HISTORICAL DEVELOPMENT OF HEMIPTERA INFRAORDER NEPOMORPHA (HETEROPTERA)

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NOTES ON ENGLISH TRANSLATION

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This translation was made for my own use rather than for publication; accuracy therefore takes precedence over elegance. Miss Vaitaitis has kept it as literal and as close to the original Russian style and wording as possible. Questions regarding the meaning of specific passages should be addressed to her. Revisions in the translation were made only after consultation with Miss Vaitaitis. The pencilled comments (or protests!) in the margins are my own, and may be noted or disregarded at the reader's discretion; in many cases they do not reflect Dr. Popov's views.

The typed numbers at the top right corner of each page, and along the right-hand margin, denote pages of the Russian book.

"Condensed" and "respirators" should be changed to "flattened" and "spiracles", respectively.

The following figure captions are incorrect in the Russian original: Fig. 7: captions to 7a and 7b are reversed. Fig. 24: both 24a and 24b are of adult; 24a is midsagittal, 24b is parasagittal.

Two rather serious errors in the descriptions should be pointed out: (1) The sclerite labelled "epm_3" (Ch. III) and referred to, in Ch. V, as the "metathoracic epimere", is actually the metathoracic episternum. It is not serially homologous with "epm_2", which is correctly labelled and described. (2) In Ch. VI and elsewhere: the anteclypeus of modern Corixidae, although expanded, is not, as Dr. Popov claims, fused with the head capsule. Such fusion occurs only in Notonectidae, Naucoridae, Gelastocoridae, and Ochteridae; in these groups the anteclypeus fuses with the loral lobes but not with the maxillary ones. The corixid anteclypeus is free, like that of Nepidae and Belostomatidae (Parsons, 1965; Can. J. Zool. 43: 161-166).

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TABLE OF CONTENTS

	Manuscript	Book
Forward	1	3-4
Introduction	2-4	5-8
I. History of the study	5-8	9-13
II. Geological and geographical distribution of the extinct Nepomorpha	9-21	14-28
III. General morphological survey of the Nepomorpha	22-39	29-83
IV. Systematics of the Infraorder Nepomorpha and some questions on the general classification of the Heteroptera	40-51	84-97
V. Taxonomic section	52-104	98-175
Infraorder Nepomorpha	52	98
Superfam. Gelastocoroidea Kirkaldy 1897	52-55	98-103
Superfam. Nepoidea Latreille 1802	55-67	103-121
Superfam. Corixoidea Leach 1815	67-78	121-138
Superfam. Naucoroidea Fallen 1814	78-93	138-159
Superfam. Notonectoidea Leach 1815	93-104	159-175
VI. Origin and basic directions of evolution of the Infraorder Nepomorpha	105-129	176-208
Basic directions of morphogenesis in evolution, morphological prototypes of the infraorder, and phylogenetic interrelationships with the Infraorder Leptopodidomorpha	105-114	176-188
Phylogeny of Superfam. Nepoidea	114-117	188-192
Phylogeny of Superfam. Gelastocoroidea	117-119	192-193
Phylogeny of Superfam. Corixoidea	119-125	193-202
Phylogeny of Superfam. Naucoroidea	125-128	202-205
Phylogeny of Superfam. Notonectoidea	128-129	206-208
Russian Bibliography	130-132	209-211
List of word designations to figures	133-135	225-226
Explanation of Plates	136-137	227-228

Figure captions

	Manuscript	Book
Ch. III and IV	138	
Ch. V	139-140	
Ch. VI	141	

FOREWORD

Brought to the attention of the reader is an investigation devoted to a survey of the historical development of one group of Heteroptera insects of the infraorder Nepomorpha. It is based on the study of diverse extinct Heteroptera and a comprehensive examination of the features of presently living representatives of the infraorder.

The author sets out the results of the investigation in six chapters, beginning with an historical study, a geological-geographical section, a survey of morphological features, then the taxonomy and descriptive part, and ending with an examination of the phylogenetic relationships of the entire infraorder as a whole and the superfamilies comprising it.

The geological-geographical section includes a survey of all known fossil finds of Nepomorpha and partly of other Heteroptera. Lists are given of all localities (29 in all) indicating species found, and conditions of burial of the studied insects are discussed. This chapter undoubtedly will have important comparative significance for later investigators.

The extensive, well illustrated morphological chapter reports the basic data on structure necessary for understanding the phylogenetic relationships and taxonomy of the studied insects. This section of the investigation is based primarily on zoological data, and in many cases all the available data on extinct forms have been utilized. Thus, the morphological survey is the main source of factual evidence of the various taxonomic-phylogenetic generalizations.

The survey of taxonomy is not limited to the Nepomorpha: at the beginning of the chapter, the author provides a division of the entire order Heteroptera into large taxons, infraorders and superfamilies. Critically examining the schemes of other authors, the author sets out his taxonojic scheme of the whole order, subdividing it into six infraorders and later in more detail establishes the division of the infraorders Nepomorpha and Leptopodidomorpha[1] into superfamilies and families. This taxonomic survey is undoubtedly very useful in bringing order and precision into the interrelationships of the large taxons of the known groups of aquatic Heteroptera.

The taxonomic portion includes descriptions of all large taxons of the infraorder - 5 superfamilies, 12 families (of which two are new), 22 subfamilies (of which four are new) and some new tribes (5), genera (12) and species (13) of Mesozoic and Cainozoic fauna. These descriptions, apart from the diagnostic features, include data on distribution and ecology. Thevalue of this taxonomic survey is great as a guideline for later investigators of the fauna of the geologic past, on the one hand, and is a basis for phylogenetic surveys on the corresponding groups of the Nepomorpha, on the other.

Finally, the last chapter is a survey of the directions of the evolution of the Nepomorpha, where the phylogenetic interrelationships of this infraorder with the one closest to it, Gerromorpha, are examined, and then the phylogenies of the separate superfamilies are described. The comprehensiveness of the argumentation in the discussion of the paths of phylogeny is noteworthy. Basic is the appraisal of the biological adaptations which have occurred in the history of these insects - first of all of feeding (predatory or vegetarian), respiration (in connection with the transition to an aquatic form of life), ontogenesis (with respect to the features of embryological development), and finally the methods of movement (with an examination of the features of the transformation of leg structure). All this gives depth and interest to the phylogenetic section.

In conclusion, first of all the originality of the entire work must be emphasized: up to now no phylogenetic investigations have appeared for the order Heteroptera, and even for the whole superorder Rhynchota, based on a complex study of living fauna and the fossil material on such a select scale - on the level of taxons of large ranks, infraorders and superfamilies. As a result, we can with confidence recognize that our knowledge of the paths of evolution of one large and important in many respects order of winged insects has been considerably increased. This monograph on the evolution of aquatic Heteroptera is one of the most far reaching steps in the study of the historical development of insects, conducted by the Paleontological Institute of the Academy of Sciences of the USSR. B.B. ROHDENDORF

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[1] Apparently, the correct name must be considered "Gerromorpha."

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INTRODUCTION

Real Heteroptera, or bugs, have been investigated by many taxonomists and morphologists. The reason for this interest in them is the extreme diversity of their ecology: from quickly moving physophags (Cydnidae) and mitsetophags (Aradidae, Brachyrrhynchidae) to the living pelagic forms, which live on the ocean's surface and are active predators (Hallobatinae, Gerridae).

The diversity of the form of life, the habitation in different ecological conditions led to considerably diversified morphological adaptations (structure of head, thorax, abdomen, terminalia, the numerous sexual isolating mechanisms, etc.) and the existence of a comparatively large number of species. An estimate of the number of the latter varies from 23,000 (Beier, 1937) to 26,000 (Obenberger, 1958) or even to 40,000 (Bei-Bienko, 1967). In my opinion, the most realistic figure is 30,000 (or somewhat more) living species (considering that each year approximately 100 to 300 new species are described), of which about 1,600 species belong to the aquatic group of bugs of the infraorder Nepomorpha.

Notwithstanding the abundance of taxonomic and morphological literature on this question, only comparatively few authors have devoted their works to the evolution of the bugs. Most investigations on the question of the phylogeny of the Heteroptera are based exclusively on morphological and ecological material, often devoid of explanations of any determining morphogenetic processes or even more of paleontological argumentation. The latter is excused by the lack of studies of described paleontological material (particularly from Mesozoic deposits). This approach is characteristic with respect to the existing literature on the evolution of large taxons of the order.

Recently more than 50 Mesozoic representatives of the order Heteroptera have been described, of which about 10 belong to the Nepomorpha (=Hydrocorisae, Cryptocerata). The taxonomic position in a number of cases has been incorrectly determined, and the quality of many descriptions leaves much to be desired. As for the described Cainozoic Heteroptera, their number is high (over 500 species), and their family belonging more or less clear.

The status of the study of Paleocene and Neocene aquatic Heteroptera is analogous to that of other orders of insects: the general volume of material is large, but it has been superficially described, basically in the past century by investigators of a wide profile (Germar, Deichmuller, Heer, Oppenheim, Scudder, Handlirsch, and others), and at present the material is difficult to obtain for revision. Besides, for the separate groups of the order the material is very irregularly distributed.

There are great difficulties in utilizing the described fossil bugs in clearing 6 up their phylogenetic relationships within the order: the lack of a proper standard of description (the basic mass of species was described in the 19th century!), the small difference of the Cainozoic forms from the Recent and because of this the possibility of reconstructing only the last stages of formation of the living fauna (mainly, evolution on the generic level), and also in many cases the poor preservation of the remains. Thus, research of the rich material of Mesozoic Heteroptera preserved in the collections of the Paleontological Museum of the Academy of Sciences, USSR, is highly desirable. It would also be useful to conduct a revision of the fossil Heteroptera described earlier from foreign collections.

In the present paper, I have limited the examination to one of the most specialized groups of bugs, which are adapted to an aquatic or littoral form of life, the infraorder Nepomorpha (=Cryptocerata, aquatic), which is considerably less in size than the infraorder of terrestrial bugs (=Gymnocerata, terrestrial). This investigation is only the first step in a planned study of the Heteroptera, basically Cainozoic, both from our own and from foreign territories. The infraorder Nepomorpha was chosen because they are the most complete in paleontological material in comparison with other groups of bugs. Actually, eight families of aquatic bugs are represented in the Mesozoic, and remains of representatives of the living families Naucoridae, Corixidae and Notonectidae are found in Lower Jurassic deposits.

The basic collection of Mesozoic Nepomorpha (except the Jurassic of West Europe) is concentrated in the Paleontological Institute of the Academy of Sciences, USSR. They number over 2,000 determinable specimens, preserved basically from the Mesozoic deposits of Central Asia and Eastern Siberia. Of the Cainozoic aquatic bugs within the USSR, only the material found in Mesozoic deposits of the North Caucasus, Central Asia (Central Tien-Shan) and West Siberia have been used, comprisong about 100 specimens of aquatic bugs of the family Corixidae and one belostomid specimen. Also studied were Mesozoic bugs from the collection of the Munich Paleontological Museum (11 specimens), which holds most of the types of aquatic Heteroptera from the Upper Jurassic localities of Bavaria (FRG, Solnhofen shales). From the British Museum of Natural History in London were received 60 specimens collected from Solnhofen and the locality of Ridgeway (Upper Jurassic, England), and also a few specimens of Corixidae from the Oligocene deposits of Florissant (Colorado, USA). Also studied were eight specimens of Upper Oligocene Notonectidae from Rott (Baden), kindly sent by Prof. W. Struve from the Geological Museum of Frankfurt-on-Main. Thanks to the kindness of Dr. J. Kukalova (Prague, CSSR), I studied the original of the recently described Oligocene belostomid Lethocerus sulcifemoralis Rih. et Kuk. from North Bohemia. Several species were studied from enlarged photographs.

Thus, I studied many Mesozoic Heteroptera, described from West Europe, first hand. Unfortunately, the few Cainozoic West European aquatic bugs remain partly uninvestigated and the description in a number of cases was obtained only from literature.

In working up the descriptive and particularly the morphological sections, the fairly extensive material on living aquatic Heteroptera from both the temperate zones and the subtropical and tropical regions of the earth was used.

In the present work are given descriptions of the overwhelming majority of extinct 7
genera of aquatic Heteroptera; species are described only if they are new or needed in a sub-generic survey. Most species are understood only through corresponding genera. Besides, I propose a new system of the order Heteroptera with a different size and names (not typological) of superfamilies, joined into six new taxonomic units - infraorders.

I have established the new families Shurabellidae (Corixoidea) and Mesotrephidae (Notonectoidea), subfamilies Stygeonepinae (Belostomatidae), Ijanectinae (Corixidae), Sphaerodemopsinae (Naucoridae) and tribes Liadonaucorini, Nectonaucorini, Angaronectini, Aidiini, Cataractocorini, and Coleopterocorini (Naucoridae). Also described are new species, which, with a few exceptions, belong to new genera. Laccotrephes incertus sp.nov. (Nepidae), Lethocerus turgaicus sp.nov., Stygeonepa foersteri sp.nov. (Belostomatidae), Ijanecta angarica sp.nov., Gazimuria scutellata sp.nov., Mesosigara kryshtofovichi, sp. nov., Diacorixa miocaenica sp.nov. (Corixidae), Liadonaucoris rohdendorfi sp.nov., Heleonaucoris maculipennis sp.nov., Angaronecta longirostris sp.nov. (Naucoridae), Mesotrephes striata sp.nov. (Mesotrephidae), Pelonecta solenhofeni sp.nov. and Liadonecta tomiensis sp.nov. (Notonectidae). For Corixa florissantella Cock. the new genus Sigaretta gen.nov. was established, and also redescribed were Sphaerodemopsis jurassica (Opp.), Mesonepa primordialis (Germ.), Mesobelostomum deperditum (Germ.), Clypostemma xyphiale I. Pop., Karataviella brachyptera B.-M., Shurabella lepyroniopsis B.-M. and Nepidium stolones West. The synonymy of some extinct aquatic Heteroptera was established.

The studied Nepomorpha belong to 12 families, 22 subfamilies, 36 genera and 67 speices, of which the overwhelming majority of genera and species are encountered almost exclusively in the fossil state. Described for the first time in the present work are 34 taxons, including one infraorder, two families, four subfamilies, five tribes, 11 genera and 12 species.

At present the accumulation of factual material on Mesozoic representatives of the infraorder, of course, has not been exhausted and thus is far from sufficient for final conclusions about the evolution of the infraorder and the order as a whole; all the more so since the littoral families Gelastocoridae and Ochteridae, which stand, in the opinion of contemporary hemipterologists (China, 1955; Miyamoto, 1961; Parsons, 1965, 1962a), at the base of the phylogenetic tree of Nepomorpha, have not been found in either Mesozoic or Cainozoic deposits. Available paleontological data shed light only on some stages of evolution. Such, for example, is the statement of the existence of numerous Nepoidea in the late Jurassic in West Europe and Corixoidea and Notonectoidea in the early Jurassic of Asia. Thus, the study of the evolution of the order as a whole requires a special and as far as possible comprehensive comparative investigation of its living representatives.

The data obtained in the process of studying both fossil (mainly Mesozoic) and living fauna, unfortunately, did not provide material for resolving judgment on the origin of the infraorder Nepomorpha, and the phylogenetic ties of the order Heteroptera with the related to it order Homoptera. However, the investigation of living material and paleontological finds proved sufficient for a preliminary clarification of the phylogenies of families within the infraorder, for enlightening the separate evolutionary moments in the families of aquatic Heteroptera, except the littoral Gelastocoroidea, and also the path of historical development of the aquatic group of bugs of this infraorder as a whole. The paleontological material which I studied showed that the fossil fauna of the bugs, particularly in the Mesozoic, in the num- 8
ber of large taxons (not below subfamilies) not only do not yield to living, but even in a number of cases somewhat exceed them. Thus, of 11 families of the infraorder, seven are found in the Mesozoic, two of which are now completely extinct. Apparently, the infraorder Nepomorpha as a whole did not flourish at that time, which is particularly true, from my point of view, for the families Nepidae, Pleidae, Helotrephidae, and the littoral family Ochteridae.

The author takes this opportunity to express his sincere appreciation to the persons who gave him ecological material on living aquatic bugs for study and permanent use - Prof. T. L. Jaczewski, Zoological Institute, PAN, Warsaw, Poland; Prof. J. W. Evans, Sydney, Australia; Dr. A. Menke, University of California, Davis, USA; Dr. D. Lauck, Humbold State College, Arcata, USA; Prof. J. Carayon, National Museum of Natural History, Paris, France; Dr. E. C. Young, University of Canterbury, Christchurch, New Zealand; Dr. J. D. Lattin, Oregon State University, Corvallis, USA; Prof. Ira La Rivers, University of Nevada, Reno, USA; Prof. A. W. Wroblewski, Zoological Institute, PAN, Poznan, Poland, and I. M. Kirchner, Zoological Institute, Academy of Sciences, USSR, Leningrad. With thanks is noted the great help of the following people in the loan of fossil material from foreign collections: Prof. W. Struve, Natur-Museum und Forschungs-Institut, Senckenberg, Frankfurt-am-Main, BRD; Dr. R. Forster, University Institute of Paleontology and Historical Geology, Munich, BRD; Dr. R. Backer and Dr. S. Morris, British Museum (N.H.), London, England; Dr. R. Wooton, Exeter University, Exeter, England; Dr. F. Bachmayer, Natural History Museum, Vienna, Austria, and Dr. J. Kukalova, Karlova University, Prague, CSSR.

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⑤

CHAPTER I

HISTORY OF THE STUDY

For the most authentic studies of the historical development of any group of animals, in this case bugs, the most complete and comprehensive data are needed not only on the occurrence of extinct forms, but also on the diversity of the examined group, the originality of its conditions of existence, history and phylogeny, not to mention the morphological side of the study. Naturally, thus, the most complete objects are the Recent, not living on earth, fauna of Heteroptera, which are the best preserved and most easily obtainable for such a comprehensive study. Thus the greatest attention will be given to an analysis of living forms.

We find the first mention of aquatic bugs in the work of Aldrovandi (1618), "De animabilis insectis." Somewhat later, in 1634, Mouffet, in "Insectorum theatrum," published drawings of representatives of the genera Nepa, Ranatra and Notonecta. Good drawings of aquatic bugs appear in Merian (1726), who also drew belostomids attacking a frog. Numerous studies followed, Frisch (1727-1728), Swammerdam (1737-1738), and also Linnaeus, Rosel Geoffroy, Fabricius and many other later authors, who took up both the taxonomy of aquatic Heteroptera and their biology.

The literature dealing with the taxonomy and faunistics of living aquatic bugs is so erroneous that it can be dealt with at a glance.

The most serious account of the study of aquatic Heteroptera was done by Kirkaldy (1897, 1898, 1904, 1906, 1907, 1909), who embraced in his studies almost the entirety of this group on a worldwide scale. Besides a taxonomic development of the separate families (Notonectidae, Naucoridae, Nepidae, Belostomatidae), he presented a list of all the then known genera of this group (Kirkaldy, 1906). Almost simultaneously the Russian hemipterologist V. F. Oshanin made two complete catalogues of Heteroptera of the Palearctic Region (1906, 1909, 1910, 1912), and somewhat later an analogous catalogue of the bugs of North America appeared by the Mexican Van Duzee (1917).

Particularly good progress has been attained in the course of the last decade, when our knowledge with respect to taxonomy, morphology and the form of life of aquatic Heteroptera, not only of the temperate but also of the tropical zones, increased considerably. Right, we do not yet have complete catalogues for the world fauna of the infraorder Nepomorpha or for some families of terrestrial bugs. There is a great number of monographs of surveys or general summaries on separate groups or regions, and also very many partial taxonomic works and an enormous number of articles on the ecology and biology of aquatic bugs. Of the largest contemporary studies, we must note, in the first place, the general summaries of the group of 10
Heteroptera by Poisson (1924, 1949, 1951) and Usinger (1956), the monograph by Hungerford on the biology and ecology of aquatic bugs (1919), and also on the Corixidae of the Western Hemisphere (1948). On the aquatic bugs of Africa, there are a number of works by Hutchinson (1929, 1930, 1932, 1933) and Poisson (1950, 1955, 1963, and others); Arabia, Brown (1945); West Europe, Jaczewski (1924, 1925, 1934), Jordan (1935, 1950), Vrublevsky (1958), Poisson (1957), Stichel (1925-1938, 1955), Macan (1956), Leston (Southwood, Leston, 1959) and others; European USSR, Kirichenko, (1930, 1940, 1951), Jaczewski (Jaczewski, Kirchner, 1964); Turkey, Hoberlandt (1948a); on the oriental aquatic Heteroptera, Paiva (1918), Esaki (1926), Lundblad (1933a, 1934), Hoffmann(1925, 1927, 1930ab, 1930-1931, 1933ab, 1941) and others; Japan, Matsumura (1905, 1915), Horvath (1879, 1905), Uhler (1896-1897) and others; Australia and New Zealand, White, 1878), Hutton(1904), Hale (1922, 1923ab, 1924abBg, 1935), Myers (1922, 1926; Myers, China 1928), Tillyard (1926), Hungerford (1933b, 1943, 1947), Young (1962) and others; Canada, Brooks and Kelton (1967); Cuba, Palmau (1967); Trinidad and Tobago, Hynes (1948); Central and South America, Melin (1928), De Carlo (1930, 1931, 1932, 1934, 1938, 1951, 1964)and others.

Many families were especially studied for an extent of many years by different specialists. The beginning of a detailed study of the largest and most numerous species of the family Corixidae is connected with the appearance in the 19th century of the works of Leach (1818) and Sahlberg (1819). The next step in the matter of the study of this group of bugs was the works of Fieber (1848, 1851, 1861), Flor (1860), Douglas and Scott (1865), Thomson (1869), White (1873), Puton (1880), Sahlberg (1875), Saunders (1875, 1892), Wallengren (1894), and some others. Particularly important are the already mentioned works of Kirkaldy, who gave a description of the different species of Corixidae on a new, higher level, and also established the synonymy of a whole number of genera. Later followed the taxonomic-faunistic works of Horvath (1904, 1926), Abbot (1912, 1917, 1918), Lindberg (1922), Deay (1935) and others, and also the numerous articles of Hungerford, including his study on the monograph of Croixidae of the Western Hemisphere (1948). Already for many years the Corixidae had been intensively studied by the renowned Polish hemipterologist T. Jaczewski (1924, 1926, 1928, 1929ab, 1931ab, 1933, 1934, 1936, 1939; 1960abB, 1961, 1962ab, 1963ab, 1964, 1968 and others). Many hemipterologists studied European and North American Corixidae (Poisson, 1924, 1938, 1951, 1957; Lundblad, 1925aB, 1926, 1927, 1928aBc, 1929, 1936; Poisson, Jaczewski, 1928; Walton, 1936; Jordan, 1937; Macan, 1939, 1941, 1954ab; China, 1943; Griffit, 1945; Wagner, 1947, 1952; Horegott, Jordan, 1954; Leston, 1955ab; Lansbury, 1955, 1960; Roubal, 1957; Šoos, 1961). The subfamily Micronectinae presently in its entire taxonomy has been developed by Wroblewski(1960ab, 1962ab, 1963ab, 1964ab, 1967, 1968).

The family Notonectidae has also been intensively studied by many investigators. The earliest works which appeared on this group of bugs are "Classification of Notonectiden," Leach (1818), the works of Spinola (1837, 1840) and Fieber (1851).

The next most important stage in the knowledge of the family Notonectidae as a whole, again, was done by Kirkaldy. The most important of his articles must be 11 considered the revision of the family Notonectidae (1897) and one of his last works, "Uber Notonectiden," (1904) in which he examined all of the then known species and established the synonymy of different taxons. Finally, his last fundamental survey together with Bueno is a catalogue of American aquatic and semi-aquatic Heteroptera (1909). Bueno also is the author of a number of specialized works on aquatic bugs (1902ab, 1905, 1908, 1925). In 1923 Hale published descriptions of new species from Australia, Lundblad described many species from the oriental region (1933), and finally, in Jaczewski's works (1949, 1958), besides new descriptions, the taxonomy of the Notonectidae was considerably improved.

The third stage in the study of the Notonectidae consists of the numerous works of the greatest specialist of this group of aquatic bugs, the already mentioned Hungerford, of which must be selected his monograph on the genus Notonecta (1933), then the works of Esaki (1915), Brooks (1948, 1951), Truxal (1953), the many which followed in the knowledge of the oriental fauna of Notonectidae by Lansbury (1962, 1963, 1964ab, 1965ab, 1966, 1968), and also the great number of articles of other hemipterologists: Poisson, Jordan, Leston, Jaczewski, Kirichenko, Leon, Fernando, Nieser and others.

The family Naucoridae, most representatives of which live within the Palearctic, in the past was studied by Stal (1965, 1870, 1897), Puton (1880) and Montandon (1895, 1897ab, 1898). Usinger made intensive studies in the 40's (1938, 1941, 1946, 1947), and also Hungerford (1941, 1942). Presently Naucoridae of the Western Hemisphere are actively being studied by the American hemipterologist La Rivers (1951, 1953, 1956, etc.). Naucoridae of other regions have been studied incidentally, although with less completeness, by many other hemipterologists.

The families of aquatic scorpions (Nepidae) and Belostomatidae, at the beginning of the 20th century, were studied by the Swedish hemipterologists Stal and Montandon. The early work of Ferrari (1888) dealing with Nepidae is also noteworthy. Much was done for the knowledge of these families by the Japanese hemipterologist Esaki (1926b, 1928) and by the above-mentioned works of De Carlo from Argentina. Recently, the taxonomy of the Belostomatidae has been worked out by the American entomologists Menke and Lauck (1961), in the practically complete studies of the Belostomatidae of the Western Hemisphere (Lauck, 1958, 1959, 1962, 1963; Menke, 1958, 1959, 1960, 1961, 1962, 1963abc, 1965, 1966; Menke, Lauck, 1962; Menke, Truxal, 1966).

The family Pleidae was partly studied by various authors, Stal, Kirkaldy, Poisson, etc. Finally, the last family, not known in a fossil state, the Helotrephidae, have been studied basically by the English hemipterologist China (1932, 1935, 1936, 1940).

The special group within the Nepomorpha which forms the two littoral families Gelastocoridae and Ochteridae also has been given attention by investigators. The first studies on representatives of these families were done by Latreille (1802) and Leach (1815). Later the families were studied in detail by many hemipterologists (Westwood, 1840; Spinola, 1850b; Fieber, 1861, Stal, 1865, 1870; Kirkaldy, 1897, 1906; Reuter, 1910; Horvath, 1911; Hungerford, 1922; Martin, 1928; Schell, 1943; Poisson, 1951, 1957; Todd, 1955, 1956, 1961, and others).

Such in a very compressed view is the character of the state of the study of the living representatives of the present Heteroptera of the infraorder Nepomorpha; it was not possible for me to give the numerous available works on morphology, ecology, and biology of aquatic bugs, although some parts of these are given later in the text. Considerably poorer is the history of the study of fossil forms of the infraorder of aquatic bugs.

The first data on fossil Heteroptera of the infraorder we find in Serres (1829) and Berendt (1830), who collected two representatives of aquatic scorpions from Oligocene localities of Europe. Later in Oligocene deposits of Western Europe and America were found two more species of Heteroptera belonging to the families Nepidae and Notonectidae (Hope, 1847), and also the first aquatic bugs from the rich Upper Oligocene localities of Rott in West Germany (Germar, 1837; Heyden, 1859). Subsequently, from Rott were described four more aquatic bugs belonging to the families Corixidae, Notonectidae and Nepidae (Deichmuller, 1881; Schlechtendal, 1894; Statz, 1950, and Jordan, 1953).

Germar first described Jurassic Heteroptera (Mesonepa primordalis Germ. and Mesobelostomum deperditum Germ.) from the lithographic shales of Bavaria (Solnhofen), which he (and all later authors who have studied this fauna) placed in the living families Nepidae and Belostomatidae (Germar, 1839). On the basis of my study of the types of these species, they belong only to the one family Belostomatidae. Subsequently, from Solnhofen, some remains were described which were placed in the aquatic bugs (Weyenbergh, 1869; Deichmuller, 1886, Oppenheim, 1888; Handlirsch, 1906). However, some of these turn out to belong to earlier described species; others were incorrectly determined and actually belong to insects of other orders.

Of the oldest representatives of Heteroptera described at the beginning of this century by Handlirsch (1906) which come from the Liassic deposits of West Europe (Dobbertin), one belongs to the living family Naucoridae. Another representative of the early Jurassic aquatic bugs described from Braunschweig (FRG), Megalocoris laticlavus Bode (1953), apparently belongs to a special, still not described, Jurassic family.

A great number of Nepomorpha are known from the Neocene localities of West Europe and North America. Heer (1853, 1865) described the rich Upper Miocene fauna of Oeningen (Bavaria), where he found five species of aquatic bugs of the families Naucoridae, Nepidae, Belostomatidae, and Corixidae. Later to these were added two more representatives of the families Notonectidae and Belostomatidae (Schöberlin, 1888). Thus, from this one locality were found representatives of most living aquatic families (five out of nine). From Oligocene deposits of Florissant, Colorado, at first Scudder (1881, 1890) and then Cockerell (1906, 1908), Hungerford (1932) and Lauck (1960) described eight representatives of aquatic bugs of the family Nepidae (one species), Naucoridae (two species), Notonectidae (one species), and Corixidae (four species). Quite a few Heteroptera were found in the Upper Oligocene deposits of Rott (FRG), of which Germar (1837) described one species of Belostomatidae, Heyden (1859) one species of Notonectidae, Deichmuller (1881) one species of Notonectidae, Schlechtendal (1894, 1898) two species of Naucoridae and Corixidae and Statz (1950) two species of Corixidae. Piton published descriptions of two new species of the recent genera Naucoris and Notonecta from Mio-Pliocene deposits of South France (Piton, 1942; Piton, Theobald, 1935). Hutchinson (1942) noted a subfossil representative of the Notonectidae, Buenoa Kirk., from late-glacial deposits of North America. 13 Later from Pleistocene deposits of California, two speciesof Nepidae and one species of Notonectidae were described also (Pierce, 1948). The quality of the recent works of the German hemipterologist K. Jordan (1967), with a description of Pliocene bugs from the locality of Willerhaus (GDR) is regrettable. As for the above-mentioned work of A. Bode (1953) on Liassic bugs, this article is also not suitable for any conclusions. Although among the described Heteroptera, there are real aquatic forms, one out of two of the newly established monotypic families treated as aquatic I am forced to make some reproofs about.

Jordan established the new family Pseudonepidae for Pseudonepa bitarsalis Jordan, which has two-segmented tarsi of all pairs of legs, non-walking fore legs and weakly developed claws. Judging by the description and figure (which, however, are entirely unsatisfactory), this specimen cannot be considered as belonging either to a representative of aquatic bugs or in any way at all to the Heteroptera. More likely, this is some kind of orthopteroid insect, the ovipositor of which was taken by Jordan to be the respiratory tube.

On the other hand, most forms described as terrestrial bugs, including Atoposita angulosa Jordan, separated into a special family, apparently belong to the genus Naucoris (Naucoridae). It is possible that they actually all belong to one species.

The existence in Pliocene times of individuals different from living families is entirely very improbable.

Until recently, fossil aquatic Heteroptera within the USSR were not known. However, now, thanks mainly to the recent finds of the expeditions of the Paleontological Institute, USSR, Academy of Sciences, we have been able to add considerably to our knowledge of fossil Nepomorpha from the territory of the USSR. The first aquatic Heteroptera described from our territory must be considered the Liassic Shurabella lepyroniopsis B.-M. and the Upper Jurassic Karataviella brachyptera B.-M. from Central Asia, at first incorrectly placed in the cicadas of the superfamily Jassoidea (Becker-Migdisova, 1949). Subsequently, their belonging to the superfamily Corixoidea was cleared up. Later another species of the Upper Jurassic locality of Karatau (South Kazakhstan) was described, which belongs in the Notonectidae (B.-M., Popov, 1963). Very recently from the same locality of Karatau, Popov described five more species of aquatic bugs, one of which belongs to the special Jurassic family of pleid-like Scaphocoridae (1968).

Besides, from the Lower Cretaceous deposits of the Transbaikals, I recently described the new subfamily Clypostemmatinae (Notonectidae). In this subfamily the Upper Oligocene bugs from Rott have been included which were originally described as Notonecta primaeva Heyd. and later put into the special genus Clematina Popov (1964). Subsequently, from the same locality were described two more species of the living family Corixidae (Popov, 1966).

These data conclude our knowledge about fossil aquatic Heteroptera of the infraorder Nepomorpha. Completely lacking are any data on representatives of the aquatic families Helotrephidae, Pleidae and what is particularly annoying, presently entirely missing from paleontological annals are the plesiomorphic, littoral families Gelastocoridae, and particularly, Ochteridae, from which the studied aquatic bugs derive phylogenetically.

CHAPTER II

GEOLOGICAL AND GEOGRAPHICAL DISTRIBUTION OF THE EXTINCT NEPOMORPHA

Remains of fossil Heteroptera, as with most fossil insects, very rarely are of a completely preserved body; as a rule, only the tegmen, pronotum, abdomen or strongly dismembered body devoid of terminalia are preserved; finds of hind wings are extremely rare. In burial, in most cases, the body of the insect was carried more or less far by water torrents, in the process of which, it, as a rule, was macerated and the skeleton partly destroyed and deformed. Because of this, even relatively well preserved insect remains are usually only of parts of the dorsal and ventral sides of the body without antennae and legs. A determination of the taxonomic position of the insect from such an imprint is not always possible. In connection, with this, most systems of fossil insects in one degree or another are parataxonomic.

In some special conditions, fossilization and the definite composition of the containing rock can also create other difficulties. Thus, in the process of the study of the fauna of the Liassic locality of Shurab, it was found that the fine-grained and argillaceous rock containing insect remains had undergone compression or tension. This very much distorted the dimensions and form of the specimens, including remains of the aquatic bug Shurabella lepyroniopsis B.-M. From the figures (Table 1, fs. 1-2), it is distinctly visible that two specimens which are set in a row on the same plane almost at right angles to each other have an entirely different form and body proportion. This was the reason for the incorrect placing of the same species into different genera. An analogous taxonomic error was made in another case when from the Jurassic locality of Karatau two different species of the genus Karataviella were described: K. brachyptera B.-M. and K. brachynota B.-M. (1949), which turn out in the same manner to beidentical (Popov, 1962). In this case, the original error was because of the different degree of maceration of the specimens. Similar distortions were found, for example, in the numerous finds of beetles from Dzhailiaucho (South Fergana) in Ponomarekno's work (1969) and the Hymenoptera from the same locality in Rasnitsin's work (1969). In cases of asymmetry of the specimen, different methods of restoration changed the symmetry and proportions by means of coordinated reorganization or photography under correspondingly select angle (D'Arcy Thomson, 1942; Sdzuy, 1962, and others).

Among fossil true Heteroptera of the infraorder Nepomorpha, up to now only aquatic forms are known (Hydrocorisae), and in the past century as far as that goes, mainly only this group of aquatic bugs (except the very doubtful Oligocene Necygonus rotundatus Scudder, incorrectly put in the Gelastocoridae, and the very similar to Gelastocoridae, according to the drawing, Miocene Diplonychus rotundatus Heer).

Remains of fossil Heteroptera, particularly aquatic, until recently were known mainly from Tertiary and Jurassic deposits of West Europe and North America. 15 Unfortunately, many of the fossil forms up to now remain almost not studied. Within the USSR, fossil aquatic bugs were found only recently, some of them (Shurabella lepyroniopsis B.-M., Karataviella brachyptera B.-M.) earlier were considered representatives of another order - Homoptera.

MESOZOIC NEPOMORPHA

The first certain remains of aquatic bugs are found in the lower Jurassic[1], particularly in the Upper Lias of Western Germany (Handlirsch, 1906-1908, 1939). They were

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[1] In my study of remains placed in the genus Triassocoris from the Upper Triassic of Australia (Denmark Hill), it seems that one part of the species belongs to the special family Actinoscytinidae of terrestrial Heteroptera and the other part to Homoptera. Thus, the earlier discussed presumption that Triassocoris is a possible ancestor of the group Naucoridae (Becker-Migdisova, 1962) cannot now be accepted.

put into several special families (Aphlebocoridae, Archegocimicidae, Progonocimicidae, Apopnidae and Probascanionidae), but unfortunately any serious discussion is hardly possible because of the extremely unsatisfactory descriptions and drawings. This is true with respect not only to species established by Handlirsch, but also for the forms later described by Bode (1953) from the same locality.

Within the USSR, the first aquatic bugs were found in deposits of the Lower Jurassic in Central Asia[2], and also West and East Siberia. The original early Jurassic fauna of the group is represented here by the special superfamilies Corixoidea and Notonectoidea and also the superfamily Naucoridoidea.

One Liassic family, Shurabellidae, which was found in deposits of the Lower Jurassic close to Shurab (Fergana)[3] belongs to the Corixoidea. Remains of the presently single representative (Shurabella lepyroniopsis B.-M.) of this endemic specialized family were collected in a great quantity (about 1,000 specimens). It is most probable that Shurabella lived in the zone of humid and warm ginko-sago forests on the north shore of the tropical sea Tetis (Sinitsin, 1962). It is interesting to note that, besides the abovementioned species, other unquestionable remains of aquatic Heteroptera have not yet been found here.

Burial occurred in the locality of Shurab, apparently on the spot of silty shallows with rich vegetation, which is verified by the large number of vegetative remains. Remains of aquatic bugs here are often represented by complete remains of the body. As for the precise age of this locality, a determination now is difficult to make. Some authors consider it Lower Liassic (Martynov, 1937, 1938; Martynova, 1949; Rohdendor, 1957), and others Mid or Upper Liassic (Kuzichkina, Repman and Sikstel , 1958).

Early representatives of Naucoridae (Liadonaucoris rohdendorfi, sp.n.) have been found in another Central Asian locality of approximately the same age (Kizil-kia in South Fergana).

Families of true Notonectidae and Corixidae, represented by one monotypic genus each, 16
are known from the Lower and Mid-Jurassic deposits of Siberia. A few of their remains are found in different localities of approximately the same age (Kuznetzk Basin, Tom River; and East Siberia, Iya River).

In the Lower Jurassic locality of East Transbaikals (Gazimur) was found one of the first certain representatives of living Corixidae which belongs to a special monotypic genus, Gazimuria, gen.n., and which I have put into the living Australian relict subfamily Diaprepocorinae. This find of a Corixoidea in the Lower Jurassic of Angarida, apparently, is indirect evidence of their derivation from the common Nepomorpha stem before the isolation of the Notonectidae and Naucoridae.

These finds in Central Asia and East Siberia, comparatively speaking ,also complete our data on the early Jurassic fossil Nepomorpha in the USSR.

Thus, one of the earliest known aquatic bugs of the families Shurabellidae and Corixidae (Diaprepocorinae) appeared at least no later than the early Liassic on the territory of ancient Angarida in its western and southwestern regions. The most ancient true Notonectidae (Liadonecta tomiensis, sp.n.) also existed then. Within the territory of the present Central Asia there appeared at the same time side by side with Corixidae also the first representatives of the Naucoridae. The Liassic fauna of aqatic Heteroptera of Fennoscandia (West Europe) are entirely different from those of Angarida. Considering the Liassic finds in FRG (Braunschweig), despite their being somewhat problematic, it is possible to speak preliminarily about the beginning of a special early Jurassic Hemiptera-fauna of Fennoscandia, most families of which are never again met anywhere. On the western edge of Angarida at the same time began to appear the first representatives of Living Corixidae (the subfamily Diaprepocorinae), Notonectidae and Naucoridae, the development of which originated under conditions of a humid moderate climate in the zone of conifer-ginko (sagos) forests (Sinitsin, 1962).

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[2] In 1970, in the Upper Triassic,(Norris layer) in South Kirghiz (Madigen horizon), N. I. Novozhilov found a specimen of an abdomen of Naucoridae, which must be considered for now as the oldest fossil find of aquatic bugs.

[3] I take this opportunity to thank N. I. Novozhilov for help and consultation on the Lower Jurassic localities of the USSR.

Mid Jurassic Heteroptera fauna presently remain unknown (if only the above listed Siberian localities do not actually belong to the Dogger), and more or less significant complexes of Heteroptera are found only in later deposits.

Thus, the subsequent actually known Heteroptera fauna belong to the late Jurassic times (beginning with the late Dogger). On the one hand, still preserved here in places are significant complexes consisting mainly of Mid-Jurassic elements and, apparently, even elements of early Jurassic fauna. First of all, to this locality must be placed the entirely special and isolated lagune fauna of the Solnhofen lithographic shales of the FRG (Solnhofen, Eichstatt, Schernfeld, Langenaltheim, etc.)

On the site of a former sea, the Upper Jurassic locality in Bavaria[1] was formed by a saltish lagune of the south shore of Fennoscandia representing an arm about 100 km long and approximately 30 km wide (Kuhn, 1961) and arose because of the sharp cutback and shallowing of the epicontinental basin of the European cycle. The lagune was a flat basin about 0.5-12.0 m deep, separated on the south from the sea by a number of barrier reefs with fairly wide straits. The conditions in the lagune were normal, without 17 heightened salinity or hydrogen sulphide. From time to time the lagune dried up considerably and then, apparently, somewhat smaller lagunes were formed, including the Solnhofen and Eichstatt (Mayr, 1967). Evidently, burial occurred in lime-argillaceous silt. The lime matter was formed by dissolution of the coral reefs found on the south and southwest of the Titon Sea and brought into the lagune by currents (Rothpletz, 1909; Abel, 1924; Schwertschlater, 1925; Kuhn, 1957). Besides, some of the remains were preserved in argillaceous alluvia of the river mouths (Kuhn, 1961), and also as a result of the movement of water in running with the sea, when the raised silt was brought into the lagune (Mayr, 1967).

The reason for the death of animals in the lagune is explained, on the one hand, by the periodic widespread droughts, as a result of which the temperature and salinity of the water rose sharply with a simultaneous lowering in the accumulation of O_2 (Barthel, 1964; Mayr, 1967) and, on the other hand, by superfluous freshening because of deposits resembling present tropical cloudbursts, along with currents of water with matter (Walther, 1904). It must be noted that Mayr's suggestion (1967) regarding the entering nature of insect fauna of the Solnhofen and Eichstatt lagunes to a considerable degree is exaggerated, since the aquatic bug fauna appear on the local scene later in the course of this period. This is particularly true for Nepoidea, which are preserved by whole undamaged specimens in large numbers. The ecology of living forms also verifies my opinion. The conditions of the Solnhofen and Eichstatt lagunes, apparently, were not entirely identical, which, to some degree, is verified by the composition of the buried animal remains. This region then belonged to the zone of hybrid cicadophyte-conifer-ginko forests with a tropical climate (Sinitsin, 1966).

