and Nepidae seem to offer a striking similarity in the above respects. (How naucorid eggs behave still seems uncertain. Eggs of ochter-)* Therefore it seems to me the Notonectoideae form a not unnatural systematic group around these 2 ~~enlarged~~ families (and probably also the Aepophilidae), the representatives of which are either gymnocerate or cryptocerate according to the different conditions of life. The sternum also remains compound in these last, a fact which has probably been conditioned by the biological conditions (see page 6). [*insert: ids, nerthrids, dipsocorids, and aepophilids have not yet been examined).

Only the position of the Corixidae seems problematical to me. That is, it is not quite impossible that they are to be placed opposite all other Heteroptera and form a Suborder, Sandaliorrhyncha Börner ("Zur Systematik der Hexapoden" (Zool.Anzeig.1904:611 et seq.), equivalent to all the remaining Heteroptera. This Suborder, now represented only by highly specialized forms, has already branched off independently from the Palaeohemiptera. But the ancestors of such a Suborder still remain unknown to us for it is doubtless wrong to consider the present Corixidae as a low-standing group, as Börner did, which Handlirsch has already convincingly explained. It seems to me that the Corixidae show differences in the deviating structure of head and mouthparts, the peculiar forelegs, the metasternum, the asymmetrical abdomen in the ♂, as well as in the development of the remarkable stridulating apparatus, not only in comparison with the Notonectidae but also with all other Cryptoceratae, which can hardly be derived from the organization of these. With all that it is not my intention to speak out against derivation of Corixidae from the Notonectidae. Leuckart has demonstrated that the micropylar apparatus of the eggs of these two families has developed entirely according to the same type. The fact that I deviate, for the rest, from Kirkaldy relative to the mutual kindred relationships of the separate Notonectoidea families will be further demonstrated by the exposition below (see page 21-22).

The classification of Heteroptera proposed by Kirkaldy seems to me to be deficient especially in the following points:

By the bi-partition into Trochalopoda and Pagiopoda based on the structure of the hind coxae, inter-related families are placed in different Superfamilies and, on the other hand, heterophyletic families are placed in the same Superfamily.

The Superfamilies are not naturally delimited thereby, but rather they contain either too many or too few families (Nepoidea, Miroidea, and Notonectoidea).

Also the Superfamily Cimicoideae seems to consist partly of heterophyletic families.

By the fact that the author considers the trochalopodous forms as the primitive ones, families of lower organization prove to be derived from those of higher organization (Nabidae from Myodochidae).

Therefore he also happens to designate an already rather specialized type ("Cimicina" = Asopina) as the primitive type of Heteroptera.

Just as wrongly, he designates the Notonectoidea as the most specialized whereas on the contrary they include the family (Ochteridae) which probably comes closest to the Proto-Heteroptera.

de la Torre Bueno's "Some recent contributions to hemipterology" (1909:294 et seq.) became known to me only after the beginning of this paper was already printed. In this discussion he partially criticized Kirkaldy's phylogenetic views. For the above reason I could not refer to it in Chapter I. His remarks chiefly concern the families Notonectoidea and Nepoideae. Of the former he considers the families Acanthiidae (more correctly Acanthiadae), Ochteridae, Naucoridae, with which he united the Nerthridae, and Belostomatidae as a developmental series in which the first forms the most primitive, the last the most highly specialized steps. It is evident from the above exposition that my views diverge from those of the author; the reasons for this have already been set forth in detail, as well as the reasons for the view that the Nepidae and Gerridae do not belong (as Torre Bueno still thinks) to the family complex of the Reduviidae etc. Here it may only be stated that Torre Bueno considers the families Notonectidae and Corixidae (among the Notonectoidea) as differing just as much from each other as from all the remaining families and that he maintains that the families Hydrometridae and Mesoveliidae (more correctly Mesoveliadae) are to be seperated from the Gerridae as independent families, the former being more closely related to the reduviids, the other with the nabids. On this I will only remark that it is evident from the egg structure, among other things, that the similarity between the reduviids and the hydrometrids is only a superficial one. On the other hand, with respect to the relationship between the Mesoveliadae and the Nabidae, it is not impossible that Torre Bueno is on the right track. The internal anatomy of these families has been quite unknown hitherto and even the eggs have not yet been investigated.

3. Handlirsch's System. [Diagrammed on page 47 of the text].

Handlirsch's System deviates substantially from that of Kirkaldy. Certainly it has the cleaving of the Hemiptera stem into two great sections in common therewith. But whereas Kirkaldy following Schioedte's example, used the structure of the hind coxae as basis for division, Handlirsch on the other hand still maintained the old division into Gymnocerata and Cryptocerata (= Geocorisae and Hydrocorisae). He had probably perceived the above emphasized weakness in Schioedte's system and also considered this author's view that the shortness of the antennae in Cryptoceratae is less hereditary than adaptive in nature and therefore of no use as the main basis for division, as insufficiently grounded. That is, he emphasized the fact that the Cryptoceratae had already branched off from the Protoheteroptera in the Lias and that as early as in the upper Jurassic the Cryptoceratae and Gymnoceratae sharply differed and the former were even predominant. He also derived all present Cryptoceratae from these cryptocerates.

Still Handlirsch shared Osborn's view (see page 18 [of the text]) that the cryptocerate families were originally derived from secondary adaptive forms which came from low-standing, shore-inhabiting land bugs, probably reminiscent of Saldidae (Acanthiadae); and rejected Borner's concept that the Gymnoceratae were supposed to have descended from the highly specialized Cryptoceratae as impossible.

Since Handlirsch therefore designated the Protoheteroptera as acanthiad-like, he thereby also expressed the view that the pagiopodous forms are primitive and the trochalopodous arose later. I am in complete agreement with this view. But I believe that the Protoheteroptera have their nearest relatives among now-living forms, in another family than in the Acanthiadae, that is, in the Ochteridae which Handlirsch placed among the Cryptoceratae. It is to be noted that it does in fact come very close to the Acanthiadae and, having been separated from the Hydrocorisae by several authors, has been placed right beside the Acanthiadae among the Geocorisae. (See page 31). In my opinion, perhaps all the cryptocerate as well as some gymnocerate families (Acanthoideae and perhaps Gerroideae also) arose from forms which come close to this family. But besides that a few other gymnocerate family-complexes have independently developed from similar primitive forms.

That is, it is certainly probable, as Handlirsch believed, that present-day cryptocerate families are homophyletic in that adaptation to life in the water showed up early and these waterbugs later became repeatedly specialized, transmitting the once acquired adaptation characters, of course. But it is not therefore excluded that gymnocerate families also belong to the same Phylum. I have already stated above (page 18-19) that I considered the Superfamily Notonectoideae Kirk. as a not unnatural systematic unit and pointed out the characteristic structure of the eggs common to families belonging here. For just as certainly as the hind coxae change their form according to way of life, the antennae are very plastic in the same way. Acanthiadae and Gerridae living in air on the surface of the earth or the surface of the water, have long free antennae; waterbugs, on the other hand, have very short and concealed antennae. The shortness of the antennae in Ochteridae is harder to understand. But this too is explained by the way of life of larvae and nymphs, ~~as~~ since Leon Dufour (1833:195) reported, they live in small tunnels under moist sand where long antennae would naturally be a hindrance to them. The basic division of the Heteroptera into 2 sections — Gymnocerata and Cryptocerata — must therefore certainly be designated as artificial in that the Acanthiadae and Gerridae as well as the gymnocerate families most olcsely related to them seem to be more closely related to the Cryptoceratae than to the remaining Gymnoceratae. Therefore I cannot consent to the cleaving of Heteroptera accepted by Handlirsch but am rather, as already stated, of opinion that the Heteroptera stem had been divided into several primitive branches one of which had ramified both into cryptocerate families and into a few gymnocerate families related to them.

After these general remarks we will consider Handlirsch's diagrammatic presentation of kindred relationships of his Cryptoceratae in somewhat more detail. As main stem thereof he gives the Naucoridae, from which the Ochteridae (=Pelogonidae) and Notonectidae issued at about the same time, as well as Nepidae and Belostomidae somewhat later. As for Ochteridae, I have already expressed the view that just this small family is to be considered as the most primitive of all now-living Heteroptera. It seems wrong to me (see pages 2, 4) for forms with ocelli and 4-segmented beak like the Ochteridae to be derived from forms which do without ocelli and have only a 3-segmented beak like the Naucoridae. Probably the Nerthridae (=Galgulidae) come from the Ochteridae, as Handlirsch also reports. Of the remaining above mentioned families, it seems to me the Belostomidae is very primitive both as a result of the venation of the membrane and the occurrence of labial palpi, although the beak has already become 3-segmented. The Nepidae are very closely related to the Belostomidae (see page 17) and can perhaps even be considered as having descended from them, become adapted to life on the bottom of the water, and therefore as trochalopodous forms. The Naucoridae* seem to me to be related to both the foregoing, though they are clearly less primitive. The Notonectidae seem to have branched off from these families independently, their primitive forms still have a 4-segmented beak (Notonectina). The membrane which is qüite without veins is further evidence of this. As for the Corixidae, which Handlirsch derives from the Notonectidae, I have already expressed my views above (see page 19).

---

*. Following Stal's example, I consider the Aphelochiridae as only a subfamily of the Naucoridae.

Handlirsch divides the Gymnoceratae into 2 great trunks. The first (and older one) typically characterized by the absence of claw-arolia is further divided into 3 branches*. Furthermore from the first of these, which begins with the Velocipedidae, spring the Saldidae (=Acanthiadae and Leptopodidae), Isometopidae, and Anthocoridae (in which the Microphysidae and Termatophylidae are doubtless also included); then from the Isometopidae come the Capsidae (=Miridae), and from the Anthocoridae the Ceratocombidae (=Dipsocoridae and Schizopteridae), and later the Cimicidae. According to Handlirsch, the 2nd branch includes 4 families: Hydrometridae** (which certainly also includes the Gerridae and Veliadae) as the most primitive from which the Mesoveliidae and later (questionably) the Hebridae sprang; the Aepophilidae were also questionably derived from the Mesoveliidae. The 3rd branch begins with the Reduviidae from which sprouted 3 small families, the Nabidae, Henicocephalidae, and Phymatidae (=Macrocephalidae).

---

*. Claw-arolia show up only in the Miridae and Hebriade, yet are frequently lacking in the former. If present, the Miridae are readily separated from the families of the second branch by the formation of the antennae. The systematic position of the Hebridae still remains somewhat doubtful.

**. If these 3 families are united, this family must be called Gerridae and not Hydrometridae because the name Gerris originates from 1794, and that of Hydrometra from 1797.

The families of the first branch certainly seem to me to be heterophyletic. Future investigation of the eggs of the different families will probably confirm the fact that this is so. Velocipedid eggs have not yet been examined and will remain unknown for a long time yet on account of the great rarity of spp. belonging here. But the velocipedids and the acanthiads are no doubt so closely related that even their eggs must be developed essentially ~~according~~ to the same type. Acanthiad eggs are not even mentioned in Leuckardt's frequently cited, meritorious work, but they are now being examined by my brother Dr. Enzio Reuter at my suggestion. The result of his examination is that the micropylar apparatus of these eggs occupies a central and apical position and thereby deviates widely from the structure of the same apparatus in the other families brought together with the Acanthiadae by Handlirsch in his first branch the eggs of which, on the contrary, agree with those of families belonging to the 3rd or nabid branch. Unfortunately we could not get mature eggs of Leptopodidae, but since the ♀ ventral and genital segments developed absolutely according to the same strikingly peculiar type as those of the Acanthiadae it is probable that the eggs of the two families are also substantially alike***.

***. I previously I expressed the opinion that the Leptopodidae were most closely related to the Nabidae and referred in this respect to the structure of the beak and the agreement in the peculiar structure of the femora with those of Reduviolina. But now I find that the similar structure of the genital segments confirms relationship with the Acanthiadae.

Therefore in my opinion, only the three above-named families can be counted for the Velocipedidae branch, they also show great similarity in habitus with one another. But the above described egg-development in Acanthiadae has great similarity with that in Cryptoceratae. That family was therefore probably not without basis, placed by Kirkaldy together with these in the Superfamily Notonectoideae (Kirkaldy's Acanthiidae also includes the Velocipedidae and Leptopodidae). The relationship with the Ochteridae is striking and was also emphasized by Leon Dufour with respect to the internal anatomy. Still the Velocipedidae, Acanthiadae, and Leptopodidae must be considered as an independent branch of the common trunk, in which the antennae have become long and projecting as a result of life on the surface of the ground or in the air, and the meso- and meta-sterna are no longer compound [or composite]

Judging from the development of the eggs, so far as they are known,* the above named second branch, the Hydrometridae, branch of Handlirsch, is to be brought over to the great circle of forms called Notonectoideae by Kirkaldy, as a separate branch. Still the family Hebridae, which Handlirsch questionably derived from Hydrometridae, almost certainly does not belong thereto. A rostral sheath like that of the Hebridae cannot be derived from such a rostral sheath as that of Hydrometridae. Finally, as above pointed out, the Aepophilidae are to be placed in the vicinity of Acanthiadae. It cannot be right to let this pagiopodous family descend from trochalopodous ancestors, as Handlirsch proposed, even though doubtfully. On the other hand, of course, there is no obstacle to derivation of the trochalopodous Hydrometridae and Mesoveliidae from ancestors common to these families and acanthiad-analogues. Of course those families may have developed from pagiopodous ancestors just as the Nepidae developed from Belosotmidae among the cryptocerates. I am again calling attention to the fact that Osborn in his diagrammatic representation of the phylogeny of Heteroptera even directly (which is still not right) derived his Hydrobatidae (=Gerridae) and Limnobatidae (=Hydrometridae) from the Saldidae (=Acanthiadae). In any case the families belonging to the hydrometrid branch are to be considered as more highly specialized than the families of the velocipedid branch. This is so not only because they are trochalopodous, a fact which indicates a later development (see page 6), but also with respect to the structure of the hemelytra. Kirkaldy**, that is, was probably not wrong when he conceived of the completely membranous or in any case homogeneous elytra as proof of higher specialization.

---

*. This is so with eggs of Hydrometra, Gerris, and Velia which were accurately described by Leuckart. In the case of the eggs of these genera which do without the operculum, the micropyl apparatus is centrally placed and shows only 1 or 2 micropyles in which respect it shows significant similarity with the eggs of some waterbugs (Notonecta, Corixa).

**. "Some remarks on the Phylogeny of the Hemiptera-Heteroptera" (Canad.Entom. 1908;358).

The families Isometopidae, Capsidae, Anthocoridae, Ceratocombidae and Cimicidae ø are still left of the above cited first branch. But these very substantially agree, as already set forth, with the families of the 3rd branch in structure of the micropyle apparatus of the eggs and are doubtless, since they also show remarkable similarities in other respects, to be considered as homophyletic with them, even though the phylum was divided rather soon into two small branches, the one represented by the aforesaid families, the other by Handlirsch's third branch.

The former includes families whose meso- and meta-sternum are still compound and which therefore must be considered as lagging behind to a certain extent on a more primitive step in development although some of them are still highly specialized in several other respects. Also the ♀ of all these families is provided with a saw case. Such a thing is found, to be sure, in the Nabidae belonging to the 2nd branchlet but they are distinguished by the structure of the thorax [or sternum] and also approach the Reduviidae in general habitus. øø

ø. Handlirsch made no mention of Polyctenidae in his diagrammatic representation of Heteroptera phylogeny. For this family see page 19.

ø. The outlines of the different parts are indistinct in Cimicidae.

øø. The view expressed earlier (1909;1) that the anthocoride perhaps came from the nabid-branch must be given up, mainly on the ground that the thoracic pleura of the former are compound, of the latter simple and accordingly must represent a later step in development.

Handlirsch considered the families Isometopidae and Anthocoridae as primitive. From the former he derived the Capsidae, from the latter Ceratocombidae and Cimicidae. I cannot go along with him in this concept. In the first place, in my opinion, the Ceratocombidae does not belong to this family complex at all (see page 18). In the second place, it seems more correct to me to divide the anthocorids up into 3 families (Anthocoridae, Microphysidae, and Termatophylidae), and in the third place it seems to me impossible to derive some of the families belonging to this group from others of the same but rather [it seems to me] they are to be considered as independent small branches of the same branch, although they do stand very close together.

As is known, the isometopids have very few representatives and doubtless represent an old family that is dying out. But that the Capsidae (Miridae) which are now so numerous, cannot be derived at least directly from present isometopids is evident from the fact that the Miridae have to show, among them, characters which are more primitive than those which characterize the Isometopidae as, for instance, the structure of the membrane of some Restheniaria, the occurrence of a hamus of the wing-cell in many genera, while this has disappeared in the Isometopidae. Furthermore the Isometopidae already seem to be rather strictly specialized in a certain direction, whereas the Miridae still have very variable forms to show, none of which, however, exhibit stronger similarity to the isometopids. On the other hand, for example, several Fulviaria are very similar in habitus to the Termatophylidae so that is is hard to explain this similarity only as convergence dependent on accidental circumstances and in fact, Puton (1888:106) questioned whether the Termetophylidae were to be united to the Capsidae or with the Anthocoridae. Now since it has been revealed that the Termatophylidae do without ocelli just like the capsids, the similarity pointed out becomes even greater. Accordingly it is still less permissible to derive the capsids from the termatophylids than from the isometopids because the beak of the former already shows a more highly specialized type (1st segment greatly abbreviated) and the termatophylids even in other respects such as in the structure of the apex of the head and also the ventral and ♀ genital segments conform to the anthocorid type which was developed in a definitely different direction. On the other hand, the great similarity of certain capsids with the termatophylids can be understood as a reminiscence from still older times when the capsid and anthocorid types had not yet been separated. Loss of ocelli in Termatophylidae doubtless showed up quite independent of the same loss in the Capsidae and therefore represents only an analogous phenomenon.

As is evident from what has been said above, the Termatophylidae, Microphysidae, Anthocoridae, and Cimicidae agree in several essential respects and form a type separated off from the Miridae (Capsidae) and Isometopidae. In the Miridae and Isometopidae, that is, the posterior margins of all ventral segments conceal the anterior margin of the following segments, while in the anthocorids and, according to Poppius's investigations, also in the Microphysidae, Termatophylidae, and Cimicidae, the anterior ventral segments are contiguous only by the margins (as in Nabidae, Reduviidae, etc.) (see also Schioedte "Nogle nye Hovedsaetninger af Rhynchoternes Morphologie og Systematik":249). In the former, the two ♀ genital segments are entirely free as in Nabidae, in the latter, on the contrary, only the lobes of the 2nd genital segment are free while those of the 7th (apparently 6th) ventral segment - first drawn out lateral backward from it - for the most part are covered in such a way that a triangular little lobe is visible only at the outer margin and sometimes also a little piece at the base of the saw case. Also the structure of the head is different in the two groups. In the anthocorids and their relatives, the always horizontal head is distinctly truncate on the apex. If, therefore the aforesaid families certainly belong to two definitely separate directions, it still does not seem right to me to consider them only as subfamilies of only two families (Cimicidae and Miridae). If, for instance, the Pyrrhocoridae is once raised to a separate family on the basis of venation of the membrane and absence of ocelli, then it seems to me just as correct to separate the termatophylids from the anthocorids. The

Microphysidae, which Fieber has already separated from the anthocorids, likewise a substantially different structure of the membrane. Furthermore the strongly expressed sexual dimorphism which is always strictly carried out, is extraordinarily characteristic for this family; this dimorphism has no counterpart among the Anthocoridae. To this is added the different number of tarsal and rostral segments which still seems to me to be of less importance. (The microphysid genus Nabidomorpha Popp., as stated earlier, has only 3 visible rostral segment, just like the anthocorids.) These two families, the Termatophylidae and the Microphysidae seem to me to represent a lower type than the Anthocoridae, in certain respects. Evidence of that, it seems to me, is the still typically 4-segmented beak, but also the fact that it is now very poor in spp., supports the concept that it belongs to an older circle of forms. On the other hand, the Anthocoridae which have shown relatively numerous genera and spp., at present, probably are of later origin, of which fact the reduction of rostral segments showing up in them seems to be evidence. Finally the Cimicidae are quite peculiar and probably later appearing parasitic forms of adaptation whose great affinity to the anthocorids can hardly be disputed today. However it would be wrong to conceive of them as only anthocorids which have become adapted to parasitism, as Flor (1860) wanted to do. This author knew only Cimex lectularius and did not know that several distinctly different types of genera were joined onto the genus Cimex and with it formed a small systematic group characterized by common characters. The structure of the head and pronotum thereof is so different from that of the Anthocorid type that it can hardly be conceived of as a subfamily of the latter. Here brachypterism has become a true family character; of millions of bedbugs, not a single alate bug has ever been observed. The lack of ocelli in Cimicidae is a further phenomenon which goes together with the constant brachypterism and which has become a family character just as that has.

If therefore the Cimicidae can be considered as highly specialized forms without hesitation, it may, as already indicated, be more difficult to decide which of all the six above-mentioned families is to be considered as the most primitive. Here I call attention to the fact that Brullé (1835) has already placed the Miriae at the lowermost terminus of the Heteroptera system and that the author (1875, 1878), Puton (1886), and Saunders (1876, 1892) have considered the Capsidae as the lowermost among the Gymnoceratae. If, as above proved, this is not correct, this family and the Isometopidae with a very distinct 4-segmented beak, represent in the aforesaid family complex with respect to structure of the rostral sheath, a more primitive level in development just as certainly as do the Termatophylidae and Microphysidae whose 1st rostral segment has already been greatly reduced in length. One genus of the microphydids (Nabidomorpha Popp.) has even become recently known whose rostral sheath showed only 3 visible segments. The sheath has only 3 segments in all the remaining families. As for the membrane, none of the above-mentioned families shows the primitive venation like the Nabidae and Velocipedidae. But there are some Restheniaria genera (Resthenia Spin., Platytylus Fieb.) among the Miridae whose membrane is provided with distinct radiating veins which go out from the cell-veins toward the margins and probably represent the last traces of the radiating venation which has been characteristic for the nabid and velocipedid membrane and presumably just as characteristic for mirid ancestors. But the venation of the membrane, as soon, that is, as it has developed, has become strongly reduced in the families belonging to the branch that is under discussion, in such a way that it forms only one or a pair of basal cells (Miridae, Termatophylidae) which sometimes show a pair of short off-shoots (Isometopidae, Microphysidae), or even in such a way that it consists of from 1 to 4 longitudinal veins which issue from a sometimes very indistinct narrow cell adjacent to the suture of the membrane and of these only very rarely (Physopleurella Reut., Buchananiella Reut., and sometimes Cardiastethus Fieb.) the 2 inner ones run together before the apex and form a triangular cell. It is indeed difficult to say which of these types correspond to a higher development. But here it should be stated that the anthocorid type of venation first showed up simultaneously with reduction of the rostral segments.