The deposits we are discussing have usually been placed in the Portland, i.e., the uppermost Jurassic. However, in the Reports of the 22nd International Geological Congress, G. J. Krimholtz, V. A. Vakhrameev and others (1964) suggested dropping the use of the term "Portland" because of the non-synonymous lower borders of the Portland and the lack of coordination in the stratigraphic sections of the continental and sea facets, and adopting the more correct name - Titonic layer - for designating the entire interval from Kimeridge to the beginning of the Cretaceous. Most recently (1967), Mayr dated the Bavarian shales Kimeridge or Lower Titon, i.e., Upper Cretaceous.

All the bug remains of these localities were initially put into four living families:[1] Nepidae, Belostomatidae, Naucoridae and Notonectidae (Handlirsch, 1906-1908). The revision I made of the greater portion of the earlier described material disclosed a different map of the faunistic complex of the Bavarian locality. It was found that

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~~1 (16)~~ I wish to thank Prof. R. F. Gecker for help and consultation on this locality.

1 (17) Mesocorixa tenuelytris (Germ.), described as a representatives of the aquatic family Corixidae, as established by Alten (1958), actually is a synonym of the Mesozoic blattid Lithoblatta lithophila (Germ.)

⑫

Notonectites elterleini (Deichm.), "Naucoris" lapidaria Germ. (=Palaeoheteroptera Men.), Mesonepa primordialis (Germ.), Mesobelostomum deperditum (Germ.), and Laccotrephes incertus, sp.n., which I have described below, are representatives of living Notonectidae, Naucoridae, Nepidae and Belostomatidae. The greatest specification is present in the Nepoidea, particularly the belostomatid complex of the genera Mesonepa, Mesobelostomum and Stygeonepa. Thus, the first two genera belong to living subfamilies of the Belostomatidae. According to level of organization, the West European aquatic scorpions 18 cannot be considered primitive and are fully similar to living representatives of two families of this superfamily, Nepidae and Belostomatidae. In degree of specialization and diversity, Jurassic Nepoidea [barely yield to] living forms. (has almost as much as)

Thus, the Nepomorpha fauna of the Solnhofen shales is very original and specified and in some forms (Stygeonepa) does not have close analogies among living (except families of true aquatic Nepidae) or among other known ancient fauna. Considering the finds in the close in age localities in England (Ridgeway) and Kazakhstan (Karatau), Nepoidea from the Solnhofen shales of Bavaria can be considered, apparently, as autochthonic-estuary forms. In support of this is also the lack of any traces of aquatic bug fauna in analogous littoral shales of the same age in France (Cerin), FRG (Würtemburg, Nusplingen), Spain (Sierra Montsech), Australia (Talbrager), Congo (Kinshasa), South America, etc., and even the lack of Nepidae in the above-mentioned localities.

From another Upper Jurassic locality of West Europe (Ridgeway, England), placed in the Oxford layer (Purbeck)[1], only one true representative of aquatic bugs is known - Nepidium stolones Watw., which, in my point of view, belongs to the living family Notonectidae.

For the Mid-Mesozoic localities of Asian USSR, abundance of living families, usually represented by several genera, is characteristic. Thus, in the Upper Jurassic deposits of South Kazakhstan (Karatau), we find four genera of Naucoridae, of which only one (Aidium Y. Pop.) belongs to the special tribe Aidiini.

The presence of a huge number of remains of representatives of the now living family Corixidae must be noted - Karataviella brachyptera B.-M. (over 1,000). Like Gazimuria gen.n., this genus belongs to the living relict subfamily Diaprepocorinae. Another genus of this family, Archaeocorixa V. Pop, I separated into the new subfamily Archaecorixinae (Popov, 1968); some later Mesozoic forms belong to this subfamily (see below). Only one genus of Notonectidae is found in Karatau (Asionecta Y. Pop.). Besides, the special Jurassic chelotrephoid family Scaphocoridae (apparently endemic) of the superfamily Notonectoidea is represented here. Aquatic bugs found in Karatua comprise about 90% of all Heteroptera known from this locality, which in its turn comprises 6.6% of the whole number of insects (Panfilov, 1968). The locality of Karatau was formed on the site of a small lake or number of small lake reservoirs (Gecker, 1948; Panfilov, 1968). At least some aquatic bugs (for example, Karataviella B.-M.), judging from the preservation of the remains, were brought into the lake from rivers. Insect parts are very bouyant and sink only after 10-15 days (judging from my experiments), so that they have already lost their terminalia. As for Corixidae, phytozoophagous, they prefer to stick close to vegetative undergrowth in more or less shallow areas in which there are plankton. However, according to data of Yakovlev (1962), the Jurassic lake was weak in aquatic vegetation and plankton, which one again verifies the transport of Corixidae remains from outside to the place of burial. According to later data (Gallitsky, Gecker, Kostenko, Sakulina, 1968), the Karatau reservoir was a lake with fresh hard water, rich in Ca and Mg, the surroundings of which on rocky areas had sparse tree growth, 19 mainly conifers and bennettites, and also ferns and ginkos. The seasonal climate changes alternated between dry and wet periods. The character of the flora of the Kara-bastau series indicates an aridization of the climate in comparison with the older series of the Jurassic of Karatau (Vakhrameev, 1964).

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[1] During the above-mentimed Congress, a colloquium of the Congress also recommended avoiding the use of the term "Purback" as a designation of the sublayer of the Oxford layer (Krimholtz, Vakhrameev and others, 1964).

There is no single opinion regarding the precise age of the locality of the Jurassic lake Karatau. Most authors consider it Late Jurassic (Martynov, 1925ab; Gecker, 1948; Yakovlev, 1965a). Rohdendorf definitely considers the Karatau deposits as Mid-Jurssic. By later investigators (Gallitsky and others, 1968), the insect bearing thickness was separated into a special Kara-bastau series of Late Jurassic age, dated Kellov-Titon on the basis of the latest spore-pollen studies (Murakhovskaya, 1968; Sakulina, 1968). However, even the latest complicated study of the insect fauna does not allow making a definite determination of their age (Survey - "Jurassic Insects of Karatau," 1968).

In connection with this, it is not without interest to set forth the basic data on the Karatau bug fauna which I have at hand. Of 11 families, seven are living; among the rest, two are clearly specialized aquatic families (Scaphocoridae and Karanabidae), and the other two terrestrial families (Mesopentacoridae and Actinoscytinidae) apparently are phylogenetically relicts of the early Mesozoic. This is especially correct for the latter, which was richly represented in the Triassic and Liassic. In connection with this, of great interest is the Upper Liassic bug Megalocoris laticlavus Bode from Braunschweig (1953), which, in my opinion, belongs to a special family. Besides, Eogerridium gracile Bode from the same locality, which was incorrectly placed by Bode (1953) in the terrestrial Liassic family Diatilidae[1]," judging from the figure, is similar to the Karatau Karanabis kiritshenkoi B.-M. With respect to this, the opinion of V. N. Yakovlev (1967) is interesting, who noticed the considerable similarity of the Upper Jurassic Karatau fish with those of the Mid-Jurassic of Ust-Balei.

At the same time, the Karatau form has some traits in common with the clearly younger fauna of the Tmnsbaikals (Bais), the age of which presently has been determined as Lower Cretaceous (Kolesnikov, 1964). Here we already see another map: endemic and the more relict Jurassic families are entirely missing. The most numerous are Notonectidae and Corixidae, the latter represented by two genera (Diapherinus Y. Pop. and Baissocorixa Y. Pop.) of the special subfamily Archaecorixinae, found in Karatau. The peculiarity of the basin locality is that burial was directly on site (in situ), without any significant crrying by water currents from without, as occurred in all previous (except, possibly, Solnhofen) localities and, thanks to this, the most complete preservation of insect remains.

The character of burial in the numerous Bais layers is extremely diverse. According[2] to facial conditions (Sukacheva, 1968; Rasnitsin, 1969), they fall into three types: layers of deposits of which conditions for burial were unfavorable (23 and 19), and layers with conditions most favorable for burial and development of aquatic fauna (2, 4, 7, 21, 22, 25, 31 and 35). Actually, the data on bugs in general also verifies such a subdivision of layers (Table 1).

TABLE 1   20

DISTRIBUTION OF FINDS OF REPRESENTATIVES OF VARIOUS FAMILIES OF AQUATIC BUGS IN THE INSECT-BEARING LAYERS OF THE LOCALITY OF BAIS

Number of finds and percent of entire number of aquatic bugs in layer (in brackets)

	Distribution of finds according to layer						In All
Families	2	4	19	25	31	35	
Notonectidae	12(60)	-	5(100)	-	51(96)	2(40)	74(82,2)
Corixidae (Diapherinus)	4(20)	-	-	-	1(2)	-	5(5,6)
Corixidae (Baissocorixa)	4(20)	1(100)	-	1(100)	-	4(60)	10(11)
Naucoridae	-	-	-	-	1(2)	-	1(1, 2)

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[1] In my opinion, the family Diatilidae is not independent but identical to the othr Liassic family Protocoridae.

[2] Numbering of layers of the Bais locality given according to Martinson (1961).

It is remarkable that among Notonectidae remains specimens of larvae were found, and in the 31st layer larvae of all five ages were found. Thus, we concluded that the Notonectidae were buried without being transported - in situ. Besides, the distribution of the two basic groups of bugs is such that the majority of the Notonectidae are in the 31st layer (96%) and the Corixidae ain the second layer (40%). Thus, their percentage ratio in the first case is 96 and two, and in the second 60 and 40%. As is known, the Notonectidae prefer a more or less undergrowth vegetative locality (at rest they adhere to plant stems); Corixidae, on the other hand, try to stay on smaller areas free from vegetation, in a condition of rest placing the hind legs on the ground. The distribution of finds of these aquatic Heteroptera justifies suggesting a lessening of depth and changing character of the vegetation of the reservoir from the 35th to the second layer (Sukacheva, 1968).

As for the age of the Bais finds, here again we have no single opinion: some authors consider this locality Late Jurassic (Martynova, 1961; Chernova, 1961; Novozhilov, 1954, 1963), others early Cretaceous (Martinson, 1961; Kolesnikov, 1964; Yakovlev, 1965a). In my opinion the most correct conclusion was given by Kolesnikov (1964) in his work on the stratigraphy of the continental Mesozoic deposits of the Transbaikals. He puts the Bais layer in the Bais series of the Vitim tableland and thinks that the fauna of molluscs, conches and fish sufficiently correctly indicate their Lower Cretaceous age (Lower Neokom). Kolesnikov suggests a border with the Lower Cretaceous/Upper Jurassic Romanovsk series, according to the coarse-pebbly conglomerate and phonglomerate. In his article on the border of the Jurassic and Cretaceous in East Asia, Yakovlev (1965a) finally comes to the conclusion that whichever horizons have Lycoptera and corresponding insect fauna anywhere are Lower Cretaceous.

The climate in the Late Jurassic and Early Cretaceous (Neokom) times in Kazakhstan and Siberia, where the localities of Karatau and Bais are found, was getting considerably arid: the forest vegetation disappeared, xerophilous, sparse tree growth and savannas appeared, and in connection with this carbon accumulation ended. The number of ferns and ginkos diminished; conifers and cicadophytes became the host group (Sinitsin, 1966).

As follows from the above discussion, in the Jurassic period occurred the development of the basic living aquatic families of the infraorder Nepomorpha, belonging mainly to the Corixoidea, Naucoroidea, Notonectoidea and Nepoidea. The superfamily Corixoidea, 21 apparently isolated at the end of the Triassic, was represented by the special Early Jurassic family Shurabellidae. To this time belongs the appearance of the first representatives of true Corixidae (Gazimuria), which I have put in the living relict subfamily Diaprepocorinae. In the Late Jurassic, along with the superfamily Diaprepocorinae, was found the first representative of the Mid-Mesozoic subfamily Archaeocorixinae, which according to paleontological finds, was the most diversely represented in the Lower Cretaceous. Naucoridae and Notonectidae also appear no later than the Early Jurassic in the living families Naucoridae and Notonectidae. In the Upper Jurassic, Notonectidae and Naucoridae are represented by Late Jurassic and three living subfamilies. The third group of aquatic bugs dominant in the Mesozoic is the superfamily of aquatic scorpions Nepoidea, represented by the original Belostomatid-nepid complex in the Torton age. Thus, the original Mid-Mesozoic fauna of aquatic bugs, on the one hand, is represented already by a considerable number of now living families (Nepidae, Corixidae,Naucoridae, Notonectidae), on the other hand, includes still one original only to the Jurassic family Scaphocoridae and, in the richness of large taxons,has almost as many as living fauna (such are the remarkable Jurassic subfamily of the Belostomatidae, Stygeonepinae, and Naucoridae, Sphaerodemopsinae, or the early representatives of the Mesozoic subfamily of the Corixidae, Archaeocorixinae). This latter phenomenon is particularly true for the superfamily Nepoidea with its diverse Jurassic genera of aquatic bugs (Stygeonepa, Mesobelostomum, Mesonepa and others). Characteristic also is the existence of the living genus of aquatic scorpions, Laccotrephes, in the Upper Jurassic of Bavaria.

Finds of Cretaceous insects are extremely few. As for Cretaceous Heteroptera, besides the two finds of terrestrial bugs from Northeast China (Ping, 1928), up to now nothing has been found. With respect to Heteroptera, I have filled this gap only to a small degree in the present study with material on finds from two Upper Cretaceous deposits (Turon and Maastricht) in South Kazakhstan and the Far East.

The Upper Cretaceous locality of Kizil-Jar is found in the northwestern part of Karatau and is a mound, the argillaceous layer of which contains both vegetative remains and insect bodies. This layer was separated into the Beleutin series (Nikiforova, 1960), the age of which was determined as Turon-Santon. However, the question of the age of the insect bearing layer has not yet been determined. Many paleobotanists consider these deposits to be Senoman-Turon (Yarmolenko, 1935; Vakhrameev, 1952; Baikovskaya, 1956). Once even the possibility of Paleocene age was suggested (Yarmolenko, 1935). However, most authors prefer to consider them Turon (Yanshin, 1953; Samsonov, 1966), or Turon-Santon (Nikiforova, 1960).

The climate of the Turon era in this region was sufficiently hot and relatively dry. According to Vakhrameev (1952), the locality of Kizil-Jar was found within the limits of an arid zone. Vegetation was represented mainly (75%) by diverse plane trees and other arboreals, and also shrubbery characteristic for tropical and sub-tropical regions. On the basis of this, the conclusion was made that the Turon forest of Kizil-Jar in richness is closer to the tropical jungle than to the forest of the temperate zone, but with an admixture of subtropical forms of dry-loving type (Samsonov, 1966). These arboreal and shrubbery associations grew on a comparatively small territory near the shore of the Turon Sea. In Samsonov's opinion (1955), this locality represented a wasteland connected with a sea lagune, which was fresh because of the rivers running into it.

In the Cretaceous locality in South Kazakhstan, a special Cretaceous family of 22
aquatic bugs was found, Mesotrephidae, which is somewhat similar, on the one hand, with the living families Pleidae and Helotrephidae and, on the other, resembles the Jurassic family Scaphocoridae. These finds confirm the early isolation of the helotrephoid branch and its existence in the course of a very long time. From the same locality, in the collection of the Paleontological Institute, there are about ten undescribed Heteroptera remains of the ligeid-coreid complex, and the oldest of the up to now known Tingidae was actually found.[1]

Of special interest is another, later Asiatic Upper Cretaceous locality, Cagayan, Pri-Amur. In the Mid-Amurian depression are widely distributed weakly cemented, loose sand-argillaceous deposits, which are separated into the Cagayan synclose (Krishtofovich, Baikovskaya, 1966). The latter is divided into three series: Archarin and Tyukan, dated in Senon time, and Kivdin, placed in the Paleocene (Kirshtofovich, Baikovskaya, 1966). A. N. Krishtofovich considers the Cretaceous series of the synclose to be Danish; recently, on the basis of data of a spore-pollen analysis, their age was determined to be Maastricht (Bratseva, 1966, 1969). The climate of the Pri-Amur at the end of the Cretaceous was warm-moderate with some xerothermization. The vegetation was primarily represented by trochodendron forests with a considerable intermixture of plane trees and some conifers (Taxodium dubium, Metaseguoia disticha and others). In character of vegetation, Cagayan was close to the warm-moderate Late Cretaceous flora of the Arctic, Greenland and North America.

In Cagayan deposits which belong to the Tyukan series, in the lower course of the Bureya River, one representative of Corixidae was found, Mesosigara kryshtofovichi, sp.n., which was put in the Mid-Mesozoic subfamily Archaecorixinae. However, this Corixidae, the closest ancestral form of which survived the great readjustment of the entire continental flora and fauna in connection with the further aridization of the climate of Eurasia and formation of the zone of warm temperate climate (Sinitsin, 1966), along

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[1] Tingiopsis reticulata B.-M., described from the Trias of Central Asia as a representative of the bug Tingidae (1953, 1963), was correctly transferred to the order Homoptera (Evans, 1957, Drake, Rudhoff, 1966).

with the preservation of the basic characteristics of the archedictyon, already had some characteristics of the Cainozoic Corixinae - terminally reduced venation and embolium rim and, also, apparently, asymmetry of the last abdominal male segments. Thus, this form permits leading to the Cainozoic Corixinae directly from the Mesozoic Archaecorixinae.

A reconstruction of the complete map of the geographical distribution of the Mesozoic Nepomorpha on the basis of the paleontological material known to us is not presently possible. This is particularly so in the distribution of genera and more so of species. We do not know one species found at two points at all remote from each other.

The distribution of families in the Mid-Mesozoic is given in Table 2.

As can be seen from Table 2, the first characteristic of the Mid-Mesozoic fauna is the wide distribution of the families Notonectidae and Naucoridae, so that the latter in West Europe and in Kazakhstan are represented by three genera. The second characteristic is the presence of the special Jurassic specialized family Scaphocoridae of the superfamily Notonectoidea.

Comparing Mesozoic forms with living ones related to them, we can note only separate 23
instances of zoogeographical sequence. Thus, representatives of the subfamily Diaprepocorinae, known now only in southeastern Australia, in Tasmania and New Zealand, are found in the Lower or Mid-Jurassic of the Far East and Upper Jurassic of Kazakhstan.

Some mass aquatic bugs, such as the Liassic Shurabella lepyroniopsis B.-M., the Upper Jurassic Karataviella brachyptera B.-M., the Lower Cretaceous Clypostemma xyphiale Y. Pop. and Baissocorixa jaczewskii Y. Pop., can have the same stratigraphical importance as, for example, the Lower Cretaceous fish Lycoptera middendorfii Mill. and others.

TABLE 2

DISTRIBUTION OF FAMILIES OF AQUATIC BUGS FROM AVAILABLE FINDS IN THE UPPER JURASSIC-LOWER CRETACEOUS

Figures indicate number of genera

Locality	Family					
	Nepidae	Belostomatidae	Naucoridae	Notonectidae	Corixidae	Scaphocoridae
England (Ridgeway)	-	-	-	1	-	-
FRG (Bavaria)	1	3	3	1	-	-
Kazakhstan (Karatau)	-	-	4	1	2	1
Transbaikals (Bais)	-	-	1	1	2	-

BASIC LOCALITIES OF MESOZOIC NEPOMORPHA

1. <u>Sai Sagul</u> (Shurab III), Kirghiz, Oshsk Prov., Batkensk region. Found 12 km southwest of the Shurab River. About 1,000 specimens of Heteroptera collected, mainly aquatic Shurabellidae, and about 20 specimens of terrestrial Actinoscytinidae in the lower insect-bearing horizon of argillaceous shales. Age of deposit determined as Mid- or Upper-Lias (Kuzichkina, Repman and Sikstel, 1958). Collection of the Paleontological Institute of Science (PIN) Nos. 495, 1724, 2032 and 2061 (Becker-Migdisova, 1949).

   Shurabella Lepyroniopsis B.-M.

2. <u>Kizil-Kia,</u> Kirghiz SSR, Oshsk Prov., Near Kizil-Kia in 1937, B. B. Rohdendorf found one specimen of an aquatic bug of the family Naucoridae in deposits of the Lower Lias (Martynov, 1937; according to Kuzichkin, Repman, Sikstel, 1958 - Mid or Upper Lias). Collection PIN No. 166.

   Liadonaucoris rohdendorfi Y. Pop., sp. n.

3. Cherni Etap (Black Stop), West Siberia, Kuznetzk Basin, Kemerov Prov., Krapivinsk region. In 1948, Lebedev found one specimen of a Liassic Notonectidae on the left bank of the Tom River above the village of Cherni Etap II (Tersiusk series, Lower or Mid-Jurassic). Collection PIN No. 1068.

Liadonecta tomiensis, sp.n.

4. Iya, East Siberia, Irkutsk Prov., Tulun region. The 1959 Expedition of the Paleontological Institute collected on the left bank of the Iya River in the region of the town of Vladimirov, in deposits of Ust-Balei horizon, four specimens of numphs of aquatic Corixidae. Rasnitsin (1969) notes the closeness of the Liadoxyella Hart. representatives found in these deposits to those from the Liassic deposits of South Fergana. Collection PIN No. 1669.

Ijanecta angarica, sp.n.

5. Gazimur, Southeast Transbaikals, Chitin Prov. The Jurassic study party of the Chitin Geological Department (1958-1961), near Borov on the right shore of the Gazimur River, in the Aleurol-Akatuev series, found some specimens of aquatic Corixidae, which 24 Martynova preliminarily placed in the family Notonectidae (Kolosnitsina, 1962). The locality is dated from sea fauna remains as Mid or Upper Lias (Mushnikov, Apashkina, Olexin, 1966).

Gazimuria scutellata, sp.n.

6. Braunschweig, FRG. Locality of Upper Lias age in which were found about 50 specimens of Cryptocerata. Of 26 described species, only one can be placed in the aquatic bugs (apparently to a new family), conditionally placed by Bode (1958) in the family Archaegocimicidae.

Megalocoris laticlavus Bode, 1953.

7. Dobbertin, Meklenburg. Locality of Upper Lias age in which was found a large number of Heteroptera remains, belonging almost exclusively to terrestrial bugs. Only one form is an aquatic Naucoridae. It was incorrectly separated by Handlirsch into the special family Aphelocoridae (1906-1908).

Aphlebocoris punctata Handlirsch, 1906.

8. Bavaria. Solnhofen, Eichstatt, Schernfeld, Langenaltheim. FRG. Lithographic shales in the region of Eichstatt represent lagune deposits, by the name of Solnhofen, formed in the Late Jurassic in the sea lagune of the south shore of Fennoscandia (Kuhn, 1961). About 100 Heteroptera remains were found in this locality, of which about fifteen belong to the superfamily Nepoidea, and also to the families Notonectidae and Naucoridae. According to the paleoentomologist F. Carpenter (1932), the aquatic bugs were preserved in salty deposits and fell there by means of flight from neighboring fresh reservoirs. The Solnhofen deposits are placed into the Uppermost Jurassic (Portland). Preservation of the material in many cases is very poor and thus a large part precludes re-examination of the already described species, leaving them mostly in a parataxonomic state. (Germar, 1839; Quenstedt, 1852; Weyenbergh, 1869, 1873, 1874; Assmann, 1877; Deichmuller, 1881, 1886; Oppenheim, 1888; Haase, 1890; Meunier, 1897, 1898, 1900; Handlirsch, 1906).

Presently the described remains are preserved in various West European museums - in Munich, Frankfurt-am-Main (FRG), Rostok (GDR), London, etc., and also in some museums of the USA (Carnegia Museum and Museum of Comparative Zoology in Cambridge).

Mesobelostomum deperditum (Germar, 1839)
Mesonepa primordialis (Germar, 1839)
Stygeonepa foersteri, sp.nov.
Laccotrephes incertus, sp.nov.
Pelonecta solnhofeni, sp.nov.
"Naucoris" lapidarius Weyenbergh, 1869
Notonectites elterleini Deichmuller, 1886
Sphaerodemopsis jurassica (Oppenheim, 1888).

9. Ridgeway, England, Dorchester. Locality of Upper Jurassic age, in which in 1853, Fisher found 12 insect specimens. Among the found specimens were two Heteroptera which belong to aquatic bugs and were preliminarily placed in the family Naucoridae (Westwood, 1854; Handlirsch, 1906). Actually, in body form they resemble Naucoridae; however, in structure of the preserved body parts, they are typical Notonectidae.

Nepidium stolones West., 1854.

10. Karatau, South Kazakhstan, Chimkent Prov., Algabassregion. One of the richest localities, located in the southwest part of the Karatau Mountains, in which in the course of many years, beginning with the collections of A. V. Martynov (1924), about 18,000 fossil insects have been collected (Panfilov, 1968). Over 1,000 specimens belong to representatives of the Heteroptera. The basic finds were made close to the village of Michailovka (confluence of Aulie and Kara-bastau) and at the village of Uspensk (near Galkino), and belong to the Karabastau series. Age of the locality is considered to be Upper Jurassic (Kellov-Titon). Collection PIN Nos. 124, 126-135, 138-142, 152, 167, 172, 183-185, 965, 1789, 2066, 2231, 2239, 2255, 2384, 2452, 2554 (Becker-Migdisova, 1949; Becker-Migdisova, Popov, 1963; Popov, 1961, 1962, 1968).

Aidium pleurale Y. Popov, 1968
Nectonaucoris lariversi Y. Popov, 1968
Nectodes maculatus Y. Popov, 1968
Heleonaucoris maculipennis, sp.nov.
Asionecta curtipes, Y.Popov, 1963
Karataviella brachyptera Becker-Migdisova, 1948
Achaecorixa lata Y. Popov, 1968
Scaphocoris karatavicus Y. Popov, 1968.

12. Bais. Transbaikals, Buriat ASSR, Eravin region. The basic collections were made by the Paleoentomological Expeditions of 1958 and 1961. Over 200 Heteroptera specimens 25 were collected, of which about 50 are aquatic. As already stated, according to Kolesnikov (1964), this locality belongs to the Bais series and is considered to be Lower Cretaceous (Neokom). Collections PIN Nos. 1668, 1989 (Popov, 1964; 1966).

Angaronecta longirostris, sp. nov.
Clypostemma xyphiale Y. Popov, 1964
Diapherinus ornatipennis Y. Popov, 1966
Baissocorixa jaczewskii Y. Popov, 1966.

13. Kizil-Jar. South Kazakhstan, Kizil-Ordin Prov., Chiliisk region. The Paleontomological Expedition in 1963 collected about ten specimens of terrestrial and four of aquatic Mesozoic chelotrephoid Heteroptera of the Mesotrephidae in the Upper Cretaceous (Turon) deposits of Beleutin series on northwest sectors of Karatau. Collection PIN No. 2383.

Mesotrephes striata, sp. nov.

14. Bureya, Khabarov Territory, Amur Prov., Archarin region. In 1914, A. Krishtofovich found several specimens of Corixidae in Upper Cretaceous deposits of the Tyukan series (Maastrich-dat) on the Bureya River at Cagayan. Collection PIN No. 324.

Mesosigara kryshtofovichii, sp. nov.

CAINOZOIC HETEROPTERA

According to the number of specimens found and described (over 500 species), Tertiary bugs considerably exceed Mesozoic. Right, the number of Cainozoic localities exceeds the number of Mesozoic. Most finds were made in West Europe and North America. In Tertiary deposits, we already find not one new family which would be absent in living fauna; the entire make up of the living Heteroptera fauna is unusually similar to that in the Paleocene, and particularly, the Neocene period: many genera are found in fossil state and are identical to recent fauna.

Nepomorpha in the Paleocene and Neocene (more precisely, in the Oligocene and Miocene) are represented by five living families (Nepidae, Belostomatidae, Naucoridae, Notonectidae, Corixidae), the largest number of species of which is over 40. Representatives of these families belong to now living genera, possibly with some exceptions. Thus, the Upper Oligocene Notonectidae from Rott, Clematina primaeva (Heyd.), still preserves some traits of the Mesozoic subfamily Clypostemmatinae. How strongly different from each other in specific and generic composition are the Neocene and Paleocene representatives of aquatic bugs is now difficult to judge, and because of this, except for a review of the already known Cainozoic material, new finds are also needed.

The Quartenary period was not completely favorable to burial and preservation of insect remains and we know very little about either the changes of the local fauna or the general appearance of the gradually changing fauna of the large territories during, for example, the glacial freezes and thaws.

In sum, we know not more than ten remains of Quartenary aquatic Heteroptera of the families Nepidae, Notonectidae and Corixidae. There is also mention of a find of a Holocene belostomid, Lethocerus americanus (Leidy), in Pleistocene deposits near Los Angeles (Lauck, Menke, 1961).

Real Paleocene Heteroptera fauna of West Europe developed in the zone of changing subtropical evergreen vegetation (Poltav, Turgan flora), located in the tropical humid lithogenetic zone of Mediterranean type with subtropical, close to tropical, climate (humid-subtropical). In the Miocene, the vegetation remained basically of the same but more Turgan type, i.e., leaf shedding. Because of reduction of the water of the ancient Tetis, the climate often became subtropical with further continentalization 26
and aridization, particularly in the Asiatic part of Eurasia (Kazakhstan, South Siberia). On this territory, the forest vegetation represents a mixture of derivatives of Turgan and Poltav flora, which formed a new type of Neocene flora--the ancient Mediterranean (Kornilova, 1966). The savannas began to be replaced by degrees and at the end of the Miocene, beginning of the Pliocene, all of the subtropical savanna had disappeared and basically the steppes remained. In the Pliocene a gradual general cooling and continentalization of the climate began, the flora of the Mediterranean region became xerophilous, in Europe the displacement to the south of the geobotanical zone occurred, in Siberia the dark coniferous forest appeared (first stage of the taiga), in Tien-Shan the Neocene turgan flora formed, and the desert landscape of Central Asia and Kazakhstan appeared, etc. (Sinitsin, 1966).

Of the fossil insect bearing Tertiary deposits of the territory of the USSR, we are interested in the Miocene locality of Chon-Tuz in the upper reaches of the Chu River (North Kirghiz).[1] In the layer of lake shales and aleurolites with conglomerate layers (breccia and gravellites of 300 to 1,500 m thickness) in the southern part of the Kochkor diggings, numerous insect remains were found. Besides insects, these deposits (Martynov, 1938; Becker-Migdisova ,Martynova, 1951) contain fish also (Yakovlev, 1959), and numerous flora remains (Kornilova, 1966), which most authors place in the Mid-Miocene (Sikstel, 1939; Petrushevsky, 1948; Kornilova, 1962, 1966). A preliminary determination of the flora by I. V. Palibinin and M. D. Zalessky indicates also Sarmat age. A later spore-pollen data analysis (Abuzyarova, 1954) determined the age of the deposits as Lower-Mid Miocene. To the latter determination of dating the age, add also S. A. Tarasov (1968), who separated these deposits into the Shabirkol series.

As to the conditions in which the development of the Miocene aquatic bugs occurred, some data have been provided by A. V. Martynov (1938), who discussed the existence of a large lake with fresh, or at times weakly salty, water which was not very deep. S. A. Tarasov (1968) comes to the same conclusion on the basis of the presence of a large number of tiny-fragmented thin layered rocks of lake genesis and the lack of salt bearing rock.

Such are the general traits of the characteristics of the Cainozoic aquatic Heteroptera and the conditions in which they developed.

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[1] I take this opportunity to express thanks to the science student of the Paleontological Institute, V. I. Zhegalle, who was of great help in the locality characteristics.

BASIC LOCALITIES OF CAINOZOIC NEPOMORPHA

1. Baltic Amber, Pribaltic. About 50 specimens of bugs have been found in the Lower Oligocene amber. Only one specimen is a Nepomorpha representative. Also in the collections of the PIN, Academy of Sciences (AN), USSR, there are specimens of undescribed Corixidae nymphs.

Nepa sp. Berendt, 1830.

2. Aix-en-Provence, France, Provence. Over 30 specimens were collected from deposits of the Mid-Oligocene, including one Notonectidae and one supposed aqutic Nepidae.

Nepa? Serres, 1829
Notonecta sp. Hope, 1847.

3. Rott, FRG, Rhine Region. About 650 specimens were found in the locality of Upper Oligocene age, of which about 600 belong to aquatic bugs. 47 species of terrestrial and 12 species of aquatic Heteroptera have been described (Germar, 1837; Heyden, 1859; 27 Deichmuller, 1881; Schlechtendal, 1892, 1894, 1898; Statz, 1950; Statz, Wagner, 1960; Jordan, 1953), of which the Corixidae designated by Statz as Corixa vidua is apprently identical to Corixa rhenana Stz. (Statz, 1950). Besides this, it is possible that all of the Corixidae belong to one species.

"Belostoma" goldfussi Germar, 1837
Naucoris rottensis Schlechtendal, 1898
Clematina primaeva (Heyden, 1859)
Soevenia heydeni (Deichmuller, 1881)
Corixa elegans Schlechtendal, 1894
Corixa rhenana Statz, 1950
Corixa vidua Statz, 1950.

4. Florissant. USA, Colorado. One of the richest Cainozoic localities from which 153 species of Heteroptera have been described, including six species of Nepomorpha.[1] Its age was determined earlier as Miocene (Scudder, 1881, 1890; Cockerell, 1908; Hungerford, 1932; MacGiniti, 1953; Lauck, 1960), now as Mid or even Lower Oligocene, MacGiniti, 1960).

Nepa vulcanica Cockerell, 1908
(Discostoma) sp. Scudder, 1890[2]
Notonecta emersoni Scudder, 1890
Notonecta (Paranecta) binuda Lauck, 1960
Corixa immersa Scudder, 1890[3]
Corixa vanduzeei Scudder, 1890
Sigaretta florissantella (Cockerell, 1908).

5. Dečin, CSSR, North Czechoslovakia. One representative of Belostomatidae has been described from Oligo-Miocene deposits at the village of the Lower Dolni Bechlejovice (Riha, Kukalova, 1967).

Lethocerus sulcifemoralis Rh. et Kuk.

6. Kutschlin, CSSR, Czechoslovakia. A single bug specimen was found (Notonectidae) in deposits of the Lower Miocene (Deichmuller, 1881; Statz, 1950).

Soevenia kutschlini (Deichmuller, 1881).

7. Oeningen, FRG, Baden. 94 species of bugs have been described from an Upper Miocene locality, eight of which belong to Nepomorpha[4] (Keferstein, 1834; Heer, 1853; 1865; Schöberlin, 1888).

Nepa, Keferstein, 1834
Nepa Schöberlin, 1888
"Belostomates" speciosa Heer, 1865
"Belostomates" harrisi Schöberlin, 1888
Naucoris dilatatus Heer, 1853
(Diplonychus) rotundatus Heer, 1853[5]
Corixa fasciolata Heer, 1853.

8. Chon-Tuz, Northeast Kirghiz, Kochkor region. In 1938, A. Y. Petrosian, and in 1942 the Expedition of the PIN, USSR, in the south side of Tersk-Alatau (Central Tien-Shan, in the Kochkor diggings on the right bank of the Chon-Tuz River, in Miocene deposits of the Shabirkol series, collected about 150 specimens of Heteroptera, among which about 90 belong to aquatic bugs of the family Corixidae. Collection PIN No. 372.

Diacorixa miocaenica Y. Popov, sp. nov.

9. Tara, West Siberia, Omsk Prov. In beds of Miocene age, on the left bank of the Abrosimovki River, at the village of Ekaterinoslav 10-12 km south of Tara, on the Irtysh, a specimen of a true Belostomatidae was found.

Lethocerus turgaicus Y. Popov, sp. nov.

10. Stavropol, 1 (Voroshilov), North Caucasus, Stavropol region, Balka Vishnevaya, 2 km above the mouth, west bank of Lake Sengileev. In 1939, the Expedition of the Paleontological Institute found a single specimen of an aquatic Corixidae in spaniodont argillaceous layers among numerous Heteroptera. Collection PIN No. 254/2962.

Sigara sp.

11. Lac Chambon, France, Central Massif. Four species have been described from deposits of Mio-Pliocene age, two of which belong to Notonectidae and Naucoridae (Piton, Theobald, 1935; Piton, 1942).

Naucoris crassus Piton, 1935
Notonecta arvernica Piton, 1942.

12. Willerhaus, South Saxony, near Gartz. 21 Heteroptera species were described from deposits of Upper Pliocene age, four of which belong to Naucoridae (Jordan, 1967). 28

"Cydnopsis" ventralis Jord.
"Cydnopsis" affinis Jord.
"Coreides" latus Jord.
"Atoposita" angulosa Jord.

13. Re, Italy. In literature appears one specimen of an indeterminate bug from Quarternary deposits (Benassi, 1896).

Corixa sp. Benassi, 1896.

14. Mac-Kitrik, USA, California. Two species have been described of aquatic Nepidae and one species of Naucoridae from layers of Pleistocene age (Pierce, 1948).

Ranatra asphalti Pierce, 1948
Ranatra besscomi Pierce, 1948
Notonecta (Paranecta) badia Pierce, 1948.

15. Boryslaw, West Ukraine, Lvov Prov. Four species of Corixidae have been described from a Pleistocene locality (Lomnicki, 1894; Jaczewski, 1923, 1929, 1949), one of them recent (S. producta Rt).

Sigara (Arctocorisa) horvathi (Lomnicki, 1894)
Sigara (Callicorixa) producta (Reuter, 1880)
Sigara glacialis Lomnicki, 1894
Sigara boryslavica Lomnicki, 1894.

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[1] As drawn and described by Scudder, Necygonus rotundata Scudder in no way corresponds to characteristics of the family Gelastocoridae.

[2] Most likely this is the genus Naucoris L.

[3] It is more probable that this species is identical with Corixa vanduzei Scd., which actually differs only slightly in dimensions of the ninth segment.

[4] Judging from Heer's drawing, Nepa atavina Heer (Heer, 1853, t.X, fig. 9ab) can in no way be put in the aquatic bugs.

[5] It is possible that this is a representative of littoral Gelastocoridae.

CHAPTER III

GENERAL MORPHOLOGICAL SURVEY OF THE NEPOMORPHA

The body structure of true Heteroptera as a whole has been studied sufficiently completely beginning with the works of Dufour(1833) and Geise (1883). This problem has interested many investigators in our century (Taylor, 1918; Hoke, 1926; Tanaka, 1926; Ekblom, 1926, 1930; Weber, 1930; Snodgrass, 1935, 1938; Elson, 1937; Spooner, 1938; Butt, 1943; Larsen, 1945ab, 1950; Southwood, 1955, 1956; Poisson, 1957; Pendergrast, 1957; Scudder, 1959; Miyamoto, 1961, and many others). However, studies which give a detailed account of the basic body sections and their comparative-morphological analysis are still very few (Becker, 1929; Wefelscheid, 1912; Ferriere, 1914; Hamilton, 1931; Rawat, 1939; Griffith, 1945; Sutton, 1951; Marks, 1958, 1959; Benwitz, 1959; Parsons, 1958, 1959, 1960, 1962, 1963, 1964, 1965, 1966ab, 1967, and others).

A detailed examination of the structure of Heteroptera of the infraorder Nepomorpha does not fall within the problems of this study. Except for a general plan of the body structure, I have touched upon only those morphological features which play an especially important role in the restoration of the path of historical development of the infraorder and explain the phylogenetic relationships of the basic taxons included in it. Besides, I propose a new interpretation of the separate elements of the skeleton.

GENERAL STRUCTURAL CHARACTERISTICS

Families of the infraorder Nepomorpha are characterized by sufficiently clearly expressed adaptive traits, which along with other features, sufficiently clearly separate one from the other. The body plan is flat and narrow in the Corixidae; cigar-like and in sections almost three-edged in Notonectidae; flat, widely-oval or almost disc-like in most Naucoridae; flat, more or less oval in Belostomatidae; elongated, baton-like in Ranatrinae and flat, oblong-oval in most Nepinae (Nepidae); short, with roof-shaped folding wings in Pleidae and Scaphocoridae; finally, more or less oval and fairly strongly convex in Ochteridae, Gelastocoridae, Helotrephidae and Mesotrephidae. The mouth apparatus is scraping-sucking in Corixidae and thrusting-sucking in the rest of the Nepomorpha. The fore legs are grasping in Gelastocoridae Naucoridae and in all families of the Nepoidea; in male Corixidae the tarsi are often spade-like (palae). The hind legs are usually natatory, often with more or less flattened tarsal segments and with a developed dense brush of hairs in Corixidae, Angarocorini (Naucoridae), or even like very broad paddles in Stygeonepinae (Belostomatidae). The usually non-flattened hind tarsal segments, covered with thick hairs, are characteristic for Notonectidae and most Naucoridae. The hind tarsi of Pleidae, Aphelocheirinae and Crypocricinae (Naucoridae), Helotrephidae and Mesotre- 30
phidae differ in the presence of sparse long hairs. Walking hind legs are peculiar to Nepidae and Helotrephidae. In Nepidae, the coxae are well separated and the sternal region of the thorax is well developed; in all remaining Nepomorpha, the coxae are pushed together and adjoin by the inner sides, and the sternal region is strongly reduced. In most male Corixidae, the abdominal segments are asymmetrical, with a split eighth segment. In Nepidae, long (but in Belostomatidae and Stygeonepinae, short) respiratory tubes are developed.

The use of the above-listed morphological features of representatives of these families often makes it possible to determine fossil remains accurately and dependably, not only from the whole body, but also from partially preserved body parts.

BODY STRUCTURE OF THE IMAGO

distinguished separated

The Nepomorpha head frequently is more or less pulled into the prothorax and fairly sharply articulated from it. In some Helotrephidae (Paskia, Idiocoris), in contrast to all other Heteroptera (even the overwhelming majority of all other insects in general), the head and prothorax are fused without any traces of articulation (f. 107) and form the so-called cephalothorax (cephalonotum). In representatives of the families Nepidae and Naucoridae, the head is especially deeply pulled in, so that a large part of it is found in a special cavity of the pronotum (f. 1). In the other Nepomorpha, the fore margin of the pronotum is more or less straight, and the head is weakly or entirely not drawn in. In a number of cases, the almost complete fusion of the anterior sclerites of the head (clypeus, frons, vertex, genae) does not allow precisely discerning their borders, which are visible topographically only at the point of articulation of the separate muscles, the fore "tentorial"[1] pits, some internal skeletal parts of the head or along the direction of the facial sutures.

The mouth organs are like a rostrum, attached to the fore part of the head and formed of the labium, the mandibulae and maxillae, which are transmuted into long stylets. In a state of rest, the rostrum usually lies under the thorax, but during feeding it usually stands at a right angle to the body, so that the rostrum is shortened, freeing the tips of both pairs of maxillae/mandibulae.

The labium is segmented, usually consisting of four segments; the basal segment is joined by means of a membrane to the ventral sector of the head capsule. The labium serves as a case for the mandibular and maxillary stylets. The basic modifications of the Nepomorpha labium are shown in figure 2.

The mandibulae are represented by two thrusting mandibular stylets which lie, as a rule, with respect to the maxillary stylets, ventrally within the head (f. 3) and laterally within the labium (f. 4). They serve to pierce the body of the prey and fix the rostrum in it. The base of the mandibular stylet is widened and serves as a place of attachment of the muscle-retractors, which, in their turn, are directly attached to the head capsule. The stylets have another point of articulation to the inner wall of the head at the lateral end of the loro-genal suture by means of the 31
so-called mandibular lever. This lever is a plate which lies horizontally in the head and serves to support the mandibular stylets and direct their movement. The apex of the lateral surface of the mandibles bears somewhat sabre-like projections, the apices of which are directed backward, which facilitates the fixation of the mandibles in the body of the victim during sucking (f. 5).