A character common to the families of this branch - as soon as the elytra have once succeeded in developing - is the more or less marked development of the so-called cuneus which is separated from the corium, especially in Miridae and Isometopidae, by a distinct fracture. But the fact that some Miridae genera (Lygaeocoytus Reut., Myrmecophyes Osh., Pithanus Fieb., Myrmecoris Gorski) show up which do without this fracture, seems to the author to indicate which ones - like present representatives of families of Handlirsch's 3rd branch (Nabidae etc.) - had still developed no cuneus. Since such atavistic results [or products] as these and the peculiar membrane structure of some Restheniaria discussed above occur among Miridae perhaps, with reference to the primitive structure of the beak, sufficient ground could be found for considering this family as the most primitive of the branch. Meanwhile it has become specialized in several important respects, namely, in the disappearance of the ocelli and in the development of claw-arolia which are absent in all the remaining families, as well as in the reduction of nymphal dorsal glands (see page 10-11). The occurrence of ocelli is as earlier pointed out,*~~is~~ the most primitive typical character and the absence thereof, as in the waterbugs, is always an acquired character. In the 6th Chapter, I am going to present proof that the Miridae also come from ancestors which had ~~also~~ been provided with ocelli just as the related isometopids, microphysids, and anthocorids are today. It is possible that these ancestors resembled the isometopids for, as has already been demonstrated, the Miridae are most closely related to this one of all the families.
*insert: for the Heteroptera,

As stated above, the families under discussion show distinct relationship with Handlirsch's family group including the Reduviidae, Nabidae, Henicocephalidae, and Phymatidae. In all these the pieces [?sclerites] of the meso- and meta-sterna - which are characteristically still delimited for the basic type of Heteroptera - have been completely fused so that they seem to be entirely simple. Furthermore also the hind coxae have become rotatory so that the insects in question are to be considered as trochalopodous.

Handlirsch designated the Reduviidae as the basic type of this family complex and let the other 3 families radiate from that. However, Kirkaldy was decidedly right when he considered the Nabidae as the most primitive. In it the venation of the membrane is continued right up to the same primitive standard as in the Velocipedidae in the 1st branch. (The presence of an embolium in the nabid subfamily Pachynomina and Nabina is likewise a primitive character (see page 5). The subfamily Reduviolina, which mostly does without the embolium, is therefore to be considered as more highly specialized, this being also evident from the fact that in some genera of this subfamily the venation of the membrane even in the long-winged form is more or less reduced (Arachnocoris Scott, Arbela Stål) and that even the beak of one genus, Scotomedes Stål, is 3-segmented, at least externally.) The beak also still has the primitive 4 segments, although the first one is greatly shortened; 3 segments are supposed to occur only in the genus Scotomedes Stål which is unknown to me. Moreover, the beak of a few genera in Nabina, as well as spp. in Pachynomina, is short, very powerful and on the whole strongly reminiscent of the beak of reduviids.

In reduviids, macrocephalids, and henicocephalids the first segment of the beak is always no longer visible and the beak has become so short that it does not reach beyond the prosternum. Of the reduviids, spp. of the subfamily Piratina Stål, show very great similarity in habitus with the nabids which indeed had been combined in one family with the reduviids by all authors before Fieber (1861) and also by several authors after that, and had been placed beside the Piratina. One could therefore be inclined to derive the reduviids as a branch from the nabids in which the number of rostral segments and the venation of the membrane had been reduced. But in the reduviids there is a contrivance which they have in common with the macrocephalids: the very characteristic stridulation groove of the prosternum. Furthermore the spp. of these two families lay their eggs quite free [i.e., in the open] and their ♀ genital organs are therefore developed according to a type deviating from that of the nabids.

27

and doing without the saw sheath altogether. Those two circumstances seem to mean a common origin. But to derive both reduviids and macrocephalids directly from the nabids seems risky to me for the macrocephalids show too great differences to justify such a concept. Neither is it exactly possible to consider the macrocephalids only as highly specialized reduviids because their membrane is still very frequently found on a distinctly more primitive level of development than the reduviid membrane with its greatly reduced venation. Therefore it seems presumable to me that all the four above-mentioned families belonging to the same complex ~~of nabid-like ancestors~~ come from nabid-like ancestors, but that the Phylum branched into 3 branches one of which, the Nabidae, still has several primitive characters whereas the other 2 are more highly specialized. Of the latter, one soon again divided into two small branches, the reduviids and macrocephalids; the other included the hemicocephalids (see page 17).

The second great Gymnoceratae trunk of Handlirsh's very soon divided into two branches; the Coreidae and the Pentatomidae. Later the author mentioned the pentatomids as a quite independent group which certainly is completely right. He derived the Lygaeidae (=Myodochidae), Pyrrhocoridae, and also the Aradidae, Tingididae, and Berytidae (=Neididae) from the Coreidae. This phylogeny is certainly for the most part only supported on weak grounds. The fact that the dorsal glands of coreid nymphs show a reduction of the primitive type which is still present in myodochids, pyrrhocorids, and aradids, is quite decisive evidence against such a concept. No more can the Tingididae derive from the Coreidae since the latter have dorsal glands on the 5th and 6 segments, never on the 4th as do the former (see page 10-11). Also I can form no firm opinion on the kindred relations of most of these families. Still I find this much certain; the pyrrhocorids and coreids cannot be considered as homophyletic (see p.15) Investigation of the internal anatomy and the eggs of myodochids, aradids, tingidids, and neidids ~~for a correct understanding of~~ is absolutely necessary for a correct understanding of these families (see p. 15). Likewise it seems to me the Aradidae [ought] to be removed from the circle of relationship of the above-mentioned families (see p.29). On the other hand, we may assume with great probability that the neidids are closely related to the myodochids, as already demonstrated by Stål (1874). The membrane with only 5 veins, as in the myodochids, is especially worthy of note. Still it seems to me Stål went too far when he united it with the latter as a subfamily. (So did Kirkaldy since he did not mention the Neididae at all in his diagram). They have very little in common with the Coreidae from which Handlirsch derived them. Handlirsch himself has demonstrated (see p.19) that all the abdominal spiracles of the Neididae are dorsal. Both for this and for many other reasons (for example, the characteristic formation of antennae and legs, as well as the presence of only 2 nymphal dorsal glands) this family must be considered as still more highly specialized than the Myodochidae.

Therefore in my opinion, as is evident from the differing egg-structure of the Pentatomidae, Coreidae, and Pyrrhocoridae, Handlirsch's second Gymnoceratae trunk is to be divided up into at least 3 independent branches.

In comparison to Kirkaldy's system, Handlirsch's has a decided advantage in the fact that the author considers the primitive Heteroptera as pagiopodous and derives the trochalopodous families from such. But the fact that I cannot agree with his phylogenetic points of view comes from the circumstance that he artificially divides the Heteroptera with respect to a single adaptive character (projecting or short antennae); and that he combines frequently heterophyletic families in the same branches.

4. My Own System.

The family tree (see Plate) was very kindly drawn by a zoologist, Mr. Fachmann, according to my instructions.

I have already given reasons for my deviating views in the above remarks on Kirkaldy's and Handlirsch's phylogenetic diagrams in such detail that it is sufficient now to uniformly summarize the results thereof, especially since in Chapter IV I will characterize the systematic groups again.

One substantial difference between my System and those of Kirkaldy and Handlirsch is the rejection of the artificial bi-partition of Heteroptera based on a single adaptive character. In my opinion, the Protoheteroptera developed in several (about 6) different directions. I consider the differing formation of the micropyle apparatus of the egg as very characteristic for these directions. The families that show similarity in this respect also prove to be related in others. Thus, for instance, the correctness of bringing the families designated by Kirkaldy as Notonectoideae together is justified by the structure of the micropyle apparatus which is essentially in agreement. But the same thing shows that the Gerridae are also to be reckoned with the same superfamily most naturally. A second very striking proof of the significance of the aforesaid micropyle apparatus is the distinct relationship of the families provided with parietal micropyles, which families, however, were unnaturally separated by Kirkaldy's and Handlirsch's divisions. Only it is to be regretted that the eggs of all families have not yet been investigated. The placement of some families must therefore still be considered as provisional. I will call attention to these families below.

[Agreeing] with Handlirsch and in opposition to Kirkaldy, I am considering the pagiopodous forms as more primitive. The trochalopodous forms developed gradually and often heterophyletically from these. This took place very early in some directions of development so that the now-existing, most primitive forms thereof are only trochalopodous, while at the same time other primitive characters, for example the structure of the sternum [or thorax] show a later level of development.

Branch I (Hydrobiotica)* of the Heteroptera stem (Protoheteroptera) includes only pagiopodous forms, with few exceptions. So far as the eggs are known, they do without the operculum and the micropyle apparatus is apical and central with only one or in any case only a few micropyles (For eggs of Naucoris see page 11). The families belonging to this Branch, all of which are without claw-arolia, are largely water-animals in that they either creep about on the bottom of the water-pond, swim in the water, or paddle around on the water surface. Others, on the other hand, are land bugs but mostly still live in moist places. The antennae are differently modified according to way of life, being short and concealed in the bugs living in the water, long-projecting and mostly filiform in bugs living on the water surface and on the surface of the ground, finally projecting but short in some families whose larvae and nymphs, at least in the Ochteridae, lead a subterranean way of life.

This first Branch is divided into 4 branches, also representing many superfamilies, the first of which, Ochteroideae, is conceived as a direct continuation of the Branch (see page 13). Probably the family Nerthridae issues from this. The peculiar family Peloridiidae (see page 1)** certainly also belongs to the same circle of relationship. The second branch, the superfamily Notonectoideae, still characterized by a compound sternum, is divided into several (4 or 5) small branches. The most primitive of these is the Belostomatidae from which the trochalopodous Nepidae originated, as well as probably the still more highly specialized Naucoridae. The Notonectidae (see page 22) seem to have branched off independently from these. Whether the family Corixidae sprang from the Notonectidae or quite independently, and whether it is to be counted among the Heteroptera at all must be left undecided (see page 19). The third branch, the superfamily Acanthioideae, all of whose representatives have long antennae and simple meso- and meta-sterna, but are still pagiopodous, sends out 4 small branches of which the family Velocipedidae is the most primitive as is evident from the venation of the membrane and the structure of the ♀ genital segments. The family Aepophilidae (page 16) adapted for life under water came forth in the vicinity of this small branch. The Acanthiadae and Loptopodidae are somewhat more highly specialized. The 4th branch, Gerroideae, which also has long filiform antennae∅ and simple meso- and meta-sterna, but is characterized by homogeneous elytra and has become trochalopodous as a result of way of life (water-runners), is divided into 4 small branches, the families Gerridae, Veliadae, Hydrometridae, and Mesoveliadae but of these the place of the latter is uncertain. It may perhaps belong to Branch III (page 19).

Branch II (Trichotelocera) embraces only a single superfamily Dipsocoroideae, divided into 2 families Schizopteridae and Dipsocoridae which, especially the former, seem to be very primitive in many respects (page 18). However it is doubtful whether erection of this Branch is well grounded. Possibly the superfamily Dipsocoroideae is only a branch of Branch I. Its internal anatomy as well as the structure of the eggs is still completely unknown. Until research has settled this question, it seems to me that the quite peculiar formation of the antennae, reminiscent of that in Cicadaria, provisionally justifies separating the Dipsocoroideae from the other Heteroptera as an independent Branch.