In manner of attachment and in form, there are four types of mandibular levers (f. 6) (Ekblom, 1929). The first type of lever is triangular, attached to a membrane, which surrounds the base of the mandibular stylet. The second type of lever is three-branching, directly attached by one end to the stylet. The third type of lever is triangular, the fore end of which, turned downward, is directly contiguous to the stylet, and the hind to the head capsule. The fourth type is a quadrangular lever with double walls, which lie close to the base of the stylet, but are not fused with it. Spooner (1938), who studied a large portion of the families in detail, found, in the families which I include in the Nepomorpha (except Corixidae), the second type of lever. The third type is inherent only to the Corixidae, and the fourth to the littoral families Ochteridae and Gelastocoridae. All terrestrial Heteroptera have the first type of lever.

The maxillae are represented by maxillary stylets, which serve to carry food and inject saliva. On the inner side of each stylet there are two grooves which, when folded, form two canals: the upper, feeding and lower (usually much more narrow), salivary (f. 4). In form, the maxillary stylets are similar to the mandibular;

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[1] Bugs have no real tentorium (see below). However, I have preserved the term "tentorial" pits, accepted in hemipterological literature, since the true nature of these indentations has not been established.

however, their base is slightly thicker, since it serves as the place of articulation of the muscle-retractors and muscle-protractors. These muscles are attached directly to the head capsule. The other point of articulation of the stylets is the maxillary lever like a thin, curved bar (f. 5), which is attached to one of the hypopharyngeal wings and is not connected to any muscle (f. 3). Often, the right and left stylets are different from each other. There is a system of hairs and stylets on the apex of the maxillary stylet which, as Parsons (1959) suggests, help in filtering the sucked in food.

The labrum is attached to the ventral or distal margin of the clypeus, particularly 34 to the fore margin of the anteclypeus and to the maxillary plates with the help of a narrow membrane. It is usually triangular (fs. 8a, 15a, 16)[1], wider in Gelastocoridae and Naucoridae (fs. 9a, 14a) and narrower in Nepidae, Belostomatidae (fs. 11a, 12a, 13a) and particularly in Corixidae (fs. 18, 19).

The clypeus, on the outside in terrestrial Heteroptera, is divided into two parts: anteclypeus and postclypeus. The hind border of the latter is not clearly or not at all pronounced. On the sides, the anteclypeus is distinctly separated by deep clypeoloral sutures (suturae clypeolorales), which in the common ancestor of the Nepomorpha, apparently, reached the fore "tentorial" pits. In most aquatic bugs, these sutures are missing. In the superfamily Nepoidea, they are distinct but are strongly shortened due to the complete or almost complete fusion of the proximal part of the postclypeus with the laterally situated sclerites (lorae) (f. 7). The anteclypeus usually is completely fused with the postclypeus without any distinct sutures. However, in some fossil aquatic bugs (Clypostemma xyphiale Y. Pop.), these parts are divided by the clypeal suture (sutura clypealis). In places, the inner surface of the anteclypeus and the labrum forms a membranous roof of the fore section of the food canal or cibarium, the so-called epipharynx. This section of the food canal sucks in food because of the vertical movement of the epipharyngeal surface and thus is often called the food pump. We will use this term from now on.

The maxillary plates (laminae maxillares) are situated on the dorsal surface of the epicranium (fs. 8-17). A large portion of them are submerged within the head, from the skeleton of which they leave at the level of the fore and hind "tentorial" pits. 35 These plates are delimited from the loral plates by the loro-genal sutures and situated laterally at the fore margin of the clypeus. In Nepomorpha, the outer sclerite is proximally fused with the genal region, having only one more or less clearly marked suture - the loro-genal, which is differently developed in representatives of different families (f. 7).

The loral or mandibular plates (loral plates, mandibular plates, paraclypeus, jugum) are formed by the emergence onto the dorsal surface of the so-called loral fields or lorae (lorae, laminae mandibulares), which are the inner side walls of the food pump, forming the hypopharynx. The loral plates are well developed in all families of the infraorder (fs. 8-17) and separated from the surrounding sclerites by the loro-genal (suturae lorogenales) or clypeo-loral (suturae clypeolarales) sutures (f. 7). The loral plates border the genal region only along the distal part of the strongly shortened loro-genal suture; however, for the greatest extent they are fused with the genae.

The genae and postgenae are strongly spread out and completely fused with their surrounding sclerites without any traces of articulation. Only remnants occur of the already above-mentioned loro-genal and ventral (apparently, hypostomal)(sutura ventralis) sutures, the latter coming from below along the central line.

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[1] Spooner (1938) isolated three types of labrum structure: a wide wing-shaped labrum is met in Naucoridae, Notonectidae and Corixidae of the Nepomorpha; a long and narrow triangular labrum in Belostomatidae; a wide wing-shaped labrum with long, epipharyngeal projection in Ochteridae and Gelastocoridae. However, this division is morphologically incorrect, all the more so since there is a transitional form between the first two types.

The postgenal bridge or genopont (genopons, pons postgenalis) is formed, in my opinion, by the accretion of the ventral margins of the postgenae and, apparently, the hypostomi also, which sometimes are divided (particularly in the nymphs) by longitudinal sutures. From the caudal side of the epicranium, the above-mentioned sclerites occupy a sector in the closing of the foramen occipitale. From the outside, the genopons is usually smooth (fs. 9b, 11B), weakly-knobbed (f. 10b) or with a strongly developed mound (f. 14b).

In hemipterological literature, this region is usually called the gular plate or gula, which basically is an independent sclerite of the neck membrane. However, in this case apparently, the process of strengthening of the ventral part of the head occurs in a different way, namely, by the growth and closing of the medio-ventral margins of the head capsule. Snodgrass (1960) holds a similar point of view, calling this formation in the Notonectidae and Naucoridae the postgenal bridge. Some other investigators (MacGillivray, 1923; Spooner, 1938) also held the opinion that the occipital aperture in bugs is closed not by the gular plate itself, but by the so-called genopont. The preservation, in nymphs, of some forms of hypostomal sutures (and, apparently, distal parts of the post-occipital) permits suggesting that the foramen occipitale is closed not by the post-genal, but by the hypostomal (+post-oscipital ?) bridge. For convenience, I will conditionally designate this sclerite as post-occipital.

The frons gets smaller in those cases where the dimensions of the vertex, eyes and clypeus increase. We can judge the dimensions of the latter only from the position of the fore "tentorial" pits, which appear on the hind border of the clypeus, since the frons-clypeal, or epistomal, suture is missing in Heteroptera.

The vertex in Nepomorpha occupies the uppermost part of the head capsule and, as a rule, is not large. Its size depends on the form of the head.

Completely missing in real Heteroptera is the system of strongly chitinized internal supporting bars perpendicular to the surface of the head capsule - the so-called tentorium, which is so characteristic for Homoptera, where they, besides fixing 41
the mouth apparatus for work, serve as the site of attachment of the muscles connected with them. For directing the maxillary stylets in the head capsule of bugs there are structures which resemble tentorials, like the so-called hypopharyngeal projections or wings (f. 3), to which the throat muscles, and also the maxillary levers, are articulated. The hypopharyngeal wings have been designated in hemipterological literature (Hamilton, 1931; Butt, 1943; Guadri, 1951; Benwitz, 1956; Parsons, 1959, 1960, 1962, 1963, 1964, 1966; Matsuda, 1965) as "hind plates of the hypopharynx" (Snodgrass, 1938), "sclerotized plates of the genal apodeme" (Rawat, 1939), "maxillary coverings" (Sprague, 1956), and finally, as parts of the tentorium (Ekblom, 1926; Becker, 1929). All these supporting structures, ~~are~~ on a level with the tentorium, are present in Homoptera. Thus, the corresponding parts of the endoskeleton of the head of bugs in no way can be considered as rudiments of the tentorium.

The reason for the loss (if Heteroptera arose directly from the Homoptera) of one of the basic supporting structures of the epicranium in Heteroptera apparently must be looked for in the transition from phytophagy to zoophagy, where an unusually powerful cibarium pump, available in cicadas, is necessary, but consequently, not a tentorium. In bugs, undoubtedly, phytophagy is a secondary phenomenon, all the more so since vegetarianness often bears the character of phytozoophagy.

The structure of the special filtering system in the fore section of the food canal (cibarium), which is very characteristic for most Nepomorpha, deserves special attention - the so-called pharyngeal teeth, which are very significant for understanding the historical development of the entire group of aquatic bugs as a whole. This system has recently been studied in detail by the Canadian morphologist, Parsons (1959, 1965, 1966, etc.).

As is known, the food pump, or cibarium, is a canal which begins from the place where the mandibular and maxillary stylets part and is situated in the dorso-medial part of the head capsule (f. 18). The dorsal surface of the pump (roof) is partly a membranous epipharyngeal formation of the inner surface of the anteclypeus; the ventral is the chitinized dorsal surface of the hypopharynx (Parsons, 1966). In the widened central portion of the food pump on the epipharyngeal surface is an original system of parallel, low, flat riblets which are joined into two as the so-called transverse plates in the families Ochteridae (f. 19ab), Gelastocoridae (f. 20ab), and Naucoridae (f. 21ab), or in an unpaired transverse plate in Notonectidae (f. 22), and Corixidae (fs. 23, 24ab). These riblets bear a small thickening or elevation, which is repeated at regular intervals and thus creates an original covering. Thus, in the beginning they were called "striped plates" (Parsons, 1959). In Ochteridae, these plates divide into fore and hind sections: the fore section consists of riblets with thickenings, almost analogous to those in the family Gelastocoridae, and thus creating stripes directed slantingly with respect to the longitudinal axis; in the hind section the elevations of the riblets are smaller and closer, perpendicular to those in the fore section (f. 20b). The transverse plates, together with the opposing projections and hairs on the hypopharyngeal surface of the food pump, bear the function of pulverizing and filtering food particles. Sometimes, these plates are devoid of riblets, creating a stripedness;* for example in the hind sector of the unpaired transverse plates of Notonectidae (f. 22). The projections and thickenings of the epipharynx, in this case, basically bear the 44 function of pulverizing food particles, and the hypopharyngeal surface is furnished only with hairs and participates only in filtering. In Naucoridae this filtering apparatus is somewhat more complicated in structure and consists of a pair of transverse plates, furnished with numerous longitudinal rows of teeth, with corresponding fore and hind sectors (f. 21b). The filtering function of the transverse plates in Naucoridae was studied experimentally by M. Parsons (1966). Note: I didn't experiment (M.C.P.)

*zone?

The construction of the filtering apparatus is of an entirely different form in Corixidae. Here we find the greatest complexity of the transverse plates, which have been studied by a number of authors. Just as in the above-mentioned families (except Gelastocoridae), the unpaired transverse plate is divided into fore and hind sections, each of which, in its turn, is articulated into two zones (f. 23). The strong development and complexity of the filtering apparatus of Corixidae is caused first of all by a special (for aquatic bugs) type of feeding - phytophagy (more precisely, detrito- and algophary), which requires intensive pulverization and filtering of the food substrate. The basic pulverization of the food takes place in the first two zones, and filtering occurs in the third zone. The trans- 45 verse fold, as in Notonectidae and Naucoridae, is furnished with long filtering hairs on the inner side.

In Nepidae and Belostomatidae, the filtering apparatus is weakly developed. It is represented by two rows of longitudinal projections on the epipharynx, situated laterally from the central line, and by two analogous formations on the hypopharyngeal side. The projections of the epipharynx bear a row of small sclerotized stylet-like projections, which in Belostomatidae are dorso-laterally curved (f. 25). In Ranatra (Nepidae), the sclerotized projections on the epipharyngeal side (f. 26) are extremely small, directed vertically downward and resemble those in Saldidae. At the same time, in Nepa the corresponding region is smooth and apparently devoid of any projections.

The maxillary glands of Notonectidae, Naucoridae, Pleidae, Corixidae and Belostomatidae are localized basically at the base of the rostrum (fs. 27a-B). In Nepidae they partially (f. 27B) or wholly come into the prothoracic sector. Around the discharging pores there are hairs which are especially developed in Notonectidae and Pleidae. In Corixidae and Naucoridae, these hairs are weakly developed. Not one opinion exists presently as to the relative function of these glands.

According to Poisson, their secretion, dispersed close to the victim, either paralyzes it or frightens predators (Poisson, 1958; Benwitz, 1956). Khanna (1964) considers that the secretion of the maxillary glands serves only as lubrication for the stylets of the rostrum. The excretory function of these glands was suggested by M. Bordas (1905), E.G. Becker (1929), and L. V. Puchkova (1965).

Nepomorpha antennae, as a rule, are very shortened, shorter than the head, and at rest are concealed on the lower side of the body in special depressions, so that seen from above they are almost not visible. Apparently, this is connected with the aquatic or littoral form of life. Usually they consist of three or four segments and are attached, as a rule, under the eyes. The form and hairy cover of the antennae vary greatly in the different families. In Corixidae and Naucoridae, the antennae are four-segmented, more or less cylindrical, the second and third segments almost bare. In Naucoridae, these segments are covered with long hairs (f. 28). In Notonectidae, the antennae are either four-segmented - Notonecta, Enithares, Martarega (then all 50
segments are cylindrical, f. 29) - or three-segmented (Anisopinae). In this case, as a rule, the last segment is condensed and stretched. In Nepidae, the the antennae are three-segmented, of fairly original form, almost naked (f. 30). Antennae are very variable in representatives of the family Belostomatidae (Lauck, Menke, 1961). Here we find both three-segmented (fs. 31z-i) and four-segmented antennae (fs. 31a-zh). In this case, it is possible to follow the paths of change from the most simple line of antennae, for example in Belostoma and Abedus (fs. 31 z-i), to their highly unusual structure, for example, in Lethocerus or in Horvathinia and Limnogeton (fs. 31a-B). In Pleidae, the antennae are always three-segmented, cylindrical (f. 32), whereas in the related family Helotrephidae, the antennae are two- (f. 33) or even one-segmented (Idiocerinae). Some Naucoridae (Aphelocheirinae, Potamocorinae) and Ochteridae have the longest among Nepomorpha four-segmented antennae, which are only slightly shorter than the head (f. 34) and are not hidden in the furrows. In Naucoridae, they 51
even bend onto the dorsal side of the head(f. 15).

The thorax in true aquatic Heteroptera is usually a compact formation, with more or less whole segments, Pleurites ~~are most often~~ expressed (fs. 35-45). , for the most part, are

The prothorax is more or less mobole, sometimes partially (Pleidae, Helotrephidae, Scaphocoridae) or completely (subfamily Idiocorinae in the family Helotrephidae) fused with the head, clearly visible from above like a fairly large pronotum. In Nepidae and Belostomatidae, the pronotum is divided by a transverse break into fore and hind fields; in aquatic scorpions it is highly sculptured, but in other families smooth or punctured (in Pleidae).

The lateral margins of the pronotum are usually strongly wrapped onto the ventral side and often fused with the thoracic pleurites. Only in bugs of families Belostomatidae and Notonectidae are the notopleural sutures more or less marked (fs. 39, 45). In the family Naucoridae and particularly the Nepidae, there is a place of fusion of the pronotum with the ventral sclerites. Thus, in Nepinae the epimeres and episterna do not have notopleural sutures and, are wholly accreted with the lateral margins of the pronotum (f. 37). In Ranatrinae, there are remains of epimeres at the base of the strongly moved forward coxae (f. 38). In Corixidae, the sides of the pronotum are 52
expressed as small, clearly visible lobes; the basisternite is hidden (fs. 40, 41). The coxal cavities in aquatic bugs, as a rule, are closed.

The mesothorax in aquatic bugs is of more monotypic structure. The characteristic feature is the close junction of the sternal region and the pleurites, of ten divided by the pleuro-sternal suture, which occupies a variable position, but is always longitudinal. Exceptions in this respect are the plesiomorphic Ochteridae (f. 39) and the specialized Pleidae (f. 44), in which the basisternite is a separate sclerite. In the family Notonectidae (f. 45), this fissure runs vertically and takes up only a

portion of the basisternum and episternum (pre-episternum according to Matsuda, 1962), already fused into a single sclerite. In most Corixidae, for example in Hesperocorixa (Matsuda, 1962) and Corixa, the pleurosternal suture is developed: it is particularly distinct, deep and complete in Sigara. In all other families, the basisternum and episternum are completely fused without any traces of sutures. The basisternum, usually along a central line, is more or less curved. Only in Nepidae, in connection with strongly moved apart coxae, is this sclerite fairly convex. Thus, the segmentation of the sternopleural region in aquatic groups of Heteroptera is lost as a result of the almost complete fusion of the separate sclerites. Apart from the visible junction of the episternal region in living aquatic bugs (except Nepidae), an outgrowth of 53
its hind section also occurred, with the formation of the so-called supracoxal sector (Matsuda, 1962), which completely covers the base of the coxae. In Notonectidae, Naucoridae, Belostomatidae, Pleidae, this region is well developed, in Corixidae, weaker, in Helotrephidae, represented as a narrow transverse stripe. The epimeral region is also developed, but basically in back and laterally. It is always separated from the episternal region by a deep suture which runs from the place of articulation of the mid coxae to the base of the wing. I am designating this suture as pleural. On the inner side, this suture corresponds to a comb, or columella. This region occupies the most lateral position in Notonectidae, in that the epimere is moved slightly onto the dorsal side so that its inner region (anepimere) is not visible from below (f. 45). In most Corixidae (except the South American Tenagobia), this sclerite is weakly developed and less moved.

Its segmentation into an- and catepimeres occurs only in some forms. This segmentation is most distinct in the oriental Xenocorixa and partly in the primitive Australian genus Diaprepocoris (f. 40). In Naucoridae and Belostomatidae, in connection with the unusually strongly developed episternal region and strong dorso-ventral flattening of the thorax, the epimeres are very small. Well developed in some aquatic bugs (Helotrephidae, Pleidae) and also littoral forms (Ochteridae, Gelastocoridae), is the central projection of the hind margin of the basisternite (mesocyphus)(fs. 35, 36, 44), which is just noticeable in representatives of the families Belostomatidae, Corixidae and most Naucoridae (fs. 39, 40, 41, 43) and is entirely missing in aquatic scorpions and some Notonectidae (fs. 37, 38). The catepimere (external epimere, according to Matsuda, 1962), in the hind lateral corner, bears a cone-shaped projections, which holds 54
(clasps) the tegmen in a state of rest. The trochantin is often well developed but, as a rule, is partly covered by the episternite. It is present in Notonectidae and in most Corixidae (except Tenagobia), but is missing in Helotrephidae and Pleidae.

In structure of the ventral side of the thorax, Nepidae occupy a special position, having preserved moved apart coxae and the position of the sclerites connected with this. Their basisternum, which is completely without any traces of a suture, is fused with an unsegmented (?) episternal region. The epimere is also represented as a single sclerite (fs. 37, 38).

The metathorax in structure of the ventral side is general similar to the mesothorax. Division of the basisternum and episternum by a sternopleural suture is missing in most aquatic bugs. The episternum has a constant division into a very small anepisternum, which often is not visible from above, and a very strongly developed catepisternum, which covers the base of the hind coxae. Fused with the proepisternum, the basisternite is best developed in Nepidae, Belostomatidae and Notonectidae (fs. 37, 38, 39, 45). In the latter, there is a well developed central projection of the hind margin of the basisternite (metacyphus). In Corixidae, Naucoridae, and the littoral bugs (fs. 35, 36, 40-43), the basisternite occupies a much smaller place; the metacyphus is often strongly developed (except representatives of the genus Tenagobia). 55
And, finally, in Nepidae (fs. 37, 38), the basisternite is like a convex transverse plate with fused pro- and anbasisternum, divided only by a deep longitudinal indentation.

The epimeres of the metathorax are most strongly developed in Pleidae (f. 44) and in some Helotrephidae, where the unsegmented epimeral sclerite occupies a considerable portion of the ventral surface of the thorax, wholly covering the anepisternum and partly the catepimere of the mesothorax. A feature of the pleural region of the metathorax of aquatic Heteroptera is the lateral articulation of the proepisternum to the strongly overgrown catepisternum, and not to the anepisternum, as is usual.

The strongly developed catepisternal region in Nepomorpha in front usually fully or partially covers the anepimere and hind margin of the bases of the hind coxae. It usually fixes the position of the coxae for rowing movements of the hind legs. In aquatic scorpions (Nepidae), the hind coxae are very far apart, since their legs are adapted basically for walking and not for swimming. The epimeral region in all Nepomorpha is weakly developed. In some forms, the epimeres are completely covered by the catepisternum, for example, in Belostomatidae (f. 39), Naucoridae (f. 43), 58 Helotrephidae; in others, it is partly visible from above, as in Corixidae (fs. 40, 41) and Nepidae (f. 37). In Notonectidae, the epimeres are covered by the tegmen. In aquatic scorpions, due to the special position of the coxae, one more section of the sternal region is preserved - the furkasternite (f. 37).

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Laterally to the metacyphus in some aquatic bugs is preserved a narrow, triangular plate, called the ventropleurite, which conjecturally is treated as the anopleural ring of the subcoxa (Matsuda, 1962). This sclerite partly (in some Notonectidae) or completely (Notonectidae, Corixidae) is fused with the catepimere. Along the fore margin of the episternite runs the shallow canal of the odor glands, the fore part of which usually is covered by the epimere of the mesothorax, as, for example, in Notonectidae or in the overwhelming majority of the Corixidae. In Tenagobia (Micronectinae), this canal is open for its entire extent and consists of two parts.

The legs in aquatic Heteroptera consist of the coxae, trochanter, femor, tibia and tarsus; the tarsi in their turn consist of the tarsus proper and the pretarsus.

The fore legs are usually very different from the mid and hind legs and, as a rule, bear the function of seizing and holding prey; however, the degree of adaptation in Nepomorpha is variably expressed (f. 46). The most specialized forms, in this respect, are representatives of the superfamily Nepoidea. Their fore legs have forward directed coxae, which permits increasing the width of the capture. The best developed seizing legs are found in the extinct Stygeonepinae (f. 77), and also in the living Nepidae and Belostomatidae. In them, the femora are usually strongly widened and, due to the elongation of the coxae, are borne in front of the head, the tibia are somewhat shorter than the femora and, in a state of rest, fold beyond the sharp thorn at the base of the femora, often secured here with the help of a clawlike tarsus (f. 1) However, the number of tarsal segments and degree of development of the claws in living forms of Belostomatidae vary greatly. The highest degree of specialization for seizure occurs in living aquatic scorpions of the subfamily Ranatrinae (Nepidae). These are predators which lie in wait and possess unusually strongly elongated coxae, the length of which twice exceeds the length of the head together with the forward elongated rostrum, due to which the basal part of the legs is carried far beyond the head. Their femora are more than twice longer than the thin and comparatively short tibia.

In living Naucoridae, we find fairly original preying legs, the femora of which are the most strongly thickened; for example, in the American genus Ambrysus, their length exceeds the width only 1.5 times, but the tibia is fused with the tarsus like a sharp, slightly curved needle. In this family, as in the above-mentioned family Belostomatidae, and also in Gelastocoridae, there is a great number of forms with less specialized seizing legs. Often the fore femora are as wide as those of the mid and hind legs, the tibia are almost straight, the tarsi two or three-segmented, rarely one-segmented, divided by a pair of divided claws.

The least specialized seizing legs, the structure of which is almost identical to the mid and hind legs, we find in all representatives of the littoral family Ochteridae, and in Notonectidae, and also in some Naucoridae, for example, Aphelocheirinae. The fore legs of Corixidae are of special structure in connection with their algophagy and detriphagy, and also the development of a special stridulating apparatus on the tarsi and femora. In them, the femora are strongly thickened, short, their length less than 1.5 times greater than the width, the tibia are very short, almost twice smaller than the femora, and the tarsi are one-segmented. In the 59 tribe Cymatiini, sexual dimorphism does not appear in the structure of the tarsi. In other Corixidae, the male tarsi are converted into a free pala, which is furnished with long, strong stylets and hairs, and also stridulating teeth (see further on), placed in one or two rows. The inner surface of the femora often bears a small section, the so-called pars stridens, covered with a great number of tiny teeth. In the female, the tarsi is simple, narrow,also armed with stylets and hairs. In the subfamily Micronectinae, the femora and tibia are somewhat thickened, the tarsi are of free form, but do not form the above-mentioned palae. In the subfamily Diaprepocorinae, the slightly thickened femora are almost equal or just shorter than the tibia, which are fused with the tarsi. In both latter subfamilies, the stridulatory apparatus on the fore legs is not developed, the tarsi in both sexes are identically constructed. The stridulators, like the stridulating combs on the tibia, appear also in some Notonectidae (Anisopinae).

Coxae in all Nepomorpha (except the superfamily Nepoidea) are long and directed backward, but their length usually depends on the form of the trochanter and the place of attachment of the latter to the coxae. In some cases(superfamily Nepoidea), the coxae can be spherical, partially sunk into coxal pits, able to move together with the legs (pagiopod type). In most cases, coxae are elongated, remain practically immobile in movement of the insect (trochalopod type). Usually in the latter type, the coxae have special lateral projections which fix the movement of the legs.

The Heteroptera pretarsus is the most apical part of the tarsus, consisting of a kind of drawn out plate, empodium, parempodium, areola, stylet and claws (f. 47). The base of the pretarsus is a drawn out plate, which has been studied in detail by 60 Dashman (1958), who established the diversity of the structures and made them suitable as family characteristics. The drawn out plate consists of straight rows of tiny, scale-like chitinized plates which lie one on the other. Its functional significance is to give increased flexibility to the pretarsus. In form, the drawn out plate is spade-like (Notonectidae), very transverse (Gelastocoridae, Nepidae), or weakly transverse (Naucoridae, Belostomatidae, Corixidae). The empodium is usually furnished with a parempodium but then, as a rule, the stylets are missing (Gelastocoridae, Naucoridae, Notonectidae, Nepidae) or, if they are present, the parempodium is missing (most of the Belostomatidae).

The claws usually are attached to the distal part of the drawn out plate and in each family there are numerous variants of structure: from very short and divided the entire length to unpaired, claw-like formation.

The mid legs of aquatic Heteroptera, more alike in structure and form, bear a different function (f. 48). In swimming, they usually do not participate. In the subfamily Notonectinae, the mid legs, analogous in structure and form to the fore, apart 61 from participating in swimming, are apparently also used in holding prey, since they have sharp and straight claws, which are curved only at the very end. In the subfamily Anisopinae (Notonectidae), the mid legs are longer and thicker, but the claws are as curved and sharp and, evidently, also used for holding the victim. In Naucoridae, the mid legs are thin, with a pair of straight, sharp claws, curved only at the very end. In Corixidae, they are very long, somewhat shorter than the tarsus, weakly curved the entire length and bear the function of attaching to the substrate at rest. In

Belostomatidae (f. 63), the mid legs are similar in form and structure to the hind, in that on the outer and inner hind margins of the femora, at the places of attachment to the trochanter, there are small projections which limit the movement of the legs to one plane - horizontal, necessary for swimming; the inner side of the tibia is covered with one row of dense, long hairs. In aquatic Nepidae, and also 62 in Gelastocoridae, the mid legs in all details repeat the structure and form of the hind legs, only slightly exceeding them in length. In Helotrephidae, on the other hand, the mid legs repeat the structure of the fore. The tarsi of the mid legs in Belostomatidae, Corixidae, Naucoridae and some Pleidae are two-segmented, in Nepidae, Helotrephidae and some Corixidae, one-segmented but long. The center coxae in all representatives of Nepomorpha, except Nepidae, are closed.

The hind legs in most bugs are adapted for swimming (f. 49). In living aquatic Heteroptera tht swim well, the legs are relatively shorter, and the tarsi longer than in the related terrestrial and some fossil aquatic forms. That is, the legs work with a greater frequency. The best rowing legs are in Belostomatidae and Corixidae. In the Belostomatidae, the femora are flattened and bear projections on the apex, limiting movement, the tibia are flattened and somewhat widened at the apex, forming a single flat oar out of the femur and tibia. The inner surface of the tibia and tarsus is thickly covered with a one-row brush of dense and long hairs. The two-segmented tarsi are also flattened. The coxae have limiting projections analogous to the mid coxae (f. 39). The highest degree of specialization is found in the Jurassic belostomatid Stygeonepinae (fs. 77ab). In living Corixidae, the most strongly developed and condensed is the two-segmented hind tarsus (f. 49ab), which is furnished with a special system of strong outer and thin inner swimming hairs, which are especially significant in increasing the effectiveness of the rowing thrust. As Schenke studies (1965) showed, each hair is connected with the surface of the legs by means of a specialized joint and is furnished with a restriction which prevents ~~is a~~ bend of the hair in an undesirable direction. The tibia is somewhat shorter than the tarsus; the coxae are also furnished with projections limiting the movement of the legs only in one plane (fs. 40, 41). An original type of swimming leg is found in the extinct Shurabellidae, which have thin hind legs with a thick brush of long, swimming hairs (f. 79). Farther in degree of adaptation to swimming are the Notonectidae, in which a not-widened two-segmented tarsus is almost equal in length to the tibia and thickly covered with long hairs placed in one row. Their legs are longer than in Corixidae, the coxae also have limiting projectiong (f. 49). In Naucoridae, Helotrephidae and Pleidae, the legs are less adapted to swimming, the innder surface of the long tibia is covered with dense hairs of moderate length, the two-segmented (in Helotrephidae, three-segmented) tarsi are considerably shorter than the femora. Finally, the aquatic scorpions have preserved true walking legs with one-segmented, long tarsi. In Belostomatidae, Naucoridae, Helotrephidae and especially in Nepidae, the claws are well developed. In Notonectidae and Corixidae, the claws are reduced.

In aquatic bugs, both fore and hind wings are well developed (except Pleidae, in which the hind wings are strongly reduced). The Corixidae fly especially well. The fore wings, or tegmen, usually are strongly chitinized, the hind wings membranous. At rest, the wings usually fold flat on the abdomen, so that the anal margins of the tegmen are contiguous, and the membranous, apical portion of one tegmen lies on the corresponding region of the other. Thus, the fore wings in a state of rest usually lie flat against the thorax with the help of a cone-shaped projection of the same part of the epimeres which is moved to the dorsal side. In its turn, this projection comes deep into the costal margin of the fore wing. Besides, usually the thickened part in the rest of the margin of the tegmen comes beyond the lateral side of the abdomen (connexivum) and thus further strengthens the folded tegmen in a state of rest.

The tegmen (hemelytrae) usually have a more or less chitinized basal sector and a membranous apex, rarely are entirely coriaceous - in Helotrephidae, Mesotrophidae, Pleidae and in the overwhelming majority of Corixidae (f. 50). The chitinized tegmen with membranous apex is undoubtedly characteristic for the initial type of structure of the true bugs. However, there are cases of half or almost half membranization, for example, in representatives of the subfamily Anisopinae (family Notonectidae). In most aquatic bugs, as a rule, the tegmen reach the apex of the abdomen (not counting the respiratory tubes in Nepidae and Belostomatidae). True brachyptery among aquatic bugs is unusual and encountered only in Aphelocheirinae and Cryphocricinae (Naucoridae), full-winged individuals of which are very rare. In Nepidae and Naucoridae, the wings are not longer than the abdomen, in Belostomatidae even somewhat shorter. The tegmen of many aquatic bugs are smooth (Belostomatidae, most Naucoridae, Corixidae) or slightly sculptured (some Ochteridae, Nepidae, Naucoridae, Helotrephidae). In Gelastocoridae, the sculpture is very much developed. They usually do not have venation (Naucoridae, Notonectidae, living Corixidae, and others); rarely venation is partially preserved (Nepidae) or almost completely (Belostomatidae and the Mesozoic Shurabellidae).

The basic chitinized portion of the tegmen bears the name of corium. Just behind it, the locking part of the tegmen, or clavus, which at rest lies along the scutellum, is usually similar in structure to the corium, most often not very long (except Corixoidea and some Nepoidea), almost linear. Very rarely the clavus disappears, fusing completely with the basal part of the tegmen (Helotrephidae, some Naucoridae). The outer (fore) part of the wing often is separated into a special sector - the embolium, which is delimited by a nodal fissure (fracture). In Corixidae, at the site of the embolium and farther to the wing apex,there is a very narrow sector, the basal plane of which is almost perpendicular to the surface of the tegmen, which can be called the embolium rim. Right, Hungerford (1948) used the name "embolium groove" for this sector of the wing, later used also by Poisson (1957). However, to me the use of the above-suggested term "embolium rim" seems more correct, since its distal part does not form a groove; it is strongly condensed and situated on the same plane with the corium, and the nodal fissure in a number of cases is missing.

The apical part of the tegmen is usually membranous (membrana). In Corixidae, Naucoridae, Notonectidae, it is completely devoid of venation. In Nepidae and Och- teridae (fs. 50, 66), there is a free set of veins on it. In Corixidae, a weak, light stripe can be distinguished between the corium and the very chitinized membrane (Heliocorisa, Vermicorixa, Sigara and others); rarely the entire apical sector of the tegmen is of a lighter color (Ramphocorixa, Agraptocorixa, Morphocorixa and others). In Heterocorixa, the left tegmen, lying on the right, has a true membrane. From the outside the right and left tegmen close at the inner side of the clavus, forming a claval suture (commissura clavi), the length of which varies in different families. The venation of the fore wings of most aquatic bugs is very reduced and is usually represented by only one, rarely two, anal veins on the clavus. The most complete venation is found in the Belostomatidae, in which the radial (R) and medial (M) veins are present, strongly moved toward the fore margin of the wing, often fused at the root of the wing. The fore margin of the wing is strongly curved on the ventral 65 side, so that the visible fore veins turn out to be the fusing subcostal, radial vein and radial sector (RS). The cubital vein (Cu) is strongly moved to the anal. In most Belostomatidae, as in Corixidae, there is a nodal fissure. In aquatic scorpions, the venation is weakly expressed and the basic veins are thin, whereas the membrane has preserved a rich set of veins (f. 69). In fossil Belostomatidae (Mesonepa), the venation is more or less complete and resembles that of living Belostomatidae (f. 73).

The hind wings are always membranous, transparent, soft. At rest, they fold completely under the tegmen and partly the scutellum, bending along a longitudinal fold, which separates the jugal lobe. In some Helotrephidae and Pleidae, the hind wings are missing. The wing is differentiated into a basal sector, or archeala, into which come the basic veins R, M and Cu, and the accessory neala, in which are located the anal (A1, A3) and jugal (Ju1,2) veins. The wing surface is divided into four lobes: fore, pre-anal, anal and jugal. The wing is joined to the thorax by means of strongly developed axillary and medial plates.

The general plan of distribution of the basal sclerites of the hind wing in aquatic Heteroptera is considerably different from that in other insects and, particularly, in terrestrial bugs. Due to the reduction of C and Sc, the 2nd axillary plate (Ax2) is moved to the fore margin of the wing and occupies a distal position with respect to the first axillary plate (Ax1), from which R comes (f. 51). The first medial plate (Med1), which corresponds to the medial distal, according to Snodgrass (1938), or mid plate, according to Puchkova (1961), also changes its position, moving to the first axillary plate. This sclerite sometimes is actually divided into outer and inner parts (for example, in Notonectidae) or here has only a stretching, as in Corixidae. The veins M, CuA and CuP come into it. The second medial proximal plate (Med2) occupies a distal position, is usually strongly elongated, and A1[1] and A2 leave from it. The third axillary plate (Ax3) usually has three longitudinal branches: outer, fore and hind. In Nepidae, the medial humeral plates are fused and appear as a large chitinized section at the base of the wing, continuing far along the hind cubital and anal veins. In Aphelocheirinae (Naucoridae), the sclerotized basal sector of the wing arose because of the spread of the second medial plate along the anal and jugal veins. The membrane of the hind wing is divided by longitudinal folds into a number of lobes, which I distinguish according to Puchkova's terminology (1961). 67
A characteristic feature of aquatic bugs is the strongly developed anojugal region, or neala, which is delimited from the archeala by the anal fold (plica analis). In some forms, for example, in the families Naucoridae and Corixidae, there is a small fold, named by some authors the preanal (Puchkova, 1961). It begins in the central part of the anal fold; in most Nepomorpha this fold is not expressed. The distal sector of the anal and preanal fold (plica anterior analis) forms the preanal lobe (lobus praeanalis), in which there is often a cubital vein (CuP), especially distinct in Corixidae. The jugal fold (plica jugalis) begins from the very base of the wing behind the apex of the outer sector of the third axillary sclerite and separates the jugal lobe (lobus jugalis) from the anal. The jugal lobe in aquatic Heteroptera is very well developed. It is especially large in Ochteridae, Corixidae and in some Notonectidae. In Nepidae, this lobe has a semi-round form or is triangular, as in Belostomatidae. At the ends of the folds, the outer margin of the wing is usually more or less truncated (f. 52).

For aquatic bugs, as, apparently, for the overwhelming majority of terrestrial ones, the lack of a free Sc is characteristic. The radial, medial and cubital veins are always well developed. R leaves from the second axillary sclerite, occupies a marginal position and, as a rule, almost reaches the apex of the wing. M begins in the first medial plate and is the most mobile component in the system of basic veins of the archeala. In some families (Ochteridae, Corixidae), in its proximal sector, it is completely fused with R, in others separated from the latter its entire extent (Nepidae, Naucoridae, Notonectidae). In the distal sector, M fused with Cu and later, joining with R (directly with the aid of the crossvein r-m), forms a cell. This cell is well expressed in most terrestrial Heteroptera; in Ochteridae, Corixidae and in some Naucoridae (Aphelocheirinae), it is practically missing. In the latter, the medial vein is interrupted in the central sector, forming a wing cell between R and Cu, which appear only like slanting cross short sectors. This cell, due to the reduction of the venation, is entirely missing in Helotrephidae. The fore cubital vein also leaves from the first medial plate and in its distal sector usually fuses with M (Nepidae, Aphelocheirinae, Corixidae) or fuses only at one point (Notonectidae) or is even joined with M by means of a crossvein m-cu. Now and then (in Corixidae), apparently, remains of the second branch of the cubital vein (CuP) are present in

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[1] In my opinion,,some authors incorrectly consider A1 to be CuP (Pcu), Puchkova, 1961; Davis, 1961.

the preanal region (f. 51). The venation in the anojugal lobe of the hind wings is considerably reduced, and its homologization in a number of cases is made difficult. In the anal sector, A1 distally usually comes close to A2 (Naucoridae, Notonectidae). Sometimes they diverge (Aphelocheirinae) or are parallel, and later fuse with each 68 other (Nepidae), or, finally, are joined by the crossvein a1-a2 (Corixidae). The distal ends of these veins, as a rule, gradually disappear, not reaching the outer margin of the wing. In aquatic Nepidae, the lower margin of the chitinized sector of the wing between A1 and A2 bears traces of five-six parallel branches. In the jugal lobe there is usually one vein only, which leaves J1. In Nepidae and Belostomatidae, in connection with the development of this lobe, a second jugal (J2) is also well developed. In Corixidae, a residual trace of this vein has been preserved. Usually the second jugal vein is expressed as a short curved arc.

Besides the above-mentioned crossveins (r-m, m-cu, a1-a2) and remains of these in the preanal and anal lobes, in the families Nepidae, Belostomatidae and Corixidae are preserved traces of a rich archedictyon on the archeala of the hind wing, which apparently has a secondary character. The presence of such a supporting "lattice" is, apparently, an important adaptation to flight for such large flying forms as the aquatic scorpions or belostomids.

In conclusion, it must be stated that the homology of some basic veins of the ano-jugal sector in aquatic and in terrestrial bugs has still not been conclusively explained. Thus, with respect to the Nepomorpha, the first vein from the fore margin is treated as the radial, is independent or in some cases partly fused with the medial (Davis, 1961; Puchkova, 1961). Some authors consider it the sub-cubital (Poisson, 1957), which is actually missing in these insects. The remains of Sc are fused at the very base with R. Correspondingly, Poisson designates the medial vein as the radial, and the cubital as the medial. Different from Western authors, L. V. Puchkova (1961) entirely correctly pointed out the anojugal region to be the jugal region and designated the veins in it as jugal.

The abdomen consists of 11 segments. The first tergite and the first two sternites are almost entirely reduced. The 2nd-7th segments, designated as pregenital, are of identical structure in females and males (except Corixidae), except that the seventh sternite in females is often represented as single, the so-called subgenital plate, devoid of the central fin and having great taxonomic significance in the families Nepidae and Belostomatidae. The eighth and ninth segments (genital) are greatly variable and adapted for sexual functions. The eighth segment often completely covers the following ninth, which in males forms the genital capsule. The ninth and 11th segments (postgenital) are strongly reduced. The tenth is transformed into the anal ring, the 11th into its valve.

Each segment consists of the dorsal part (tergite) and the ventral (sternite), from each of which additional sclerites are separated laterally: the latero-tergites (paratergites) and laterosternites (parasternites), which are accreted (f. 53). The laterotergites are strongly moved onto the ventral side and bear stigma (respirators); they are always clearly separated from the tergites on the dorsal surface by a longitudinal pressed in fissure and often slightly raised like a condensed outer lateral cushion of the abdomen, the so-called abdominal rim (connexivum). Thus, the abdominal rim is two-layered, fromed by the laterotergites folded in two. The sclerites, situated between the sternites and the laterotergites, usually are called parasternites (laterosternites). Sometimes the parasternites are curved inward, for example, in Ranatrinae (Nepidae), and are not visible from the outside (fs. 38, 53).

The abdominal sclerites are joined by an intersegmental membrane, which, together with the two-layered abdominal rim, can stretch considerably by taking a considerable portion of food and even during copulation (Poisson, 1957). The borders of the ter- 69 gites usually are straight or with small projections on the central segments; the sternal borders are straight, angular or arched, for example, in male Corixidae (f. 41).

The digestive system consists of the basic digestive apparatus (fore, mid and hind gut), and its appendages, such as the salivary glands and malphigian tubes (f. 54). As a rule, the digestive tract exceeds the body length almost twice, and in some cases its length is three tims greater than the body length (Belostomatidae).

The fore gut is almost entirely situated in the prothorax and is represented by the esophagus[1]. In Ochteridae, Gelastocoridae, Pleidae, Notonectinae, the esophagus is short, especially in representatives of the latter family. In all other Nepomorpha, mainly, Nerthrinae (Gelastocoridae), Corixidae, Ranatrinae (Nepidae), Anisopinae (Notonectidae), Naucoridae the esophagus is long.