Branch III (Anonychia) is well characterized by the peculiar structure of the micropyle apparatus of the eggs (numerous parietal micropyles). The antennae typically have the last 2 segments slenderer or they are filiform. If there is an exception in this respect, the last two segments, very rarely only the last (Macrocephalidae) are thick (in the latter case however the beak is only 3-segmented). The claws are provided with arolia only in one family, Miridae, and here too, not always so provided. This Branch is divided into 3 branches. From the first branch, the pagiopodous superfamily Cimicoideae, characterized by a compound sternum, arose in diverging directions on the one hand, Isometopidae and Miridae and on the other the Microphysidae, Termatophylidae, Anthocoridae, and Cimicidae (pages 23-24) and also perhaps Polyctenidae. The second branch, the trochalopodous superfamily Reduvioideae, characterized by simple meso- and meta-sterna, further divides into 4 small branches, the Nabidae which includes the most primitive forms (page 26); the highly specialized Henicocephalidae, and then the Reduviidae and Macrocephalidae which are closely related to each other. A 3rd branch, the superfamily Aradoideae is probably to be added to these two branches; it also has simple meso- and meta-sterna and rotatory hind coxae but its beak is straight and not curved. This branch is perhaps divided into 2 small branches, the new family Joppeicidae and the Aradidae. The former includes only a single genus which was previously counted among the Aradidae (Puton (1881;122)) or Myodochidae (Bergroth 1898;188). The following prove that the later concept is decidedly wrong: the beak with only 3 segments, the 2-segmented tarsi, the claws entirely without arolia, and finally the structure of the ♀ genital segments which certainly are cleft in the middle but bear no saw case. This small family also deviates from the Aradidae by several characters: the occurrence of ocelli, the last thin antennal segments, and the venation of the membrane in which 3 respects they are very strongly reminiscent of anthocorids. The structure of the eggs is still unknown but the for the most part striking characters seem to point [illegible] family to its place in Branch III. Although the relationship with the aradids is not very conspicuous it still does not seem to be wholly i

---

*. This name does not characterize all forms belonging here, certainly, for a few (Acanthioideae) are land bugs for the most part. However, with the sole exception of the Leptopodidae, they live on the banks of bodies of water or in moist places. Naming can never be fully adequate. It must be considered sufficient when it designates the typical forms of the respective groups. These remarks refer both to the above and to other names used below.

**. This family was not mentioned at all by Handlirsch, it was united by Kirkaldy (1906) with the Ochteridae without basis.

∅. Except for the genus Rheumatobates Bergr. and a few related ones whose antennae in the ♂ have been quite peculiarly transformed.

that this family also had the same origin. It had previously been derived from the pentatomids (Tessaratomina) by Kirkaldy and from the Coreidae by Handlirsch, but in my opinion without reason. Although the 3-segmented beak of Aradidae can be derived from the 4-segmented beak of pentatomids or coreids, it is still rather improbable that the claw-arolia acquired by this family have been lost again. Indeed the formation of the antennae strongly deviates from that typical for Branch III. But the formation of the antennae has frequently proved to be of little importance in systematic respects. The placement of the two aforesaid families, Joppeicidae and Aradidae must be considered as only provisional until the structure of their eggs and their internal anatomy has been sufficiently investigated. Here it may still only be noted that the similarity of Aradidae with Tingididae, as a result of which most authors placed these families beside each other, is very superficial. Certainly the tarsi in both of these families are only 2-segmented. Such tarsi, however, are also found in several families of Branch III (Microphysidae, Joppeicidae, Macrocephalidae) and the groove- [or channel-, gutter-, etc.] formation of the gula which is also common to both families, also shows up in the Macrocephalidae. These phenomena are independently acquired characters which do not depend upon any closer blood relationship.

The peculiar, striking similarity in venation of the membrane in primitive Nabidae of Branch III and Velocipedidae and Ochteridae of Branch I seems to indicate that these two Branches may have had the same origin a long ways back.

In Branch IV (Onychiophora), which coincides with the superfamily Neidoideae, I am provisionally combining families whose claws are always provided with arolia, whose antennae are filiform or the last segment is more or less thickened, and whose membrane is never provided with many parallel veins. Unfortunately the eggs of only a single family (Pyrrhocoridae) have been examined. They are without operculum and also are otherwise differently formed from those of all other families, even from those of Coreidae (page 11) for which reason this family cannot be united with the Coreidae in the same branch. If the eggs of the other families of Branch IV prove to be formed the same as in Pyrrhocoridae, the questionable relationship will be confirmed. Until then, the belonging at least of Piesmidae (page 15), Tingididae, and Hebridae to this branch is more or less problematicas. As I picture it to myself, the Branch is divided into 2 branches, the families Pyrrhocoridae and Myodochidae, which have specialized in diverging direction (page 15). Without doubt the Neididae and perhaps also the Piesmidae and Tingididae issue from the latter branch. In the occurrence of ocelli, in the scutellum not concealed by the pronotum, and in the venation of the membrane (in macropterous forms), the Piesmidae have characters which are reminiscent of Myodochidae. Future investigation of the eggs will decide whether the Hebridae in fact also belong to this Branch. The structure of the beak and the claws provided with arolia show that this family in any case cannot be referred to the Gerroideae.

Branch V (Polyneuria) includes the superfamily Coreoideae with the family Coreidae. The membrane venation in this family shows great similarity with that of the Pentatomoideae (see Branch VI) and Branches V and VI perhaps long since sprang from one family-branch. In any case, the substantial difference in structure of the head, in the typical number of antennal segments and in the structure of the eggs (page 11) are enough to keep these two Branches separated for now.

Branch VI (Peltocephala), finally, is identical with the superfamily Pentatomoideae. The family Pentatomidae is a more primitive branch of this Branch, the Urolabididae and Thyreocoridae are more highly specialized. Perhaps a few of the pentatomid subfamilies cited by Kirkaldy in his 1909 Catalog deserve to be considered as independent families such as Coptosominae, Scutellerinae, etc., for example. But unfortunately I am not now able to engage in studies of this question.

[illegible] Characteristics of the Superfamilies and Families plus a historical survey of earlier views.

31.

In the following characterizations, the characters whose validity does not yet seem to be sufficiently verified, are given in parentheses. Primitive characters are in italics. Where the hemelytra are described, the descriptions always refer to the conditions in Forma macroptera. The family Polyctenidae has been omitted from the families because it is unknown to me in nature and all previous descriptions are not sufficient to determine its position in the System. Thus, for instance, Speiser completely overlooked such an important structure as the genital segments.

Series I Hydrobiotica: *Unguiculi destitute of arolia.* Metasternum destitute of orificia or very rarely (Velocipedidae) provided with very minute orificia. Nymphs without orificia of the dorsal glands or provided with a single orificium only on the 4th abdominal segment. Ova destitute of operculum, with a few central apical micropyles (Eggs of the families Ochteridae, Nerthridae, Leptopodidae, Velocipedidae, Aepophilidae, and Mesoveliadae not yet examined.).

This series corresponds to the Hydrocorisae Latr., or Cryptocerata Fieb., plus the Oculatae Latr. (Riparii Burm.) and Ploteres Latr. (Amphibicorisae Leon Duf.). The recently erected family Aepophilidae also belongs here. In Kirkaldy's System, the Series is represented by his superfamily Notonectoideae, by the Nepoideae families Nepidae and Gerridae, as well as by the Miroideae family Aepophilidae; in Handlirsch's System by his Cryptocerata, as well as by the gymnocerate families Velocipedidae, Saldidae, Hydrometridae, Mesoveliidae, and Aepophilidae.

Superfamily Ochteroideae: *Ocelli two* or very rarely none, in this case the diaphanous hemelytra would show *ramose veins*, producing a great many cells. Antennae 4 or 3 segmented, simple, very short, never longer than the head, often concealed. *Meso- and meta-sterna composite.* Acetabula of front legs excised with [or by] the posterior margin of the prosternum. *Hind coxae cardinate* [i.e., hinged]. Legs never natatorial. (Abdominal *spiracles 2-7 ventral*). Nymphs without orificia of the dorsal glands (sec. Kirkaldy).

This Superfamily coincides with the cryptocerate subsection Litoralis Fieb. Of the families belonging here, the first, as is evident from the following exposition, has frequently been placed in the Gymnoceratae. In fact it seems to connect the superfamily Notonectoideae with the superfamily Acanthioideae and probably contains the most primitive forms of still living Heteroptera (page 13). Blanchard (1852) even went so far as to separate it from these (Prostomophora) and combine it with the Homoptera under the name of Hipostomophora.

Phalanx I Ochteriformes: *Ocelli present. Antennae 4-segmented. Beak 4-segmented. Hemelytra of macropterous form composed of clavus, corium, embolium, and hardly separate membrane.*

Family I Ochteridae: *Clypeus turning backward. Antennae freely projecting.* Beak long, with short, thick, *ring-like basal segment.* *Membrane with oblong areolae, in 2 rows circumscribed by a strong vein, on the margin with inconspicuous, radiating veins. Front legs equal to the middle legs, cursorial. Front and middle tarsi one-segmented, hind tarsi 2-segmented, all bi-unguiculate.* Last ventral (genital) segment in the ♀ cleft in the middle, inclosing [or confining] the terebra.

The kindred relationships of Ochteridae (=Pelogonidae) to the Acanthioideae on the one hand and to the Notonectoideae (Cryptoceratae) on the other, have been variously interpreted by different authors. The genus Octerus (Pelogonus) was referred to the Geocorisae (Aurocorisae of Westwood) by several authors and placed in the vicinity of

Acanthiae or Leptopoda, as did Latreille (1825, Oculatae) [others named, page 61 of text]. It was referred to Reduvites, which belongs to Laporte's Section Haemathelges with a few cryptocerate families, by Laporte (1832) along with Leptopus. Stål placed it (1864) as a separate family between Hydrobatida (=Gerridae) and Mononychida (=Nerthridae p.); Brullé (1835), Blanchard (1840), Lucas (1849) placed it together with the Nerthridae between Nepidae and Leptopodidae as the family Galgulidae. Amyot (1848) placed it opposite the remaining Cryptoceratae, Occulticornes, as a separate tripe the Brevicornes. Other authors [many named, page 61 of text] brought it under the Hydrocorisae (Cryptocerata). Schioedte (1869) placed it among his Pagiopoda between Acanthiae and Naucorides; and Kirkaldy (1908) put it together as a small group with the Acanthiidae in his superfamily Notonectoideae.

Family II Nerthridae: Clypeus turning backward. Antennae hidden. Beak short. Membrane on the posterior margin irregularly areolate or destitute of veins. Legs differently formed, the front legs raptorial. Front tarsi 1-segmented.

The Nerthridae (=Galgulidae and Mononychidae) were very frequently combined as a separate subfamily with the foregoing family. [Authors who did so named, page 61 of text]. Spinola placed it (1840) as a "tribe" of its own between the Hydrocorisae and Amphibicorisae, while the Ochteridae were referred to the Geocorysae. In Westwood (1840) the Nerthridae (Galgulidae) form the first family among his Aurocorisa; while the Ochteridae were placed in the second (Acanthiidae). Amyot and Serville (1843) set it up under the name Bigemmes as the first family of the Hydrocorisae, while the Ochteridae are found beside the Acanthiadae in the geocoriaad family Nudirostres. Just so did Dohrn (1859) and Walker (1873). Amyot (1848) likewise separated the two families from each other in that he transferred the Nerthridae to the tribe Occulticornes, the Ochteridae to the tribe Brevicornes. Fieber (1851), Champion (1901), and Handlirsch (1908) considered the two families as separate from each other. Stahl [sic!] (1864) placed the Mononychida between Pelogonida and Naucorida. Kirkaldy still in 1906 treated Ochteridae and Nerthridae as separate families but united them later on in 1907. Still later, in 1909 (page XXIV) he placed some genera of this family (Mononyx etc.) under the Naucoridae. Finally de la Torre Bueno united the Nerthridae and Naucoridae. (Page 20)

Phalanx II Peloridiiformes: Ocelli absent. Antennae 3-segmented, the last segment submammilla-form—pointed on the end, on the apex itself (seen under the microscope). Beak going out between the front coxae, 3-segmented, with the basal segment hidden between the lamellae of the prostethium. Hemelytra diaphanous showing ramose veins producing a great many cells.

Family III Peloridiidae: Head seen from below horizontally sub-planate, posteriorly depressed in a broadly triangular process, and very closely pressed to the prostethium and connate with it, apically trilobate, produced and separated from it by a carinula and transverse depressions. Legs simple, formed alike. Tarsi 2-segmented.

A single genus, Peloridium Bredd. (page 2).

Superfamily II Notonectoidae: Ocelli absent. Antennae very short, shorter than the head, subocular, more or less hidden. Hemelytra for the most part provided with an embolium. Meso- and meta-sterna composite. Hind coxae mostly cardinate. Hind legs mostly natatorial. Nymphs without orificia of the dorsal glands.