The mid gut in most cases consists of two sectors (Nepidae, Belostomatidae, Helotrephidae, Corixidae), sometimes weakly expressed (Notonectidae and Pleidae): the stomach and tubeular sector. In Ochteridae, Gelastocoridae, Notonectidae, Nepidae, Naucoridae and Corixidae, the stomach is very large and only in some Gelastocoridae (Nerthrinae) and Belostomatidae is it either short, or narrow, of comparatively small size. The tubular sector in most Nepomorpha is like a long and repeatedly curving tube (especially long and sinuous in Belostomatidae) and only Helotrephidae and Corixidae are exceptions. In littoral Nepomorpha (Ochteridae and Gelastocoridae) and in aquatic Naucoridae, besides the two above-mentioned, there is another bubble-like section of the mid gut like a thickening of the hind end of the tubular sector. 72

Between the mid and hind gut a small tubular sector is situated bearing the name of pylorus, which is considered as the foremost sector of the hind gut. In Nepomorpha, it is very short and barely distinguishable, except in Nepidae and Belostomatidae. From the pylorus come two pairs of malphigian tubes like thin and long tortuous (particularly in Nepidae) tubes, the apices of which usually are contiguous (Gelastocoridae, some Naucoridae, Notonectidae, and Corixidae), rarely joined in pairs or all togethr (Nepidae, Belostomatidae).

The hind gut in Nepomorpha always consists of two sections: ilium and rectum, which often (particularly the ilium) have thick walls. The most variable is the ilium. In most families it is fairly short (Ochteridae, some Gelastocoridae and Naucoridae, Helotrephidae, Pleidae, Corixidae), but in some aquatic bugs the ilium is long (some Gelastocoridae, Naucoridae and Notonectidae). It reaches greatest length and sinuosity in Nepidae and Belostomatidae. The rectum, as a rule, has the appearance of a bubble-shaped widening, sharply narrowed at the end, with a disappearing rectal covering. In Nepidae and Belostomatidae the rectum is strongly elongated. In Naucoridae and Pleidae, this section is provided with a diverticulum.

The salivary glands consist, together with their conductor ducts, of basic and auxillary glands; the basic salivary glands are the most variable in form and structure in each family. The basic glands are almost always dichotomous, in most cases consist of numerous bubble cells (field); however, the fore section usually is considerably smaller than the hind. This latter sometimes is like one large semi-transparent bubble-like formation, for example, in Pleidae. The exception is Helotrephidae, in which there are unusually original five-part basic glands, and the four sections consist of the above-mentioned bubble cells, the fifth like a semi-transparent bubble. The accessory glands are strongly lengthed sack-like formations; in size they often are larger than the basic glands. The structure of the accessory glands is most different in Belostomatidae, where they look like an elongated sack with very long tubular diverticulum (especially in Diplonychus).

The male genital capsule (f. 55), formed by the ninth abdominal segment, is furnished with one pair of mobile segmented more or less chitinized plates (P1, P2), the so-called parameres, moved by corresponding muscles. In some forms the parameres are strongly reduced or entirely missing. The base of the genital capsule from the inside is formed by a system of articulated plates, the so-called basals. These plates, together forming the so-called strema, envelop the phallus (or aedeagus)

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[1] The terminology and description of the structure of the digestive organs basically are taken from Miyamoto (1961).

and are its sectors. The phallus consists usually of two basic parts: the phallocum and endocum, which together form the aedeagus. In Nepomorpha the phallocum is completely membranous. The apex of the phallus is sclerotized, the phallocum is formed only by a part of the membrane, so that the movement of the phallus is regulated by the bend of the so-called ligaments, which are connected with the basal plates. In its turn, the more or less accreted basal plates form the ventral plate, by movement of which the apical part of the phallus usually is drawn backward. The structure of the phallocum of Nepomorpha, in connection with its membranous part, has not been sufficiently well studied. In Naucoridae, Pleidae, and Corixidae, the male genital segments, particularly the parameres, as a rule, are asymmetrical.

The internal reproductive organs consist of paired testicles (left and right), vasa deferentia, ductus ejaculatorius and the accessory glands, or mesodenia. In 73 all Nepomorpha, the bulbus ejaculatorius is missing, the widened part of the fore end of the ductur ejaculatorius, which is present in other bugs.

The right and left testicles consist each of 4-7 follicles or sperm tubes, which are connected together by a common peritonal jacket. The testicles are usually fairly strongly elongated, and their apical portion is spirally rolled up, as, for example, in Gelastocoridae, and the basal uncurved part cuts across the entire abdomen. The follicular cavities of each field of the testicles fall into a single vasa deferentia, which is a simple, often curved, thin tube. In some aquatic bugs (Nepidae and Belostomatidae), the latter in the distal part forms a widening which contains the vesicular seminalis (f. 56). The left and right vasa deferentia are joined into one unpaired ductus ejaculatorius, which is like a fine irregularly curved long (particularly in Ochteridae) tube, which runs directly into the aedeagus. At the base of the vasa deferentia at the point where the vasa deferentia leave, the mesodenia are revealed, delimited from them by the peritonal membrane. In some Nepomorpha, for example, in all Nepidae and Belostomatidae, the mesodenia are missing.

The female genital and anal appendages are formed of the eighth to 11th segments, and their appendages. The postgenital segments (10th and 11th) are dorsally situated, fusing laterally and ventrally with the seventh segment. The tenth segment is only an anal tube, the 11th is the anal segment proper. The ovipositor[1] (f. 57) is formed of the appendages of the eighth and ninth segments. The ventral portions of the 74 segment, the paratergites, which bear respirators, bear the basal sclerites of the first pair of folds of the ovipositor, or gonococae (=first valvifers), from which leaves the distal part of the fold, or gonapophyses (=first valvules). The first pair of folds is situated ventrally and outside, forming the basal outer part of the ovipositor. The apical part of the first gonapophyses, in connection with laying of the egg in plant tissue, sometimes is serrated and is the most chitinized (Notonectidae and Pleidae). The second pair of folds is attached by the basal part, designated as the second gonococae (=second valvifers), from which leaves the distal part of the fold, or the second gonopophyses (= second valvules). The apical tip of these folds in very rare cases, for example, in Naucoridae and Notonectidae, is also serrated. The characteristic feature of the ovipositor in bugs is the presence of a more powerful first pair of gonococae in comparison with the second. In some cases (Aphelocheirinae, Anisopinae, Gelastocoridae), the second gonopophyses are strongly reduced. The third pair of folds is formed by the projections of the second gonococae and bears the name of gonoplak (=third valvules). In most cases, the gonoplak is well developed, reaching maximal size in Naucoridae, Holotrephidae, Ochteridae and Gelastocoridae. Only in Corixidae is it entirely reduced in connection with the complete fusion of the second pair of gonococae with the ninth paratergite. From the ninth segment in bugs usually

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[1] Until recently, basically the terminology of the component parts of the insect ovipositor, particularly of Heteroptera, given by Snodgrass (1933, 1935) has been used. However, recently the Canadian entomologist Scudder conducted a number of morphological studies of the structure of the ovipositor of both insects as a whole (1957, 1961ab) and of real Heteroptera (1959) separately. He made a new interpretation of the

leaves another sclerite, the so-called gonangulum (=fore, or triangular, plate), which inside is connected to the first gonapophyses. In many Nepomorpha, this sclerotized plate is considerably reduced (Ochteridae, Gelastocoridae, Belostomatidae, Helotrephidae, Corixidae) or even entirely missing (Pleidae), but in Nepidae, Notonectidae, and some Naucoridae, the gonangulum is well developed.

The structure of the internal female reproductive organs, particularly the semen-collector, in a number of cases also has great significance as a characteristic of large taxons not only of separate families, but even of families and suborders. Their structure in most Heteroptera as a whole is subject to a single plan (f. 58). Within the female reproductive organs come the laterally situated ovaries, each of 75 which in Nepomorpha, as a rule, consists of seven egg tubes. From the ovaries come the left and right lateral oviducts, which join into a common (medial) oviduct, which in Nepidae and Belostomatidae is usually short. In its turn, the oviduct comes into the bubble-shaped copulatory pouch, or vagina, which is connected with the spermatika (semen-collector) by a long and sinuous (Gelastocoroidea, Naucoroidea, Notonectoidea) or short curved (Nepoidea) sperm duct. The spermatika in most Nepomorpha is narrow and long, like a simple weakly curved fine tube; however, in Gelastocoroidea, it is strongly widened at the apical part. In Naucoridae, Corixidae and Ochteridae, the apex of the spermatika has a long diverticulum, joining the secretory cells; the longest projection occurs in Corixidae. The cavity of the spermatiki, as a rule, is covered by a thin, semi-sclerotized cuticle (intima). In some cases,(in Gerromorpha), in the spermatiki there is a second duct, the so-called fertilizing canal, through which the sperm come to the eggs in the common oviduct through the vagina. An analogous canal we encounter in other orders also, for example, in beetles of the family Carabidae.

Organs of Respiration. Bugs usually have ten pairs of stigma and their tracheal system consists of two longitudinal dorsal stems, from which leave branches, parallel to the stigma. The basic abdominal stems do not have transverse segmental branchings, which occur only in some bugs (Belostomatidae) just in the thorax, rarely in the abdomen. The stigma of the terrestrial and amphibious bugs are furnished with closing apparatuses of different types. In aquatic they are more or less deeply set into the ~~cover~~ integument, do not have a closing apparatus, and their opening is assured by a thin perforated membrane or group of hydrophobic stylets. Aquatic species have yet othr features. All stigma in the nymphs of Nepa, for example, are ventral and situated one on the border of the fore and mid thorax (midthoracic stigma), the second on the metathorax and the third pair on the border of the abdomen and the metathorax. The other stigma lie in the pleural fold of the last abdominal segment, which forms the breathing cavity. In adult Nepa, the pair of metathoracic stigma and the first abdominal shift dorsally: a breathing siphon is formed from two symmetrical halves, joined by means of small hairs. To breath, aquatic scorpions push the apex of the siphon to the surface of the water and, due to the movement of the abdominal muscle-respirators, drive air in and out through the tenth pair of stigma, situated at the base of the siphon on the proximal plate of the anal apparatus. From time to time, the air, pulled under the tegmen, reaches the 2nd-3rd pairs of stigma, sometimes the first pair. The 4th, 5th and 9th pairs of stigma of adult Nepa do not function, and the 6th-8th are connected with the sensory static organs. Only Notonectidae have nine pairs of stigma. The stigma of their eighth segment serves for breathing (in and out); respiration also occurs through the stigma of the thoracic segments. Naucoris also almost breathes; in it the first six pairs of abdominal stigma are ventral,

? (translation is correct here)

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structure of the ovipositor in bugs, and also used the terminology first given by Grassi (1887) and subsequently by Tuxen (1956). In this paper, I am using the terminology used in the above-mentioned works of Scudder for Heteroptera, showing in brackets the widespread synonyms.

the seventh pair lies at the base of the eighth segment. Air does not come from the ventral side of the body, but from the dorsal. These bugs adjoin the surface of the water by the dorsal side of their abdomen. In Corixidae, which live at the surface of water, breathing is accomplished by the following manner: in - by the first abdominal stigma, and out by all the other stigma of the abdomen and thorax (Brocher, 1905). Corixidae, different from large aquatic bugs with an open tracheal system, get air with exceptional speed, remaining on the surface of the water for only a fraction of a second. This method of breathing permits them to run to attack prey. To implement with instant rapidity such a complicated process as the renewal 78 of air in the outer thoracic chambers of the first and second segments, under the wings of the bug and within its tracheal system, serves a complicated system of muscles in the region of the thoracic and the first two abdominal segments. At the moment of attachment of the fore end of the body of the corixid to the surface of the water, strong ventral muscles of the abdomen are compressed, curving it and opening, in the region of the thorax, an access to the atmospheric air to the organs of respiration (Larsen, 1954). The integument of aquatic bugs is covered by hydrophobic hairs, lubricated by wax secretion. On the surface of the body there are often respiratory chambers and air sacs. On the ventral surface of the abdomen, Notonectidae have rows of dense hairs (two rows along the middle and two lateral). These hairs are distributed in such a manner that they form similar canals right and left which are usually used for respiration (f. 59). The air accumulates in the cavities, the so-called air reservoirs, which are situated on the sides of the thorax, under the fore legs, and also under the pronotum or under the tegmen (Naucoridae, Notonectidae, Corixidae, Belostomatidae). This air, already used and impoverished of oxygen, serves as a gaseous reserve and plays a hydrostatic role.

Corixidae, in swimming, with the aid of the hind legs direct the currents of water 79 which concentrates the thoracic supply of air oxygen. These movements of the legs reflectorily give rise to the accumulation of carbon dioxide in the body of the insect. In such good swimmers as representatives of the families Naucoridae, Notonectidae, Corixidae and Belostomatidae, this supply of air, besides the hydrostatic role, fulfills the function of supply of oxygen and is renewed through its diffusion from water. Oxygen from the air bubble is adsorbed and changes into CO_2; O_2, dissolved in water, has a greater pressure than in the bubble, whereas the pressure of nitrogen is almost the same; thus, O_2 can be concentrated in the bubble. Nitrogen, in the end of ends, dissolves in water, and the insect surfaces to get a new supply of nitrogen, and also oxygen. Tests show that Notonecta live six hours in water containing atmospheric air and about 35 minutes in water where oxygen is dissolved and nitrogen is missing. Consequently, in the lack of nitrogen, the insect cannot get oxygen necessary for respiration. If the aquatic bug moves a little in water containing only nitrogen, then the duration of remaining under water is shortened to five minutes (Poisson, 1951). Surfacing is a feature which varies in different aquatic Heteroptera. Naucoris prefers life in water rich in oxygen, but in replenishing the air supply water penetrates the trachea; in a lower content of oxygen, water does not fill the trachea. In Corixidae and Notonectidae, smaller volumes of air supplies are found, since they discharge a small amount of CO_2 in water.

Around the stigma is a ring of hydrophilic hairs from outside and hydrophobic from within. When the insect rises to the surface of the water, the surface tension gives rise to a compression of the external hydrophilic ring and allows air to enter the stigma. During swimming the ring locks the air chamber and the hydrophobic ring impedes the penetration of water into the stigma. Respiration of young nymphs of aquatic bugs generally is cuticular. Aphelocheirinae nymphs are benthoid, like the imago, but devoid of a supply of air on the thoracic surface, which is present in the imago, and their respiration to the last imagal stage is done exclusively through the cuticle. In adult forms around each stigma is a rosette in the center of which is the trachea. The rosette is formed from chitinized exocuticular tubes, furnished with tiny pores. In the center of the rosette there is sometimes a crack - a variant of the primitive stigma. Aquatic bugs have the so-called gas plastron on the thorax, which contains a constant supply of air; the gas plastron is enclosed by a small hydrophobous hairiness, densely covering the sternite. Oxygen of the plastron diffuses in the trachea through the tiny aperture of small stigmal tubes.

STRUCTURE OF THE PREIMAGAL PHASE

Eggs of aquatic Heteroptera are very well differentiated in each family (f. 60).
The most characteristic element of the eggs of bugs is the covering, situated on the
upper pole and opening in the emergence of the nymphs from the egg(f. 61). Highly
original are the eggs in living Corixidae, which are attached to the substrate by
a special sticky disc on the stem. However, most often the egg is attached by a 80
sticky secretion of the accessory glands or is inserted into the plant tissue, as
for example, in many Notonectidae, some Naucoridae and Nepidae. Some representatives
of the family Notonectidae, for example, Notonecta glauca L., plunge each egg at
an angle for 3/4ths of its length into an aquatic plant (f. 62); others, for example,
Notonecta maculata F., stick directly to the surface of the substrate (Poisson, 1957).
Pleidae insert the eggs at one place directly into the plant tissue, just as some
Naucoridae (Iliocoris cimicoidea L.); however, others (Naucoris maculatus F.) lay
each egg singly into the plant. Some Naucoridae (Aphelocheirus) lay eggs on the
shells of lamellibranchia or under rocks on the ground (Poisson, 1957). In some
cases the eggs are laid directly on the dorsal surface of the body of the male 81
(many Belostomatidae) and stay here for ten to twelve days up to the hatching of
the nymphs (Chen, Young, 1943). These eggs usually are attached to the tegmen and
scutellum by a special substance which does not dissolve in water (f. 63).

Nymphs (f. 64). The process of hatching in some aquatic bugs, for example, in
Trichocorixa najas Kirk. (Corixidae), is connected with the osmotic expansion of
the bubbles within the egg in front of the head end of the nymph. The expanding 83
bubble breaks the corion. Then the nymph begins energetically to paddle water,
increasing in dimensions and, pressing on the bubble, breaks its wall. The process
concludes by means of the emancipation of the nymph from the surrounding covering
and emergence from the egg (Davis, 1965).

The position and degree of development of the odor glands are variable. In the imago they are situated in the metathorax, in nymphs on the abdomen. In the imago the dorso-abdominal odor glands always are completely reduced. The number of abdominal glands among nymphs is also the same. In Corixidae, the secreting pores of the gland are situated on the hind margin of the third to fifth abdominal tergites. In Naucoridae, Helotrephidae, and Pleidae, the odor glands are preserved only on the third tergite of the abdomen. In Nepidae and Notonectidae, abdominal glands are entirely missing in the larval stage.

Nymphs of aquatic bugs are still poorly studied and there are only very general data about them (Poisson, 1951, 1957; Kirichenko, 1940, 1951; Teidzo, 1959, and others). In this respect, there is some exclusion in the work of Cobben and Moller (1960) on the nymphs of the Corixidae of Holland, where descriptions and comparative characteristics of the nymphal stages of the Corixidae are given in sufficient detail.

CHAPTER IV

SYSTEMATICS OF THE INFRAORDER NEPOMORPHA AND SOME QUESTIONS ON THE GENERAL CLASSIFICATION OF THE HETEROPTERA

The phylogenetic natural system of the order Heteroptera is at present not satisfactorily worked out. A number of unclear questions exist in differentiating the order Heteroptera from the other closely related order, Homoptera, and in dividing the order into suborders and superfamilies and clarifying their true phylogenetic connections.

On the basis of recent morphological works (Carayon, 1950, 1954,; Southwood, 1955; Benwitz, 1956; Pendergrast, 1957; Snodgrass, 1960; Miyamoto, 1961; Parsons, 1959, 1960, 1962, 1963, 1964, 1966, 1967; Cobben, 1968), it is possible to divide the Homoptera and Heteroptera reliably on at least three apomorphic characteristics. The first, and in my opinion, the most important differentiating characteristic of the order of true Heteroptera is the lack of a supporting skeleton of the head - tentorium (projections of the inner walls of the head capsule) and the presence of only one supporting formation of the epicranium - hypopharyngeal wings. The second characteristic of the order is the presence of a special sclerotized formation of the caudal side of the epicranium, the so-called postgenal bridge (better known in recent literature under the name of "gula" and "gular plate", about the error of the application of which see Ch. III), which is missing in Homoptera. The third feature of Heteroptera is the different structure of the coupling of the fore and hind wings in comparison with Homoptera (f. 65). Other (basically ecological) important differences of these orders also exist, for example, the existence of true aquatic forms whose entire cycle of development takes place entirely in water, and the zoophagy of many groups of Heteroptera, not to mention true ectoparasites (Cimicidae and Polyctenidae). As for the other usually mentioned morphological features, for example, the division of the tegmen into coriaceous and membranous sectors, the position of the tegmen with respect to each other, body form, dimensions, etc., all these traits are found in different representatives of both orders. All of the above-mentioned once again emphasizes the genetic closeness of these orders and thus the difficulty of their strict division. Apparently for this reason, by some authors, particularly in the new works of Goodchild (1966) and Cobben (1968), the orders Heteroptera and Homoptera are considered only suborders. True, in the little known work of Verhoeff (1893, Vergleichende Untersuchungen uber die Abdominalsegmente der wieblichen Hemiptera-Heteroptera und-Homoptera), Homoptera and Heteroptera are even considered as a class Hemiptera s. Rhynchota, and for the Homoptera and Hemiptera there is a corresponding range of subclasses, which, of course, is a clear exaggeration.

Turning to a discussion of the division of the Heteroptera into suborders, it must be emphasized that the overwhelming majority of contemporary authors do not try to make such a division and restrict themselves only to characterization of families, 85
superfamilies and to a general series of superfamilies. The history of the division of the Heteroptera into suborders (groups) and, in connection with this, the establishment of their ecological forms, was begun by Latreille (1802, 1825) who divided the bugs into two groups: "Hydrocorises", or aquatic bugs, and "Geocorises", or terrestrial bugs. Later Dufour (1833) isolated still another group, "Amphibiocorises", in which he included also the true aquatic Corixidae. However, Borner (1904) corrected this error, separating the Corixidae into the independent group Sandaliorrehyncha. Fieber (1861) first divided the Heteroptera into two groups (Cryptocerata and Gymnocerata) on the structure of the antennae. Some other authors followed this subdivision, particularly Reuter (1912), Butler (1923), Borner (1934), Beior (1938), Poisson (1951), Obenberger (1958) and some others. Right, Poisson (1957) later rejected this principle of Heteroptera division, not however offering any other system. In the above-mentioned work of Verhoeff (1893), on the basis of a comparative

study of the female abdominal segments (mainly I, II, VII–X) of Homoptera and Heteroptera, and also on the basis of an analysis of a number of previous morphological works, the author also suggested dividing all bugs into two groups (subclasses): Hydrorhynchota (Cryptocerata) and Gymnocerata. Thus, the true aquatic Heteroptera were placed into the former group, in four orders: Corisaeformia (Corixidae), Notonectaeformia (Notonectidae), Naucoriformia (Naucoridae) and Nepaeformia (Nepidae, Belostomatidae). Kirkaldy (1907, 1909) objected to this method of dividing the Heteroptera and he divided all Heteroptera into two groups (phalanges) on the manner of the articulation of the leg coxae. Trochalopoda (with rotating coxae) and Pagiopoda (with coxae which move in one plane). Into the former group, Kirkaldy put the superfamilies Cimicoidea and Nepoidea, the latter of which contain the extremely diverse anf far from each other families Nabidae, Gerridae, Reduviidae, Nepidae, Phymatidae and Enicocephalidae. Into the other group were joined the two superfamilies "Mirioidea" and "Notonectoidea". In the latter belonged the Saldidae, Ochteridae, Naucoridae, Belostomatidae, Corixidae and Notonectidae. As can be seen from this list, the superfamily Notonectoidea is also artificial and not entirely successful. Kirkaldy's system was not recognized by later hemipterologists.

The most natural organization of the families of bugs was developed by Reuter (1910, 1912), who conducted a survey of the entire system of the Heteroptera. At this time, the division of the order into separate families had already been done by Handlirsch (1906–1908), and Reuter's scheme then numbered already 40 families (not counting Peloridiidae).

In his 1910 work, Reuter still had not divided the Heteroptera into two suborders, but had established the basic superfamilies and series of vital forms. Without discussing his scheme in detail, since it was subjected to an analysis later in Russian literature (Kirichenko, 1951), I want to point out only that my infraorder Nepomorpha fell into the series Hydrobiotica as two superfamilies: Ochteroidea, including the Ochteridae, Gelastocoridae, and Peloridiidae[1], and Notonectoidea with the families Nepidae, Belostomatidae, Naucoridae, Notonectidae and conditionally Corixidae.

Reuter's scheme was based mainly on the lack or presence of ocelli and areola, form and structure of the ovum, and also the structure of the sternal sclerites. Right, the significance of these characters has been questioned by some later authors, who have pointed out the variability of the sternal structures dependent upon the development of the wings (McAtee, 1924, 1925, 1926; McAtee, Malloch, 1933), the difficulty of using the form of the ovum for phylogenetic constructions (Ekblom, 1929) and also the unreliability of the structure of the areola for these schemes (Myers, 1924; Holway, 1935). However, despite the expressed objections, the Reuter series of Heteroptera has been used by various authors with few changes (Oshanin, 1912; Singh-Pruthi, 1925, Esaki, China, 1929, and others).

Subsequently, Reuter (1912) clearly divided the order Heteroptera into two suborders: Geocorisae (terrestrial) and Hydrocorisae (aquatic). He divided the suborder of aquatic bugs into four superfamilies: Litoralia (Gelastocoridae, Ochteridae), Nepaeformis (Nepidae, Belostomatidae, Naucoridae), Notonectaeforme (Notonectidae, Pleidae) and Corixoideae (Corixidae). The latter family Reuter, following Borner (1904) again put into the special series Sandaliorrhyncha. Placement of the littoral Ochteridae and Gelastocoridae into the group of aquatic bugs was subsequently done by Beier (1938).

Oshanin (1912) held basically to Reuter's system in the catalogue of Palearctic 87
Heteroptera, and distributed the Nepomorpha into two series: Sandaliorrhyncha (Corixidae) and Hydrobiotica. The terrestrial ones were put into five other series: Trichoteloceras, Anonychia, Onychiophora, Phloeobiotica and Polyneuria, all the Gerroidea falling into the latter.

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[1] China (1929) later correctly puts the Peloridiidae into the Homoptera.

Later China (1933) drew up a scheme (dendrogram) of the congeneric relationships of the families of all true Heteroptera, which subsequently received sufficiently wide distribution. In this scheme, the common stem of Nepoidea and Naucoroidea was indicated, the divergence of which in time is noted only as a late process. As shown in my subsequent analysis of these groups, such a close connection of the Nepoidea to the Naucoroidea is hardly expedient.[1]

Another essential moment of China's scheme is the separation of the Corixoidea after the branching off of the stems of the Nepoidea - Naucoroidea and Notonectoidea. This hardly corresponds to reality. As I proved later, the phylogenetic closeness of the two latter superfamilies and the isolation of the Corixidae are unquestionable. The opinion that the Nepidae and Belostomatidae arose from the littoral Gelastocoridae is in general correct and has subsequently been proven by many authors (China, 1955; Miyamoto, 1961; Parsons, 1965); however, in detail, China's scheme is less correct (see below). The origin of the Saldidae and Ochteridae through the specialized Gelastocoridae, in my opinion, is inadmissible. Miyamoto's work (1961) on the comparative anatomy of the digestive organs of the order Heteroptera showed sufficiently convincingly the most primitive condition of the Saldidae, not only in comparison with true aquatic (=Hydrocorisae) and semiaquatic (=Amphibiocorisae) bugs, but also evidently, with the other Heteroptera in general. China's scheme as a whole is now only of historical interest.

Also only of historical significance are the schemes of Esaki and China (1927, 1928) which are devoted to the classification of the Heteroptera connected with water. In these, the authors grouped the families into four series. The most artificial and heterogeneous is the series Telmatobia. The family Leptopodidae placed in it is only partly littoral, although its ancestors apparently existed in littoral localities, and the "family" Velocipedidae (=Scotomedidae) is actually only a subfamily, not related to aquatic bugs, of the family Nabidae (Kirichenko, 1951; Kirchner, 1966), not to mention that these families, and also the Saldidae, are not related to other members of the group Hycrocorisae (in China's understanding). The preliminarily suggested series Cephalonotera (1927), including the single family Helotrephidae (s. lato), was already in the 1927 work of Esaki and China put into the series Hydrobia, where all the other families of aquatic bugs were put. The family Corixidae was put into the special series Sandaliorrhyncha. And, finally, connected with these groups was the series Phanoptocorisa with the original family Peloridiidae - primitive Homoptera of the special suborder Coleorrhyncha (China, 1929; Evans, 1941).

In a later work, these authors (Esaki, China, 1927) united the families of aquatic bugs (Hydrocorisae) on a somewhat different principle, choosing the superfamilies Nepidae (Nepidae, Belostomatidae), Notonectoidea (Notonectidae, Naucoridae, Aphelocheiridae) and Pleoidea (Pleidae, Helotrephidae). Here were also placed the littoral Ochteridae and Gelastocoridae under the name Telmatobia, where were also included the Saldidae and Leptopodidae. As my analysis of the familial characters of this group of bugs showed, the closeness of the Notonectidae to the Pleidae is more obvious 88 and the union of these families into one superfamily is natural.

"Here" = Hydrocorisae

Butler (1923), in a monograph on the biology of the Heteroptera, following Latreille, divided the order Heteroptera into two basic groups: Cryptocerata and Gymnocerata.

Ekblom (1929), using the earlier mentioned schemes of Dufour (1833) and Borner (1904), divided all bugs into four groups on the basis of the structure of the mouth parts: Geocorisae, Hydrocorisae, Sandaliorrhyncha and Amphibiocorisae. The author considered the littoral representatives of the family Saldidae as the closest to the ancestors of the Heteroptera, according to the general structure and form of life. Based on the structural features of the mouth apparatus (mandibular and maxillary articulations) and the littoral form of life, the phylogenetic initial position of the hypothetical Protosaldidae was first more or less validly indicated by Ekblom.

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[1] It is difficult to judge a more precise time of the divergence of the various phylogenetic branches (stems) according to China's scheme, since the designiations of geologic time are missing.

Singh-Pruthi (1925) made an attempt to classify the families of true Heteroptera on the basis of the structure of the male copulatory apparatus. In the scheme he offered, all Heteroptera are distributed according to type of genitalia into two large groups: the most primitive reduviid type forms all Hydrocorisae, Amphibiocorisae and Cimicomorpha, the pentatomids all the other Geocorisae, and also Leptopodoidea. This method of classifying families was apparently not entirely successful because of the clearly one-sided analysis and presence of convergent traits in the structure of the male copulatory apparatus. However, it is interesting. The existence of convergency in the structure of the male reproductive organs and the contradiction of conclusions, based on their studies, regarding the congeneric ties of the families of Heteroptera is clearly evident in the works of Pendergrast (1957) and Kumar(1961).

The scheme of interrelationships of the families of Heteroptera constructed by Spooner (1938) on the basis of the features of the epicranial structures of the imagal and nymphal phases is noteworthy. Despite the hypothetical nature of the conclusions and the known morphological inaccuracies, this scheme is interesting. Thus, the family Corixidae is considered a very isolated and highly specialized group, representing the special sèries Sandaliorrhyncha. In form of anteclypeus, the Corixidae are preliminarily connected with the Saldidae, the hydrocorisae are a special, isolated group composed of four families: Nepidae, Belostomatidae, Naucoridae and Notonectidae. In type of structure of mandibular lever (see morphological section), Nepidae and Belostomatidae are joined into one group having a three-branching lever; Naucoridae into another, with a narrow and loop-shaped lever and, finally, the Notonectidae into the third (lever composed of two parts).

Spooner included the families Gelastocoridae (=Nerthridae) and Ochteridae (=Pelogonidae) into the series Amphibiocorisae together with the Heteroptera that live on the surface of water (Gerridae, Veliidae, Hydrometridae and others). The presence of an epipharyngeal projection and the form of the mandibular levers were used as the basis for this consolidation. However, in Ochteridae and Gelastocoridae, this projection is very short and the lever is of different type (lever not quadrangular, but almost triangular). In a number of apomorphic morphological characters (inner skeleton of the head, structure of the thoracic sclerites, etc.) and also in the form of life, as Kirichenko (1951) pointed out, these ancient families are well differentiated from the series Amphibiocorisae, which is the basic ancient stem of Nepomorpha in a wide sense. Nevertheless, the possibility of the isolation (see below) of the above-water bugs (Gerroidea) from ochterid-like ancestors cannot be excluded.

In form of anteclypeus with widened distal margins, the author places the littoral 89
families Ochteridae and Gelastocoridae close to the aquatic Naucoridae and Notonectidae, holding the opinion (subsequently supported by Parsons) that they are intermediary forms between the Hydro- and Amphibiocorisae.

In 1955 China suggested a new, more developed and substantiated phylogenetic scheme of families of aquatic Heteroptera. He placed the most generalized families Ochteridae and Gelastocoridae at the base of the phylogenetic stem of Hydrocorisae. Farther along, he put the Naucoridae, from which the Nepidae, Belostomatidae and Corixidae come independently, and also the common branch of the Helotrephidae, Pleidae and Notonectidae (see later on for more details).

The certain belonging of the Ochteridae and Gelastocoridae to the Nepomorpha (= Hydrocorisae) and their relationship to each other was definitely proven by Miyamoto (1961) on the basis of an anatomical study of the structure of the intestinal tract of representatives of 36 families of Heteroptera; by Pendergrast (1957), who studied the structure of the reproductive organs, and also by Parsons (1959, 1960, 1965, 1966), who made a detailed study of the structure of the head capsule of Nepomorpha. China also notes the isolation of the Corixidae in the framework of the Hydrocorisae and Saldidae among the Amphibiocorisae, considering the latter family the most primitive in the Heteroptera common stem. Thus, the opinion of Reuter and Beier about the necessity of placing the Ochteridae and Gelastocoridae into the group of aquatic Hydrocorisae is supported.

China removes all aquatic Heteroptera directly from the hypothetical terrestrial forms (Proto-Heteroptera); however, the presents no discussion and does not substantiate this position. He derives the other group of aquatic bugs of the series Amphibiocorisae, or Gerroidea, from saldid-like ancestors (Protosaldidae) of some kind of terrestrial Heteroptera (Proto-Heteroptera terrestrial), again with no discussion. Thus, according to China, the two basic evolutionary branches of aquatic bugs (Hydrocorisae and Amphibiocorisae) are not closely related and arise independently from different terrestrial ancestors. I cannot agree with these conclusions for reasons spelled out in Chapter VI.

In his survey of Heteroptera, Poisson (1951) divides the order Heteroptera into two suborders: Cryptocerata, or Hydrocorisae, and Gymnocerata or Geocorisae. In the suborder Crypocerata, he includes only the true aquatic bugs (Hydrocorisae sensu Latreille), represented by four superfamilies: Corixoidea (Corixidae), Notonectoidea (Notonectidae), Pleoidea (Pleidae, Helotrephidae) and Nepoidea (Nepidae, Belostomatidae, and Naucoridae). The lack of the littoral Ochteridae and Gelastocoridae and also the size of the suggested superfamilies, clearly demonstrate the error of such an interpretation of the suborder. In another of his monographs on the aquatic Heteroptera, Poisson (1957) calls into question the expediency of dividing the order of bugs according to the character of the antennae into the two groups Cryptocerata and Gymnocerata because the littoral families Ochteridae and Gelastocoridae are not inhabitants of open water and they can be considered as transitional forms between the Hydrocorisae and Amphibiocorisae. Thus, Poisson prefers to stick to the earlier suggested division of Heteroptera into four typological groups: Sandaliorrhyncha, Hydrocorisae, Amphibiocorisae, and Geocorisae (Dufour, 1833; Borner, 1904; Ekblom, 1929; Spooner, 1938 and others). In morphological structure (mouth apparatus, thoracic sclerites, etc.), Poisson proposes the heterogeneity of aquatic bugs, particularly the groups of Hydrocorisae which, in his opinion, are joined by an aquatic form of life. The error of this opinion, from my point of view, has been convincingly proven by the morphological works of the last decade.

In a general list of families and subfamilies, China and Miller (1959) offer a 90
phylogenetic scheme of families analogous to that given by China earlier (1933), wherein the Heteroptera are considered only as a suborder of the order Hemiptera. Once again the subdivision of true Heteroptera is in three groups: Hydrocorisae (including the littoral families), Amphibiocorisae and Geocorisae. Within the Geocorisae are two groups: Cimicomorpha and Pentatomomorpha. The general number of families in comparison with the former scheme is increased by one only (52); however, within the order itself there are a few changes: Aphelocheiridae are included as a subfamily in the Naucoridae and the Aepophilidae in the Saldidae; separated into independent families are the Lestoniidae from the Pentatomidae (s. lato) and Stenocephalidae from the Coreidae (s. lato), and the new family Vianaididae, close to the Tingidae, is given. The greatest changes are in the construction of phylogenetic family trees; they are distinctly seen in comparison with the above-mentioned schemes.

Pendergrast (1957) conducted a study of the reproductive organs of Heteroptera analogous to those done by Larsen (1938) and Singh-Pruthi (1925), and offered a general classification of the order. On the basis of a study of female spermatiki and the male reproductive organs (including the sex glands), all bugs were divided into four groups, one of which is represented by the entire group of aquatic Heteroptera: Naucoridae (+Apholocheiridae), Nepidae, Belostomatidae, Notonectidae, Pleidae, Corixidae, Ochteridae and Gelastocoridae. Noteworthy are Pendergrast's analysis and critical remarks of the five systems he examined (Reuter, 1912; China, 1933; Borner, 1934; Beier, 1938, Poisson, 1951), which led to the following. First, he correctly objects to placing the Corixidae into a special series, since the reproductive organs basically are of the same type as in other aquatic bugs and, particularly, the single type of female spermatiki is found in Corixidae and Naucoridae. Secondly, in his opinion, Ochteridae and Gelastocoridae must be considered as one unit with the strictly delimited group of true aquatic bugs, and joining them with the Saldidae, Leptopodidae and Leotichiidae is somewhat artificial. Thirdly, concerning the Notonectidae, he suggests following China's scheme (1933), in which the notonectids are joined with the Pleidae and Helotrephidae into one group, on the basis of the identical structure of the spermatiki. Finally, Pendergrast objects to joining the Nepidae, Belostomatidae and Naucoridae (also the Aphelocheiridae, which figures as in independent family in this work), since the spermatiki of the Naucoridae are essentially different from those of the Nepidae and Belostomatidae, and thus the superfamily Nepoidea should include only the latter two families. For a general classification of the Heteroptera, Pendergrast follows Dufour (1833), i.e., he divides the order into three basic groups, Hydrocorisae, Amphibiocorisae and Geocorisae.

We find a somewhat different and, in my opinion, poorly based division of all Heteroptera into three heterogeneous groups in Scudder (1959). The first group includes all the Pentatomomorpha, the second Cimicomorpha, Nepomorpha (=Hydrocorisae) and Gerromorpha (=Amphibiocorisae), and the third only the Corixidae. This division of the bugs, based mainly on the structure of the female genitalia, is undoubtedly to a considerable degree artificial. Of definite interest here is the somewhat isolated position of all Pentatomomorpha, and also the similarity of the female genital structure of Saldidae and Mesoveliidae, to be discussed below.

On this morphological base, Scudder suggested the following size of superfamilies: 91
Nepoidea (Nepidae, Belostomatidae), Naucoroidea (Naucoridae, Aphelocheiridae), Notonectoidea (Notonectidae, Pleidae), Ochteroidea (Ochteridae), Corixoidea (Corixidae). The structure of the genitalia in Gelastocoridae and Helotrephidae is so original that he put these families into the group Heteroptera incertae sedis.

Noteworthy are the recent morphological works of Parsons and the phylogenetic constructions connected with them (1959, 1965). This author prefers to hold to Fieber's division of real Heteroptera into the two suborders Cryptocerata and Gymnocerata. On the basis of histological studies of the midgut (Parsons, 1959), a preliminary phylogenetic scheme was constructed which differs from that of China (1955a) by connecting the Corixidae with the nepid-belostomatid complex and deriving them from the ancestral branch of Nepoidea.

On the basis of the structure of the endocranial elements of the head, and also the suctorial system of the rostrum and the structures connected with it, Parsons (1966) suggested a new scheme of phylogenetic relationships of seven families of the aquatic group of bugs which differs significantly from others, mainly from that of China (1955a): from the beginning the Nepoidea were isolated from the basic heteropteroid stem, then the Corixoidea and in turn the Gelastocoroidea and the Naucoroidea with the Notonectoidea.

Of special interest is the newest monographic work on the egg structure and embryogenesis of Heteroptera by Cobben (1968), which is a great step forward in comparison with the studies which have been available up to now on the bugs as a whole. In this work, the author, on the basis of features of egg structure, suggests dividing the Heteroptera into the following more or less, from his point of view, equivalent groups: Cimicomorpha (s. str.), Dipsocoroidea, Enicocephalidae, Joppeicidae, Reduviidae, Thaumastocoridae, Pentatomomorpha, Amphibiocorisae, and finally Hydrocorisae. From a nomenclature point of view, these groups are scarcely equivalent taxons in the rank of infraorder. Right, Cobben does recognize this indirectly, placing all groups (except the latter two) into the Geocorisae and thus specifying the non-equivalency of the latter Amphibiocorisae and Hydrocorisae, and also correctly demonstrating the polyphyletic origin of the terrestrial Heteroptera Geocorisae.

And thus the basic disagreements in the existing classification schemes of aquatic Heteroptera reduce to a determination of the placement of the littoral families Gelastocoridae, Saldidae and Ochteridae and the aquatic Corixidae, Nepidae and Belostomatidae, and also the principles of the higher classification of the order, and particularly, the establishment of the superfamily taxons and their size. Undoubtedly, the division of the order Heteroptera into the two suborders Cryptocerata (Hydrocorisae) and Gymnocerata (Geocorisae) or the series Hydrocorisae, Amphibiocorisae and Geocorisae, to a sufficient degree, is established and is more a typological than a phylogenetic division (this is particularly true in the size of the polyphyletic group Geocorisae). Their use is based more on traditional practice than on well developed scientific principles.

Thus, at present there is no one opinion on the system of the large taxons of the present Heteroptera. Up to now, some authors have considered the Heteroptera as a suborder of the Hemiptera (Rhynchota), along with the Homoptera (Brues, Melander, Carpenter, 1954; China, 1955b, China, Miller, 1959; Southwood, Leston, 1959; Goodchild, 1955; Cobben, 1968). However, another group of contemporary researchers of true Heteroptera considers them as the special order Heteroptera (Hemiptera), which, from my point of view, apparently is much more expedient (Kirichenko, 1951; Poisson, 1957; Matsuda, 1961; Becker-Migdisova, 1962; Jascewski, Kirchner, 1964, and others).

Taxonomically, the largest taxons of the order (suborder, superfamily) are still 92
insufficiently developed and, as was already discussed above, the division of the Heteroptera into a series of superfamilies , and also the establishment of superfamily ranks is far from accepted by all researchers in identical size.

In characterizing such large taxons, it is very difficult to choose traits which would strictly delimit them. Thus, the higher the rank of taxonomic unit, the more difficult it is to find unique characteristics. Many structures (external and internal) vary and cannot, naturally, serve as determining characters of the taxon. However, in some cases, one character in some taxons varies, and in others is stable, so that it can serve as a characteristic. For example, in aquatic groups of Heteroptera (Nepomorpha and Leptopodidomorpha), according to Pendergrast's data (1957), the number of ovules in the ovaries does not vary, wheras in the so-called Enicocephalomorpha, Cimicomorpha and Pentatomomorpha, this number varies from four to seven. In all primitive groups they are always seven.

As a result of an analysis of the general morphological works and studies of fossil forms, the genetic ties of the basic groups of Heteroptera and the main directions of adaptation to surrounding conditions have been preliminarily established. On the basis of this, we now suggest turning from the more or less widely accepted division of the order Heteroptera into two suborders (Cryptocerata and Gymnocerata or Saldinea and Cimicinea, sensu Popov, 1968) or series (Hydrocorisae, Amphibiocorisae and Geocorisae), to the new concept "infraorder" (an intermediary taxon between suborder and superfamily) for the taxonomy of the order Heteroptera. The introduction of infraorders, as the practice of their application has shown (Principles of Paleontology, Arthropoda, Tracheids, Chelicera, 1962), is fully justified. In any case, the division of the Heteroptera into infraorders, from my point of view, is more natural than the division suggested by various authors into suborders and series, since both these divisions had so many exceptions and, besides, in many cases, the transitions between them are so gradual, not to mention the apparent individual origin of the true terrestrial groups of bugs (on the one hand, Enicocephalomorpha+Cimicomorpha, and on the other, Pentatomomorpha). The indraordinal taxon corresponds well with the basic phylogenetic stems and evolutionary directions of development of true Heteroptera and, thus, all infraorders are strictly morphological. Probably, all the bug infraorders which I have suggested, in the degree of their supposed closeness and organization, can be joined into four independent groups, giving them the rank of suborders: 1) Nepomorpha+Leptopodidomorpha, 2) Enicocephalomorpha+Cimicomorpha, 3) Pentatomomorpha, 4) Actinoscytinomorpha (Triassocoridomorpha).

However, to finally solve this problem we still need a special study in this direction, which, apparently, will be realized in the near future by the joint efforts of a number of hemipterologists.

In general, the idea to remove the monophyletic groups of Heteroptera into the size of the infraorder I have suggested is not new and has already been discussed in one form or another. Thus, for pentatomoid and cimicoid groups the ending "morpha" has been used (Leston, Pendergrast, Southwood, 1954). Stichel (1955) gave the following names for the groups (divisions) which he isolated: Hydrocoriomorpha, Amphibiocoriomorpha, Hemicocephalomorpha of equal rank to Cimicomorpha and Pentatomorpha. An analogous attempt was undertaken (Miyamoto, 1961) on the basis of morphological studies of the digestive tract of almost all Heteroptera families: 93 Hydrocorisae, Amphibiocorisae, Dipsocorimorpha (=Henicocephalomorpha), Cimicomorpha, and Pentatomomorpha.

The order of true Heteroptera, or bugs, thus is subdivided into a series of more or less equivalent, from my point of view, infraorders: Nepomorpha (=Hydrocorisae), Leptopodidomorpha (=Amphibiocorisae), Enicocephalmorpha (=Dipsocorimorpha, Henicocephalomorpha), Cimicomorpha, Pentatomomorpha and the extinct Actinoscytinomorpha (Triassocoridomorpha). In turn, the most intersting to me systems of the related infraorders Nepomorpha and Leptopodidomorpha, I have put into the following subfamily categories:

INFRAORDER NEPOMORPHA
  Superfamily Gelastocoroidea
    Family Ochteridae Kirkaldy, 1906
    Family Gelastocoridae Kirkaldy, 1897
  Superfamily Nepoidea
    Family Nepidae Latreille, 1802
    Family Belostomatidae Leach, 1815
  Superfamily Corixoidea
    Family Corixidae Enderlein, 1912
    Family Shurabellidae, fam. nov.
  Superfamily Naucoroidea
    Family Naucoridae Fallen, 1814
  Superfamily Notonectoidea
    Family Scaphocoridae Y. Popov, 1968
    Family Mesotrephidae, fam. nov.
    Family Pleidae Fieber, 1859
    Family Helotrephidae Esaki, China, 1927
    Family Notonectidae Leach, 1815
INFRAORDER LEPTOPODIDOMORPHA
  Superfamily Leptopodoidea
    Family Leptopodidae Brulle, 1835
    Family Leotichiidae China, 1933
    Family Saldidae Costa, 1852
  Superfamily Gerroidea
    Family Mesoveliidae, Puton, 1879
    Family Hebridae Amiot, Serville, 1843
    Family Hebroveliidae Lundblad, 1939
    Family Veliidae Amiot, Serville, 1843
    Family Macroveliidae MacKinstry, 1942
    Family Gerridae Leach, 1815
    Family Hydrometridae Baer, 1860

Some of the principal differentiating traits connected with the new divisions of the closely related infraorders of aquatic bugs are the varied structure of the digestive system, the internal reproductive organs, structure of the egg, embryogenesis, and also the varied position of the antennae. Hidden antennae in the infraorder Nepomorpha is the result of adaptation to aquatic living conditions, and the corresponding changing function of this organ, which appeared originally in the littoral forms of the type of representatives of the recent family Gelastocoridae, which, as already discussed above, from time to time settles an aquatic area. Only in a few Nepomorpha do we find freely set antennae, which in some cases have a clearly secondary character, for example in the aquatic Aphelocheirinae (Naucoridae), in connection with digging in silt (Puchkova, 1964) and in others, undoubtedly, are primary, as in the littoral Ochteridae. 94

Up to now, we still have not resolved conclusively the question of the true congeneric interrelationships of the littoral families Ochteridae and Saldidae, which are placed correspondingly at the base of the phylogenetic trees of the infraorders Nepomorpha and Leptopodidomorpha. The most recent morphological investigations of Cobben (1968) proved that in structure and orientation of the micropiles, in the character of the breaking when nymphs hatch from the egg, the real aquatic and littoral Heteroptera are joined into the one group Nepomorpha and are placed, alongside sensu mihi ~~with~~ the Leptopodoidea, i.e., Leptopodidomorpha (s.m.) In structure of the mandibular levers (Bueno, 1923; Ekblom, 1929) and presence on the head of three pairs of trichobotri (China, 1955a), Saldidae are similar to the Gerroidea. However, in structure of salivary glands and malpighian tubes, Saldidae resemble the terrestrial Cimicomorpha, wheras the salivary glands of Gerridae are clearly of ochteroid type (Miyamoto, 1961). On the other hand, the structure of the hind gut of the Saldidae is similar to that of the Nepomorpha, Cimicomorpha and even the Gerroidea. The structure of the reproductive organs resembles that in Pentatomomorpha (Pendergrast, 1957). The study undertaken by Kumar (1964) of the internal structures of the male reproductive organs of Enicocephalidae and Leptopodidae also shows indirect connections of the Saldidae (through Mesoveliidae!) with the infraorder Enicocephalomorpha, which occupies an intermediary position between the Leptopodidomorpha (=Gerromorpha sensu Kumar) and Cimicomorpha. Such a mix of traits of structure of internal organs, peculiar to both Leptopodidomorpha and the the terrestrial groups of Heteroptera referred to, in Miyamoto's opinion,(1965), permits suggesting that the family Saldidae is one of the most primitive groups of bugs, occupying an intermediary position between the real terrestrial and aquatic groups of Heteroptera.

In the infraorder Nepomorpha are the most primitive representatives of the superfamily Gelastocoroidea, consisting of the two living families Ochteridae and Gelastocoridae. Spooner (1938) considered the Ochteridae and Gelastocoridae as a bridge between the aquatic and semi-aquatic groups of Heteroptera, judging them closest to the amphibial group. He proceeded from the presence in them of an epipharyngeal projection and the single type of mandibular lever.. On the basis of this, he put the Ochteridae and Gelastocoridae into the series Amphibiocorisae, and the Saldidae into the terrestrial group Geocorisae. However, subsequently, Parsons (1959) established the error of the identification of the levers in these groups. Nonetheless, many of the already mentioned later works on the taxonomy and phylogeny of the Heteroptera have convincingly shown that the littoral Ochteridae and Gelastocoridae belong to the aquatic group of Heteroptera.

The problem of the phylogenetic relationships of the littoral families Ochteridae and Gelastocoridae was solved in the morphological studies of Pendergrast (1957), Miyamoto (1961), Parsons (1959, 1960, 1962 and others) and Cobben (1965, 1968). All these authors place the Ochteridae and Gelastocoridae into the group of aquatic bugs, i.e., the infraorder Nepomorpha (=Hydrocorisae). However, opinions on their congeneric relationships with other families turn out to be different. On the basis of the structure of the reproductive organs, Pendergrast came to the conclusion that uniting the littoral families into one group was artificial, since the Ochteridae showed a greater similarity to the Naucoridae and Corixidae than to the Gelastocoridae, and the latter turned out to be closer to the Notonectidae. On

the other hand, morphological studies of the head (Parsons, 1959) and digestive
organs (Miyamoto, 1961) confirm the closeness of these two families. From my point 95
of view, the morphological data of the works of those two authors is more conclusive, since the structure of the reproductive organs is less constant, which is also evident from the recent morphological works of Kumar (1961, 1964). The greater closeness of the Gelastocoridae to the Naucoridae, Notonectidae and Corixidae than to the Nepoidea, as more specialized forms, and consequently the earlier isolation of the nepid from the ochterid branch was well proven by the studies of Parsons (1959).

In the structure of the food pump and its musculature (Parsons, 1959), Gelastocoridae show similarity to Naucoridae and Notonectidae, but in structure of labium resemble even the Nepidae. The labial musculature of the thoracic sclerites (Parsons, 1960) "labial"? (longitudinal?) typo error in book and the reproductive organs (Pendergrast, 1957) of representatives of this family also strongly resemble those of the Notonectidae. The structure of the digestive organs (Miyamoto, 1961) as a whole is closest to that of Naucoridae, evidencing similarity, on the one hand, with Ochteridae and on the other with Notonectidae.

The superfamily Nepoidea is exclusively aquatic and joins the two living families Nepidae and Belostomatidae. In structure of head capsule (not-widened distinctly marked sutures of the clypeus, weakly formed filtering system of the throat, etc.) developed venation of the fore wings, features of the respiratory system and some other characteristics, this superfamily differs sharply from all other aquatic bugs and occupies an isolated position.

The closeness of the living Nepidae and Belostomatidae was well proven by Larsen (1938), who indicated the similarity in the structure of their respiratory tube and abdominal musculature, and also by Spooner (1938), who pointed out the identical structure of the mandibular levers. Pendergrast (1957) found much similarity in these two families in the structure of the semen-holder. Miyamoto (1961) showed the undoubted similarity of the structure of their digestive organs; the American hemipterologists Lauck and Menke (1961) also showed the similarity in the structure of the antennae. The family Belostomatidae evidences the following similar characteristics with the Nepidae: 1) fore coxae are short, 2) in some Laccotrephes (Nepidae) and Lethocerus there are two furrows on the fore tibia, 3) the abdominal sternites are divided into mid section and parasternites, 4) the apical projections of the abdomen form the air canal of the respiratory tube, analogous to the siphon of Nephidae, 5) the phallus has a divided aedeagus and ventral diverticulum. However, the ability to use a shorter respiratory tube and lay eggs on the surface of plants (Nepidae lay in the tissue of plants) sharply differentiates the Belostomatidae from the Nepidae.

The superfamily Naucoroidea consists only of a single family which in number of subfamilial taxons (5) is comparable only to the Corixidae (6). In structure of digestive organs, Naucoridae resemble the littoral families of the Nepomorpha, particularly the Gelastocoridae. The structure of the basic salivary glands in some of the studied Naucoridae (Aphelocheirinae) also shows similarity with the superfamily Gelastocoroidea. The anteclypeus of Naucoroidea is similar to that in Gelastocoridea, Notonectoidea, and Corixoidea in being strongly widened and fused with the loral sclerites of the head capsule. Not fused in corixids M.C.P.

In general, among living Nepomorpha, Naucoroidea are most similar to representatives of the families Gelastocoridae and Notonectidae: form of maxillary plate, lack of a distinct stylet groove at the base of the second segment of the rostrum, presence of more than one supporting tendon between the first two segments of the rostrum, and lack of an intermediate sclerite in the latter (Parsons, 1966a) speak in favor
of their being close to these groups. In structure of spermatiki, Naucoridae are 96
similar to the Corixidae and Ochteridae (Pendergrast, 1957). The original South American subfamily Potamocorinae is similar to the primitive Helotrephidae of the Notonectoidea.

The superfamily Notonectoidea joins the three living families Helotrephidae, Pleidae and Notonectidae and the two specialized extinct Scaphocoridae and Mesotrephidae. This superfamily is represented by aquatic forms with wings which are roof-shaped when folded, an occurrence unique in the order Heteroptera and characteristic for the related order Homoptera, and, undoubtedly, in this case a convergent characteristic. Most probably the Notonectidae separated from some form of naucorid stem and evidence a fairly significant similarity with the latter. The study of the filtering system of Notonectidae in general showed a structure analagous to that of the Naucoridae, but somewhat more simple (Parsons, 1966a), and together with it the single type of modified clypeus (Parsons, 1965). In similarity of structure of the labium, living Notonectidae, just as Naucoridae, are close to the littoral family Gelastocoridae (Parsons, 1966b). With the latter family, Notonectidae (Helotrephidae and Pleidae) are similar also in structure of spermatiki and the male reproductive organs (Pendergrast, 1957). Studies of the digestive organs (Miyamoto, 1961) showed the closeness of living notonectids: Helotrephidae, Pleidae and Notonectidae, thus confirming the naturalness of their being united, which Esaki and China already suggested (Esaki, China, 1928; China, 1955).

The last superfamily I examined, the Corixoidea, is the most specialized and isolated among Nepomorpha; it consists of the very extensive living family Corixidae and the extinct lower Jurassic Shurabellidae.

Representatives of this original superfamily have separate traits of similarity not only with all aquatic bugs of the infraorders Nepomorpha, and Leptopodidomorpha (Ochteroidea, Nepidea, Naucoridea, Leptopodoidea, Gerroidea), but also with all the other terrestrial Heteroptera (in the presence of abdominal glands in the nymphal stage).

Such are the basic traits and size of the five proposed superfamilies comprising the infraorder Nepomorpha which I have established.

Key for Determining the Superfamilies and Families of the Infraorder Nepomorpha[1]

1(2) Antennae as long or longer than head, always free; claws of tarsus with areoli or without areola. Above water and littoral forms. Leptopodidomorpha

2(1) Antennae shorter than head, usually (except Ochteridae and Aphelocheirinae and Potamocorinae of the Naucoridae) concealed in pits under the eyes between the head and prothorax; tarsal claw without areola. Aquatic and littoral forms Nepomorpha

3(6) Rostrum very short and wide, semi-conical, sunk into the clypeus, indistinctly segmented, base of head lamellate, overhanging the pronotum in front; fore tarsi of males transformed into palae or almost cylindrical, bordered by hard stylets; nymphs with three dorsal abdominal apertures of odor glands. Aquatic. Corixoidea

4(5) Tegmen with leaf-like widenings along entire length of fore margin and remains of venation; hind tibia and tarsi not flattened with brush of very long swimming hairs; head narrower than pronotum. Shurabellidae.

5(4) Tegmen with not-widened fore margin; embolium rim usually well expressed 97
or nodal fissure present; venation very reduced (except Mesozoic Archaecorixinae); hind tibia and tarsi flattened and densely covered with swimming hairs; head not narrower than pronotum Corixidae

6(3) Rostrum cylindrical or conical, distinctly three- or four-segmented; fore tarsi of usual form; base of head comes into prothorax; nymphs without abdominal glands or only with one unpaired dorsal aperture of the odor glands.

7(24) Head and pronotum not fused or partially fused, but then fissure between them deep and straight; antennae three- or four-segmented.

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[1] To ease determination in many cases theses and antitheses which directly characterize family taxons are furnished with additional designations which are not in opposition.

8(11) Ocelli present; mid and hind legs not flattened, walking and not covered with swimming hairs. Littoral Gelastocoroidea

9(10) Head transverse, semi-stalked eyes widely set apart; rostrum short, does not come beyond fore coxae; antennae from above not visible, set in grooves under the eyes; fore legs seizing, femora fairly powerful and wide, with fissure or riblet on inner surface; scutellum unevenly convex. Gelastocoridae

10(9) Head with vertex slightly wider than diameter of one eye; eyes not semi-stalked; rostrum long, reaching hind coxae at least; antennae visible from above; fore legs simple, similar to mid and hind legs, running; scutellum flat. Ochteridae

11(8) Ocelli missing. Mid and hind legs, as a rule, swimming, covered with dense brush of hairs. Aquatic forms.

12(17) Body strongly condensed or widely-oval, rarely elongated; tegmen lie flat on back; coxae of fore legs attached at fore margin of prothorax; fore legs grasping.

13(14) Body widely- or elongatedly-oval; membrane without veins, tegmen with reduced venation; abdomen at apex without respiratory tube; of moderate size (Naucoroidea). Head transverse; rostrum short, conical, reaches only fore coxae, rarely comes beyond them; mid and hind legs with row of swimming stylets or almost without them Naucoridae

14(13) Body oval, elongated, tegmen with venation preserved, membrane with veins, usually forming a distinct netting; abdomen at apex with respiratory tube (siphon); large Nepoidea

15(16) Leg coxae strongly set apart, sternal region from outside strongly developed. Abdomen with very long thin respiratory tube; fore legs strongly developed, grasping; tegmen with weakly expressed venation; membrane with thick set of veins Nepidae

16(15) Leg coxae not set apart and contiguous, sternal region from outside weakly developed; abdomen with shorter, thin or widely flattened respiratory tube; venation of tegmen well expressed Belostomatidae.

17(12) Body elongated; cylindrical, from above strongly convex, tegmen lie roof-shaped (except some Helotrephidae); coxae of fore legs attached at hind margin of prothorax; fore legs simple, not grasping Notonectoidea

18(19) Body stretched out, cigar-shaped, antennae usually four-segmented; hind legs long, paddle-shaped, without distinct claws; hind tibia flattened; tarsi two-segmented, of medium size Notonectidae

19(18) Body oval, hind legs short; basically small forms

20(21) Hind margin of pronotum strongly developed and completely covers a small scutellum; tegmen with membrane; femora short and doe not project beyond lateral margin, hind tibia and one-segmented tarsi thick, tarsi covered with long swimming hairs, of medium size, not less than 4 mm. Scaphocoridae

21(20) Hind margin of pronotum less strongly developed, scutellum free; very small forms, body length not more than 2-3 mm.

22(23) Pronotum almost rectangular, transverse, scutellum relatively large, membrane missing, antennae three-segmented Pleidae

23(22) Pronotum oval, strongly transverse, scutellum very small, tegmen with membrane, lateral margins widened Mesotrephidae

24(7) Head fused with prothorax, forming cephalonotum; connection between head and prothorax usually designated by a dorsal curved suture; antennae one- or two-segmented, membrane strongly reduced. Helotrephidae.

CHAPTER V

TAXONOMIC SECTION

INFRAORDER NEPOMORPHA - INFRAORDO NOVUS

Description. Bugs of the most diverse size, from very small forms less than 1.5 mm (Helotrephidae) to the real giants among Heteroptera, reaching 110 mm (Belostomatidae). The main features which characterize the group are the structure of the digestive system - the scarcely visible pylorus, the presence of an ilium, the narrow aperture of the basic salivary glands (except Corixidae) - and also the lack of a bulbus ejaculatorius in the male reproductive organs, and the presence of strongly shortened antennae, hidden, as a rule, in special pits (grooves) directly under the eyes or between the head and the prothorax. Being basically a predatory group, representatives of the suborder, in most cases, have grasping fore legs. This group of true Heteroptera, comparatively small in size (about 1,600 species), is adapted to life in water, and also to littoral conditions. The development of aquatic vegetation, the lack of currents and large waves, small shallows favor a rich development of aquatic bugs.

Comparison. Differs from the infraorder Leptopodidomorpha in the undeveloped pylorus of the digestive system, the hidden position of the antennae, the submarine form of life in most representatives and also the difference in the structure of the mandibular levers, the absence of the head trichobotry and the second duct, connecting the semen-collector with the vagina (the so-called "fertilizing canal").

Composition. Five superfamilies: Gelastocoroidea, not known in the fossil state, live in the tropics and subtropics; the extinct Nepoidea - Jurassic of West Europe, Paleocene and Neocene of North America and West Europe; Naucoroidea - Jurassic of West Europe and Asian USSR, Cainozoic of North America and West Europe; Notonectoidea - Jurassic of West Europe, Cretaceous of Kazakhstan, Cainozoic of North America and West Europe; Corixoidea - Jurassic of Asian USSR, Cainozoic of North America and West Europe; living representatives of all the above-named superfamilies are widely distributed in all zoogeographic regions.

SUPERFAMILY GELASTOCOROIDEA Kirkaldy 1897

Description. Representatives of this superfamily are flat, thickset, with uneven, often knobby body surface. Head lies flat against the pronotum; anteclypeus in living forms is not expressed; rostrum is four-segmented, often moved to base of head; four-segmented antennae not of identical length, thus the manner of being hidden is variably expressed, but, as a rule, the antennae are hidden under the large eyes; ocelli present. Mid and hind legs are walking, coxae of the legs pagiopod. Lead a littoral form of life.

Comparison. Representatives of Gelastocoroidea differ from all other Nepomorpha (except Diaprepocorinae of the Corixidae) in the presence of ocelli and lack of swimming legs, and also the littoral form of life. 99

Composition. The families Ochteridae and Gelastocoridae are not known in the fossil state. Living representatives of these families are distributed worldwide in tropical and subtropical areas. The world fauna numbers about 130 species.

Comments. The original form of life of these insects has raised doubts on the possibility of their being placed in the aquatic or in the terrestrial group of bugs. The form of life in common with representatives of some littoral families (Saldidae, Leptopodidae and Leotichiidae), and even in some cases the similar external appearance led to their being joined with the latter, especially the Saldidae (Westwood, 1840; Dohrn, 1859).

Thanks to recent morphological studies, the Gelastocoroidea must be considered conclusively as belonging to the aquatic group of the infraorder Nepomorpha (Pendergrast, 1957; Matsuda, 1961; Parsons, 1959, 1960, 1962, 1964, 1966; Cobben, 1968).

FAMILY OCHTERIDAE Kirkaldy 1906 F. 66

Description. Body, small, oval, short, flattened out, resembling Saldidae, which live in similar biotypes. Insects of dark color, usually black-velvety with diffuse bluish spots on the tegmen and yellow-orange spots on the margins of the pronotum and tegmen. Head short; from above along the entire length of the clypeus and the frons runs a shallow central fin, eyes large, convex, two simple eyes more or less set apart and situated at the base of the head. Rostrum four-segmented, thin, very long, reaching the 11th abdominal sternite; antennae four-segmented, first two segments strongly shortened, last two segments elongated and thinner. Tegmen divide into clavus, corium, embolium and membrane: the large pentagonal cells of the latter are curved toward the inner side; the margin of the membrane has radial grooves. Venation of the hind wings very similar to that of the Notonectidae and Corixidae. Fore and mid tarsi are two-segmented, hind three-segmented, basal segment in all three pairs very small. Two simple claws on the very apex of the tarsus. Male abdominal segments asymmetrical, beginning with the sixth, but to a much lesser degree than in Corixidae. Ninth segment is very deformed, twisted, sternite is convex as well, tergal region narrow. Parameres strongly asymmetrical, left side reduced, simple; right side, on the other hand, strongly developed and of complicated structure. In females, the ovipositor is reduced. Structure of female genitalia is similar to that in Notonectidae.

Biology. These bugs form a small family of predatory insects which live along the banks of fresh reservoirs, especially running. Their ecology is still poorly studied. Some species have a wide geographical distribution. They live in moist zones along the margins of running water, where they are observed in the sand, buried under rocks, in sparse vegetation in the river. They move about by very careful and quick springs; eat small Diptera larvae which live in the pits of sand deposits along the water (Poisson, 1957), and also various crayfish side-swimmers of the genus Gammarus. They hibernate in the 4th, 5th nymphal stages and as adults, the emergence of the insects is observed in early spring. The egg before laying develops slowly and only two- 100
three eggs are found simultaneously in the oviduct. The eggs are laid in groups of 25-30 onto the surface of various objects: on grains of sand, plant remains, but not within plants. They develop about two months (Takahashi, 1923; Jaczewski, 1934; Schell, 1943; Bobb, 1951).

Comparison. This family differs from the Gelastocoridae in the considerably longer rostrum, longer antennae, homonomous legs and velvety body surface, and also the different position of the more widely set simple eyes on the head.

Composition. Two living genera[1]: Ochterus Latreille is widely distributed in the south Palearctic, in Ethiopia, Oriental and Nearctic regions; Megochterus Jaczewski in Australia. About 20 species combined.

FAMILY GELASTOCORIDAE Kirkaldy 1897 F. 67

Description. Squat, of moderate size (not more than 10 mm), whole body surface rough, usually knobby-warty, color greyish. Head in front triangular, pushed into a hollow between the fore corners of the pronotum; eyes large, reniform, highly convex and

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[1] The other described ochterid genus Ocyochterus (Drake et Gomez-Menor, 1954) from the type specimen Ochterus victor Bolivar from Ecuador, judging from the comparative characteristics given and the drawing, can hardly be considered a separate genus.

projecting dorso-laterally; ocelli usually present. Rostrum four-segmented, thick, short, reaching fore coxae. Antennae short, four-segmented, set under the eyes and hidden between the head and prothorax; the two simple eyes are drawn together and more or less far from the hind margin of the head. Pronotum large, slightly wider than the head, convex. Scutellum usually fairly large, triangular, projecting. Tegmen with clavus, corium, often with embolium and weakly expressed membrane, often partly or wholly reduced. Fore legs grasping, mid and hind of walking type. Nymphs always with simple eyes.

Biology. All species, apparently, are predatory, since their fore legs are grasping. They catch small insects which live in the same environment with them. Species of the subfamily Gelastocorinae live in mud silt or sand, along the shores of tributaries, ponds, lakes, etc. Some species of the subfamily Nerthrinae live in rotten parts of bananas (Melin, 1929) or on the ground in small groups of dry leaves, and also spend 101 much time on the ground under rocks (Kevan, Keith, 1942; Todd, 1955). Representatives of other species are encountered in small, thoroughly warmed reservoirs under rocks, semi-submerged trees or submerged plants where they crawl in search of prey; nymphs are encountered together with the imago (La Rivers, 1953). Apparently they fly poorly on what appears to be a partial reduction of the membrane of the hind wings.

They hibernate in the adult state or are active year round. The eggs are laid in the uppermost layers of sand, their coloring and structure correspond so well with the surface of the soil that it is very difficult to recognize them. One female lays up to 200 eggs in a season, from one to 13-14 eggs daily. The development from egg to imago generally lasts 60-100 days (Hungerford, 1922).

Comparison. This family differs from the Ochteridae in the strongly shortened rostrum, the fore tarsi merged with the tibia (in the case of articulation the tarsus is one-segmented), the more deeply sculptured dorsal body surface, the different position of the drawn together simple eyes, and also the grayish body coloring immitating the substrate.

Composition. Two subfamilies: Gelastocorinae Kirkaldy and Nerthrinae Kirkaldy. Not known in the fossil state, living representatives of these subfamilies are distributed in the tropical and subtropical zones of the world. The world fauna numbers about 100 species.

Table for Determining Subfamilies of the Family Gelastocoridae

1(2) Fore tarsi not fused with tibia, two well developed tarsal claws on apex of fore legs. Rostrum leaves apex of head, strong and thick, curved below and backward (f. 68a) Gelastocorinae

2(1) Fore tarsi fused with tibia; one strong claw on apex of fore legs. Rostrum leaves from ventral side of head, thinner and directed at first backward and then forward (f. 68b) Nerthrinae.

SUBFAMILY GELASTOCORINAE Kirkaldy 1897

Description. Bugs with rostrum leaving apex of head, fairly thick and curved backward. Fore legs with single articulated tarsal segment, which on the apex bears two well developed claws. Ninth male abdominal sternite completely drawn into a deepening of the body and not visible from outside. Male genitalia with hind projection (fin) first paramere strongly modified, aedeagus tubular (f. 68B), left paramere small, simple. Female abdominal segments symmetrical from below (f. 68g). 102

Composition. One genus Gelastocoris Kirkaldy and more than 30 species which are distributed in tropical and subtropical zones of the Wester Hemisphere.

SUBFAMILY NERTHRINAE Kirkaldy 1906

Description. Bugs with rostrum leaving from ventral surface of head, moderately thickened, usually directed forward at the apex. Fore legs with tarsus fused with tibia, with one well developed strong claw on the apex. Ninth male abdominal sternite clearly visible from the outside. Hind projection of male genitalia weakly expressed; right paramere strongly developed and folded longitudinally, aedeagus 103 tubular, left paramere missing; female abdominal segments from below symmetrical or asymmetrical. Very widespread brachyptery.

Composition. One genus Nerthra Say and 75 species, which are distributed in the tropical and subtropical zreas of the Western and Eastern Hemispheres.

SUPERFAMILY NEPOIDEA LATREILLE 1802

Description. Head prognathous, with well marked anteclypeus. Rostrum four-segmented, antennae very short, completely hidden, simple eyes missing. Filtering apparatus of throat consists only of a system of hairs. Fore legs are grasping, fore tarsi long, fore femora set in front of the prothorax. Tegmen with distinct venation and clearly separated membrane, often bearing numerous veins. Leg coxae trochalopod or (hind) pagiopod. True aquatic insects which live on the bottom of reservoirs or swim freely.

Comparison. Differ from other superfamilies in the grasping fore legs, clearly separated anteclypeus, rich wing venation, especially the membrane, and presence of a respiratory tube (siphon), and also the drawn apart coxae of the legs of Nepidae.

Composition. Two families: the fossil Nepidae Latreille, known from the Upper Jurassic, Paleocene and Neocene of Western Europe and North America, fossil Belostomatidae Leach from the Upper Jurassic of the Paleocene and Neocene of West Europe; families widely represented in the living fauna. Over 300 species in the world fauna.

FAMILY NEPIDAE Latreille 1802 - Aquatic Scorpions

Description., Basically large (30-45 mm), rarely of moderate size (15-20 mm) bugs. Body strongly condensed, from moderately elongated (Nepinae) to baton-like (Ranatrinae). Head small, almost horizontal, from above narrower or slightly wider than pronotum, often more or less drawn into the prothorax. Eyes most often small, as a rule, projecting, spherical. Rostrum short or strongly curved, directed forward and slightly downward, with rudiments of labial palps; mandibular lever three-branching. Antennae three-segmented, very short, concealed on the lower side of the head under the eyes. Maxillary glands developed, set at the base of the rostrum. Lateral margins of pronotum very strongly turned onto the lower side. Pleural and sternal regions of prothorax strongly fused, so that the latter often has no border with the accreted lateral margins of the pronotum. Odor glands on the metathorax missing. Trochantin well developed. Scutellum free, triangular, slightly shorter than claval suture. Tegmen with partially preserved venation like weak veins, membrane with set of veins, forming numerous cells. Hind Wings bear traces of an archedictyon. Coxal cavities are closed, coxae trochalopod, adapted to rotating, widely set apart. Fore legs grasping, coxae long, directed forward, tibia always thin, tarsi one-segmented, like a talon. Mid and hind legs walking, tibia and femora thin, linear, tarsi one-segmented, furnished with a pair of claws. Abdomen weakly widened or not widened, abdominal sternites divided by longitudinal fissures or folds into central sternites (mesosternites) and parasternites, sub-genital plate fairly wide or narrow. Genital segments 10 symmetrical. Spiracles on the ventral side of the laterotergites. Surface of head, pronotum and scutellum strongly sculptured.

Nymphs with two ventro-abdominal grooves, which take in air, which are missing in adults that have a long caudal siphon. The function of the static organ in nymphs of some genera is fulfilled by the short sensory hairs along the laterotergites on the ventral side of the abdomen. The difference in the size of the female subgenital plates in each subfamily of aquatic scorpiions is connected with the different manner of the ovipositing, according to many authors. Thus Larsén (1938) states that the female of Ranatra makes an incision with the sharp subgenital plate into the living or already withered plant and in this made cut lays the eggs by means of this same plate. Thus, the filaments of the eggs thus remain free. This process of laying is illustrated also in Hungerford's work (1920). The wide subgenital plate of the female of true Nepinae, as many foreign works show (Wiley, 1924; Hoffmann, 1927; Larsén, 1938), is not adapted to this form of egg laying, and they are laid in a strongly softened substrate, like moss, rotting vegetation or silt. The eggs at the micropyles have a variable number of so-called filaments or threads, the number of which varies from 2 to 8.

Biology. Aquatic scorpions live in standing or moderately current reservoirs, move slowly along the bottom, sometimes swarm in the silt (Népa) or move about aquatic plants (Ranatra); they swim very poorly. Predators which lie in wait, they catch prey in ambush, so that at rest the grasping legs project beyond the head, and the mid and hind legs are extended along the abdomen;. they can be found in this condition for a very long time (reflex of immobility), but on condition that the end of the respiratory tube is found above the surface of the water. They destroy many roe and young of fish, Odonata and beetle larvae, and also fall upon the eggs of crayfish and their young individuals (Sirotinina, 1921, Poisson, 1957). Nepidae hibernate usually in an aquatic milieu. According to L. V. Puchkova (1962), hibernating in the bottom silt of non-frozen springs, Nepa cinerea L. were active, had a well developed fatty body, and 2-4 dozen mature eggs were found in the ovaries of the females. Eggs are laid either on objects swimming in the water (Nepa) or on the stems or leaves of plants (Ranatra). Very characteristic for aquatic scorpions is the accumulation around their bodies of green and diatom water plants, which apparently play a symbiotic role.

Comparison. 'Nepidae differ from all families first of all in the set apart coxae of the legs, and also the considerably longer fore coxae; from the family Belostomatidae in the set apart coxae of all pairs of legs, directed forward fore coxae, and also the lack of metathoracic odor glands.

Composition. Two superfamilies: Nepinae Latreille, Upper Jurassic of West Europe, Paleocene and Neocene of North America and West Europe and Ranatrinae Douglas and Scott, which in the fossil state are known only from the Pleistocene of North America. Representatives of these subfamilies in living fauna number about 200 species, distributed in various regions of the world, primarily in the Orient, Ethiopia and neotropical regions.

Table for Determining Subfamilies of the Family Nepidae

1(2) Body oblong (except strongly elongated Austronepa). Head clearly narrower than fore margin of pronotum. Pronotum trapezoid. Coxae of fore legs short, do not project beyond fore margin of pronotum. Abdominal parasternites visible.
Nepinae

2(1) Body strongly elongated (except weakly elongated Curicta). Head wider than 105
fore margin of pronotum or almost as wide. Pronotum long, narrow. Coxae of fore legs very long, baton-like, come far beyond pronotum. Parasternites fused.
Ranatrinae.

SUBFAMILY NEPINAE Latreille 1802 F. 69

Description. Body oblong-oval, strongly flattened out dorso-ventrally; some forms are more narrow (Laccotrephes, particularly Curicta), others more wide (Nepa); length from 15 to 45 mm; head narrower than fore margin of pronotum, noticeably pulled into

a hollow of its fore margin; surface of coarse sculpturing. Eyes small, do not reach fore corners of pronotum. Pronotum always transverse, particularly in genus Nepa; fore margin strongly hollowed in the central portion, in the hind third there is a distinct cross fissure, particularly noticeable in the developed sculpturing on the surface of the pronotum; hind corners strongly bumpy, particularly in the genus Laccotrephes. Scutellum relatively large, usually with rough sculpturing. Pleural region of prothorax with distinct fissure, which separates it from the lateral margins of the pronotum. Basisternites of mid and metathorax transverse, convex, devoid of any kind of projections on hind margin. Coxae very widely set apart. Abdominal parasternites fairly developed, wide (Nepa, Laccotrephes) or (Curicta) edges of sternites are situated at an angle to the central fin, rarely almost straight the entire extent (Curicta); subgenital plate wide, strongly condensed; respiratory tubes very long (Laccotrephes) 106
or shortened (Nepa, Curicta). Eggs with two terminal filaments (f. 60b).

Composition. Nine genera, of which ~~only 7~~ 7 are known only in living fauna - Borborophyes Stal, Nepita Poisson, Nepella Poisson, Paranepa Poisson, Borborophilus Stal, Curicta Stal and Telmatotrephes Stal - distributed basically in tropical and subtropical regions of the Eastern Hemisphere (except the American genus Curicta Stal); the living genus Laccotrephes Stal is known from the Upper Jurassic of West Europe; representatives of the living genus Nepa Linnaeus are noted in the Paleocene and Neocene of North America and West Europe. Number about 90 species.

LACCOTREPHES INCERTUS Y. Popov, sp. n.[1] T. 1, F. 3; F. 70

Holotype. Coll. Munich Univ., Section of Paleontology and Historical Geology, No. 1964 XXIII 98; direct imprint of insect body; Eichstatt, lithographic shales; Upper Jurassic, Portland (found by R. Fürst, 1967).
Description. Body fairly strongly elongated (length exceeds width 2.8 times), gradually narrowing beyond widest part. Head more or less elongated, projects noticeably in front of eyes, not wider than fore margin of pronotum. Pronotum weakly transverse, barely wider than its length, noticeably narrowed in front; fore margin strongly indented in central part, hind margin less indented, lateral margins straight in first two-thirds; hind corners widely rounded and barely go beyond the base of the tegmen; surface of clearly visible sculpturing, hind third noticeably raised and in hind corners bumpy. Scutellum convex, its length equal to width, it is almost 1.5 times shorter than claval suture. Tegmen come beyond apex of abdomen (not counting the respiratory tube), venation and membrane weakly expressed on the poorly preserved body imprint. Coxae of fore legs do not reach the fore margin of the pronotum. Femora of fore legs at the base strongly narrowed and have a clear indentation, the outer margin is straight, the inner convex, gradually narrows toward the apex; length exceeds width more than four times.

Dimensions. Body length 20 mm (not counting siphon), length of tegmen 18.5 mm, width, 10 mm.
Comparison. Because of the very poor preservation, it is practically impossible to make clear distinctions amongst living species. The most distinct differences are in the form of the body and almost not sculptured surface of the pronotum. Living species are distributed basically in tropical and subtropical regions.
Material. Besides the holotype, there is one more specimen from the same locality in the Collection of the Munich University. No. 1965 III 21.

SUBFAMILY RANATRINAE Douglas, Scott 1865 F. 71

Description. Body from long-oval (Austronepini) to baton-like (Ranatra); semicylindrical. Head considerably wider (Ranatra) or almost of same width as fore margin of pronotum (Austronopa); its surface, as a rule, has a more or less smoothed sculpturing, except Austronepa. Numbers more than 100 species.

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[1] From the Latin word incertus - unclear.

Eyes large, usually noticeably project beyond fore corners of pronotum. Pronotum slightly longer than its width, especially in genus Ranatra, fore margin indented. Scutellum very small, slightly shorter than claval suture. Pleural region of prothorax completely or almost completely fused with lateral margins of pronotum. Hind basisternite with central projection between hind coxae, except genus Austronepa, which has an indented hind margin. Coxae are not very widely set apart, the distance between them does not exceed their width; fore tibia with incomplete fissure along fore margin. Abdominal parasternite wholly taken within and not visible from above; borders of sternites very straight the entire extent; sixth sternite almost as long as the preceding ones; subgenital plate of female flattened out laterally into a fin-shaped projection. Eggs have from 5 to 17 terminal filaments, distributed around the micropyles (f. 60b).

Composition. Four genera in living fauna - Ranatra Fabricius, Cercotmetus Amyot et Serville, Amphischizops Montandon and Austronepa Menke et Stange; in the fossil state representatives of the genus Ranatra are known from the Pleistocene of the USA.

FAMILY BELOSTOMATIDAE Leach 1815 - Belostomids

Description. Of medium (10-15 mm) or large (30-70 mm) size, sometimes gigantic dimensions for bugs (110 mm); dorso-ventrally flattened; from above fairly smooth. Head transverse, triangular, prognathous; eyes large, reaching the fore corners of the pronotum; ocelli missing; rostrum four-segmented, strongly curved; antennae usually four-segmented, rarely three or even two-segmented, wholly concealed in pits under the eyes, of very diversified form, particularly the second and third segments due to features of the lateral projections. Pronotum trapezoid, divided by a transverse fissure into fore and hind sectors; the fore sector has two large indentations at the base; the fore margin is weakly curved. Scutellum is large, triangular, almost equal or equal in length to the claval suture. Tegmen with rich venation, sometimes like a thick set of an archedictyon (Abedus), fore margin often slightly plate-like widened, membrane with a row of parallel veins, odor glands on metathorax present.

Leg coxae are drawn together, fore coxae are directed backward; fore legs grasping, usually the tibia and tarsus fold into a groove on the inner side of the femur or are flattened and edged by bundles of hairs and setae (f. 46B); fore tarsi are two- or three-segmented, furnished with two claws; mid and hind legs of similar structure, tibia and tarsi flattened and covered with a brush of thick swimming hairs; tarsi are furnished with two claws. The laterotergites of the abdomen occupy a considerable portion of the ventral side and are covered with long, silky, raised hairs; the female genital plate is smooth on the apex, bears one or two bundles of stylets, the apex is widely rounded or insignificantly indented; the eighth segment bears a pair of long, flattened chitinized projections, which form the respiratory tube. Family numbers about 140 species.

Biology. The preferred place of habitation of the Belostomatidae, for example the cosmopolitan genus Lethocerus Mayr, is fresh water of ponds or lakes, which contain a diverse aquatic vegetation; however, they are rarely found in channels or brooks (Menke, 1963). They are also common in marine waters of the ocean shores in deltas of alluvial rivers. According to the observations of a number of authors (Karny, 1834; 108
Dimmock, 1887; Heymons, 1915; Hungerford, 1919; Wilson, 1958), belostomids often fall upon animals much larger then themselves - fish, frogs, tritons, salamanders, aquatic serpents, and even once a woodpecker, and also on smaller objects. Thus, these bugs can be one of the basic predators in fish farms. When it bites, the large Lethocerus apparently exudes a strong toxin to paralyze a prey which exceeds it in size. Some belostomids, for example, Limnogeton fieberi Mayr, are particularly selective in the choice of prey, feeding exclusively on molluscs, and in this respect are significant in the biological struggle with molluscs - intermediate hosts of the Schistosomatidae, Trematodes (Voelker, 1966).

In the little known work of Buresch (1940), also Schumacher (1917), it is noted that Lethocerus cordofanus Mayr lives both in sea water along the entire Dalmatian shore of the Adriatic Sea and is often found on wharfs, and in weakly salt lakes (Ochridsk, Nezlobinsk). Adults and nymphs actively propagate and flourish in sea water on the Dalmatian Coast, attaining maximal number in June.

Eggs are laid in masses on the stems of aquatic vegetation. According to Rankin (1935), Lethocerus americanus (Leidy) takes somewhat more than a month to develop from the egg to an adult. Sometimes the eggs (up to 150) are laid directly on the dorsal surface of the male body (Junqua, 1955).

Belostomatidae winter under ice in the water (Hungerford, 1920) or on the bottom, buried in the silt (Wilson, 1958). They fly well from birth, sometimes in large numbers, particularly Lethocerus griseus (Say) and L. uhleri (Mont.) (Menke, 1963). Flights of some Belostomatidae (Lethocerus cordofanus Mayr, Diplonychus severinii Latr.) are connected partially with the distribution of sediments in period of rain, or even yet with phases of the moon.

Comparison. Differ from Nepidae in the pushed together leg coxae, posteriorly directed ~~behind the~~ fore coxae and character of venation.

Composition. Four subfamilies: Stygeonepinae subfam. nov. from the Upper Jurassic of West Europe; Lethocerinae Lauck et Menke from the Mesozoic and Cainozoic of West Europe and the Cainozoic of Asian USSR; living representatives are distributed worldwide; Belostomatinae Leach from the Mesozoic of West Europe, living are distributed in the Western Hemisphere; Horvathiniinae Lauck et Menke are known only from South America.

Table for Determining Subfamilies of the Family Belostomatidae

1(2) Hind tibia and tarsi unusually strongly flattened and widened like a paddle; hind femora strongly shortened; mid and hind tibia and tarsi without swimming hairs; venation strongly reduced. Stygeonepinae

2(1) Hind tibia and tarsi more or less cylindrical, with small condensed rib the entire length from the outside; hind femora almost as long as tibia; rich wing venation.