This superfamily is identical with Latreille's (1825) Hydrocorisae (except the Nerthridae) and with Fieber's cryptocerate subsection Aquatilia. Latreille had already divided the Hydrocorisae into 2 groups (tribes). In "Cat.Hemipt." (1910) Kirkaldy kept the same Classification which he based on the different insertion of the front coxae. I find it best to follow these authors.

Phalanx I Nepaeformes; Front coxae inserted on or near the anterior margin of the prosternum. Body flattened above and below or a little convex. Beak 3-segmented Front legs raptorial.

Family IV Belostomatidae; Beak short, provided with (rudimentary) labial palpi. Antennae 4-segmented, provided with lateral processes. Hemelytra provided with an embolium. Membrane mostly reticulato-venose. Hind coxae cardinate. Hind legs natatorial. Middle and hind tarsi 2-segmented, provided with sterigmata [i.e., forks or props] at the base, with 2 unguiculi. Abdomen apically with the appendages of the aidotheca [?phallotheca] short, linear-lanceolate or spatulate, not much projecting more frequently enclosed. Abdominal spiracles frequently partly atrophied.

Family V Nepidae; Beak short, provided with (rudimentary) labial palpi. Antennae 3-segmented, provided with lateral processes. Hemelytra with an indistinct embolium. Membrane mostly reticulato-venose. Hind coxae rotatory. Legs gressorial. All tarsi 1-segmented. Appendages of aidotheca elongated or very long. (Abdominal spiracles 2, 3, and 7 atrophied, 4, 5, and 6 distinct.)

The close relationship of this family with the preceding was presented in detail by Schmidt (page 17).

Family VI Naucoridae; Beak destitute of labial palpi. Antennae 4-segmented, simple. Hemelytra provided with an embolium. Membrane without veins. Hind coxae cardinate. Tarsi at least the posterior ones 2-segmented and biunguiculate. Abdomen apically without the appendages of the aidotheca. (Abdominal spiracles 2-7 ventral).

Phalanx II Notonectaeformes; Front coxae inserted on the posterior margin of the prosternum. Beak destitute of palpi. Antennae simple. Membrane destitute of veins. Front legs not at all raptorial, hind legs natatorial, coxae cardinate. Abdomen apically without appendages of the aidotheca.

See page 19 for the relationship of the Corixidae with the other 2 families.

Family VII Notonectidae; Antennae 4-segmented. Beak 4- or 3-segmented, short. Hemelytra provided with an embolium and the membrane destitute of veins, or all coriaceous. Hind coxae cardinate. Hind legs natatorial. Tarsi 2-segmented, the front ones now and then in the ♂ 1-segmented. (Abdominal spiracles 2-7 ventral). Body convex, sometimes higher.

Family VIII Corixidae; Antennae 4- or rarely 3-segmented. Front strongly turning backward. Beak unsegmented or at most 2-segmented, short, concealed under the epistoma. Hemelytra "valvantia", with linear embolium, membrane without veins. Legs differently formed, the front legs "paliferus" [?shovel-bearing], the middles ones simple, the hind legs natatorial. Hind coxae cardinate. Front tarsi 1-segmented, shovel-shaped. Abdominal segments in the ♂ irregular, in the ♀ the same [or equal]. (Abdominal spiracles 2-7 ventral).

Superfamily III Acanthioideae; Ocelli two or very rarely none, in this case the eyes are small, the hemelytra greatly abbreviated. Antennae 4-segmented, always much longer than the head. Beak 3-segmented (that of the genus Aepophilus wrongly described by Signoret and Puton (1879) as 4-segmented. The beak is in fact 3-segmented, with the 1st segment shorter than the 2nd, this and the 3rd subequal in length.) Meso- and meta-sterna simple. Hind coxae cardinate. Legs saltatorial or cursorial. Tarsi 3-segmented. Abdominal spiracles 2-7 ventral. Genital segment in the ♂ with the opening apico-dorsal, with two curved styli apically convergent.

The above-described superfamily corresponds - apart from the only later discovered Velocipedidae and Aepophilidae, - completely to the Leptopodidae of Brullé (1835).

Blanchard (1840), and Lucas (1849) to the Riparii of Burmeister (1835), Saldidae of Haerensprung (1860), Oculata Flor (1860), Oculatina Dougl. and Scott (1865), Saldidae Puton (1869, 1875, 1886, 1899), Reuter (1875), Saudners (1876), Distant (1902) and includes both Fieber's families Acanthidea (1851, Saldeae 1861) and Leptopoidae (1851 Leptopodae 1861). The relationship with Ochterus (Pelogonus) which was also discussed 34 above, has already been indicated by Latreille [and others, page 64 of text]. The genera belonging to the above-described superfamily were brought together with the reduviids and nabids by Laport (but only the genus Leptopus) in 1832 [and others, page 64 of the text]. In any case this relationship must be considered as remote. When in "Monographia Nabidarum" (1909) I derived the leptopodids from the nabidoids, this was an error in all probability. However it is to be noted that Laporte as early as 1832 referred the genus Leptopus to the Reduvites while he placed Acanthia far away from it in an entirely different tribe beside Cimex; and that Westwood (1840) also emphasized the fact that in his opinion, Leptopus is a transition to the reduviids. And in fact the leptopodids, as I noted in "Remarks on nabids", shows a certain similarity to some Nabidae (Arbela Stål), especially in the striking structure of the femora. Also the beak of the leptopodids, even if its is only 3-segmented, recalls that of the Nabidae. But since the abdomen (and no doubt the still undescribed eggs also) is very differently formed in the two families, perhaps the aforesaid similarities are quite incidental unless they are of an atavistic nature and in such case witness to the ancient common origin of Acanthioideae and Nabidoideae, which we have already pointed out (pages 29-30).

Phalanx I Acanthiiformes: Two distinct ocelli* or very rarely confluent into one**. Eyes very large, strongly prominent. Hemelytra composed of clavus, corium and membrane rarely also cuneus.

---

*. Fieber (1861) and Distant (1904) wrongly described the ocelli of Leptopodidae Cf. Reuter "On the genus Valleriola Dist." in Wien.Ent.Zeit.1907:211-214.

**. Saldoida slossoni Osb. f.brachyptera.

Family IX Velocipedidae: Antennae filiform. Beak rather long, the first segment very short. Eyes internally posteriorly slightly emarginate. Hemelytra provided with a cuneus. Membrane provided with discoidal areas and with many veins radiating from them to the margins. Two genital segments visible in the ♀, enclosing the terebra in the middle. (Dorsal glands of the nymph not yet examined).

Only a single, probably very old, genus.

Family X Acanthiadae: (The families must be called Acanthiadae, Veliadae, and Mesoveliadae and not Acanthiidae, Veliidae, and Mesoveliidae. See, for instance, Curtius and Zumpt's Latin Grammar, sections 348 and 245.). Antennae subfiliform or with the last two segments thickened. Beak long, reaching the apex of the mesosternum, first segment very short. Eyes postero-internally emarginate or sometimes only subsinuate**. Hemelytra without a cuneus. Membrane with 5 or 6 longitudinal veins forming longitudinal areolae rather far in front of the apex of the membrane. (Areola of wings narrow, divided by the hamus.) Front femora not at all thicker than the rest. Last ventral segment in the ♀ long-laminately produced backward and covering the genital segment. Nymphs with a single orificium of the dorsal gland on the anterior margin of the 4th segment.

Family XI Leptopodidae: Antennae very slender. Beak short, first segment as long as the head. Eyes subglobose. Hemelytra without a cuneus. Membrane with 4 longitudinal veins connected to the apex of the membrane by the peripheral vein. (Primary and subtended veins of wing contiguous.) Front femora a little thickened, all [genera] strongly attenuated toward the apex. 7th genital segment in the ♀ as in the preceding. (Dorsal glands of nymph not yet examined).

Although most authors consider the Leptopodidae as only a subfamily of the Acanthiadae, I still believe that Fieber was right when he described it as a separate family. Certainly the genital segments are developed according to the same type and the large projecting eyes of the two families give them great similarity in habitus. But the eyes also, when more closely examined, prove to be not at all similarly developed and the other above-described differences between the two families seem to me to be so numerous and weighty that I find Fieber's concept of the Leptopodidae as a separate family again worthy of acceptance. I am also referring here to the relationship with the Nabidae which has just been discussed above (page 34).

Phalanx II Aepophiliformes: Ocelli none. Eyes very little rounded.

Family XII Aepophilidae: Antennae with the last 2 segments rather fusiform. Hemelytra strongly abbreviated, squamiform apically externally acuminate, with the subscutellar margin oblique and sinuate. Last ventral segment not produced backward at all. Two genital segments visible in the ♀, cleft in the middle and inclosing the terebra. Nymphs without orificia of the dorsal glands.

Superfamily IV Gerroideae: Ocelli two or none. Antennae 4-segmented always much longer than the head, mostly filiform. Beak 4- or 3-segmented. Hemelytra with corium, clavus, and membrane confluent or subconfluent into one. Meso- and meta-sterna simple. Hind coxae rotatory. Connexivum turning upward. Abdominal spiracles 2-7 ventral.

So long as the kindred relations of the water bugs [or water runners] cited below as two different phalanges have not yet been unravelled, it seems advisable to me to put them together here still. The Gerroideae were previously placed opposite the Hydrocorisae and Geocorisae as a different series, the Amphibicorisae, by some authors Dufour (1833), Spinola (1840), Herrich-Schäffer*(1853), and J.Sahlberg (1875). According to others [see page 65 of text] they form a separate, the second, Subsection of Gymnocerata**. Zetterstedt (1828) referred them to the Hydrocorisae, all other authors to the Geocorisae (Aurocorisa Westw.) or Gymnocerata. Relationship with the Reduviidae is indicated by most of the authors [many named on pp.65 and 66 of text]*** because the Gerroideae were placed beside these or the next related families (Nabidae, Henicocephalidae, and - by Oshanin - before the Macrocephalidae). Amyot and Serville (1843) as well as Amyot (1848) even referred the Hydrometra with the Reduviidae to the Nudirostres and put the Ploteres (=Gerridae and Veliadae) right after this. Herrich-Schäffer (1853)*** combined the Hydrometra with the Reduvini. This concept of the relationship of the Gerroideae with the Reduvioideae still shows up in Kirkaldy's System (1902, 1907, 1908, 1909). I have already shown above (page 16) that this view is probably not right. An indication relative to closer relationship with the Acanthioideae is found in Billberg (1820) [and others, page 66 of text].*** Osborn (1895) even derives the Gerridae and Hydrometridae from the Acanthiadae (page 13).

---

*. The genus Hydrometra (Limnobates) is still referred to the Reduvini

**. Fieber also refers the family Hebroidea to this Subsection.

***. The genus Hebrus counted in.

Phalanx I Gerriformes: Hind coxae far apart, inserted on the sides of the body. Scutellum covered by a triangular prolongation of the pronotum, rarely hardly visible, or very minute, or absent. Nymphs without orificia of the dorsal glands.

Family XIII Gerridae: Head short, attenuate and sloped toward the apex. Two ocelli, sometimes very obsolete. Eyes touching the apex of pronotum. Beak 4-segmented, with 1st and 2nd segments very short. Wings with 3 lobes. [illegible] large, metasternum short. Hind coxae long, cylindrical, the middle coxae far distant from the front coxae, but strongly approaching the hind coxae. Hind legs and especially the middle legs much longer than the front legs. Tarsi 2-segmented. Unguiculi ante-apical.

Family XIV Veliadae: Head short, attenuate and inclined toward the apex. Eyes touching the apex of the pronotum. Ocelli none or obsolete. Beak 3-segmented. Pronotum posteriorly produced in a triangle. Wings with 3 lobes. Pro-, meso-, and meta-sterna subequal in length. Middle coxae almost equally distant from the front and hind coxae. Hind legs a little longer than the front ones. Femora thickened. Tarsi bi- or tri-articulate. Unguiculi ante-apical.

Most authors place this family together with the foregoing and often as a separate subfamily. However the difference between them seems to me to be so substantial that, along with Fieber (1861, Hydroessae) and Stål (1864, Veliida), I am considering it as a separate family.

Family XV Hydrometridae: Head strongly elongated, horizontal, subcylindrical, and thickened toward the apex. No ocelli. Eyes far distanct from the anterior margin of pronotum. Beak short, 3-segmented. Scutellum very minute or absent. Wings destitute of lobes. Legs filiform, graceful. Tarsi 3-segmented. Unguiculi apical.

Hydrometridae are rather unlike Gerridae in habitus and not a little reminiscent of certain linear reduviids, for example, Raphidosoma Am. and Serv. Also as above stated, ~~the genus Hydrometra (Limnobates)~~ Amyot and Serville in 1843 and Amyot in 1948 separated the genus Hydrometra (Limnobates) off from the other water-runners with the reduviids etc., in the family Nudirostres and it was also brought into Herrich-Schäffer's family Reduvini by him in 1853. Even quite recently de la Torre Bueno accepted a relationship between Hydrometridae and Reduviidae. However, I have already shown that the assumed similarity is only a superficial one (page 19-20).

Phalanx II Mesoveliiformes: Coxae contiguous. Scutellum visible. Unguiculi apical. (Orificia of dorsalis of the nymph not yet examined.)

It seems rather doubtful to me whether this Phalanx is actually related to the foregoing.* Perhaps de la Torre Bueno was right when he (page 20) considered it as close to the nabids. Investigation of the internal anatomy and the eggs will solve this problem. *insert: It is therefore placed here only provisionally.

Family XVI Mesoveliadae: Body oblong. Head oblong, attenuate toward the apex, sloped. Ocelli large. Eyes subcontiguous with the pronotum. Beak 3-segmented. Hemelytra with clavus and membrane membranaceous, corium submembranaceous. Membrane destitute of veins. Tarsi 3-segmented.

Series II Trichotelocera: Unguiculi destitute of arolia. Antennae 4-segmented, with the first 2 segments short, the last two long, slender, pilose. Hemelytra and wings with veins varying. (Eggs and also orificia of dorsalis of the nymphs not examined).

This series corresponds to the former family Dipsocoridae or Ceratocombidae. The genera Dipsocoris Hal. and Ceratocombus Bgr. were at that time described as Lygaeidae (Myodochidae). Dohrn (1859) placed the genus Dipsocoris as type of a subfamily of its own (Dipsocoridae) with the myodochids and anthocorids in the family Infericornia. The sharp-sighted Fieber (1860 and 1861) found sufficient grounds for erecting a family of its own for the animals belonging here. But later several authors [named on page 67 of the text] set it up, together with the anthocorids, microphysids, and cimicids, as a separate subfamily. Reuter (1875) and Puton (1878) added the Miridae to this complon. The above-described insects were conceived of as an independent family by Saunders (1875, between cimicids and reduviids), Reuter (1891), Lethierry and Severin (1896, between Aepophilidae and Cimicidae), Champion (1901, between Anthocoridae and Cimicidae), Distant (1904, between Acanthiadae and Cimicidae), Kirkaldy (1906 between aepophilids and acanthiads, as well as in 1907 and 1908 between mirids and aepophilids), and finally Oshanin (1910, between the aepophilids and cimicids). Both Handlirsch and Kirkaldy derived them from the Anthocoridae. I have already set forth the fact that this concept is probably incorrect (page 18). However, it seems uncertain to me whether erection of this series is completely justified or whether it should not much rather be considered as only a branch of the first Branch (page 28). The eggs of these animals have not yet been investigated. The two subfamilies which I erected in 1891, I now consider as independent families.

Superfamily V Dipsocoroideae: Tarsi 3-segmented.

Family XVII Schizopteridae: Head, seen from above, strongly transverse, deflexed [i.e., bent abruptly downward], for the most part closely appressed between the prominent front acetabula. Beak 3-segmented. Hemelytra with greatly varying structure, frequently all coriaceous.

Fam. XVIII. Dipsocoridae: Head projecting or slightly declivous. Eyes minute. Beak 3-segmented. Hemelytra with varying structure of the veins, frequently incised at the lateral margin before the apex of corium. Front acetabula not at all prominent.

Series III Anonychia: Unguiculi destitute of arolia or rarely (Miridae) provided with them, in that case the membrane is bi- or mon-areolate and the antennae typically become*graceful toward the apex. *[i.e., long and slender]. Antennae much longer than the head, 4-segmented rarely composed of many segments, with the 2nd segment the longest for the most part, the last two typically longer and slenderer, very rarely thicker than the 2nd, rarely (Macrocephalidae) only the last is thickened, in this case the unguiculi are without arolia. Hemelytra composed of clavus, corium, and membrane, at times also of embolium and cuneus, very rarely (Henicocephalidae) homogeneous, membranaceous. For the most part the metasternum is provided with orificia. Eggs operculate, with many parietal micropyles.

The Series corresponds to Dumeril's Zoadelges, not counting the genus Hydrometra, as well as to the Nation erected by Billberg, the Cimicides, except the genus Tingis. In Kirkaldy's System it is identical to the superfamily Miroideae (Dipsocoridae and Aepophilidae excepted) beside the Nepoideae families Nabidae, Reduviidae, Macrocephalidae, and Enicocephalidae. In Handlirsch, it is represented by a part of the velocipedid branch (Isometopidae, Anthocoridae, Capsidae, and Cimicidae) as well as by the reduviid branch (page 23 et seq.).

Superfamily VI Cimicoideae: Meso- and metasterna composite (sutures of the family Cimicidae obsolete). Hind coxae cardinate. Unguiculi destitute of arolia, very rarely (Miridae) provided with them. Abdominal spiracles 2-7 ventral. Styli or forceps of ♂ genitalia differently formed or only the left forceps is unfolded [or without folds]. The two genital segments in the ♀ are cleft, inclosing the terebra in the middle.

The close relationship of the families described below was already pointed out by the author in 1875 when he combined them all into one family, the Cimicidae (in addition to the Dipsocoridae - Ceratocombidae). Puton (1878, Capsides) followed the author in this concept. Later the families were again separated from each other and today I am even setting up the Termatophylina and Microphysina as separate families (page 24 et seq.). However their relationship has gradually become clear to the authors and is now generally recognized. For the rest this superfamily is identical to the superfamily Miroideae Kird. (except for the dipsocorids and aepophilids). Handlirsch combined it with the Acanthioideae (pages 21-22).

Phalanx I Miriformes: Beak 4-segmented. Ventral anterior segments covering the base of the following segment. Lobes of the ♀ genital segments visible.

Family XIX Isometopidae: Ocelli large. Hemelytra provided with a distinct cuneus. Membrane provided with 1 to 2 areoles or with only 1 vein. Unguiculi without arolia (according to Poppius). (Orificia of dorsal glands of the nymph not yet examined).

The Isometopidae were first described as a family by Fieber (1860); but right after that Baerensprung (1860) referred them to the Miridae as a tribe (Cephalocorides). Further-more they were united with these, although as a separate group , by Puton (1869, etc.), the author (1875, 1878), and Distant (1904). Still later the author (1905) recognized them as a separate family and Handlirsch (1908) followed him in this concept. The mistake in considering the isometopids as only a subfamily of the Miridae resulted in the fact that until today I had not looked at the systematic units which have been described in this discussion as subfamilies of Miridae, and which in fact are to be considered as doubtless of the same value as the subfamilies of other families.

For the rest, it may be interesting to note, with respect to the conception of the relationship of isometopids with the other related families discussed above, that the first species thereof (Isometopus intrusus) was described as an Acanthia (=Cimex) by Herrich-Schaffer and in 1853 was combined with some anthocorids in his family Xylocorides.

Family XX Miridae: Ocelli absent, at times ocelloid spots on the sites of the ocelli. Hemelytra mostly provided with a very distinct cuneus, very rarely (Myrmecoris Gorski, Pithanus Fieb., Myrmecophyes Osh.) without it. Membrane for the most part mono- or bi-areolate; very rarely (Resthenia Spin., Callichila Reut., Platytylus Fieb.) with veins radiating from the areoles or (Solenoxyphus Reut.) with reticulate veins occupying the disk or (Myrmecophyes Osh.) with irregular free veins. Unguiculi frequently provided with arolia. Nymphs with a single orificium or with 2 geminate orificia on the anterior margin of the 4th segment.

On the basis of the absence of ocelli the Miridae were long considered as related to the Pyrrhocoridae. This was done by Latreille (1825), Laporte (1832), and Spinola (1840) the last of which combined these 2 families under the name of Astemmites, as well as by Amyot and Serville (1943) [and others, page 69 of text], and finally by Osborn (1895) all of whom still put them right beside the Pyrrhocoridae. Blanchard (1852) placed them right after the Coreidae, in which connection it is to be noted that he also referred the pyrrhocorids to these. However, this artificial placement cannot withstand a sharper critique Brullé (1835) and Westwood (1840) already pointed out the relationship with the cimicids and reduviids; while Kirschbaun (1855) compared the mirids with the anthocorids on the basis of development of the cuneus. Furthermore the following authors [page 69 of text] placed them beside the anthocorids. Distant (1904) placed them between Cimicidae and Anthocoridae. Stål (1864) placed the Miridae between the Pyrrhocoridae and the Anthocoridae. The relationship between the mirids and the anthocorids, microphysids, and cimicids was even understood by Schioedte (1869) as so close that he combined them in one family to which, however, he also referred the acanthiads and the leptopodids. The author (1875) also had exaggerated this relationship since, as stated above, he erected the family Cimicidae with the subfamilies Capsina (in addition to the Isometopina), Anthocorina, Cimicina, and Ceratocombina (I have already mentioned the fact that the Ceratocombidae (Dipsocoridae) do not belong in this circle of relationship) and Puton (1878) followed him in this respect. The fact that the Miridae have again been separated from the other related families has already been discussed in the foregoing.

Phalanx Cimiciformes: Beak 3- or 4-segmented, in this case the first segment is the shortest. Unguiculi always destitute of arolia. Anterior ventral segments touching each other only by the margin. First genital segment of the ♀ with the apical margin of both lobes for the most part strongly sinuate and to be discerned as a minute triangular lobe only on the outside on the sides of the second segment; sometime outwardly on the sides of these segments and on both sides at the base of the terebra to be distinguished as a small triangular lobe. Head horizontal, apically truncate.

This Phalanx is identical with the family Acanthiidae Reut. (1871) or Cimicidae Ståhl (1873), I have motivated its division into several families on pages 23-24, in more detail.

Family XXI Termatophylidae: Ocelli absent in both sexes. Beak indistinctly 4-segmented, the first segment short. Hemelytra in both sexes with clavus, corium, embolium, cuneus, and membrane separated. Membrane with a rather large subquadrangular single area. Tarsi distinctly 3-segmented. (Orificia of dorsal glands of the nymph not yet examined).

Up to the present time the Termatophylidae were considered as only a subfamily of the Anthocoridae.

Family XXII Microphysidae: Ocelli present in the ♂, absent in the ♀ for the most part. Beak 4-segmented, very rarely (Nabidomorpha Popp.) 3-segmented. ♂♂ oblong or elongated, with the elytra without folds; ♀♀ posteriorly strongly widened, apterous, with hemelytra all coriaceous, for the most part (frequently much) shorter than the abdomen. Membrane in the ♂ with a sub-oval areola at the base sending off 2-3 veins and internally provided with a free vein. Tarsi 2-segmented. (Orificia of the dorsal glands of the nymph not yet examined),

As for the Microphysidae, so long as only the ♀ of Microphysa Westw. was known, they were considered as Myodochidae (Lygaeodes, Infericornes) especially by Burmeister (1835), Westwood (1840), and Walker (1872), or as Pyrrhocoridae (Coecigenae) by Herrich-Schäffer (1853) and Dohrn (1859). Fieber who also had learned to recognize the anthocorid-like ♂, erected a Family of its own for these animals in 1860; thereafter this family was placed in the anthocorids as a subfamily by most of the authors, but certainly without sufficient ground (see p. 23-24).