3(4) Abdominal sternites not divided by a fold; spiracles distributed in central portion of laterotergites. Belostomatinae

4(3) V-VI abdominal sternites laterally divided by a fold; spiracles situated near or on border of ventral parts of laterotergites.

5(6) The fold, ventrally delimiting the laterotergites, comes to the apex of the genital plate; second and third antennal segments with fingershaped projections; fore tarsi three-segmented with one strongly developed claw. Lethocerinae

6(5) Fold of laterotergites comes to basal corner of genital plate; second antennal segment strongly widened and flattened.; third segment large, dorsally flattened; fore tarsi one-segmented, with reduced claws. ~~N~~orvathiniinae H (typo. error in book)

Typo in book

SUBFAMILY LETHOCERINAE Lauck et Menke 1961

109

Description. Here belong the largest representatives of the family (up to 110 mm). Antennae four-segmented, 2nd-4th segments with finger-shaped projections, fourth with two small projections (f. 31a). Fore tarsi three-segmented with one strongly developed claw (f. 72a); hind tibia and tarsus strongly flattened and widened, paddle-shaped; IV-VI sternites of abdomen divided into central portion and parasternites by a weak fissure-like fold which begins at the basal corner of the genital plate (f. 72e); central portion fin-shaped; spiracles situated below at border of laterotergites; projections of eighth segment, which forms an air duct, fairly elongated, closely contiguous by its lateral margins, which are bordered by dense and long hairs. Ventral diverticulum and aedeagus of phallus of males are divided (f. 72i).

Comparison. Differ from Belostomatinae in presence of a longitudinal fold which from below separates the parasternites from the central portion of the abdomen, and also the different position of the spiracles on them; from Horvathiniinae, they differ in the different position of the ventral fold of the laterotergites, form of antennae and divided position of the diverticulum and aedeagus; besides, differ from both subfamilies in the more condensed and widened tibia and tarsi and the structure of the tarsi of the mid and hind legs.

Composition. Mesobelostomum Handlirsch from the Upper Jurassic of the FRG, extinct representatives of Lethocerus Mayr from the Upper Jurassic, Oligocene and Miocene of the FRG, Oligo-Miocene of Czechoslovakia and Oligocene of Asiatic USSR; and one living genus Benacus Stal from South and Central America; representatives of living fauna (fewer than 25 species) are widely distributed in all zoogeographic regions of tropical and subtropical zones.

GENUS MESOBELOSTOMUM Haase 1890

Scarabaeides: Germar,1830, p. 21; Giebel, 1856, p. 360; Quenstedt, 1867, p. 373; Weyenbergh, 1873, p. 239; Scudder, 1885, p. 782.

Belostoma: Hagen, 1862, p. 110, 113; Quenstedt, 1867, p. 373; Weyenbergh, 1869, p. 268; Assman, 1877, p. 192; Deichmüller, 1886, p. 61; Oppenheim, 1888, p. 233; Meunier, 1896, p. 93.

Belostomum: Weyenbergh, 1869, p. 268.

Mesobelosomum: Haase, 1890, p. 20; Handlirsch, 1906, p. 637; Handlirsch, 1925, p. 210; Carpenter, 1932, p. 119; Statz, 1950, p. 77; Kirichenko, 1951, p. 54; Kühn, 1961, p. 26, 30; 1963, p. 19.

Genotype: M. deperditum (Germ.); Upper Jurassic, lithographic shales, Eichstatt, Solnhofen, Schernfeld, FRG.

Description. Large, 50-55 mm. Head from above elongated; eyes apparently large. Pronotum strongly narrowed to fore margin, transverse, its width less than twice more than length, lateral margins indented, fore margin of fold curved. Coxae of fore pair of legs reach fore margin of pronotum; legs almost of same length, shorter than hind; tibia of mid and hind legs strongly flattened along entire outer margin like a rib; first segment of hind tarsus larger than second, claws almost straight, weakly curved their entire length. Scutellum in length almost equal to claval suture. Tegmen reach end of abdomen; veins R and RS fused their entire length into a single branching vein; M and Cu in distal portion of wing strongly branch like many parallel veins. Abdomen from below with central fin which does not reach apex.

Comparison. Mesobelostomum Handlirsch is well differentiated from the living genus 111
Lethocerus Mayr in the weakly flattened tibia and tarsi of the hind legs, considerably set apart basic veins R, RS and M, moved away from the fore margin of the tegmen, and also the membrane being not expressed and devoid of venation.

Specific Composition. Monotypic genus.

MESOBELOSTOMUM DEPERDITUM (Germar 1839) T. II, Fs. 1-3; F. 73

Scarabaeides deperditus: Germar, 1839, p. 218; Table 23, f. 17; Giebel, 1856, p. 360; Quenstedt, 1867, p. 373, Table 35, f. 5; Weyenbergh, 1873, p. 239; Scudder, 1885, p. 782, f. 994.

Belostomum hartingi: Weyenbergh, 1869, p. 268, f. 35, f. 20.

Hydrophilus deperditus: Weyenbergh, 1874, p. 83.

Belostoma deperditum: Assman, 1877, p. 192; Deichmüller, 1886, p. 61, Table 5, fs. 1-3; Oppenheim, 1888, p. 233, Table 31, f. 3; Meunier, 1896, p. 93.

Mesobelostomum deperditum: Haase, 1890, p. 20, f. 8; Handlirsch, 1906, p. 637, Table 41, fs. 22-25; Handlirsch, 1925, p. 210, f. 191; Carpenter, 1932, p. 119; Statz, 1950, p. 77; Kühn, 1961, p. 30; 1963, Table 43, f. 6.

Holotype. Coll. of Munich University, Section of Paleontology and Historical Geology, No. AS VII 43; direct imprint of body of insect; Solnhofen, FRG, lithographic shales, Upper Jurassic, Kimeridge-Titon.
Description. Body elongated, slightly widening in back. Head at base of same width as fore margin of pronotum. Width of pronotum 1.7-1.9 times more than its length, 112
lateral margins in central part slightly indented, fore margin almost twice narrower than hind; surface of pronotum weakly knobby. Tegmen with straight outer margin, R and RS fused into a single vein, slightly not reaching wing apex. M reaches wing apex where it sends a row of small parallel branches, runs along the inner wing margin and, in the distal part, dividing into a great number of small parallel branches, forms, together with the branches of M, a common distal set of veins; anal veins missing on clavus. Scutellum smooth, transversely triangular, on apex moderately sharpened, its width exceeds length almost 1.5 times. Meso- and metathorax with longitudinal central suture, most distinct at the base, in the metathorax the postepisternum and furkasternite are fused into a single sclerite and are separated by a cross suture from the basal sternal-pleural region. The trochanters of the legs are articulated to the femora on the outer side, femora of fore legs noticeably narrowed toward the apex, tibia linear; femora of mid and hind pair of legs are narrowed from the bases, slightly widened at the apex; mid tibia almost not widened toward the apex; hind tibia noticeably widened toward apex due to strongly developed outer rib-like condensation, higher at the apex; first segment of hind tarsi more than 1.5 times longer than second. Abdomen flat, its length exceeds width more than 1.5 times; central sector, delimited by a central fissure, is slightly raised roof-shaped; borders between first abdominal segments straight, beginning with fourth segment angular; respiratory tube, consisting of two folds, comes past apex of abdomen for half its length.

Dimensions. Body length 54 mm, tegmen length 41 mm, width 20 mm.

Material. Besides holotype, Oppenheim's originals from the Collection of the Munich University were examined: AS I 583 and three more specimens from the Upper Jurassic - 1961 III 100 Eichstatt, 1964 XXIII 52 and 1964 XXIII 53 from Schernfeld; three more specimens from Solnhofen were studied from the collection of the British Museum - In. 44429, In. 44431, and In. 44297, and also two specimens from the Museum of Natural History in Vienna - No. Mo 2-19 and No. 1319. Carpenter (1932) discusses the presence of eleven more specimens (Nos. 3843; 3845; 5150; 5151; 5152; 5153; 5154; 5155; 5156; 5210; 1219), preserved in the Carnegia Museum and 19 specimens in the Museum of Comparative Zoology.

GENUS LETHOCERUS Mayr 1853

Lethocerus: Mayr, 1853, p. 17[1].

Genotype. L. cordofanus Mayr 1853; living species, distributed in Ethiopia and in the southwest Palearctic region.
Description. Large, reaching 40-110 mm. Head from above convex, part of the head in front of the eyes fairly developed, clearly shorter than syntlipsis; syntlipsis from narrow to wide, convex; eyes longer than wide, outer margin noticeably convex, hind lateral corners widely rounded; rostrum relatively short and strong, first segment approximately as thick as long and comprises half the length of the second segment; second segment almost 3/4 length of third segment; antennae with unevenly developed segments, 2nd-4th with lateral projections. Side margins of pronotum slightly or distinctly convex, fore margin one half smaller than hind margin; transverse fissure 113
distinct, large and slightly constrained. Legs hairy or naked; fore femora evenly or slightly widened, bear two grooves for enclosing the lower surface of the tibia;

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[1] All synonyms of this genus are given in Lauck, Menke (1961, p. 647). The description of the genus Lethocerus Mayr is taken from this work.

syntlipsis = interoculus of Lauck + Menke 1961

Popov- "fused"
Lauck + Menke '61- "concealed"

fore tibia and tarsus are squeezed dorsally and laterally; fore tarsus three-segmented. First segment very small, to some degree fused, but visible from below; second segment short, shorter than third; rectangular or rhomboid; third segment ends in a single, large well developed claw (f. 72a). Clavus with a thin set of veins; corium with strongly anastomized, longitudinal veins; membrane of tegmen large, with numerous branching veins, which form numerous elongated cells. Pubescence of the laterotergites of the abdomen as in F. 72e. Abdominal sternites evenly covered with short, little talons; female genital plate with two bundles of stylets on apex, apex usually indented.

Comparison. Lethocerus Mayr is well differentiated from the Mesozoic genus Mesobelostomum Handl. by the flattened hind tibia and tarsi, and also the venation of the tegmen.

Specific Composition. This cosmopolitan genus of circumtropical type of dissemination numbers about 30 species, a large part of which (18 species) is dispersed in the Western Hemisphere. Five species are known in the fossil state, of which two species are from the Neocene of West Europe and three species from the Neocene of West Europe and West Siberia.

LETHOCERUS TURGAICUS Y. Popov, sp. n.[1] T. III, F. 2, F. 74

Holotype. PIN No. 1096/9; reverse imprint of fore right leg; West Siberia, Omsk Region, left bank of Abrosimovk River (tributary of Irtysh), village of Ekaterinoslav, 10-12 km from the city of Tara; Miocene.

Description. Femur strongly developed, narrows noticeably at apex, length exceeds width 2.5 times; apical inner corner well developed and projects strongly like a widely rounded projection, apical outer corner weakly developed, indentation between these corners distinct, base of femur from outside very convex and widely rounded. Tibia weakly curved, more or less narrow, lies flat, almost fused with tarsus, second segment almost three times shorter than third, claw straight, not curved. Ratio of length of femur, tibia and tarsus 50:37:15.

Dimensions. Length of femur 12 mm, tibia and tarsi 12.5 mm.

Comparison. Well differentiated from all living species in the strongly developed inner corner of the fore femur, from the Oligocene L. sulcifemoralis Riha et Kukalova in the wider femur and its apex, and also the more curved and narrow tibia with outward directed claw (f. 74).

Distribution. Miocene of West Siberia.
Material. Holotype.

SUBFAMILY HORVATHINIINAE Lauck, Menke 1961

Description. Of medium size; body elliptical. Antennae four-segmented, with differently constructed segments; first segment short; thickened, second segment fairly long, strongly condensed ventrally, with finger-shaped projection on dorsal side, 114
third segment short, with strongly set apart flattened dorsally blade-like projection, fourth segment short, elongated dorso-ventrally (f. 31b). Fore tarsi two-segmented, their segments fused with two strongly reduced claws; hind tibia and tarsi flattened, angular, slightly widened, abdominal segments divided below into a central sector and aparasternites by a shallow fold like a fissure, which comes to the basal corner of the genital plate; spiracles are located from below near the edges of the ventral parts of the laterotergites; projections of the eighth segment pulled apart, short; ventral diverticulum and aedeagus of phallus fused (f. 72).

Comparison. Differs from Belostomatinae in the presence of a fold which from below divides the parasternites from the central sector of the abdomen, and also the different arrangement of the spiracles on them; from Lethocerinae in the position of

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[1] From the paleofloristic name "turgai flora".

the ventral fold of the laterotergites, form of antennae and fused diverticulum and aedeagus. In a number of characters, it occupies an intermediary position between the two other subfamilies; segmentation of abdominal sternites as in Lethocerinae. Numbers nine species.

Composition. One living genus Horvathinia Mont. from South and Central America.

SUBFAMILY BELOSTOMATINAE Leach 1815   F. 75

Description. Of medium size, rarely large. Antennae 2-4 segmented, with finger-shaped projections on second and third segments, fourth segment finger-shaped (f. 31 115 B-i). Tibia and tarsi of mid and hind legs of same form, flattened, angular, slightly widened; fore tarsi one-three segmented, with two claws, which sometimes are accreted (f. 72B-d). Longitudinal fold of abdominal sternites ends at basal corners of genital plate (f. 72z); projections of eighth segment usually set apart, in most primitive genera are contiguous; ventral diverticulum and aedeagus of phallus fused.

Comparison. Differs from the two preceding subfamilies in the lack of a fold on the abdominal sternites and central position of the spiracles on the laterotergites. Apparently, a somewhat more specialized group than the Lethocerinae; the aedeagus and ventral diverticulum of the phallus are fused, the abdominal sternites are not differentiated, the abdominal projections of the respiratory tube do not form an air duct. Besides, the famales often lay eggs on the back of males, which also is considered a manifestation of specialization. The most primitive group, standing at the base of the phylogenetic stem of this subfamily, is considered to be the African genus Limnogeton, with weakly developed grasping fore legs and swimming mid and hind terminalia, three-segmented tarsi with two identically developed claws and fairly long projections of the air tube on the apex of the abdomen.

Composition. One genus Mesonepa Handlirsch from the Upper Jurassic of West Germany, and also five genera in living fauna - Limnogeton Mayr, Hydrocyrius Spin., Sphaero- 116 dema Lap., Belostoma Latr., and Abedus Stal, which are not known for certain in the fossil state; distributed in Neotropical, Nearctic, Ethiopian, Oriental, and southern areas of the Palearctic Regions. Number more than 100 species.

GENUS MESONEPA Handlirsch 1906

Nepa: Germar, 1839, p. 206; Giebel, 1856, p. 370; Hagen, 1862, p. 111, 113; Weyenbergh, 1869, p. 273; Assman, 1877, p. 192; Scudder, 1885, p. 782; Deichmüller, 1886, p. 60; Oppenheim, 1888, p. 234; Meunier, 1898, Table 20, fs. 59, 61.
Mesonepa: Handlirsch, 1906, p. 637; Handlirsch, 1925, p. 210; Kühn, 1961, p. 26, 30; Carpenter, 1932, p. 120.

Genotype. Nepa primordialis (Germ.); Upper Jurassic, lithographic shales, Solnhofen, FRG.

Description. Body length 24-30 cm. Head from above weakly elongated, width exceeds length twice, sintlipsis not more than diameter of eyes. Pronotum strongly transverse, fore and hind margins indented, and lateral margin indented in anterior half; in front weakly narrowed. Lateral sides of scutellum not straight. Tegmen come beyond the apex of the abdomen; between the veins M and Cu are weak cross veins; border of corium with the membrane almost straight. Coxae of fore legs reach base of head, tibia of fore legs together with one-segmented tarsus shorter than femora, mid femora slightly thicker than hind, hind tibia slightly longer than hind femora. Short respiratory tubes do not project beyond apex of tegmen.

Comparison. Very similar to living genus Belostoma Latreille in structure of strongly developed grasping fore legs, head, pronotum and tegmen. However, the one-segmented tarsus, weakly developed inner projection on apex of femur, costal margin of tegmen, which reached the membrane, and finally, the comparatively large membrane permit differentiating Mesonepa Handlirsch from the compared living genus.

Specific composition. Besides the type, one other species is known from Eichstatt, M. minor Handlirsch, 1906.

MESONEPA PRIMORDIALIS (Germar, 1939) T. 1, F. 4, F. 76

Nepa primordialis: Germar, 1839, p. 206, Table 22, f. 7; Giebel, 1856, p. 370; Hagen, 1862, p. 111, 113; Weyenbergh, 1869, p. 273, Table 35, f. 22; Assman, 1877, p. 192; Scudder, 1885, p. 782; DeichmÜller, 1886, p. 60, Table 5, f. 5; Oppenheim, 1888, p. 234, Table 31, f. 11; Meunier, 1898, Table 20, fs. 59, 61.

Mesonepa primordialis: Handlirsch, 1906, p. 637, Table 41, f. 20; Handlirsch, 1925, p. 210; Carpenter, 1932, p. 120; KÜhn, 1961, p. 210.

Holotype. Collection of Munich University, Section of Paleontology and Historical Geology. No. AS VII 349; direct imprint of insect body. Solnhofen FRG, lithographic shales, Upper Jurassic, Kimeridge-Titon.

Description. Body elongated, its length 2.5 times exceeds width, widening at center, later again narrowing toward apex. Head almost as wide as fore margin of pronotum, eyes convex, sintlipsis slightly less than diameter of eyes. Pronotum trapezoid, insignificantly narrowed to fore margin; width twice greater than length; fore margin weakly indented, hind strongly concave, lateral margins noticeably indented at fore corners; fore half, separated by a transverse fissure, is more than twice longer than hind; on hind half along central line runs a distinct longitudinal rib, continuing 117 partly also onto the fore half; along central line are two low longitudinal knobs. Scutellum with wavy lateral sides, its fore margin convex along the entire line; surface uneven, with four knobs of round form along central line, hind pair of knobs more elongated. Tegmen with costal margin reaching the membrane, forming C, Sc and R; the isolated RS reaches the membrane; M is slightly curved at the base, at the apical sector fused with the slanting cross veins which come from Cu; Cu straight, also reaching membrane; weak cross veins are found in the distal part of the tegmen and are located almost at equal distances from each other. Trochanters of legs are attached to femora on the outer side; femoraof fore pair of legs aremaximally thickened in their central portion, at apex sharply narrowed and at the very apex indented, their outer sides straight with distinct fissure along them, the inner sides strongly curved; length of femur exceeds width more than four times; fore tibia sabre-like curved along entire length, gradually thin toward the apex and end in a one-segmented tarsus like an almost straight claw. Apices of hind and particularly of mid femora are directly truncated, with the inner side indented. Tibia fairly thin, with a central fissure along the entire length, slightly narrowing toward the base. First segment of hind tarsus 3.5 times shorter than tibia.

Dimensions. Length of body 30 mm, length of tegmen 22 mm, width 13 mm. 118

Comments. Thanks to the kindness of Dr. R. Förster, who sent the type and basic originals, it was finally possible to definitively unravel (except M. minor, described by Handlirsch in 1906) the complicated and confused synonymy of this species. Oppenheim's beautifully preserved original (AS VI 9) turns out really to belong to this species. As Germar explained in studying the type specimen, Gryllites dubius Germ. (AS VII 42), synonymized by Handlirsch (1906) with M. primordialis Germ., should be placed in the Homoptera, evidently (Homoptera inc. sedis) in the Cicadellidea. Quenstedt (1852) put Scaraebeides deperdites Germ. in the family Nepidae, but he later tried to correct this error and already in the following work (1867) put it in the family Belostomatidae, as also all other authors of that time. Handlirsch (1906) established the new genus Mesonepa and, on Deichmüller's drawing (1886), separated a second species, M. minor Handl., the type specimen of which, unfortunately, is missing in the material from West Europe which I studied. The final explanation of the status of this species is deferred until a study is made of the type specimen. It is most probable that M. minor Handl. is a junior synonym of M. primordialis (Germ.).

Material. Besides the holotype, there is one more imprint of a body from the same locality as Oppenheim's original (1888).

SUBFAMILY STYGEONEPINAE Y. Popov, Subfam. Nov.

Description. Large, condensed insects, of not less than 30 mm length. Head with small eyes. Pronotum transverse, trapezoid, with concave hind margin and without transverse fissure. Scutellum large, transversely-triangular, considerably shorter than claval suture. Tegmen strongly chitinized, with traces of unclear venation, membrane weakly expressed; costal margin evenly thickened along entire length.

118

Coxae of legs set apart, diected backward; fore pair of legs of grasping type with strongly developed femora, thin tibia and one-segmented tarsus; mid and hind femora thin; hind tibia with tooth on outer margin, like tarsus strongly flattened, like a wide paddle; tibia and tarsi devoid of swimming hairs. Abdomen with strongly developed laterotergites, mid portion raised, with central fin almost its whole length; respiratory tubes present. Apparently, lived by a sea lagune and river estuaries.

Comparison. The described new subfamily is very close to the living family Belostomatidae in structure and form of scutellum, tegmen (particularly in the long clavus) and fore legs. Together with these, the clavus and the strongly sculptured pronotum resemble those in the real aquatic scorpions - Nepidae; however, in Stygeonepinae, the pronotum is more tmsverse and the scutellum is larger. Stygeonepa is one of the most specialized forms of aquatic bugs known up to now; the hind legs are widened into a fan with wide lobes, which form the short and wide tibia and strongly widened one-segmented tarsus; femora of fore legs moderately thickened with very thin, slightly curved tibia.

Composition. One genus - Stygeonepa, gen. nov.

GENUS STYGEONEPA Y. Popov, gen. nov.[1] 119

Genotype. S. foersteri sp.nov., Upper Jurassic, Portland, lithographic shales, Solnhofen, FRG.
Description. Body elongated-oval, slightly widened behind; length slightly more than twice exceeds width. Head transverse, Pronotum considerably narrowed in front, fore margin curved; its width slightly more than twice greater than length. Tegmen with remains of veins R+M and Cu; anal vein preserved on clavus; thickened costal margin runs beyond membrane; claval suture twice longer than scutellum; border of corium and membrane barely visible. Coxae of fore pair of legs reach hind margin of pronotum; trochanters large, attached to base of femur along central line; femora long, their width almost seven times less than length, with fissure along inner margin; tibia shorter than femur; mid and hind femora almost of same thickness, mid tibia thin, linear, hind short, wide, with projection on apex; tarsi very wide, equal in length to femora and almost twice longer than tibia. Abdomen very wide, its length almost equal to width; laterosternites slightly wider than mesosternites; respiratory tube long.

Specific composition. Monotypic genus.

STYGEONEPA FOERSTERI Y. Popov, sp. nov.[2] T. III, F. 1, F. 77

Holotype. Collection Munich University, Department of Paleontology and Historical Geology, No. 1952/183, direct and reverse specimens of body of insect; Langenaltheim, FRG, lithographic shales, Upper Jurassic, Kimeridge-Titon.

Description. Elongated body gradually widening in back, widest at level of third abdominal segment; its length exceeds width 2.3 times. Head, apparently, not wider or barely wider than fore margin of pronotum; eyes of medium size. Lateral margins of pronotum weakly convex, almost straight; disc in central portion with uneven elevation. Scutellum more or less convex, its width exceeds length 1.2 times. Apex of tegmen widely rounded. Costal margin of tegmen thickened like a low thin cylinder, which almost reaches the apex; veins R and M fused their entire length, fused at the base with Cu, scarcely reach the border of the membrane; membrane is large and almost devoid of veins; anal veins like a very thin line, insignificantly curved and parallel to the outer side of the clavus. Fore legs are fairly long, slightly set apart; trochanters are linear; femora weakly thickened, elongated, their length

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[1] From the Greek word styx - name of a mythical river, and the name of the genus Nepa.
[2] Named for the German zoologist R. Förster, who found this specimen.

exceeds width 7.2 times; outer margin straight, inner weakly convex, apex rounded, a weak fissure runs along the outer margin almost the entire length; tibia relatively thin, curved, gradually narrowing toward apex. Mid legs thin and long. Hind femora weakly thickened, their length exceeds width 6.5 times; tibia very short, strongly condensed, cone-like, widening toward apex, apex transversely truncated, with blunt mid tooth and small indentation from inner side, at apex their length exceeds width only 2.2 times. Outer side of tibia with longitudinal rib, strongly widened; tarsus strongly widened, 2.3 times longer than tibia; its outer surface weakly convex. Abdomen with fairly flat laterosternites and roof-shaped 121
convex mesosternites like a single longitudinal elevation, which reaches the anal plate; respiratory tube comes far beyond apex of abdomen.

Dimensions. Length of body 31 mm; length of tegmen 20 mm; width 4.2 mm.

Comments. This species is one of the most specialized forms among real aquatic Heteroptera. The analogous transformation of the hind legs into real rowing oars because of the maximal widening and flattening of the tibia and tarsus occurs only in a few other groups of arthropods. In the class of insects, in the fossil larvae of aquatic beetles of the family Coptoclavidae Ponomarenko, on account of the widened tibia and tarsus, the mid and hind legs are truly natatory; in the class of scorpionomorphs, in aquatic helicerids of the Order Eurypterida, the sixth pair of terminalia is natatory, its two last segments are widened and form the so-called oar-lobes or paddles. The hind coxae in many aquatic bugs and beetles are strongly developed and immobile, often furnished with a small projection which delimits the movement of the swimming leg to one plane. In the given representative, there is also one projection on the apex of the tibia, fixing the tarsus of the hind leg in one plane with the tibia. Judging from the unusually strongly developed oar-shaped legs and the drop-like body form, our species was an active, quick-swimming predator.

Material. Holotype (found by R. Förster in 1965).

No! AC always unfused in Corixoidea M.C.P.

SUPERFAMILY CORIXOIDEA Leach, 1815

Description. Head hypo- or opistognathus, with well designated anteclypeus in some fossil forms (Shurabella) or anteclypeus completely fused with neighboring sclerites. Rostrum strongly shortened, antennae short, completely hidden. Filtering apparatus of throat complicated or consists of a system of knobs, setae and hairs. Fore legs not grasping, hind natatory. Tegmen with strongly reduced venation, membrane devoid of veins or has disappeared. Coxae of legs pagiopod. Last segments of abdomen very strongly flattened. In living forms a stridulating apparatus is always developed. Nymphs have odor glands on the abdominal tergites. True aquatic insects, basically, algo- or detritophagous, rarely predators or phytozoophags.

cibarium + pharynx in Corixids

Comparison. Differ from other superfamilies of the Nepomorpha in the rostrum hidden under the overgrown labrum, the most complicatedly constructed filtering apparatus, the strongly flattened last abdominal segments, the stridulating apparatus, and also the presence in nymphs of abdominal odor glands.

No! Labrum hidden in labium M.C.P.

Composition. Two families: Shurabellidae, Lower Jurassic of Central Asia; Corixidae, Upper Jurassic of Kazakhstan, Lower Cretaceous of East Siberia, Paleocene and Neocene of North America, West Europe and Central Asia; in living fauna distributed worldwide.

FAMILY SHURABELLIDAE Y. Popov, Fam. Nov.

Description. Relatively small insects with condensed body, not more than 6 mm long. Pronotum transverse, with clearly expressed sculpture. Head with traces of isolated clypeus, eyes large. Scutellum triangular, somewhat shorter than claval suture.

Tegmen strongly sclerotized, fore margin widened plate-like; venation strongly strongly reduced, having only remains of Sc, R and M; membrane sclerotized and fused with clavus. Hind legs long, thin; one-segmented tarsus covered with swimming hairs. In nymphs, there are abdominal glands on the third, fourth and fifth tergites.

Comparison. Differs from Corixidae in the clypeus being clearly separated from the frons and genae, presence of riblets on the pronotum, leaf-like widened tegmen and cone-like elongated eighth tergite, and also comparatively not condensed hind legs. Together with this, the form of the head and pronotum, the character of the tegmen and the presence in the nymphs of abdominal glands permits drawing representatives of the fossil family Shurabellidae close to the true living Corixidae.

No! Not fused in Corixidae M.C.P.

Composition. One monotypic genus - Shurabella B.-M. from the Lower Jurassic of Central Asia.

GENUS SHURABELLA Becker-Migdisova 1949

Shurabella: Becker-Migdisova, 1949, p. 28-29; Becker-Migdisova, Popov, 1962, p. 225.
Coleopteropsis: Becker-Migdisova, 1949, p. 29; Becker-Migdisova, Popov, 1962, p. 226, syn. nov.

Genotype. Shurabella lepyroniopsis B.-M.; Liassic, Shurab III, Oshsk Region, Kirghiz.

Description. Body small, 5-6 mm, oval, convex from above, with small pitting. Head transverse, eyes contiguous on their inner sides with the clypeus; hind margin of head between eyes is raised like a rib. Pronotum almost three times wider than its length, smooth, with two longitudinal central ribs, which do not reach the hind margin; fore and hind margin almost straight. Tegmen longer than abdomen or just cover the caudal projections of the eighth tergite; the platelike widening is fairly wide with remains of the veins Sc and R; M is comparatively long. Tibia and tarsi of hind legs very thin. Abdomen from below with longitudinal fin along the entire length.

Specific composition: Monotypic genus.

SHURABELLA LEPYRONIOPSIS Becker-Migdisova, 1949 T. II, F. 4; T. III, Fs. 3-4, Fs. 78-79.

Shurabella lepyroniopsis B.-M.: Becker-Migdisova, 1949, p. 29; Becker-Migdisova, Popov, 1962, p. 226
Coleopteropsis dolichoptera B.-M.: Becker-Migdisova, 1949, p. 31, Becker-Migdisoava, Popov, 1962, p. 225; syn. nov.

Holotype. PIN No. 459/72; direct imprint of body without head and pronotum; Kirghiz, Fergana Valley, Oshsk Region, Shurab III (Sai Sagul); Liassic.

Description. Adult form. Body in posterior half narrows gradually toward apex. Head almost as wide as fore margin of pronotum. Eyes occupy almost the entire length of the head and in front form practically one line with the clypeus. The latter is distinct, more or less flat, does not reach the center of the head; frons and vertex fused and noticeably widen toward the base, hind margin of head with a distinct rib, especially developed, apparently, in males. Lateral margins of pronotum almost straight or slightly convex; its fore corners more or less round, hind sharp. Scutellum equal- 123
sided triangular, almost threetimes shorter than claval suture. Tegmen strongly sclerotized, with small and scattered pitting; M long, extends beyong center of wing, delimiting the clavus proper and the leaf -like widening, which in the distal part fuses with the remaining portion of the wing; apex of wing sharply-angled. Hind legs with more or less thickened femora, longer than tibia.

Dimensions: Length of body 4.5-5.5 mm; length of tegmen 4.0-4.2 mm; width 2.5 mm.

Nymphs of the III-V stages elongatedly oval. Pronotum strongly transverse, its width four times exceeds length; fore margin almost straight, parallel to hind, lateral sides straight and weakly narrowed in front; lateral corners relatively sharp. Wing case strongly shortened, far from reaches base of abdomen; lateral lobes of wing case fairly wide and directed along the body, inner sides strongly spread apart; central projection distinct and noticeably projecting; length of wing case along central line almost one and one half times exceeds length of pronotum; larval suture expressed. Abdomen gradually narrows, rounded at apex.

Dimensions. Length of body 3.2-4.5 mm, width 1.8-2.2 mm.

Comments. Originally insects of this genus were described as representatives of Homoptera, conjecturally placed in the superfamily Jassoidea or Cicadelloidea (Becker-Migdisova, 1949) on the basis of similarity of form of scutellum and known dimensions 124 of the wing-integument both in living Cercopidae and in some fossil Scytinopteridae. However, these characters turned out to be purely external and insufficient for placing them in the Homoptera. Later, after re-examination of several specimens, they were put in the order of true Heteroptera (Becker-Migdisova, Popov, 1962). As a re-examination of all the available material in the PIN collection showed, these Heteroptera must be placed in the aquatic bugs (on the presence of natatory hind legs) of the superfamily Corixoidea (on the structure of the head, structure of tegmen and presence of abdominal glands in nymphs). Division of the genera Shurabella and Coleopteropsis, based on the different form of the scutellum, turns out to be unfounded; this character reflects only the different preservation of the remains and distortion of proportions because of the strain of the rock (see Chapter II).

Material. Besides the holotypes of both species, over 800 specimens are preserved in the collection of the Paleontological Institute.

FAMILY CORIXIDAE Leach 1815

Description. Bugs of medium (8-16 mm) or small (1.5-6 mm) dimensions; body elongated, condensed, dorso-ventrally, its length approximately 2-3 times greater than the width. Pronotum and tegmen often covered from above by more or less evenly alternating black and light, basically transverse, lines (stripes). Head tucked in, fairly mobile, with large eyes, from above wide, in front triangular; its hind margin lies on the pronotum, 125 head sclerites almost completely fused. Simple eyes present only in Diaprepocorinae. Antennae very short, considerably shorter than head, three- or four-segmented, attached under the eyes and hidden between the head and prothorax. Rostrum strongly shortened, wide, semiconical, not clearly articulated, from above enveloped by the fore part of the head capsule. Mandibular and maxillary stylets short, not-thrusting, maxillary stylets widened and asymmetrical (larger left one occupies a place in the formation of the food canal, the right on the apex is toothed for mincing food), the mandibular lever is triangular. The pleural region of the thorax is strongly developed, particularly the epimeres. Well developed also is the central projection of the sternite of the metathorax (metacyphus). Coxal cavities are open; coxae are pagiopod. Scutellum is covered by the hind margin of the pronotum or remains free. The tegmen reach the apex of the abdomen, are smooth or their surface has barely noticeable transverse covering of lines (running through), particularly distinct on the pronotum, clavus and basal half of the tegmen; divided into clavus, corium, linear embolium (the embolium is missing in the African genus Stenocorixa) and membrane, which is devoid of veins and usually is similar in structure to the corium. Venation is rarely present on the tegmen (Archaecorixinae). Fore legs very short, one-segmented tarsi often fused with tibia and in males often turned into palae, set with strong setae and small stridulating teeth; adapted for seizing and filtering food, stridulating, and also for holding the female during copulation; tarsi end more or less in a developed claw. On the inner side of the fore femora (see f. 46e), there is a field of very small chitinized stridulating teeth (pars stridens). In quick movement of the fore legs along the head, the inner sides of the legs brush against the lateral margin of the head and create sound waves by means of the above-mentioned stridulating

Not EPIM. III
MCP.

teeth. The mid legs are long, thin, ending in two long claws; adapted for movement and fixation on the ground. The hind legs are adapted for swimming, longer than the others; coxae with projection on the hind margin, limiting the movement of the legs to one plane; the two-segmented tarsi are considerably flattened, the claws very short. Abdominal segments and copulatory apparatus of males, as a rule, are asymmetrical; on the sixth, sometimes on the fifth and sixth tergites in males there is usually a strigil, which consists of one or several combs or a system of saw-like teeth (Diaprepocorinae), eighth segment is not telescopic, strongly flattened, divided into two plates. Females without ovipositor. Adults with well functioning thoracic glands on 3-5th segments. Presence of developed abdominal glands, apparently, depends upon feeding specialization: in zoophagy, it is not so necessary, as in phytophagy or in mixed feeding, to have developed abdominal glands.

There are more than 520 species in the world fauna, of which about 500 are living species and more than 20 extinct.[1]

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1) Thoracic glands are on 3rd thoracic seg.
2) Adults lack glands on Abd. seg. 3-5

Biology. Corixidae are often encountered in meadows, ponds, the littoral zone of a lake; a very small number of species is known from running water (for example, some species of the genus Sigara - Kirichenko, 1940, 1951) and even from reservoirs in granite depressions (Lipin, 1950). Some species are euryhaline and can live in 126 saltish water (Halicorixa stagnalis Leach, Cymatia rogenhoferi Fieb., Sigara lateralis Leach, S. assimilis Fieb., S. concinna Fieb. Davis (1965), for example, noted an abundant population of Trichocorixa reticulata in an isolated meadow among mangrove thickets in Jamaica in water temperature of 39.5° and salinity of 43%(!). I have also observed Sigara species in dried up and strongly silted saltish meadows, entirely devoid of vegetation, in semi-desert Southeast Kazakhstan. Most live in fresh water; usually they stay on the ground, swarming in the substrate. The overwhelming majority of species possess a protective coloring. Some species are connected with large ponds, or lakes, in which they live constantly; however, they breed also in temporary small reservoirs, which they abandon when conditions become unfavorable, particularly during droughts.

Corixidae are phytozoophagous and eat basically various waterplants (Spirogyra, Mougeotia, Euglena, etc.), rarely diatoms and detritus, the organic parts of which are actively devoured by them, and also diverse benthic microfauna (Hungerford, 1919, 1948; Hale, 1922; Larsen, 1938; Kirichenko, 1940; Walton, 1943; Sutton, 1951; Pavlovsky, Lepneva, 1948). Besides, they actively fall upon larvae of Culicidae, Tendipedidae and Chironomidea (Diptera), eat branch-eared crayfish (Cladocera), small-stylet worms (Tubuficidae), Ephemeroptera nymphs, and in some cases small fish (Poisson, 1935; Sutton, 1951; Benwitz, 1956; Beresina, 1955; Jaczewski, 1961). Some forms are typical predators (Cymatia, Stenocorixa, Diaprepocoris) and often have long thin fore legs, used as grasping organs. The hind legs, besides a swimming function, also serve for cleaning the air regions, located under the pronotum and under the tegmen, and also for alleviating the distribution of air supplies with the help of the wings. In Corixidae cannibalism is observed from time to time (Poisson, 1957). In their turn, Corixidae themselves serve as an object of food for some Odonata nymphs, for example, Aeschna juncea (L.) (Staddon, Griffiths, 1967).

Among Corixidae brachypterous forms are fairly often encountered: Cymatia, Micromatia and Sigara (s. lato). The distribution of fully-winged forms is determined by migratory flights, occurring basically at night (Corixa punctata Ill., Sigara falleni Fieb., S. nigrolineata Fieb., S. lateralis Leach and others). These species, possessing positive phototropism, are easily caught in light. Migration is determined basically by biological factors, for example, overpopulation in reservoirs because of rapid reproduction, and dependency on climatic conditions - temperature, humidity, atmospheric pressure, and also on degree of ionization of the atmosphere (Lefeuvre, 1967).

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[1] The latter precise data on the specific composition of the family and lower taxons are taken from T. L. Jaczewski's manuscript, "Checklist of the Aquatic and Semi-Aquatic Heteroptera of the Holarctic," kindly lent by the author for this study.

Very important for Corixidae in moving about are the air bubbles (physical gills); with the rising of temperature the entry of O_2 is lowered and at 28° ceases entirely; with rising temperature and the corresponding lowering of retaining O_2, the urge to fly in Corixidae becomes stronger; tho the radius of flight is not more than 80 km, with passing air currents it can reach 5,000 km (Popham, 1964). Apparently, instinct is also definitely important, since in the fully-winged imago there is a tendency toward flight.

The egg is usually pear shaped, usually furnished with a stem. They are attached to submerged or swimming plants with the help of a short stem, which ends in a sticky fastening disc; rarely is the egg attached directly to a solid substrate. Corixidae have five nymphal stages. The place of attachment of the stem to the egg is opposite to the head end of the nymph. The wing case appears in the third stage; from this stage the odor glands begin to function on the third, fourth and fifth tergites, 127
Not direct transformation M.C.P. → which are subsequently changed in the adult stage into one metathoracic gland. Many Corixidae hibernate in the adult stage and only rarely in the nymphal or egg stages.

Comments. Some investigators (Hungerford, 1948; Poisson, 1957) separate three more subfamilies according to the lack of an embolium rim (Stenocorixinae), the lack of a nodal fissure and transverse furrowing of the rostrum (Cymatiinae), and also the relative dimensions of the separate parts of the head and structure of the fore margin of the wing (Heterocorixinae). However, one of the most authoritative specialists of this family - T. L. Jaczewski (1924)- questioned such a subdivision a long time ago when the subfamilies were formally established (Hungerford, 1948). From my point of view, the [illegible] separation off of the last three's subfamilies is also inexpedient and with respect to morphology little justified. The lack of a nodal fissure is also noted in the American genus Tenagobia of the subfamily Micronectinae; in some genera of Corixinae, the transverse furrowing (running through) is weakly expressed, and the ratio of dimensions of the separate parts of the head varies greatly within the family. It must be noted, however, that the structure of the genital segment in Stenocorixa really differs sharply from that in all the other Corixidae. It is undoubted that the final solution of this question will be possible only after a specialized study of these aberrant forms.

Composition. Five subfamilies: Ijanectinae - Lower Jurassic of East Siberia; Archaecorixinae - from the Upper Jurassic to the Upper Cretaceous of Kazakhstan and Siberia; Diaprepocorinae - Jurassic of East Siberia and Kazakhstan; extinct Corixinae from the Paleocene and Neocene of North America, West Europe and Central Asia; Micronectinae are not known in the fossil state; in the living fauna, Corixidae are distributed worldwide.

Determinant Table of Subfamilies of the Family Corixidae

1(2) Venation of tegmen distinct, basic veins not reduced; pronotum completely covers scutellum. Archaecorixinae
2(1) Venation of tegmen strongly reduced.
3(4) Simple eyes present on vertex; scutellum free; stridulating apparatus on sixth tergite only. Diaprepocorinae
4(3) Simple eyes missing.
5(8) Scutellum free, but covered by hind margin of pronotum
6(7) Pronotum strongly developed, weakly transverse; embolium rim of tegmen very wide and flat; stridulating apparatus missing Ijanectinae
7(6) Pronotum considerably smaller, strongly transverse; embolium rim narrower and raised; stridulating apparatus present on sixth abdominal tergite (or is missing -Tenagobia) Micronectinae
8(5) Scutellum completely or almost completely concealed by the hind margin of the pronotum; stridulating apparatus on the sixth tergite and on the fore legs - seldom missing. Corixinae

SUBFAMILY ARCHAECORIXINAE Y. Popov 1968 T. IV, Fs. 1-5, Fs. 80-81

Description. Large or medium size (not less than 4 mm). Scutellum completely covered by hind margin of pronotum. Tracery on tegmen like transverse alternating black and white stripes is missing, sometimes separate spots are present (genus Diapherinus)(f. 81a), venation distinct, Sc usually fused with R the entire length, M, as a rule, fused at the root with R and Cu or at places joins with R and Cu, 128 anal veins present; embolium rim not expressed. Male abdominal segments symmetrical (except Upper Cretaceous Mesosigara), eighth tergite often large (f. 82a). Hind legs natatory, thickly covered with hairs.

Comparison. Well differentiated from all other subfamilies by presence of distinct venation through lack of embolium rim or embolium, and also the character of fusion of the basic veins. Closest to the living subfamily Corixinae, which is considered to be the next stage of evolutionary development of the Mesozoic Corixidae.

Composition. Four genera: Archaecorixa Y. Popov, Upper Jurassic, South Kazakhstan; Diapherinus Y. Popov, Baissocorixa Y. Popov, Lower Cretaceous, Transbaikals; and Mesosigara Y. Popov, Upper Cretaceous of PriAmur.