Family XXIII Anthocoridae: Ocelli distinct in both sexes. Beak 3-segmented. Hemelytra with clavus, corium, embolium, cuneus, and membrane well separated. Membrane with a very narrow area formed from the vein which strongly approaches the membrane-suture, being slightly divergent outward, and another very short connecting vein, this area sending off 1 to 4 veins, all veins sometimes obsolete. Tarsi 3-segmented. (Nymphs with the orifice of the dorsal glands situated at the anterior margin of segments 4 to 6).

Just like the abundant relationship of the mirids, that of the Anthocoridae has also been known for a long time. Burmeister (1871) [and others, see page 71 of text] placed them all in the same family together with the myodochids; Herrich-Schäffer as early as 1835 brought them together with the acanthiads, isometopids, cimicids, reduviids, nabids, etc., in the group Tricondylae, far from the tessaracondylous myodochids. Relationship with the above-named families was also understood by Amyot (1848). As early as in 1844 Fieber had mentioned the relationship between cimicids and anthocorids and in 1851 he placed the Anthocoridea as a separate family between the Phytocoridea (=Miridae) and the Cimicoidea, as well as in 1861 between his Acanthiadae (=Cimicoidae) and Ceratocombidae (=Dipsocoridae). Flor (1860) even united the anthocorids with the cimicids and microphysids in one family and the author (1871, 1882), Stal (1873), Berg (1879), Puton (1886, 1899), and Saunders (1892) followed him in this view;

all of them incorrectly also referred the ceratocombids to the same family, considering them only as a subfamily like the foregoing. Saunders (1876) had previously placed the Anthocoridae between Microphysidae and Cimicidae and recognizing the relationship with them still retained the microphysids as a separate family. But most of the later authors put the microphysids tobether with the anthocorids as a subfamily, while, on the other hand, they found sufficient reasons for setting up the cimicids and ceratocombids as separate families. [List of authors who did so, page 71 of text]. Nor was the frankly somewhat more distant relationship of the mirids overlooked by systematists. Thus, as stated above, Fieber (1851) placed the anthocorids right after the Phytocoridea, although later on he removed the two families far from each other (1861). Kirschbaum (1855) also indicated the relationship of anthocorids and capsines (mirids). Baerensprung (1860) likewise seems not to have been a stranger to this concept, because he placed the anthocorids right before the capsids (mirids), although he let the lygaeids (myodochids) precede them and therefore certainly did not make free use of the old incorrect view on the relationship of these last two families. Furthermore the relationship with the mirids has been recognized by the following authors; Flor (1860, between Miridae and Reduviidae), Stål (1864, between Miridae and Cimicidae), Douglas and Scott (1865, between Miridae and Acanthiadae), Schioedte (1869, together with the mirids etc., in the family Acanthiae), Puton (1869, 1875, between Miridae and Acanthiadae), Berg (1879, between Miridae and Tingididae), Distant (1904, after the mirids and before the Cryptocerata), and Kirkaldy (1906, first among the pagiopods, just before the Miridae). However, it was an exaggeration to do as the author did in 1875, and Puton followed him in 1878 - i.e., bringing the Miridae together into a separate family with the other above named families, for people are not willing to ascribe the rank of a Superfamily to them. Kirkaldy also (1902) placed the mirids, anthocorids, and cimicids together in one family.

Family XXIV Cimicidae; Ocelli absent in both sexes. Clypeus triangular. Beak 3-segmented. Pronotum narrowed toward the base. Hemelytra always very short, rudimentary, destitute of membrane. Tarsi 3-segmented. (Nymphs with orifice of the dorsal glands on the anterior margin of segments 4 to 6).

Finally as concerns the cimicids, Latreille (1802) has already quite rightly (that is, insofar as these families belong not to the same superfamily but to the same series) placed them together with the nabids and reduviids in his second Division, the Cimicides. Dumeril (1806) probably also recognized their relationship with these for he made room for them in his group Zoadelges between present Miridae and Reduviidae. But in 1807, Latreille was confused by the gular groove of cimicids in that he considered them as related to the aradids and tingidids on this ground, an erroneous concept which was shared later on by Fallen (1814, 1829) [and several others, named on page 72 of text]. Remarkably enough, Blanchard (1852) referred them to the Coreitos (=Pyrrhocoridae, Cimicidae, Nabidae, and Coreidae (!)). However, Dufour (1833) had already emphasized the fact that the internal anatomy of Cimex lectularius is reminiscent of that of the reduviids. Westwood (1840) placed the cimicids between reduviids and tingidids but expressly remarked that the relationship with the former is striking. Herrich-Schäffer (1835) also referred them - as having come from the isometopids, - beside the reduviids in the first group of his Tricondylae, distant from aradids and tingidids and counted them among the Reduvini in 1853. In his catalog (1859) Dohrn took up an intermediate position in that he set up the Lecticolae (Cimicidae) as a separate family between his Corticicolae (Aradidae) and Nudirostri. Still in 1873 Walker followed a similar procedure and placed the Cimicidae as a tribe, Lecticola, after the tribe Corticicola of his Ductirostra, but expressly remarked they are more closely related to the Nudirostra especially emphasizing their affinity with the anthocorids and microphysids. The narrow relationship just with the anthocorids and the necessary separation from Aradidae had already long since been demonstrated by Fieber (1844). It is evident from the above given historical presentation of the kindred relations of anthocorids that it had been generally recognized by Flor (1840) and nearly all later authors.

Superfamily VII Reduvioideae: Meso- and metasterna simple. Hind coxae rotatory. Beak mostly arcuate. Hemelytra always destitute of cuneus. Unguiculi destitute of arolia. Abdominal spiracles 2-7 ventral.

This superfamily corresponds to the superfamily Nepoideae Kirk., with the exception of the Gerridae and Nepidae (page 17) and is entirely identical with the reduviid branch erected by Handlirsch. For earlier views on the kindred relations see above in case of the Ochteroideae, Gerroideae, Acanthioideae, and Miroideae.

Phalanx I Nabiformes: Prosternum destitute of the stridulatory sulcus. Membrane with 2 to 4 more or less entire discoidal areolae and with veins radiating from the areolae to the margins, very rarely with free longitudinal or subobsolete veins. The two genital segments of the ♀ cleft in the middle and enclosing the terebra. Front legs raptorial.

The single family belonging to the above-described Phalanx, the ♀♀ of which are still provided with a saw-sheath seems to form a transition between the foregoing superfamily and this one, to a certain extent. Reduviolus ferus was even described by Fallen (1829) and Zetterstedt (1840) as a species of Miris. To most authors, however, the nabids seem to be so closely related to the reduviids that they were placed together with them in the same family. Apart from the earlier authors, this is the case in papers by Douglas and Scott (1864) [and others named on page 73 of the text], while the nabids were set up as a separate family by Fieber (1861) [and others named on page 73 of text]. **Verhoef** (1893) placed them together with the anthocorids ~~especially far from the reduviids~~ and the Tingidids (!) particularly far from the reduviids the same as Blanchard (1852) placed them together with the pyrrhocorids, cimicids, and coreids.

Family XXV Nabidae: Ocelli distinct for the most part. Beak 4-segmented, the first segment short, very rarely (Scotomedes Stål) 3-segmented. Antennae 4- or 5-segmented. Hemelytra sometimes provided with an embolium. Tarsi 3-segmented. (Nymphs with the orifice of the dorsal glands situated at the front margin of segments 4 to 6.)

Phalanx II Reduviiformes: Beak 3-segmented, frequently powerful, arcuate. Prosternum provided with a stridulatory sulcus. Hemelytra provided with clavus, corium, and membrane destitute of cuneus. Legs raptorial. ♀ without terebra.

In most authors, the family Reduviidae occupies a very definite position in the System. The alleged kindred relations have already been mentioned above. Only more recently have the kindred relations between the reduviids and macrocephalids been clearly understood (see right below).

Family XXVI Reduviidae: Antennae for the most part fractate, with 4 or more segments, for the most part slenderer toward the apex. Scutellum small or mediocre. Membrane provided with 2 or 3 areas. Tarsi most frequently 3-segmented, very rarely 2-segmented, sometimes heteromerus, the front tarsi rarely uniarticulate. (Nymphs with the orifice of the dorsal glands situated at the anterior margin of segments 4 to 6).

The subfamily Emesina was considered as a separate family by Mulsant and Rey (1873) as well as by Osborn (1895). But the absence of ocelli is characteristic not only for this subfamily but also for the subfamily Tribolocephalina and the subfamily Saiscina and even shows up in different genera of other subfamilies. The peculiar structure of the forelegs likewise does not occur exclusively in the Emesina but it also occurs in the ocelli-bearing subfamily Bactrodina. Therefore it seems to me to be most correct to retain the Emesina as only a subfamily of the Reduviidae.

Family XXVII Macrocephalidae; Head provided with a rostral sulcus below. An nae 4-segmented, with the 4th segment clavate or fusiform and much larger than the 3r Scutellum always produced backward beyond the metanotum, frequently large and conceali the greater part of the wings. Membrane provided with several veins which are frequent reticulately united. Forelegs strongly thickened. Tarsi 2-segmented. (Nymphs with the orifice of the dorsal glands situated at the anterior margin of segments 5-6.)

The majority of authors have wrongly placed the macrocephalids in the vicinity of the aradids and tingidids, on the basis of the formation of the gula and the number of tarsal segments. [Authors who did so named at top of page 74 of text]. Perhaps Herric Schäffer (1853) had already had a presentiment of the relationship with the reduviids for he placed his Spissipedes (Macrocephalidae) right before the Corticicolae (Aradidae) to be sure - but at the same time after the Reduvini. Rambur (1842) and Baerensprung (1860) likewise placed them between the acanthiids (cimicids) and reduviids, in which it is to be noted especially that this author considered them as related to the aradids. However, the relationship with the reduviids had already been understood by Laporte (183 in that this author placed his Phymatites (Macrocephalidae) in the tribe Haemathelges with the Reduvites; while he referred the tingidids and aradids to the tribe Anthothelges. This relationship was first expressly emphasized by Fieber (1844) although he later (1861) seems to have given up this concept. Schioedte (1869) no less definitely indicated this relationship and even united the phymatids and reduviids in one family Puton (1869) placed the phymatids right after the reduviids, but later placed them beside the aradids and the author (1884) ranked them right before the reduviids. Berg (1879) placed them between the aradids and nabids. Finally Handlirsch (1897) expressly discussed the reasons for the kindred relations between macrocephalids and reduviids (see page 18 of the text] and of the later authors, Oshanin (1908) and Kirkaldy (1908) agreed to the view defended by him (see also Handlirsch 1908).

Phalanx III Henicocephaliformes; Beak 3-segmented. Prosternum without the stridulatory sulcus. Hemelytra all membranaceous, provided with longitudinal and a few transverse veins. Legs rather short. ♀ without terebra.

The eggs of this animal have not yet been investigated and therefore its position must be considered as provisional. The relationship with the reduviids or nabids, however, has been accepted by all the authors who have known it.

Family XXVIII Henicocephalidae; Head constricted at the base and behind the eyes, swollen between the strictures [or compressions]. Ocelli distinct, situated anteriorly in the swollen part of the head. Antennae 4-segmented. Pronotum divided into 3 lobes. Metasternum destitute of orificia. Front tibiae gradually wider toward the apex, compressed. Front tarsi 1-segmented, the hind tarsi 3-segmented. (Orificia of dorsal glands of the nymph not yet examined.)

Superfamily VIII Aradoideae; Meso- and meta-sterna simple. Hind coxae rotatory. Beak 3-segmented, straight. Antennae 4-segmented. Hemelytra always without the cuneus. Legs regularly formed. Tarsi destitute of arolia. ♀ without terebra.

The systematic position of the two families entered together below can only be definitively established after the eggs themselves have been investigated (see page 30).

Family XXIX Joppeicidae; Head subtriangular, coarctate [i.e., contracted] before the apex, destitute of antenniferous tubercles. Ocelli distinct (Puton - 1881 - wrongly stated "ocelli invisible". See Bergroth 1898:188). Beak projecting, acuminate. Antennae with the last 2 segments slender. Margins of scutellum and corium carinate. Membrane large hyaline with 4 free longitudinal veins. Metasternum without orificia. Tarsi 2-segmented. Abdominal spiracles 2-7 ventral. (Orificia of dorsal glands of the nymph not yet examined.)

The only genus which forms this family has been counted among the aradids by Puton and the myodochids (lygaeids) by Bergroth (1898). The reasons why these views must be considered wrong have been given in detail on page 30 .

Family XXX Aradidae: Body oval, dorsally and ventrally depressed. Head horizontal, prolonged between the antennae, provided with a mostly sharp antenniferous tubercle on either side, ventrally (as well as the pectus) with a median sulcus for receiving the beak. Eyes projecting. Ocelli absent. Beak turned backward, received in the sulcus of head and pectus. Antennae for the most part strong, with the last 2 segments not at all or little slenderer than the second, sometimes thicker than this, the last shortly acuminate. Membrane provided with several irregular veins here and there joined, or without veins. Legs short. Tarsi 2-segmented. (Situation of spiracles variable. Nymphs with the orificium of the dorsal glands situated at the anterior margin of segments 4-6).

The aradids have been placed right beside the tingidids by most of the authors, both when they were put together with them in one family as did Latreille (1802, 1807, 1825) [and others named on page 75 of the text] and when they were interpreted as different families. The Aradidae and Tingididae have been separated by one or more families only by a few authors. Thus they were separated by the Hebridae by Douglas and Scott (1865) or by the macrocephalids (phymatids) by Stål (1868) [etc., see page 75 of text], or by both these families by Puton (1875, 1878). Handlirsch (1908) derived the aradids besides the tingidids, from the coreids, Kirkaldy (1907, 1908, and 1908) from the pantatomids (cimicids). I have already stated the reasons why I consider all these views as untenable (page 30).

Series IV Onychiophora: Unguiculi always provided with arolia. Beak 4-segmented. Antennae longer (for the most part much longer) than the head, 4- or very rarely 5-segmented, with the last 2 segments filiform or the last segment thicker, never slenderer than the preceding. Hemelytra of varying structure, always destitute of a cuneus. Membrane never provided with many dense longitudinal veins. Meso- and metasterna simple. Hind coxae rotatory.

The blood relationship of the families brought together below has not yet been definitively demonstrated in several cases. Putting them together is therefore to be considered as only provisional (page 30).

Superfamily IX Neidoideae: Antennae 4-segmented. Hemelytra composed of clavus, corium, and membrane or homogeneous, reticulate.

Phalanx I Pyrrhocoriformes: Membrane with more than 5 veins, frequently united here and there. Ocelli absent.

For reasons why I consider this and the following Phalanx as well-separated branches of the same branch, see page 15.

Family XXXI Pyrrhocoridae: Beak free. Head with lateral antenniferous tubercles. Hemelytra composed of clavus, corium, and membrane. ♀ destitute of terebra. Tarsi 3 segmented. (Abdominal segments [illegible] to 7 ventral. Nymphs with orificia of dorsal glands situated at the anterior margin of segments 4 to 6).

This family has been united by several authors, mostly as a subfamily, with the myodochidae (Lygaeidae). Thus did [for names of authors see page 78 of text]. Others (Laporte 1832, Spinola 184[illegible]) put them together with the [illegible] on the basis of the absence of ocelli. They were considered as a separate family, closely related to the Myodochidae by Amyot and Serville (1843) [and others, see page 76 of text]. Blanchard (1852) very strangely combined the pyrrhocorids, cimicids, nabids, and coreids in his family the Coreitos. It may still be mentioned that Verhoeff (1893) put the pyrrhocorids far from the myodochids in the same "suborder" (Pentatomina) with the Pentatomidae sensu [illegible]

[illegible] II Neidiformes: Membrane with 5 veins at most. Hemelytra sometimes all for the greater part densely reticulate.

Family XXXII Myodochidae: Ocelli present. Beak free. Head with lateral antenniferous tubercles, not constricted before the ocelli. Hemelytra composed of clavus, corium, and membrane. Membrane provided with 5 longitudinal veins. The 2 genital segments of the ♀ cleft in the middle and inclosing the terebra. Tarsi 3-segmented. (Abdominal spiracles mostly dorsal in part. Nymphs with orificium of dorsal glands situated at the anterior margin of segments 4 to 6 or sometimes (for example Eulygaeus, Cymus, Platyplax) only of 5 to 6.).

This family has been placed right beside the coreids by most authors, or has been separated from then by the neidids (Berytidae) which was separated off from the same later. Sometimes the pyrrhocorids have shoved in between the coreids and myodochids. As for the views on kindred relations of the myodochids and pyrrhocorids, see above under the Pyrrhocoridae. As for the relationship with neidids and piesmids see immediately below. Kirkaldy derived the myodochids through the pyrrhocorids from the cimicids (pentatomids), on the other hand, Handlirsch derived them from the coreids. (For remarks on this see pages 15 and 27).

Family XXXIII Neididae: Ocelli present. Head constricted before the ocelli. Eyes far from the base of the head. Beak free. Antennae geniculate, the first segment long, clavate. Scutellum very minute. Hemelytra composed of clavus, corium, and membrane. Membrane provided with 4 or 5 veins. Legs long or rather long. Femora apically clavate. Tarsi 3-segmented. (The 2 genital segments of the ♀ cleft, but the terebra not at all extended between the lobes thereof (See Flor Rhynch.Livl., I:200). Spiracles of the abdominal segments all dorsal. Nymphs with the orificium of the dorsal glands situated at the anterior margin [of segments] 5 to 6).

The Neididae had been united with the Coreidae until, recognized by Fieber (1851) as a separate family, they were thereafter placed right beside them. However, Stål (1873) found that they are more closely related to the myodochids (lygaeids) than to the coreids for which reason he united them to the former as a subfamily and the author (1882) and Berg (1884) joined him in this view. Kirkaldy who did not mention the neidids in his (1909) system at all, was also of the same opinion. On the other hand, Handlirsch derived the Berytidae from the Coreidae (page 27), in 1908.

Family XXXIV Piesmidae: Ocelli at least in the macroptera present. Head with the juga freely produced at the apex, resembling two cornicles, with the bucculae moderately raised not produced either anteriorly or posteriorly, not anteriorly convergent. Pronotum without the angular posterior process, very obtusely rounded at the base. Hemelytra densely reticulate-punctate, with the clavus distinct, the membrane of the macropterous form membranaceous, broadly "valvans" [?valvate or ?lobate], provided with four longitudinal veins, coriaceous at the base. Tarsi 2-segmented. Abdominal spiracles 2 to 6 situated on the dorsal pleura. Nymphs with orificium of dorsal glands situated at the anterior margin of segments 4 to 5.

These insects have been interpreted as a subfamily of the tingidids by nearly all the authors. However, the relationship with the Myodochidae (Lygaeidae) has been emphasized several times. Some authors have even united them with the Lygaeidae, as did Spinola (1840), Herrich-Schäffer (1853), Flor (1860), and Snellen van Vollenhofen (1870). I must confess that I consider the difference between them and the Tingididae so substantial that I believe it to be most correct to set them up as a family separated off from the Tingididae (note, page 15 [in parentheses, in the first paragraph]).

Family XXXV Tingididae: Ocelli absent. Head with the juga not at all produced at the apex, with the bucculae all raised, forming a rostral sulcus which is anteriorly closed for the most part. Pronotum for the most part posteriorly angularly produced and concealing the scutellum. Hemelytra reticulate with the clavus for the most part deficient or connate with the corium, membrane always all coriaceous or reticulate. Tarsi 2-segmented. (Abdominal spiracles 2 to 7 ventral. Nymphs with the orificium of the dorsal glands situated at the anterior margin of segments 4 to 5.)

This family was placed beside the aradids by all the authors. See above under the family [illegible] for the systematic position thereof.

[illegible]: Antennae 5-segmented, with the first 2 segments thickened, short, the last 2 filiform. Hemelytra with narrowly triangular corium, with clavus and [illegible] membranaceous, the latter large, without veins.

[illegible] Ocelli present. Head ventrally with a deep sulcus for receiving the first segment of the beak. Pectus provided with a longitudinal sulcus. Legs rather short. Tarsi 2-segmented. Abdominal spiracles 2 to 7 ventral. (Orificia of dorsal glands of the nymph not yet examined).

The [illegible] were combined by Brulle (1835) [and others, named on page 78 of the text] with the families which form the present-day Gerridae sensu latissimo (Amphibicorisae Duf., Hydrodromica Fieb.), or they were placed beside these by Berg (1884). On the other hand they were brought by Amyot and Serville (1843), Flor (1860), Douglas and Scott (1865), Puton (1875, 1878, 1886, 1899), and Saunders (1892) into the circle of relationship of the tingidids. Lethierry and Severin (1896) placed them between the aradids and gerrids (hydrometrids) as did Distant (1904), Champion (1898), and Oshanin (1908). Finally Herrich-Schäffer (1853) referred them to his Lygaeodea. Their position in the System is still questionable for Handlirsch (1908).

Series Polyneuria: Unguiculi provided with arolia. Beak 4-segmented. Antennae much longer than the head, 4-segmented, the whole to be observed from above. Head neither clypeate nor transversely impressed before the ocelli, with antenniferous tubercles occupying the upper part of the head or the latero-upper part. Meso- and metasterna always simple. Hemelytra provided with clavus, corium, and membrane. Membrane with a great many, sometimes anastomosing, veins. (Ova operculate, with only 2 micropyles one of which is situated in the front part near the apex).

This series is wholly identical with the Coreidae of later authors. According to Kirkaldy it comes from the Pentatomidae (Cimicidae); according to Handlirsch (1908) it has the same origin as these. For my views on their phylogeny see page 30).

Superfamily I Coreoideae and Family XXXVII Coreidae: Ocelli present. Scutellum small or mediocre, shorter than the abdomen by at least half. Hind femora often thickened. Tarsi 3-segmented. ♀ destitute of terebra. (Abdominal spiracles 2 to 7 ventral. Nymphs with orificium of dorsal glands situated at the anterior margin of segments 5 to 6).

Possibly this superfamily deserves to be divided into several families. Mulsant and Rey (page 12 [of the text]) erected 3 families corresponding to this family. Unfortunately it is no longer possible for me to study the question more thoroughly.

Series VI Peltocephala: Unguiculi provided with arolia. Beak 4-segmented. Head very frequently distinctly clypeate. Antennae longer (often much longer) than the head, inserted under the lateral margins of the head, with 5 segments for the most part, rarely 3, 4, or more than 5, at least the first segment at the base not discerned from above. Ocelli for the most part distinct. Meso- and metasterna always simple. Hemelytra composed of clavus, corium, and membrane. Membrane for the most part with a great many veins, rarely with a few. (Abdominal spiracles 2 to 7 ventral, the 2nd often covered by the metathorax. Nymphs with the orificium of the dorsal glands situated at the anterior margin of segments 4 to 6, the orificium of the 4th segment sometimes twinned. (Ova short operculate, with the margin of the operculum surrounded by more or less numerous slender micropyles.)

This Series, which includes a single superfamily Pentatomoideae, certainly deserves to be divided into several families (Pentatomidae, Urolabididae, Thyreocoridae etc.). Unfortunately I have neglected to study this question in more detail and must therefore waive such a presentation.