Determinant Table of Genera of the Subfamilies of the Archaecorixinae

1(2) R and M not fused in distal portion of tegmen; M leaves R. Archaecorixa
2(1) Veins R and M fused with each other in distal half of tegmen; M leaves Cu.
3(4) Anal veins missing; male abdominal segments asymmetrical. Mesosigara
4(3) Anal veins distinct; male abdominal segments symmetrical.
5(6) Sc fused with R the entire length; M fused with R at center of tegmen; nodal fissure clearly expressed; tracery spotted; membrane not expressed. Diapherinus
6(5) Sc fused with R only at basal sector of tegmen; M fused with R beyond center of tegmen; nodal fissure missing; tegmen unicolor; membrane distinct. Baissocorixa

GENUS MESOSIGARA Y. Popov, gen. nov.[1] 129

Genotype. M. kryshtofovichi, sp. nov.; Upper Cretaceous, Bureya River, Cagayan village, Kabarov Province.

Description. Comparatively small (4.5-6.0 mm), not colored, lateral lobe of pronotum separated by a fissure, mesothorax from above with longitudinal central fissure. R fused with Sc its entire length, M at base fused with Cu; anal veins missing, last male abdominal segments asymmetrical.

Comparison. Similar to Baissocorixa Y. Popov from the Mesozoic of the Transbaikals in the structure of the pronotum and character of the venation. However, the fusion of R and Sc and the structure of the last abdominal segments strongly differentiate it from this genus. By the middle of the Cretaceous period, apparently, one of the first abdominal strigils began to form in the Archaecorixinae and, connected with it, the asymmetry of the abdominal segments, beginning with the last, arose. These are the smallest representatives of the superfamily Archaecorixinae. In the author's opinion, they are evidently the connecting link between this group and the living subfamily Corixinae.

MESOSIGARA KRYSHTOFOVICHI Y. Popov, sp. nov.[2] T. IV, F. 4, F. 82

Holotype: PIN 324/2a; direct imprint of insect body. Kabarov Province, Amur Region, Arkharin District, Bureya River, Cagayan Village; Tiukan Series, Upper Cretaceous (Dat - Maastricht).

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[1] From the Greek word mesos - central, and the name of the genus Sigara.

[2] Named for the well known paleobotanist A. N. Krishtofovich, who found the specimens.

Description. Body dark, cigar-shaped; head, pronotum, and tegmen dark-brown. Lateral lobes of prothorax tongue-shaped, directly truncated at the apex. Mesothorax with shallow central fissure the entire length. Tegmen with clearly expressed venation: Sc and R fused the entire length; M fused at basal sector with Cu, its central sector free, but the distal sector is fused with the vein Sc+R; Cu, after dividing from M, is free and runs along the entire claval margin; anal veins are not expressed on the clavus. Tarsi of fore legs one-segmented, narrow, mid tarsi long, thin, ratio of length of hind tibia and tarsal segments is 5:5:3 (fs. 82bB). Hind femora not thickened. Sixth abdominal segment in males is asymmetrical. Eighth sternite is like two crescent-shaped plates.

Dimensions. Length (Holotype 324/2) 4.5 mm, width (Paratype 324) 1.8 mm.

Material. Besides the holotype, there are three other specimens of bodies: 324/2 b-g (collected by A. N. Krishtofovich in 1914).

SUBFAMILY DIAPREPOCORINAE Lundblad 1928 T. V, F. 1

Description. Medium sized (5-10 mm). Elongated. More or less unicolor, pronotum in front darker, scutellum usually darkest. Head with two simple eyes on the vertex; antennae four-segmented. Pronotum not less than twice wider than its length, usually with weakly expressed cross and longitudinal fins. Scutellum large, triangular, not 130 covered by the hind margin of the pronotum. Tegmen with weakly expressed venation like traces of Sc, R and Al; membrane expressed; embolium rim not distinct, nodal fissure often missing. Male abdominal segments symmetrical; on sixth tergite often (living genus Diaprepocoris) strigil present like little saws and comb. Fore tarsus and tibia not fused; fore tarsal claw large; hind legs densely covered with swimming hairs.

Comparison. Well differentiated from all other Corixidae by the presence of simple eyes on the vertex, from Micronectinae besides by the four-segmented antennae and form of the claw of the fore tarsus, from Archaecorixinae and Corixinae by the free scutellum.

Composition. Three genera: Gazimuria, gen. nov., Upper Liassic of East Transbaikals, Karataviella B.-M., Upper Jurassic of South Kazakhstan, and the living Diaprepocoris Hale, distributed in southern Australia, Tasmania, and New Zealand. Three species in living fauna.

Determinant Table of Genera of Subfamily Diaprepocorinae[1]

1(2) Pronotum not less than five times wider than its length. Diaprepocoris
2(1) Pronotum not more than three times wider than its length.
3(4) Scutellum 1.7-1.8 times narrower than hind margin of pronotum; venation strongly reduced and only Al represented Karataviella
4(3) Scutellum large, almost as wide as hind margin of pronotum; venatim is represented by veins R, M and Cu. Gazimuria

GENUS GAZIMURIA Y. Popov, gen. nov.[2]

Genotype. G. scutellata sp. nov., Lower Jurassic, Akutaev Series, Chitin Province, East Transbaikals.

Description. Of medium size 9-10 mm. Head as wide as pronotum, from front moderately convex, hind margin of vertex between eyes with low longitudinal cylinder, at its hind margin there is a short cross rib. Fore margin of pronotum in central portion

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[1] Unfortunately, the monotypic genus Corixanecta Wlt. remains unknown to the author. Judging from the drawing, given in Hungerford's monograph (1948), this genus is very similar to Diaprepocoris Hall., appearing to be, most likely, a synonym of the latter.

[2] For the locality of Gazimur.

straight. Scutellum large, not less than twice shorter than claval suture. Tegmen with distinct veins R, M and Cu. Mid legs thin, long; first segment of hind tarsus shorter than tibia.

Comparison. In general plan of structure similar to the Upper Jurassic genus 131 Karataviella B.-M. from South Kazakhstan; however, well differentiated from it in more transverse pronotum, larger scutellum, presence of fin on head, and also form of body.

Specific Composition. Monotypic genus.

GAZIMURIA SCUTELLATA Y. Popov, sp. nov.[1] T. V, F. 2, F. 83

Holotype: PIN 1328/4; direct and reverse imprint of body; East Transbaikals, Chitin Province, right bank of Gazimur River (tributary of Amur), village of Borovsk; Liassic, Akutaev layer.

Description. Body elongated, in back slightly widened, pronotum and scutellum strongly convex, head of same width as fore margin of pronotum; latter 3.5 times wider than its length. Frons and vertex convex; width of vertex wider than eyes at base of tibia; central longitudinal fin short, does not reach fore margin of head. Pronotum more than 3.5 times shorter than width, in front slightly widened, central portion of fore margin and hind margin straight and parallel, lateral portions of fore margin slightly slantingly truncated, fore corners sharp, hind blunt. Scutellum triangular, its length slightly less than lateral side; its fore end barely narrower than pronotum. Tegmen smooth, tracery missing. Hind femora thicker than tibia and tarsi ; hind tibia shorter than tarsi ; second segment of hind tarsi slightly shorter than tibia. Abdomen gradually widens backward, segments almost 132 of equal length, borders of tergites straight, last segments symmetrical, hind margin of seventh tergite with lateral projections.

Dimensions. Length of body 9.2 mm, length of tegmen 7.2 mm; width 3.2 mm.

Material. Besides the holotype, six more specimens of bodies from the same locality.

GENUS KARATAVIELLA Becker-Migdisova 1949 T. V, Fs. 3-4, F. 84

Karataviella: Becker-Migdisova, 1949, p. 25; Rohdendorf, 1957, p. 86; Becker-Migdisova, Popov, 1962, p. 225; Popov, 1962, p. 106; 1963, p. 148.

Genotype. K. brachyptera B.-M.; Upper Jurassic, Villages of Mikhailovka and Uspensk (Galkino), Chayan Region, Chimkent Province, South Kazakhstan.

Description. Body elongated, cigar-shaped, in back gradually narrowing, 7.5-8.5 mm. Head almost as wide as fore margin of pronotum, width of vertex exceeds width of eye. Pronotum with weakly expressed central and transverse ribs. Its width exceeds length twice. Scutellum triangular, its length at center line almost 1.5 times less than length of lateral side. Tegmen smooth, light-brown, without tracery. Only A1 preserved on clavus. Abdomen with almost identical segments, their borders straight, eighth segment strongly developed and slightly exceeds seventh. Last segments symmetrical.

Comparison. Differs from other genera of subfamily in strongly reduced venation, form of pronotum and its sculpturing like weak riblets.

Specific Composition. Monotypic genus.

SUBFAMILY IJANECTINAE Y. Popov, Subfam. Nov.

Description. Medium sized, about 5-8 mm. Body fairly wide. Pronotum strongly developed, weakly transverse. Scutellum small, free. Tegmen with completely reduced venation; fore margin of wing like wide and flat embolium rim, nodal fissure present; membrane distinct. Hind legs flattened.

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[1] From the Latin word scutellum .

Comparison. Well differentiated from the other subfamilies in strongly developed wide and flattened embolium rim, resembling that in the Liassic Shurabellidae.

Composition. Subfamily monotypic. One genus, Ijanecta Y. Pop. from the Lower Jurassic of East Siberia.

GENUS IJANECTA Y. Popov, gen. nov.

Genotype. I. angarica, sp. nov., Upper Liassic of East Siberia.
Description. Pronotum not more than 2.5 times wider than its length; shoulder corners distinctly expressed, not rounded. Scutellum completely free. Tegmen wide, convex, nodal fissure approximately at level of apex of clavus; membrane completely devoid of veins. Seventh segment of abdomen with two small projections along hind margin.

Specific Composition. Monotypic genus.

IJANECTA ANGARICA Y. Popov, sp. nov.[1] T. V, Fs. 5-6, F. 85 133

Holotype: PIN 1487/111; imago; direct and reverse imprints of body; East Siberia, Irkutsk Region, Village of Vladimirovka, Upper Liassic.

Description. Adult form. Body oval, weakly elongated, from above noticeably convex. Pronotum ellipsoid, transverse, strongly convex, its width exceeds length twice; hind lateral margins slightly concave. Scutellum very small, its length four times smaller than length of claval suture. Tegmen reach apex of abdomen; clavus wide, its length exceeds width slightly more than twice. Membrane large, occupies almost one third of tegmen. Eighth abdominal segment like strongly flattened and slightly set apart plates with slightly sharpened apices. Length of imprint of body 6 mm, width 3.8 mm, length of tegmen 4.7 mm.

Nymph. Body elongated, parallel-sided. Head (together with eyes) strongly transverse. Pronotum more than four times wider than its length; fore margin almost straight, parallel to hind, lateral sides strongly narrowed in front, hind margin straight, curves upward at lateral sides; shoulder corners sharp, slightly projecting outward. Wing case shortened, but reaches first tergites of abdomen, lateral lobes fairly wide, directed parallelly along body, their inner sides weakly set apart; central projection distinct; length of wing case along central line equal to length of pronotum. Tarsi and tibia flattened; tarsi thickly covered with strongly shortened swimming hairs. Abdomen narrowed at apical quarter and rounded at apex.

Dimensions. Length of body 4-5 mm; width 2.0-2.2 mm.

Material. Besides holotype, three more specimens from same locality.

SUBFAMILY MICRONECTINAE Jaczewski 1924 F. 86 134

Description. Small (1.5-6.0 mm), elongated. More or less uniform in color, pronotum and scutellum slightly darker. Antennae three-segmented, third segment longest and covered with dense hairs. Pronotum transverse, not more than 2.5 times wider than its length, smooth. Scutellum not covered by hind margin of pronotum. Tegmen with reduced venation; embolium rim well developed, wide; nodal fissure present or missing. Fore tarsus and tibia not fused, claw on apex of tarsus in males blade-like; claw on hind tarsus attached at very apex of last segment. Abdominal segments and male copulatory apparatus asymmetrical. Ninth tergite with indentation on apex; on sixth tergite there is a small strigil, like a system of combs on a stem. Fully winged or short winged forms.

Comparison. Easily differentiated from the other subfamilies in the small dimensions. Besides, differentiated from Archaecorixinae in the lack of venation on the tegmen, from Diapropocorinae in the lack of simple eyes on the vertex and different type of stridulators, from Corixinae in the free scutellum (except Oligocene genus Sigaretta Y. Pop.), not covered by hind margin of pronotum.

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[1] From the River Angara and the Latin word nectos - swimming.

134

Composition. Three genera in living fauna - Micronecta Kirkaldy, Synaptonecta Lundblad and Tenagobia Bergroth, including more than 130 species; unknown in fossil state; distributed worldwide, except Nearctic region (only one species, Tenagobia mexicana Deay, penetrates into the Sonor subregion).

SUBFAMILY CORIXINAE Leach 1815 F. 87 135

Description. Medium (5-9 mm) or large sized (12-16 mm), rarely small, elongated. Upper side of body usually like alternating cross dark and light stripes. Surface of pronotum and tegmen with barely visible small fissures (running through). Antennae four-segmented, third segment longest. Pronotum weakly transverse, usually its width exceeds length 1.5 times; hind margin completely covers scutellum. Scutellum very small, triangular. Tegmen with strongly reduced venation; embolium rim strongly developed, wide, covered in fore section with white film like hoarfrost; nodal furrow, as a rule, present; precubital field like a narrow stripe, gradually narrowing and crossing from a vertical to a horizontal plane (like the embolium on the fore margin of the tegmen); membrane at base as hard as corium, or, in very rare cases, more or less membranous (Heterocorixa), the border between them is usually missing or is visible as a weak light stripe (Sigara, Glaenocorisa, Graptocorisa, Corisella, Ahualtea[1], Pseudocorixa and others). Fore tarsus and tibia often fused into a single tibio-tarsus, claw on apex always thorn-like; claw on hind tarsus projects from the side before the apex of the last segment. On the fore tibia and tarsus there usually is a system of stridulating teeth and setae. The male abdominal segments are asymmetrical from the left or the right side; ninth sternite deeply split along the center; on sixth tergite the strigil is of the most diversified form, in rare cases it is missing (Callicorixa, Neocorixa, Cymatia).

Comparison. Differs from Archaecorixinae in the lack of venation on the tegmen, from Diaprepocorinae and Micronectinae in the scutellum completely hidden under the pronotum and the system of stridulators.

Composition. About 30 genera, of which two are found only in the fossil state: Sigaretta gen. nov. from the Oligocene of North America and Diacorixa gen. nov. from the Miocene of Central Asia; extinct representatives of the genus Corixa Geoffr. from the Oligocene, Miocene and Pleistocene of North America and West Europe; representatives of living fauna (over 350 species) are widely distributed in all zoogeographic regions.

Determinant Table of Genera of Subfamilies of Corixinae Found in the Fossil State 136

1(2) Scutellum partially covered by hind margin of pronotum; asymmetry of male abdominal segments weakly expressed Sigaretta
2(1) Scutellum completely covered by hind margin of pronotum; asymmetry of male abdominal segments distinct.
3(4) Tegmen with remains of Cu; embolium rim moderately developed, flat; asymmetry of male abdominal segments right-sided. Diacorixa
4(3) Tegmen without Cu; embolium rim strongly developed, high; asymmetry of male abdominal segments left-sided.[1] Corixa

GENUS SIGARETTA Y. Popov, gen. nov.[2]

Genotype. Corixa florissantella Cockerell 1906; Oligocene, Colorado, USA

Description. Small 5.8-6.5 mm, colored. Head in front convex. Pronotum large, but only partly covers scutellum, with longitudinal central fin along entire length.

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[1] Krizousacorixa Hung.

[1] In the size I adopt, the genus Corixa does not include as a subgenus Hesperocorixa Kirk. with right-sided asymmetry of the abdomen (Kirchner, Yachevsky, 1964).

[2] From the name of the genus Sigara.

Tegmen with well developed embolium rim; anal vein preserved on clavus. Border of corium and membrane scarcely visible. Eighth tergite strongly developed. Strigil missing, asymmetry of abdomen weakly expressed.

Comparison. The redescribed Paleocene representative of Corixidae differs sharply from all living representatives of the subfamily Corixinae first of all in the presence of a scutellum which is still not completely covered by a well developed pronotum.

Comments. Apparently this is a relict form, still preserved from the Cretaceous or even the Jurassic periods. This Paleocene Corixid, apparently, is phylogenetically closest to the genus Cymatia Flor.

Specific Composition. Monotypic genus.

SIGARETTA FLORISSANTELLA (Cockerell 1906), comb. nov. T. VI, Fs 1-3, F. 88

Corixa florissantella: Cockerell, 1906; Handlirsch, 1906, p. 209.

Lectotype: British Museum (N.H.), Paleontology Dept., No. 8424a; direct imprint of body; Florissant, Colorado, USA, Oligocene.

Description. Body dark-brown, cigar-shaped, widest at level of scutellum; its length exceeds width approximately four times. Head almost as wide as fore margin of pronotum. Frons convex. Vertex narrower than diameter of eyes. Width of pronotum exceeds its length more than twice; fore margin almost straight, lateral margins strongly or evenly rounded, hind projects backward in an arch; longitudinal fin distinct, developed along entire line of pronotum. Tegmen smooth, colored, embolium well preserved; postcubital field weakly expressed, only one weakly curved anal vein preserved on clavus, situated along its center. Mesothorax in fore part from above with longitudinal shallow furrow; scutum of metathorax like wide long cross stripes; hind legs fairly long, come far beyond end of abdomen, second segment of hind tarsi twice shorter than first. Abdominal segments unevenly developed, third tergite with projection on posterior side, larger than the rest, 4th-7th more or less of 137 equal size, eighth tergite strongly developed and like a transverse pentagonal plate.

Dimensions. Length 6.1 mm; width 1.5 mm.

Material. Besides the lectotype from this locality there are two more specimens of bodies; British Museum, 8424b and 8425.

GENUS DIACORIXA Y. Popov, gen. nov.[1]

Genotype. D. miocaenica, sp. nov.; Miocene, Chon-Tuz River, Central Kirghiz.

Description. Medium sized 10-11.5 mm. Head of males with indentation on frons. Mesothorax from above with furrow along entire length. Tegmen with moderately developed flat embolium rim; R+M and remains of Cu present; on border of corium and membrane is a well expressed light stripe. Asymmetry of male abdominal segments right-sided.

Comparison. The described representative of the new genus Diacorixa is very similar to the living Corixidae genera Sigara Fabr. and Corixa Geoffr. and some close genera of the subfamily Corixinae. However, the presence of a deep furrow along the entire length of the pronotum (in living representatives, it is well expressed only in the fore third and sometimes continues like a weak trace on the remaining portion, as in species of the genus Corixa Geoffr.), presence of remains of a cubital vein, insufficiently well developed longitudinal fracture of fore margin of tegmen (embolium rim), and also lack of the tracery which is characteristic for most genera of the subfamily Corixinae of cross alternating dark and light stripes on the pronotum and tegmen sharply differentiate this Miocene genus from all living genera of this subfamily.

Specific Composition. Monotypic genus.

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[1] From the Greek word dia - between, among and coris - bug.

DIACORIXA MIOCAENICA Y. Popov, sp. nov.[2]   T. VI, Fs. 3-4, F. 89

Holotype: PIN 372/16; direct imprint of insect body; Kirghiz SSR, Kochkor Region, right bank of Chon-Tuz River, Miocene.

Description. Body dark-brown, almost black; pronotum light-brown, tegmen light with dark stripes along cubital vein and at outer corners of membrane. Spotting light-brown, small and delicate, denser at inner corners of corium. Body form cigar-shaped, widest at level of apex of clavus; ratio of length to width equals 2.5:1.

Head (together with eyes) almost as wide as fore margin of pronotum. Frons flat, in males concave in front.

Pronotum entirely covers scutellum. Tegmen light, with small spotting, tracery 138 of cross stripes entirely not expressed; embolium flat, linear, projects beyond center of tegmen; postcubital field on same plane as dorsal surface of body, on corium only one vein, Sc+R+M preserved, occupying a section in the fracture of the fore margin of the tegmen and the remainder of the cubital vein (Cu), dark-brown color. Mesothorax with well expressed deep longitudinal furrow, from above running the entire length of it. First segment of hind tarsus more than three times smaller than second segment (f. 89b).

Assymetry in male abdominal segments right-sided.

Material. Besides the holotype, 90 other specimens of Corixidae are preserved in the collection of the Paleontological Institute (collected by A. Y. Petrosian, 1938; O. M. Martynova, 1942).

SUPERFAMILY NAUCOROIDEA Fallen 1814

Description. Of medium size. Body flattened dorso-ventrally. Head opistognathous, very rarely almost prognathous; outer sclerites of head not isolated, anteclypeus not separated. Antennae four-segmented, as a rule, strongly shortened. Rostrum of variable length. Simple eyes missing. Tegmen, as a rule, with completed reduced venation. Nymphs sometimes with odor gland on abdominal tergites. Aquatic.

Comparison. Differ from Nepoidea in strongly fused cranial sclerites (anteclypeus not isolated) and lack of respiratory tubes on end of abdomen; from Notonectoidea in dorso-ventral flattened abdomen and opistognathal head; from Corixoidea in free rostrum and less flattened or entirely not flattened hind legs.

FAMILY NAUCORIDAE Fallen 1814

Description. Body 5-15 mm, strongly flattened, oval, without hairs. Eyes usually do not project from head and pronotum contour. Head transverse, its fore margin does not protrude. Rostrum, as a rule, is short (except extinct Angaronectini and relict Aphelocheirinae and Potamocorinae), three- or four-segmented, does not project beyond or slightly projects beyond hind margin of head, mandibular lever is thin, loop-shaped. Antennae four-segmented, shorter than head, compact, as a rule, hidden (except Aphelocheirinae and Potomocorinae) and located under the eyes. Not in III M.C.P. Pleural region of thorax, particularly the epimeres, is strongly developed. Opening of odor glands on metathorax is missing. Scutellum is free, triangular, not shorter than claval suture. Tegmen divided into clavus, corium, embolium and distinctly separate membrane, wholly devoid of veins. Coxal cavities are open, coxae pagiopod. Fore legs strongly thickened, grasping, fore coxae are attached at the fore margin 139 of the prothorax or below it; hind legs natatory; tarsi of fore legs one- or two-segmented, tarsi of mid and hind legs two-segmented with two claws, tibia and femur of medium size. Abdomen fairly strongly widened, hind corners of tergites slightly project beyond margin of following tergite, respiratory tubes missing. Surface of body smooth, brilliant. In nymphs, abdominal odor gland is paired (Aphelocheirinae, Naucorinae) or unpaired, but strongly bifurcated and with two outlets (Potamocorinae).

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[2] From discovery in Miocene

Biology. Live in water, on aquatic plants of the shores of ponds, lakes and other standing reservoirs with 15-20° temperature. Most of the time they usually hang over the surface of water or cling to branches of plants. Swim ventral side down, with the aid of the hind legs, which are usually covered with swimming hairs (except the extinct tribe Aidiini and the living subfamily Potomocorinae), the dorsal side of the abdomen adjoining the surface of the water. Their green, yellow-green or yellow-brown coloring merges well with the background of the surrounding vegetation and ground. Hibernate under plant remains.

Some species of the American genus Ambrysus (A. mormon Mont.) live in streams with a rocky bottom, swimming among rocks in search of prey. They primarily stick to quiet or slowly running water along banks of streams, but can swim also in deeper water, where the current is quick (Usinger, 1946). La Rivers observed this species in the salt lake of Lachontan in Nevada (USA). The shore of this lake is rocky; its salinity has been determined as 1/10 the salinity of seawater. So long as its salinity, apparently, gradually increases with time, it will be possible in the future to trace the limit of salt concentration with which Ambrysus naucorids can live.

This investigator collected naucorids in two also unusual types of reservoirs in Nevada with strongly mineralized water and very high temperature. In one case La Rivers found a few individuals of apparently narrowly endemic species (Ambrysus Mormon Mont., Pelocoris shoshone La Riv.) and even a specially specific genus Usingerina, which lived in a warm spring with flowing, quickly running water of 24-32° temperature, and pH 7.3-7.5 (La Rivers, 1950). In another case, in a stream with 36° temperature, he observed in fairly large numbers very small naucorids, representatives of the endemic species Ambrysus funebris La Riv. This original, in essence, benthic naucorid basically crawls among rocks, looking for prey, and swims poorly and reluctantly (La Rivers, 1951). The unusual similarity of this naucorid with aquatic scorpions (Nepidae) was noticed: the stretching directly forward of large enlarged fore femora with grasping tibia. La Rivers also noted that naucorids of one population rarely attack those of another and, together with this, the limited possibility of recognizing objects for a distance not more than 1.5-2 cm, which is the reason for frequent errors in selection of victims (La Rivers, 1951).

Males and rarely females stridulate. When irritated, naucorids exude an acrid liquid from the rectal ampule. Nymphs and adults have odor glands. Eggs are laid either in the tissue of aquatic plants or on the surface of rocks. Eggs are semi-oval, often with a small button-shaped micropyle on the fore end. The freshly laid egg is creamy-white, in ripening it becomes grey with reddish spots. Their laying occurs in spring and the beginning of summer (Usinger, 1946). In temperate zones, Naucoridae usually have one or two generations per year, the general span of development of the nymphal stage takes about three months (Poisson, 1957). Embryonic development 2-3 weeks. In this respect, Aphelocheirinae are somewhat different from other naucorids. 140
According to observations in natural conditions, and also in laboratory tests (Krajewski, 1966), it was established that egg-laying in Aphelocheirus aestivalis (Fabr.) lasts all the summer months; from the egg, laid in the first half of the summer, after 2.5-3 months, the nymph is born, and the eggs laid in the second half of the summer, hibernate. Nymphs of the III-V stages, and also the imago are encountered year round. Nymphs already from the first stage eat fairly large animals; according to observations of Sirotinina(1921), nymphs of Ilyocoris cimicoidea L. sucked nymphs of Notonecta, which exceed them in dimensions. The predators destroy various aquatic insect larvae, small fish and prey even on fresh water trouser-leg? molluscs (Limnaeus, Planorbis).

Aphelocheirinae - primarily benthic reophils - live on the bottom of quick-current rivers, streams and in large reservoirs with flowing water, under rocks, in depths of snags and among plants, and also buried in sand. However, Aphelochierinae can live also in standing pools in lakes and in saltwater reservoirs. Their existence in this kind of reservoir is possible from the point of view of the physiology of breathing, and has been corroborated by tests (Thorpe, 1965). Their respiratory plastron, located on the ventral side of the abdomen, is covered by small and dense hydrophobic hairs. Adapted to breathing oxygen dissolved in water, they thus do not surface to renew a supply of air. After being laid, eggs stick to rocks and shells of various molluscs (Unio, Anodonta). They are encountered at a depth of 0.5 to 7 m, mainly on the rocky and also argillaceous or sandy bottom. Nymphs live together with the imago. They cycle of development is fairly prolonged; for example, in Sweden, it takes two years (Poisson, 1951). Adults live more than one year and they hibernate in various stages (egg, larval and adult). Predators, they eat mainly Trichoptera larvae (Hydropsyche ornatula McL.), chironomids and crayfish; they lead a nocturnal form of life (Sirotinina, 1921; Kirichenko, 1940).

Comments. Presently all living representatives of the family Naucoridae are divided into eight subfamilies: Naucorinae, Limnocorinae, Laccocorinae, Cheirochelinae, Ambrysinae, Cryphocricinae, Potamocorinae and Aphelocheirinae. This classification was first proposed by R. Usinger (1941) and subsequently accepted almost without change by all hemipterologists. Only the status of the specialized Aphelocheirinae, which many authors accept as a separate family, remains questionable. However, there are a whole number of little known tropical genera whose taxonomic position among subfamilies is not entirely clear. The preliminary comparative-morphological analysis which I conducted of the external structure of the head, ventral and dorsal sides of the body (Popov, 1970) led to the conclusion that the differentiating indicators used for characteristics of subfamilies can hardly serve as subfamilial indicators for a whole number of reasons. It is most probable that a large portion of subfamily taxons are really only tribal groupings which can be considered only as tribes.

The new taxonomic structure of living Naucoridae which I proposed (Popov, 1970) reduces the number of subfamilies to four - Naucorinae, Cryphocricinae, Potamocorinae, Aphelocheirinae, including the remaining "subfamilies" as the tribes Limnocorini, Laccocorini, Cheirochelini and Ambrysini in the Naucorinae.

Composition. Five subfamilies: the extinct Sphaerodemopsinae - Upper Jurassic of West Europe; the only relict subfamilies known for certain in the fossil state are the Naucorinae in the Lower and Upper Jurassic of Asiatic USSR, the Paleocene and 141 the Neocene of North America and West Europe, which in living fauna are represented in all parts of the world; the recent Aphelocheirinae are distributed in the entire Eastern Hemisphere, Potamocorinae and Cryphocricinae in the Western Hemisphere. The world fauna of this family number more than 280 species, of which about 10 are extinct.

Table for Determining Subfamilies of the Family Naucoridae

1(6) Head narrow, weakly transverse, strongly projecting in front of the eyes. Eyes strongly developed, convex. Rostrum and antennae long or short. Body surface very rough from above.

2(5) Rostrum long and thin, at least as long as fore femora. Antennae come beyond margin of head and thus are visible from above. Tarsi of fore legs mobile, with two strongly developed claws.

3(4) Rostrum very long, reaching at least mid coxae, apical segment considerably shorter than preceding one. Fore tarsi two-segmented, basal segment very small. Male genitalia asymmetrical. Usually brachypterous forms of medium size. Aphelocheirinae

4(3) Rostrum considerably shorter, reaching only fore coxae, last two segments of same length. Fore tarsi one-segmented. Male genitalia symmetrical, very small, macropterous forms only. Potamocorinae

5(2) Rostrum very short, considerably shorter than fore femora. Antennae short and entirely hidden under the head. Lateral margins of pronotum corrugated. Tarsi of fore legs one-segmented and more or less fused with tibia, claws completely reduced. Cryphocricinae

6(1) Head wide, strongly transverse, does not project or weakly projects in front of eyes. Eyes developed, strongly condensed. Rostrum and antennae always short (except Mesozoic Angaronectini). Lateral margins of pronotum smooth, tarsi of fore legs more or less fused with tibia and usually with one-two claws, or claws completely reduced. Surface smooth.

7(8) Tegmen strongly chitinized, like flat elytrae, clavus unusually long and reaches distal part of wing, forming a straight line together with the inner margin of corium. Very large Sphaerodemopsinae

8(7) Tegmen significantly smaller, chitinized, usually with well expressed membrane, clavus short, rarely longer than scutellum. Of medium size. Naucorinae.

SUBFAMILY SPHAERODEMOPSINAE Y. Popov, Subfam. Nov.

Description. Rather large, about 15 mm. Body in back widely rounded, hind femora weakly thickened. Tegmen strongly chitinized, clavus strongly developed and occupies almost one third of tegmen, membrane missing. Abdomen wide, borders of segments at base straight.

Comparison. Differ from all known subfamilies in strongly chitinized tegmen (like elytra of beetles) and strongly developed clavus. In degree of chitinization,of the tegmen resemble living neotropical Potamocorinae (genus Coleopterocoris Hung.) and some Naucorinae (genus Melloiella De Carlo) but differ in the strongly developed chitinized clavus and dimensions (for example, more than ten times larger than Coleopterocoris Hung.).

GENUS SPHAERODEMOPSIS Handlirsch 1906 142

Sphaerodema: Oppenheim, 1888, p. 235.
Sphaerodemopsis: Handlirsch, 1906, p. 543.

Genotype. S. jurassica (Opp.), Upper Jurassic, Eichstatt, FRG.
Description. Body oval, weakly elongated, greatest width at level of base of abdomen. Tegmen with fairly wide and long clavus, reaching almost to apex of wing. Base of scutellum strongly raised. Abdominal sternites of equal size, VII sternite developed best.

Generic Composition. Monotypic genus.

SPHAERODEMOPSIS JURASSICA (Oppenheim, 1888) T. VII, Fs. 3-4, F. 90

Sphaerodema jurassicum: Oppenheim, 1888, p. 235, T. 18, F. 90.
Sphaerodemopsis jurassica: Handlirsch, 1906, p. 543.

Holotype. Collection of Munich University, Department of Paleontology and Historical Geology, No. AS V2V, direct imprint of body of insect; Eichstatt, FRG, lithographic shales, Upper Jurassic, Kimeridge-Titon.

Description. Scutellum large, strongly elongated, at base strongly raised like a semi-round horny elevation. Tegmen strongly convex from above, smooth, with very long wide clavus, reaching apical fourth of wing; fore margin of tegmen strongly curved, especially in central portion, hind margin straight, apex slightly directly truncated; length of tegmen 15 mm, width 7 mm, length of clavus 10 mm, width 3 mm. Borders of abdominal segments meet at center at somewhat of an angle, particularly the last abdominal sternites (except VII) are more or less evenly developed.

Dimensions. Length of body 18-22 mm, width 12-14 mm.

Material. Besides holotype, one more specimen No. AS I 728 from the same locality.

Comments. The imprint of the body (holotype) which is the basis for the description is very stretched (almost 1.5 times); thus the description does not always concur with the drawing given of the distorted specimen.

143

SUBFAMILY NAUCORINAE Fallen 1914

Naucorinae: Fallen, 1914, p. 3,15.
Laccocorinae: Stal, 1876, p. 142.
Limnocorinae: Stal, 1876, p. 142.
Ambrysinae: Usinger, p. 8, 9.
Cheirochelinae: Montandon, 1897, p. 367.
Laccocorini: Popov, 1970, p. 97.
Ambrysini: Popov, 1970, p. 97.
Ambrysini: Popov, 1970, p. 97.
Cheirochelini: Popov, 1970, p. 97.

Description. Body flattened, oval or ovally elongated, from above slightly convex, with smooth surface; from light-green to dark-brown color. Medium or large (5-15 mm). Head strongly transverse and often strongly elongated into the prothorax; its fore margin usually does not project in front of the eyes. Eyes more or less flat, as a rule large. Antennae short and do not project beyond lateral margins of head. Labrum usually well developed (except Cheirochelini) and on apex rounded. Rostrum short with three visible segments (except Mesozoic Angaronectini), opisto- or hypognathous; if reaches or slightly extends beyond fore margin of prothorax, then never reaches fore coxae. Postgenal bridge, or genapont, long or short, often raised like a rib. Pronotum transverse, fore margin usually concave, hind margin straight for entire extent. Sternal parts of thorax often raised like a fin of variable height; pleural regions well developed and, as a rule, fused with sternal without any traces of sutures. Tegmen usually well developed and reach apex of abdomen, embolium distinctly expressed (except Laccocorini). Fore legs grasping with strongly thickened femora, curved tibia and, as a rule, more or less fused into one or two-segmented tarsi; mid and hind femora and tibia thin (only in Naucorini they are slightly widened), tarsi two- or three-segmented, with well developed two claws. Abdomen with differently developed laterotergites, sometimes not seen from below; spiracles usually occupy central position between laterotergite and sternal suture, the latter often not expressed.

Comparison. Differs from all families in the wide and strongly transverse head, flattened eyes and smooth body surface, and also the short rostrum (except Cryphocricinae). Differs from Cryphocricinae in the strongly sclerotized head capsule, weakly indented fore and smooth not-crimped lateral margins of the pronotum and the character of the abdominal spiracles.

Composition. Eight tribes, three of which (Liadonaucorini, Aidiini and Angaronectini) are found in the Mesozoic of Asia; the fourth, Naucorini, appears in the Jurassic of Central Asia and survives to the present, its living representatives distributed worldwide. Living representatives at the present time number about 225 species.

GENUS LIADONAUCORIS Y. Popov, gen. nov.[1]

Genotype. L. rohdendorfi sp. nov., Liassic, Central Asia, Fergana.
Description. Surface of dorsal side of body slightly rough, especially the scutellum. Scutellum transversely triangular. Embolium of tegmen not expressed; venation very reduced, only the radial and anal veins are distinctly preserved. Abdomen with distinct elevation in central part of last segments, on ventral side of sixth sternite strongly narrowed.

Specific Composition. Monotypic genus.

LIADONAUCORIS ROHDENDORFI Y. Popov, sp. nov.[2] T. VII, F. 1, F. 91

Holotype. PIN 166/2,3; direct and reverse imprints of body; head and pronotum missing. Central Asia, Kirghiz SSR, Oshsk Prov., Kizil-Kia city, Liassic.

Description. Body oval, weakly elongated. Mesonotum strongly transverse, width 145 four times more than length; scutellum flat, surface noticeably rough, apical portion in transverse wavy fissures; fore margin in central portion slightly curved, lateral sides straight. The radial vein is almost parallel to the outer margin of the tegmen and reaches its center; clavus fairly wide. Length of tegmen exceeds their width approximately 2.5 times, claval suture 1.5 times longer than scutellum, lateral margins of tegmen flattened. Visible portion of abdomen consists of five last segments; borders between them straight; fourth-fifth segments almost of same size; hind margin of sixth segment with very deep indentation, seventh segment with angular fore margin and strongly rounded in back, noticeably more than the others; eighth segment like two lateral curved plates, almost meeting behind seventh segment.

Dimensions. Length of body imprint 5.5 mm, width 4 mm, length of tegmen 5.5 mm.

Material. Holotype (collected by B. B. Rohdendorf in 1937).

TRIBE AIDIINI Y. Popov, trib. nov. Figs. 92 a, b

Description. Relatively small. Fore margin of pronotum weakly concave. Tegmen with only one expressed anal vein, narrow long embolium present. Sternal and pleural regions well developed; basisternum of mesothorax separated, furkasternite also developed. Fore margin of abdominal sternites jut forward angularly. Epimeres of metathorax strongly developed and widened blade-like. Hind legs, particularly the tibia and tarsi, long and thin, devoid of swimming hairs. Abdomen below without longitudinal central fin.

No! Episterna

Comparison. Differs in strongly developed sterno-pleural region of thorax, especially strongly set apart epimeres of metathorax, and also very thin hind legs.

Composition. Single monotypic genus Aidium Y. Popov, in Upper Jurassic of Kazakhstan.

TRIBE ANGARONECTINI Y. Popov, trib. nov.

Description. Fairly large. Head strongly transverse, rostrum opistognathous; labrum almost triangular; rostrum thick, four-segmented, very long, reaching hind margin of prothorax. Pronotum more or less trapezoid with concave fore margin. Propleura with clearly expressed borders of sclerites, episterna partly fused with sternite; epimeres of meso- and metathorax strongly developed. Fore legs noticeably shortened; femora of all legs thickened; tibia and tarsi of mid and hind legs flattened, pro- 146 with long swimming hairs; hind tarsi one-segmented; coxae of fore legs set far from fore margin of prothorax. Abdomen with visible first sternite, apical sternites along central line raised.

No! EM II + ES III

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[1] From Liassic locality and name of genus Naucoris.
[2] Named for the entomologist B. B. Rohdendorf, who found the imprint.

Dotorminant Table of Tribes of the Subfamily Naucorinae

No!
Episterna

1(2) Epimeres of metathorax form blade-like widening , covering the entire hind coxae. Hind legs, especially tibia and tarsi, long and thin, not covered with swimming hairs. Aidiini

2(1) Epimeres of metathorax do not form blade-like widening. Hind legs covered, as a rule, by swimming hairs.

3(4) Clavus of tegmen long, considerably longer than scutellum; corium with radial vein. Liadonaucorini

4(3) Clavus smaller than scutellum or equal to it in length.

5(6) Rostrum long, comes beyond fore coxae and reaches hind margin of metathorax. Tibia and tarsi of mid and hind legs strongly flattened and thickly covered with swimming hairs. Large. Angaronectini

6(5) Rostrum very short, thick at base, conically narrowing toward apex, does not 144 come beyond fore margin of prothorax.

7(8) Epimeres of prothorax strongly set apart and fully cover hind part of sternite. The fields surrounding the spiracles are smooth, beyond each spiracle there is a transverse row of small, smooths areas. Always fully winged. Ambrysini

8(7) Epimeres of prothorax developed, but do not meet and do not cover hind part of sternite.

9(10) Rostrum attached in a deep indentation on the lower side of the head some distance from the fore margin, which projects beyond the eyes in lamellar fashion; labrum usually strongly reduced. Cheirochelini

10(9) Rostrum leaves from fore margin of head; fore margin of head does not project in front of eyes; labrum distinctly and well developed.

11(12) Fore tarsi two-segmented with two claws, often hardly noticeable. Fore margin of head strongly curves below and backward, thus the rostrum distinctly leaves behind it; labrum sharpened at apex. Mid and hind femora on inner side, besides the two usual rows of short setae along the inner surface, have two additional rows of barely visible setae (stylets?). Laccocorini

12(11) Fore tarsi one-segmented, with one very small, barely differentiated claw or without it. Fore margin of head usually less curved, sloping strongly backward. Hind and mid femora without distinct additional row of stylets.

13(14) Inner margins of eyes spread forward. Rostrum opistognathous. Meso- and metathorax with projecting longitudinal fin, wide and bearing pits along the center. Body widely oval, flattened. Limnocorini

14(13) Inner margins of eyes meet in front. Rostrum hypognathous. Meso- and metathorax with small, thin lamellar fin or without it. Body strongly convex; large forms. Naucorini.

TRIBE LIADONAUCORINI Y. Popov, trib. nov.

Description. Fairly small forms. Tegmen longer than abdomen, embolium not expressed; radial vein present on corium; claval suture longer than scutellum. Abdomen with fin on ventral side.

Comparison. Differs from other tribes in very long clavus, considerably exceeding length of scutellum, and presence of distinct, unreduced radial vein on fore wings.

Composition. Single genus Liadonaucoris Y. Popov in the Lower Jurassic of Central Asia.

Comparison. This subfamily differs from the others (except Aphelocheirinae) in the unusually long (for Naucorids) rostrum, which comes beyond hind margin of prothorax and consists of four distinct segments, and also the outer anterior sternite. Besides, the strongly moved backward fore coxae and strongly flattened tibia and tarsi of the mid and hind legs also differentiate it from the others. In size of fore legs and character of segmentation of the pleural region and degree of flattening of the hind legs, this family can approach only the living Palearctic subfamily Naucorinae.

Composition. Monotypic subfamily - genus Angaronecta gen. nov. from the Lower Cretaceous of East Siberia.

GENUS ANGARONECTA Y. Popov, gen. nov.[1]

Genotype. A. longirostris, sp. nov.; Lower Cretaceous, Baisinsk Series, Vitim River.

Description. Head not more than twice wider than its length: labrum entirely on
ventral side of head, with weakly sharpened apex; rostrum comes beyond hind margin
of prothorax, its segments almost of identical length. Pronotum transverse, its
width more than twice exceeds length; lateral margins noticeably narrowed in front.
Sternal region of mesothorax well developed and fused with episterna, epimeres large.
Width of fore femora almost twice less than their length; tibia and tarsi, except
the fore, are flattened, tarsi of hind legs almost equal in length to the tibia;
apex of hind tarsi with two claws. Abdomen slightly transverse, strongly narrowing
toward apex; anterior sternite reaches lateral margins of abdomen; borders of seg- 147
ments more or less straight or slightly curved; central sector of fourth-seventh
sternites distinctly raised, eighth sternite does not come beyond seventh.

Specific Composition. Monotypic genus.

ANGARONECTA LONGIROSTRIS Y. Popov, sp. nov.[1] T. VII, F. 5, F. 93

Holotype. PIN 1668/1742; direct and reverse imprints of body; Buriat ASSR, Eravnin Province, left bank of Vitim River, lower mouth of Bais River, Lower Cretaceous, Baisinsk Series, Baisin layer 31 (Martinson, 1961).

Description. Body oval, slightly widening in back, widest at level of second-third
abdominal sternites; dorsal and ventral sides weakly convex. Head slightly projects
beyond fore margin of pronotum; length of part of head visible from below almost
four times exceeds width; labrum at apical sector strongly rounded and does not cover
first segment of rostrum; rostrum gradually narrows to apex. Pronotum transverse, its
width exceeds length almost 2.5 times, fore margin weakly indented, hind straight,
lateral margins slightly rounded, almost straight with narrow lateral rim along
entire margin; pleural region of prothorax without clear episternal and epimeral
sutures, which in front of coxal cavities are widely fused. Hind margin of sternite
of mesothorax with small central projection (mesocyphus) and longitudinal suture on
it, lateral sides of episterna reach hind lateral corners of prothorax. Metathorax
with weakly developed sternal region, also completely fused with episterna, like a
small fairly wide tongue with curved hind margin; epimeres strongly developed, 148
episterna almost rectangular, considerably larger than those of mesothorax; epimeres triangular
M.C.P. with elongated inner side. Fore legs short, apices of femora do not reach lateral
sides of pronotum, femora strongly flattened, especially in central portion, inner
side before the apex with small indentation and fin along the margin; tibia and one-
segmented tarsus considerably shorter than femora. Mid legs natatory, femora more
or less thickened; tibia flattened, almost 1.5 times shorter than femora; first
segment of tarsus also flattened and covered with swimming hairs. Hind legs natatory,

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[1] From the paleogeographical name Angarida and the Greek word noctos - swimming.

[1] From the Latin words longus, long, and rostrum.

tibia and one-segmented tarsi strongly flattened and covered with long, dense swimming hairs, which on tarsi are longer than their width; inner margin of tibia set with small talons. Abdomen of round form, widest at second and third segments, its width barely greater than length; segments almost of equal width, their posterior lateral corners slightly sharpened and project slightly beyond the following ones; anterior sternite partly covered by epimeres of metathorax and hind coxae; central portion of fourth-seventh sternites strongly convex, particularly on sixth-seventh sternites; eighth sternite like two paired plates, sharpened on apices and out off by the seventh sternite.

EPISTERNA

Dimensions. Length of body 14 mm, width 8 mm.

Material. Holotype.

TRIBE NAUCORINI Fallen, 1814 T. VII, F. 2

Naucoridei: Fallen, 1814, p. 3, 15.
Naucoraria: Stal, 1876, p. 142.
Naucorinae: Usinger, 1941, p. 8.
Naucorinae: China, Miller, 1959, p. 16.
Naucorini: Popov, 1970, p. 97.

Description. Body moderately flattened, oval, brilliant, from above fairly convex, usually of green or yellow-green color; fairly large (10-15 mm). Head weakly withdrawn into the prothorax; fore margin does not protrude in front of the eyes; inner margins of eyes meet. Labrum moderately developed, rounded at apex. Rostrum short, hypognathous, from base widening conically toward apex and does not reach fore margin of prothorax. Genapont fairly long, usually with rib. Fore margin of pronotum weakly curved. Fore, mid and metathorax often with low lamellar fin, pitted. Tegmen always well developed and reach apex of abdomen. Fore legs grasping, femora strongly thickened, tibia curved and fused with one-segmented tarsi. Mid and hind femora without longitudinal rows of setae along inner surface, with only two distinct rows of short setae (stylets?). Mid and hind tarsi two-segmented, with two claws. Ventral surface of abdomen without central longitudinal fin. Laterotergites of abdomen well developed, wide, [illegible] spiracle [illegible] close to parasternal fissure, which is distinctly expressed.

Comparison. Differs from Angaronectini in the very short rostrum, from Liadonaucorini in the structure of the tegmen, from Aidiini in the not set apart epimeres of the metathorax and thicker hind tibia, from Cheirochelini and Ambrysini in the weakly indented fore margin of the pronotum, from Laccocorini and Limnocorini in the hypognathous rostrum.

EPISTERNA

Composition. Eleven genera and about 50 species, of which five genera[1] are found 149
in the fossil state: Nectonaucoris Y. Popov, Nectodes Y. Popov and Heleonaucoris, gen. nov., Upper Jurassic, Kazakhstan, Discostoma Scudder, Oligocene of North America and Ilyocoris Stal, Paleocene and Neocene of West Europe.

Determinant Table of General of the Tribe Naucorini, Found in Fossil State[2]

1(2) Tegmen with unexpressed embolium; clavus with small dark spots. Nectonaucoris
2(1) Tegmen with distinct embolium; clavus with light large spot or unicolored.
3(4) Embolium narrow and expressed only at base of tegmen; corium spotty. Heleonaucoris
4(3) Embolium wide and clearly expressed along entire line; corium unicolored.
5(6) Clavus almost 2.5 times shorter than tegmen, unicolored; membrane takes up almost half of tegmen; tegmen not shorter than 10 mm. Ilyocoris
6(5) Clavus less than two times shorter than tegmon, spotty; membrane significantly shorter and occupies about one third area of tegmon; shorter than 7 mm. Nectodes.

GENUS HELEONAUCORIS Y. Popov, gen. nov.

Genotype. H. maculipennis, sp. nov.
Description. Large, not less than 15 mm. Clavus moderately developed, more than twice shorter than length of tegmen; anal vein clearly expressed. Embolium differentiated only at base of tegmen; border of corium and membrane indistinct, membrane less than half of tegmen and does not reach apex of clavus. Apex of tegmen with distinct outer and inner corners, its outer margin straight.

Comparison. Differs from other genera of this tribe in weakly developed embolium, spotty tracery of tegmen and large dimensions (except Ilyocoris). Differs from the most similar to it Mesozoic genus Nectodes from the same locality of Karatau in the considerably shorter clavus, narrow embolium, expressed only at the base of the tegmen, and directly truncated apex of tegmen. In coloring resembles the living tropical genus Heleocoris of the tribe Laccocorini.

Specific Composition. Genotype.

HELEONAUCORIS MACULIPENNIS, Y. Popov, sp. nov. T. VII, F. 6, F. 94

Holotype: Pin 2066/3680, positive and negative imprints of right tegmen; Upper Jurassic of South Kazakhstan (Karatau mountains), locality of Michailovka.

Description. Tegmen elongated, length exceeds width three times. Clavus dis- 150
tinctly widened at apex; moderately wide, length exceeds width more than 3.5 times;
anal vein very weakly curved, almost straight. Corium with clearly expressed
embolium at basal sector of tegmen, length of differentiated portion of embolium
3.5 mm. Coloring clear, like separate clear spots at basal half of wing (f. 94),
distal half light.

Dimensions. Length of tegmen 12 mm, width 4 mm.

Material. Holotype.

TRIBE AMBRYSINI Usinger 1941 F. 95

Ambrysinae: Usinger, 1941, p. 9-11.
Ambrysinae: China, Miller, 1959, p. 16.
Ambrysini: Popov, p. 97, p.p. excl. Melloiella et Carvalhoiella.

Description. Body moderately flattened, oval, usually of various shades of green color; mid or large size (7-15 mm). Head strongly drawn into prothorax; fore margin of head does not project in front of large, flat eyes. Labrum well developed, its apex rounded. Rostrum short, directed below, leaving fore margin of head, from base conically narrowing toward apex and not reaching fore margin of prothorax. Genapont long, in central portion there is a longitudinal fin-shaped elevation on it.

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[1] The Jurassic genus Palaeoheteroptera Meun. was established on the genotype of "Naucoris" carinata Opp. (Meunier, 1900). At my instructions, the types of "Naucoris" carinata Opp. (1882, XVI 34) and "Naucoris" lapidaris Weynb. (1 584) from the Munich Museum were located. The first type specimen is a blattid (Blattidae), apparently Lithoblatta lithophilla (Germ.) (Handlirsch, 1906). Thus, the genus Palaeoheteroptera, established earlier (Meunier, 1900) than the genus Lithoblatta, must be considered an old synonym of the latter.

The second type specimen ("Naucoris lapidaria Weyenb.) is very poorly preserved; its drawing, accompanying the original description, does not correspond with the specimen; it cannot be ruled out that it really should be placed in the Naucoridae; however, it is not possible to determine its true taxonomic position.

[2] Since the American Oligocene Discostoma Scudder most likely is a synonym of the genus Ilyocoris Stal, it is not included in this table.

Fore margin of pronotum sharply concave. Epimeres of prothorax strongly overgrown and protrude as lamellar projections onto hind part of sternite, joining along the central line and completely covering its base. Tegmen well developed and always reach apex of abdomen. Fore legs grasping, femora strongly thickened, sometimes become almost spherical, tibia more or less curved and fused with one-segmented tarsi; mid and hind tibia and tarsi moderately thin, tarsi three-segmented with well developed paired claws. Laterotergites of abdomen weakly or entirely not expressed; spiracles are located close to clearly expressed parasternal fissure. Always fully winged.

Comparison. Differs from the other tribes of the subfamily in the strongly overgrown epimeres of the prothorax, which fuse in back of the coxae; besides, from the Angaronectini in the short rostrum and from Aidiini in the non-widened epimeres of the metathorax.

EPISTERNA

Composition. One genus[1] and about 70 species in living fauna; in fossil state not 151 known; living representatives are distributed in the Nearctic and neotropical regions.

TRIBE CHEIROCHELINI Montandon 1897 F. 96

Cheirochelinae: Montandon, 1897, p. 367.
Cheirochelinae: Usinger, 1941, p. 8.
Cheirochelinae: China, Miller, 1959, p. 16.
Cheirochelini: Popov, 1970, p. 97.

Description. Body strongly flattened, oval, of medium size. Head round-triangular, strongly elongated into the prothorax; fore margin strongly projects in front of small eyes. Labrum strongly reduced. Rostrum very short, directed below, base of first segment submerged within the head and protrudes fairly far from its fore margin. Genapont long and not high. Fore margin of pronotum sharply concave. Tegmen developed, but often do not reach apex of abdomen. Fore legs grasping, femora strongly thickened, tibia curved and more or less fused with one-segmented 152 tarsi; mid and hind tibia and tarsi fairly thin and thickly covered with swimming hairs, tarsi three-segmented. Laterotergites of abdomen not expressed; spiracles occupy central position between margin of abdomen and clearly expressed parasternal fissure.

Comparison. Differs from the other tribes in that the rostrum leaves some distance from the fore margin of the head and the strongly reduced labrum; from Angaronectini in the short rostrum; from Aidiini in the not-widened epimeres of the metathorax.

EPISTERNA

Composition. Six genera and 11 species; not known in the fossil state; all distributed in the Oriental region.

TRIBE LACCOCORINI Stal 1876 F. 97

Laccocoraria: Stal, 1876, p. 142.
Laccocorinae: Usinger, 1941, p. 8.
Laccocorinae: China, Miller, 1959, p. 16.
Laccocorini: Popov, 1970, p. 97.

Description. Body moderately flattened, oval or ovally-elongated, of yellow-brown color and medium size (7-12 mm). Head strongly transverse, slightly drawn into

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[1] Two other monotypic genera, Melloiella De Carlo and Carvalhoiella De Carlo, from South America, have been placed in this group along with the type of the genus Ambrysus Stal. Unfortunately, the first genus is known only from the drawing from above and the other remains in general inaccessible to the author. Since the taxonomic position and basic morphology of these genera remain unclear, they for now are not included in any of the tribes included in the subfamily Naucorinae.

prothorax; fore margin of its frons-clypeal portion curves downward and backward, not projecting in front of the large, flat eyes. Labrum strongly developed and at apex distinctly sharpened. Rostrum, because clypeus is strongly curved onto the ventral side, leaves some distance from the fore margin of the head; short, directed backward, reaches or slightly comes beyond fore margin of prothorax. Genapont very short, without longitudinal fin or elevation. Fore margin of pronotum weakly indented, almost straight. Prothorax with large sternal elevation like a fin. Tegmen well developed and reach apex of abdomen, embolium not expressed. Fore legs less modified for grasping, femora almost not widened, tibia straight with two-segmented tarsi, furnished at apex with two small claws, which are well developed on mid and hind tarsi; mid and hind femora on lower side with two longitudinal rows of very small setae along with the two usual rows of short setae (stylets?) along the inner surface. Laterotergites of abdomen developed; spiracles occupy a more or less central position or are located somewhat closer to the weakly expressed parasternal fissure.

EPISTERNA

Comparison. Differs from Angaronectini in strongly shortened rostrum, from Aidiini in the not-widened epimeres of metathorax, from Liadonaucorini in short clavus, from Limnocorini in two-segmented fore tarsi, from the other tribes in opistognathous rostrum and weakly concave fore margin of pronotum.

Composition. Eight genera and about 60 species in living fauna; in fossil state not known; distributed in Neotropical, Ethiopia, Oriental and Australian regions.

TRIBE LIMNOCORINI Stal 1876 F. 98

Limnocoraria: Stal, p. 142	Limnocorinae: China, Miller, 1959, p. 16.
Limnocorinae: Usinger, 1941, p. 8.	Limnocorini: Popov, 1970, p. 97.

Description. Body moderately flattened, widely oval, small or of medium size (5.2-11 mm). Head weakly drawn into prothorax, fore margin does not project in front 153 of large, flat eyes; inner margins of eyes spread apart in front. Labrum well developed, apex noticeably rounded. Rostrum short, directed backward, from base narrows conically toward apex, reaches or slightly comes beyond fore margin of prothorax. Genapont very short, often ending in a sharp rib at base of head. Fore margin of pronotum weakly concave; prothorax with large sternal elevation like a fin; meso- and metathorax with wide projecting sternal fin in small pits along center. Tegmen always well developed and reach apex of abdomen. Fore legs grasping, femora strongly thickened, tibia curved and fused with one-segmented tarsi; mid and hind femora with only two usual rows of short setae (stylets?) on inner side. Laterotergites of abdomen weakly developed, narrow; spiracles stand far from laterotergites, parasternal fissure not expressed.

EPISTERNA

Comparison. Differs from Angaronectini in strongly shortened rostrum, from Aidiini in not-widened epimeres of metathorax, from Liadonaucorini in structure of tegmen, from Cheirochelini and Ambrysini in backward directed rostrum and weakly concave fore margin of pronotum; from Laccocorini in one-segmented fore tarsi and sharpened at apex labrum, from Naucorini in "opistognathous" rostrum, different divergence of inner margins of eyes, and also flatter and wider body.

Composition. Two genera and about 35 species; in fossil state not known; distributed only in Neotropical and Nearctic regions.

SUBFAMILY CRYPHOCRICINAE Montandon 1897

Cryptocricinae: Montandon, 1897, p. 6, p.p. excl. Ambrysus.
Cryphocricinae: Champion, 1901, p. 354.
Cryphocricinae: Usinger, 1941, p. 8.
Ambrysinae: Usinger, 1941, p. 11-12; p.p. quoad Cataractocoris.
Cryphocricinae: Usinger, 1947, p. 353.
Cryphocricinae: China, Miller, 1959, p. 16.

"genal sclerite" = Max. plate

Description. Body more or less convex, from above rough, in small granules; of variable size (6.5-14 mm). Head with rostrum directed forward, strongly drawn into pronotum; fore margin noticeably projects in front of relatively small and convex eyes. Antennae short and entirely concealed under lateral margins of head. Labrum well developed, slightly elongated and weakly rounded at apex, hanging over at fore margin of head; genal sclerites distinctly separated and project in front of head. Rostrum three-segmented, strongly shortened, conically anrrowing toward apex and directed forward and slightly below. Genapont long with central fin along entire line. Pronotum transverse, lateral margins goffered, fore margin strongly concave, hind quarter of pronotum more convex and separated by a distinct furrow; sternite of prothorax is completely open fron the back or covered at the base by accreted epimeres; sternites of meso- and metathorax flat, not raised like a fin. Tegmen often underdeveloped. Fore legs grasping, femora strongly thickened, tibia curved and fused with one-segmented tarsi; mid and hind femora thin, flattened, tarsi three-segmented with unusually strongly developed paired claws. Laterotergites of abdomen developed; spiracles located close to the laterotergites; parasternal fissure clearly expressed. Brachypterous forms fairly common.

Comparison. Differs from all subfamilies in rostrum directed forward, clearly expressed genal lamellae pushed in front of head, goffered margins of pronotum, and also dorsal surface of body roughened in small granules.

Composition. Two monotypic tribes - Cryphocricini and Cataractocorini, not known in fossil state; distributed in Nearctic (Sonor region) and Neotropical regions.

Comments: As recently shown in the preliminary comparative-morphological study made of the external structures of representatives of the genera Ambrysus, Cataractocoris and Cryphocricos (Popov, 1970), up to now placed in different subfamilies (Montandon, 1897 a,B; Usinger, 1941, 1947; Poisson, 1951, 1957, and others), the genus Cataractocoris in a whole number of congeneric apomorphic characters (basically the structure of the head and dorsal side of the body), from my point of view, demonstrates greater similarity to the other Neotropical genus Cryphocricos than to the genus Ambrysus which is combined with it. The latter genus, in its turn, is more closely related to genera of the subfamily Naucorinae and particularly to the tribe Cheirochelini. In connection with this, it was suggested to transfer the genus Cataractocoris from the higher subfamily Ambrysinae (sensu Usinger) to the subfamily Cryphocricinae and at the same time to isolate the tribes Cryphocricini and Cataractocorini as separate monotypic taxons. Also, the genus Ambrysus, which possesses more differences than relationships, but is, in my point of view, most closely related to Naucorinae of the Eastern Hemisphere, is included as a subfamily of the Naucorinae (sensu mihi) as an independent tribe Ambrysini (Popov, 1970).

to Naucorinae

Determinant Table of Tribes of the Subfamily Cryphocricinae

1(2) Epimeres of prothorax overgrown, covering the base of a small poststernite. Ventral surface of abdomen pubescent. Fields surrounding spiracles smooth, beyond each spiracle there is a transverse row of small smooth areas. Always completely winged — Cataractocorini

2(1) Epimors of thorax developed, but do not meet behind completely open and large poststernite. Ventral abdominal surface lacks pubescence. Around each spiracle are perforated disc-formed fields. Sharply dimorphic, more commonly brachypterous forms. — Cryphycricini

TRIBE CRYPHOCRICINI Montandon 1897 F. 99

Description. Body strongly flattened, especially below, ovally elongated (macropterous forms) or widely oval (brachypterous forms); of medium size or small (6.5 - 11.5 mm). Rostrum directed forward, very short; eyes strongly convex, genal plates strongly project forward, genapont long, raised like a fin. Prothorax with strongly developed poststernite; epimeres lie flat against sternal portion and are separated by simple fissures; meso- and metathorax with strongly integrated sterno-pleural region, only pleural fissure preserved. Tegmen, as a rule, weakly developed and far from reach apex of abdomen. Ventral surface of abdomen not pubescent; laterotergites weakly developed; spiracles situated along laterotergites like perforated disc-shaped fields; parasternal fissure well 156 expressed. Usually brachypterous forms.

Comparison. Differs from representatives of the second tribe in structure of strongly flattened ventral side of body, structure of sterno-pleural region of thorax and special morphology of spiracles of abdomen, and also strongly developed brachyptery.

Composition. One genus, 11 species.

TRIBE CATARACTOCORINI Y. Popov, trib. nov. F. 100

Cryptocricinae: Montandon, 1897, p. 125, p.p. excl. Ambrysus.
Ambrysinae: Usinger, 1941, p. 11-12, p.p. quoad Cataractocoris.
Cataractocorini: Popov, 1970, p. 97.

Description. Body more or less flattened, widely oval, fairly large (12-14 mm). Rostrum less prognathous and slightly longer than in representatives of type of tribe; eyes large, convex; genal lamollae noticeably project forward; genapont long, strongly elevated like a central fin. Prothorax with weakly developed poststernite, covered at the base by strongly overgrown epimeres; mesothorax with distinctly expressed sterno-pleural and epimeral fissures, which are separated by corresponding sternal region and anepimeres. Tegmen well developed and always reach apex of abdomen. Ventral surface of abdomen covered with hairs; laterotergites well developed, more or less wide; spiracles located close to margin of abdomen, of usual structure; parasternal fissure most distinct on VII-VIII sternites. Always fully winged forms.

Comparison. Differs first of all in structure of ventral side of body, less prognathous and slightly longer rostrum, and also less pushed forward lamellae and larger eyes.

Composition. Single genus with two species.

SUBFAMILY APHELOCHEIRINAE Fieber 1860 F. 101

Description. Body strongly flattened, ovally convex (macropterous forms) or widely oval (brachypterous forms), of medium size (8-10 mm). Head with opistognathous rostrum, spherical-triangular, frons from above visible, fore margin projects in front of eyes noticeably. Antennae thin, fairly long, slightly projecting beyond lateral margins of head and thus visible from above. Labrum transverse, apex rounded, located on ventral side. Rostrum three-segmented, thin and very long, reaching mid coxae; basal segment very short, second segment slightly longer than third. Fore legs weakly adapted for grasping; femora weakly thickened, tibia straight, tarsi mobile, two-segmented, ending in two claws, as well developed as on the other legs. In brachypterous forms, tegmen are slightly rounded and do not reach or barely reach first visible abdominal segment; in macropterous forms, tegmen come beyond apex of abdomen, but are noticeably narrower than it. Spiracles visible and surrounded by a rosette of radial branches. Male genital segments asymmetrical; right parameres strongly curved and small, left parameres more curved and massive. Brachypterous forms are most frequently encountered.

No! 4 segments - M.C.P.

Comments. Many authors have placed the genus Aphelocheirus into an independent 157 family (Douglas, Scott, 1865; Handlirsch, 1906-1908, 1925; Melander, Brues, 1932; Kirichenko, 1951; Poisson, 1951, 1957; Southwood, Leston, 1959 and others). At the same time, other researchers include this genus in the family Naucoridae as a separate subfamily.(Stal, 1876; Kirkaldy, 1906; Oshanin, 1906-1909; Beier, 1938; Usinger, 1941; China, Miller, 1959 and others). Later specialized morphological studies (Miyamoto, 1961; Parsons, 1966) and a taxonomic analysis of living and fossil naucorids have forced me to agree that this highly specialized genus belongs to the family Naucoridae only as a special subfamily.

Comparison. Differs from representatives of other taxons (except Potamocorinae and Angaronectini) in the unusually long and thin rostrum, reaching the mid coxae, and also the fairly long antennae visible from above.

Composition. One genus Aphelocheirus Westw. (f. 100), which is not known as a fossil; living fauna number about 30 species, distributed in the Palearctic, Ethiopian and Australian regions.

SUBFAMILY POTAMOCORINAE Usinger 1941

Description. Body moderately flattened, oval-convex, very small, about 2.7-2.8 mm. Head with opistognathous rostrum, rounded-triangular, fore margin strongly projects in front of small (especially in Coleopterocoris) eyes. Antennae four-segmented, fairly long, thin, noticeably projecting beyond lateral margins of head and thus visible from above. Eyes strongly moved onto ventral side of head, occupying there the same area as on the dorsal side. Labrum transverse, on apex round. Rostrum ? → three-segmented, thin, relatively short, reaching fore coxae, basal segment short, last two segments of equal length. Postgenal bridge (genapont) long, without longitudinal fin (elevation) or widely raised. Pronotum strongly transverse; its fore margin noticeably indented, but straight in central portion, hind margin also indented into the wide base of the neighboring scutellum. Tegmen always well developed; embolium expressed. Prothorax evenlyconvex, mesothorax slightly raised. Fore legs weakly grasping; femora more or less developed, tibia straight, tarsi one-segmented, furnished with two claws, also well developed, as on remaining legs. Spiracles reduced. Abdomen without central fin below; male genital segments symmetrical.

Comparison. Differs from all other subfamilies (except Aphelocheirinae) in fairly 158 long antennae, visible from above, and also thin and longer rostrum (except Aphelocheirinae and Angaronectini, in which rostrum is even longer).

Composition. Two tribes: Potamocorini and Coleopterocorini, which are not known as fossils; distributed in South America.

Determinant Table of Tribes of Subfamily Potamocorinae

1(2) Eyes large, more or less close together; scutellum very large, tegmen clearly delimited into clavus, corium and membrane, margins parallel. Potamocorini

2(1) Eyes small, widely set apart; scutellum considerably smaller, tegmen strongly chitinized, like elytra, do not subdivide into separate parts, lateral margins not parallel. Coleopterocorini

TRIBE POTAMOCORINI Usinger 1941 F. 102

Description. Body elongated. Head with large more or less flattened eyes; genapont slightly shortened, flat. Scutellum strongly developed, triangular; tegmen well developed, punctured, with distinctly expressed embolium, clavus and large membrane. Legs thin, hind tibia and tarsi covered only with thin setae.

Comparison. Differs from other tribe in large eyes, more triangular scutellum, less sclerotized, differentiated tegmen, and also lack of swimming hairs on hind legs.

Composition. Monotypic tribe with single species from Brazil.

TRIBE COLEOPTEROCORINI Y. Popov, trib. nov. F. 103 159

Description. Body ovally-elongated. Head with small eyes, distance between which more than 2.5 times diameter of eyes, genapont long, evenly convex. Scutellum strongly transverse, more or less triangular. Tegmen strongly sclerotized, not divided into separate parts. Legs fairly long, hind tibia and tarsi with swimming hairs on inner side.

Comparison. Differs from type of tribe in small widely distributed eyes, strongly transverse and small in dimensions scutellum, strongly sclerotized tegmen and presence of swimming hairs on hind legs.

Composition. Monotypic tribe with single species from Paraguay.

SUPERFAMILY NOTONECTOIDEA Leach 1815

Description. Body from 2 to 18 mm, flat below and convex above, rarely/only flattened (Idiocorinae, Helotrephidae). Head hypognathous or opistognathous; outer sclerites strongly fused, anteclypeus not distinctly designated (except Mesozoic subfamily Clypostemmatinae, Notonectidae). Antennae strongly shortened and not visible from above, usually three-four segmented, rarely one or two-segmented. Simple eyes missing. Scutellum triangular, of variable size. Tegmen flat with reduced venation. Fore legs simple, not grasping; coxae of legs drawn together. Aquatic. In nymphs of some Notonectidae there is one unpaired abdominal odor gland.

Comparison. Differs from all superfamilies in strongly convex dorsal side of body with wings folding roof-shaped (except some Helotrephidae).

Composition. Five families: Scaphocoridae, Upper Jurassic of South Kazakhstan; Mesotrephidae, Upper Cretaceous of South Kazakhstan; Notonectidae, known from the Liassic of South Siberia, Upper Jurassic of West Europe and South Kazakhstan, Lower Cretaceous of East Siberia and Paleocene and Neocene of North America and West Europe; Pleidae and Helotrephidae not known as fossils; representatives of living fauna are widely distributed in all zoogeographical regions. World fauna number more than 250 species.

FAMILY SCAPHOCORIDAE Y. Popov 1968 T. VIII, F. 1, F. 104

Description. Body short, boat-shaped, compressed from the sides with roof-shaped tegmen folded like the bottom of a boat. Of medium size (4-6 mm). Head hypognathous, strongly transverse, apparently partly accreted with the thorax; eyes comparatively small and do not touch fore margin of pronotum, which is strongly developed and covers the scutellum. Scutellum very small. Tegmen sclerotized, embolium not expressed; completely covers abdomen, claval suture long, more than three times exceeds length of scutellum; membrane devoid of veins and occupies almost one third of tegmen. Hind legs not very long, oar-shaped; tarsi one-segmented and covered with thick swimming hairs.

Comparison. Differs from all families of the superfamily in strongly developed
pronotum, completely covering scutellum, and one-segmented hind tarsi; from Helo-
trephidae and Mesotrephidae in more convex pleid body; from Pleidae and Notonectidae 160
in strongly transverse head and somewhat small eyes.

Composition. Monotypic family - genus Scaphocoris Y. Popov; from Upper Jurassic of Kazakhstan.

FAMILY MESOTREPHIDAE Y. Popov, Fam. Nov.

Description. Small, not more than 3 mm long; dorsal side elevated roof-shaped, ventral flat. Head strongly tucked under and completely hidden by pronotum from above. Pronotum transverse, convex, of ellyptic form. Scutellum small, triangular, not covered by pronotum. Tegmen reach apex of abdomen; fore margin widened in lamellar form; venation strongly reduced, remains of veins along outer margin and anal vein on clavus present; latter well developed; membrane weakly expressed. Legs not swimming, hind tarsi longer than tibia, apparently two-segmented. Tracery usually present.

Comparison. The described Mesozoic Hemiptera resembles representatives of the recent families Pleidae and Helotrephidae in form of body and non-swimming legs. The pronotum, apparently entirely concealing the head, is similar to that of the Upper Jurassic Scaphocoridae. The small triangular scutellum resembles that of living South American Neotrephinae (Helotrephidae). In general plan of structure, this family is closest to the Jurassic Scaphocoridae, apparently being its descendent. Arthropods However, the form of the pronotum which is unusual for Arth?, the strongly widened outer margins of the tegmen, similar to those of living Belostomatidae, and the hind tarsi distinctly differentiate the Cretaceous family from all others.

Composition. One monotypic genus, Mesotrephes gen. nov., from the Upper Cretaceous of Kazakhstan.

GENUS MESOTREPHES Y. Popov, gen. nov.[1]

Genotype: M. striata, sp. nov.; Upper Cretaceous of South Kazakhstan.
Description. Pronotum strongly transverse, not wider than base of tegmen, lateral
margins rounded. Scutellum very small, more than three times shorter than claval 161
suture. Roof-shaped tegmen like a turned over boat bottom; their fore margin widened
lamellar like with remains of one vein along margin; clavus strongly developed and
occupies a considerable portion of the tegmen surface; anal vein runs along entire
clavus. Hind legs relatively short; tibia and tarsi of hind legs considerably thinner
than femora; hind tibia shorter than tarsus and femora. Tracery on dorsal side of
body distinct.

Specific Composition. Monotypic genus.

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[1] From Greek words for center and flattened.

MESOTREPHES STRIATA Y. Popov, sp. nov.[1] T. VIII, F. 2, F. 105

Holotype. PIN 2382/133; direct and obverse imprints of body; South Kazakhstan, Kizil-Ordin Province, Chiliis District, northeast spurs of Karatau mountains; Upper Cretaceous (Turon-Santon).

Description. Body oval, widest in central portion at level of claval suture. Tracery like distinct longitudinal dark-brown stripes on entire dorsal surface of body. Pronotum strongly convex, barely narrower than base of tegmen; its width exceeds length almost twice; fore margin evenly curved, hind widely rounded and somewhat stretched backward, its lateral sides slightly indented, lateral corners strongly rounded; three longitudinal stripes are wide and close to the center. Tegmen long, come beyond abdominal apex; lateral lamellar widenings occupy more than half the length of tegmen; vein (apparently Sc+R) is situated along entire widening, but does not reach base of tegmen, where there is another weak vein; lateral fore corners strongly rounded; clavus wide, its length slightly more than three times greater than width; apex of tegmen widely rounded; anal vein curved and runs along entire clavus. Triangular scutellum slightly transverse with sharp apex; lateral sides darkly-brown. Corium with three longitudinal stripes; most narrow inner one comes only slightly onto weakly expressed membrane, and outer one is the widest, central reaches apex of tegmen; clavus with two stripes: outer is wide and short, taking up a portion of the anal vein, and the inner one is long, running along the entire clavus, partially taking up the lateral side of the scutellum. Hind legs small; femora weakly thickened, evenly wide along entire length; tibia short, almost 1.5 times shorter than femora and tarsi taken separately; tarsi very long, almost equal in length to femora, slightly thinner than tibia.

Dimensions. Length of body 2.8 mm.

Material. Besides holotype, two other specimens of body from Karatau - PIN 2382/132 and 2783/255.

FAMILY HELOTREPHIDAE Esaki,China 1927 162

Description. Very small forms (1.3-5 mm). Body more or less flat, especially in Idiocorinae, oval, without hairs. Head fused with thorax in greater (Idiocorinae, Neotrephinae) or lesser (Helotrephinae) degree, forming in separate cases the so-called cephalothorax. Antennae reduced (one to two segments) and shortened, entirely hidden under the eyes. Simple eyes missing. Scutellum free, triangular and often strongly elongated. Pleural region well developed, especially epimeres; projections of meso-and metathorax very small, usually like setae. Openings of odor glands present on metathorax. Tegmen strongly sclerotized, clavus usually missing, membrane not expressed. Hind wings reduced. Coxal cavities open, coxae pagiopod. Legs moderately long, number of tarsal segments varies strongly; pretarsus provided with two claws, seta-like areola and membranous tube-like empodium. In nymphs, there is an unpaired gland on the dorsal side of the second segment of the abdomen, similar to Pleidae and Notonectidae. Male genital segments asymmetrical and moved to the left. The biology of these bugs is almost unknown.

EM II + ES III? →
or only 1 of these?

Comparison. Differs from other families in fused head and pronotum; from Scaphocoridae in scutellum not covered by pronotum and hind one-segmented legs; from Mesotrephidae in flatter body and form of pronotum, and also head less moved below; from Pleidae and Notonectidae in strongly reduced one or two-segmented antennae and less convex body.

Composition. Three subfamilies in living fauna: Helotrephinae, Neotrephinae and Idiocoriniae, not known as fossils; distributed in tropical belt and numbers about 20 species.

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[1] From Latin word for striped.

Determinant Table of Subfamilies of the Family Helotrephidae

1(2) Number of tarsal segments 3-3-3; dorsal surface of head separated from ventral by a distinct thin rib; scutellum at base wider than its length; female with ovipositor Neotrephinae

2(1) Number of tarsal segments 1-1-2; dorsal surface of head not separated from ventral by a thin rib or, if separated, then scutellum considerably longer than wide; scutellum of equal width and length; female without ovipositor.

3(4) Body flattened; suture between head and pronotum missing; antennae one-segmented, strongly condensed. Idiocorinae

4(3) Body strongly convex; suture between head and pronotum distinct; antennae two-segmented. Helotrephinae.

SUBFAMILY HELOTREPHINAE Esaki, China 1927 F. 106

Description. Body of these small bugs very convex and resembles Pleidae. Suture between head and pronotum sufficiently distinct and, as a rule, strongly wavy. Antennae always two-segmented. Fore and mid tarsi one-segmented, hind two-segmented. Live in standing water of small reservoirs and lakes. This subfamily, apparently, is the most primitive among all the other subfamilies.

Comparison. Differs from Neotrephinae and Idiocorinae in hemispherical body, from Neotrephinae in number of tarsal segments (1-1-2) and lack of ovipositor in females, from Idiocorinae in distinct suture between head and pronotum.

Composition. Eight endemic genera: Helotrephes Stal, Esakiella China, Tiphotrephes 163
Esaki et China, Hydrotrephes China, Limnotrephes Esaki et China, Idiotrephes Lundblad, Paralimnotrephes Poisson and Heterotrephes Esaki et Miyamoto.

SUBFAMILY NEOTREPHINAE China 1940 F. 107

Description. Body more or less flat, from above with fairly large, densely set pits. Head transverse; dorsal and ventral surface separated by distinct longitudinal rib; suture between head and pronotum weakly expressed and not wavy. Eyes relatively small and in shallow cavities. Scutellum short, slightly transverse. Tegmen without any kind of subdivision. Legs thin, long; tarsi of all pairs of legs three-segmented. Females have reduced ovipositor. Live in mountain streams, which are devoid of vegetation and have very quick currents, in the deepenings between rocks, on the bottom of which there is a thin layer of silt. Very sparse, only two to three specimens live in one of these deependings within one to two kilometers.

Comparison. Differs from Helotrephinae and Idiocorinae in three-segmented tarsi and presence of an ovipositor.

Composition. Two genera from South America, Neotrephes China and Paratrephes China.

SUBFAMILY IDIOCORINAE Esaki, China 1927 F. 108

Description. Body fairly strongly flattened. Brachypterous forms occur. Head and thorax completely fused, without any traces of sutures. Antennae one-segmented, strongly shortened, flattened and hidden under the eyes. Scutellum very long. Tegmen not subdivided into clavus, corium and membrane. Legs of moderate length, fore and mid tarsi one-segmented, hind two-segmented. Representatives of both genera were found under small rocks in Lake Tanganyika. Male genital segments 164
asymmetrical and moved to the left. The most specialized family.

Comparison. Differs from Helotrephinae and Neotrephinae in complete fusion of head and thorax.

Composition. Two genera from Central Africa - Idiocoris Esaki et China and Paskia Esaki.

FAMILY PLEIDAE Fieber 1851 F. 109

Description. Small aquatic bugs (2-3 mm). Body strongly shortened, its length approximately only two times larger than width, compressed at sides, from above strongly convex, below flattened. Head and pronotum partially accreted; head hypognathous, wide, with small eyes, sclerites strongly fused. Antennae three-segmented, strongly shortened and completely hidden under head. Rostrum four-segmented, relatively short, slightly projecting beyond fore coxae. Scutellum small, free, scarcely transverse. Tegmen lie on dorsal side roof-shaped, project beyond abdominal apex; strongly sclerotized and covered by a dense sculpturing 165 like small multi-angular pits; they are almost triangular, divide into clavus and corium, membrane strongly reduced and practically missing; tegmen do not lie ono on the other in posterior half of body, forming a straight suture. Hind wings, as a rule, strongly reduced. Pleural region of thorax well developed, especially epimeres; sternites of meso- and metathorax with distinct central projections on hind margin, especially developed metacyphus. Coxal cavities open; coxae pagiopod. Odor glands of metathorax present. Legs not very long, hind evenly covered with fairly long hairs; tarsi of all pairs of legs three-segmented, of walking, suction-adhering type, provided with two claws; pretarsus with a pair of seta-like areolae and central membranous empodium. Nymphs with unpaired central gland on dorsal surface of abdomen. Males make sound with the aid of the hind margin of the prothorax, wich looks like a saw, directed toward the mesothorax. Swim on the back, ventral side above. Predators. Live in standing waters of ponds and lakes with plentiful vegetation, including saline. In moderate latitudes, hibernate in the adult stage. Female lays eggs in plant tissue. In some places, for example, Plea atomaria Fall. are actively eaten by grey mullet families of Atherinidae (Tinarelli, 1962).

EmII and EsIII?

Comparison. Differ from Scaphocoridae and Mesotrephidae in narrower and more convex body and less moved below head, and also free scutellum and few hairs on hind legs (Scaphocoridae); from Helotrephidae in less reduced three-segmented antennae and body form; from Notonectidae in more shortened body, three-segmented antennae and considerably smaller dimensions.

Composition. One genus Plea, which contains about 20 species, not known as fossils, representatives of living fauna are distributed everywhere.

FAMILY NOTONECTIDAE Leach 1815

Description. Small and medium size (4.2-18 mm). Body elongated, torpedo-shaped (especially genera Anisops and Martarega), length approximately 2.5-4 times greater than width, with sides compressed, dorsal side strongly convex like the bottom of a boat, abdominal flat. Head opistognathous, head sclerites almost always fused. Vertex occupies uppermost portion of head, the size of which depends strongly on the size of the eyes. Anterior sector of clypeus (anteclypeus) is weakly expressed and is separated from the sides of the head only by sutures (except fossil subfamily Clypostemmatinae, which characteristically has a distinct subdivision of the fore and hind parts of the clypeus). Antennae four-segmented, rarely three-segmented (genus Nychia), very short, shorter than head, set under the eyes and hidden between the head and thorax. Rostrum four-segmented, short, reaches only to coxae of fore legs; mandibular lever three-branching. No labial palps. Eyes large, reniform, occupy the greater portion of the dorsal surface of the head, in some cases almost fusing at their inner sides (genera Anisops and Martarega). Simple eyes missing. Pleural region of thorax well developed, especially episterna of metathorax; sternal projection fairly large and occurs usually at metathorax (metacyphus). Coxal cavities open; coxae pagiopod. Odor glands of metathorax

correctly described here M.L.P.

weakly developed. Scutellum large, triangular, free. From below the thorax is covered with bundles of long and dense hairs. Tegmen smooth or almost smooth, divide into clavus, corium and embolium and membrane, devoid of veins. Fore and mid legs adapted for grabbing prey and operate with the aid of strongly developed 166 claws; hind legs long, slightly flattened, covered with dense swimming hairs; mid femora have a comb for cleaning the rostrum, analogous adaptation for cleaning occurs also on mid and hind tibia; tarsi two and three-segmented, sometimes one-segmented (genus Anisops), provided with two claws, which are strongly reduced on hind legs; hind legs are provided with sensory organs; glandular ducts also open on the legs secreting a substance that notonectids use to lubricate the body and tegmen to keep from getting wet. The abdomen from below has a central longitudinal fin, densely covered along the sides with long hairs, forming, together with the hairs on the lateral margins, two stripes ie, furrows - air chambers; apex of abdomen is also covered with thick hairs; respiratory tube is missing. Females have ovipositor. Male genital segments symmetrical or asymmetrical. On male legs a stridulatory apparatus like teeth or a comb is often developed. Swim on the back, abdomen side on top.

Biology.[1] Notonectidae live in fresh water; settle basically various puddles, brooks with weakly running water, ponds, primarily in zones well warmed by the sun, rarely in the shade of aquatic plants. Some species live in somewhat marshy water. Other species prefer water devoid of any vegetation, for example, various cement reservoirs. Different from Anisops, which willingly remain in depths because of the presence of long setae on the fore legs which allow them to dive easily into depths, Notonecta abide basically at an angle to the surface of the water, having contact with air. In this position the body forms an angle by which the mid legs touch the water film, and the hind legs are directed forward and in case of danger permit instantaneous rowing. Representatives of the genus Enithares usually catch onto semisubmerged objects or run about the stems of aquatic plants to replenish the supply of air (Hale, 1923). Anisopinae prefer more running water and usually balance themselves in the active state under the surface of the water, although they have been noted (Anisops breddini Kirk.) in hugh numbers in fish ponds in Singapore and Malaya (Leong, 1962).

Notonectids are predatory and in places incur appreciable harm to fish farms, following the young in the period of their emergence from their roe, beginning already with the nymphal stage of the fifth instar (Gorai, Chaudhuri, 1962). How Notonectidae can be serious competitors and dangerous for young fish, is shown by data of N. Berezina (1955), whose studies show that in spawning ponds in an area 0.01 hectares, in one day 2.5-3.5 thousand young fish were eaten by Notonecta glauca L. But basically they prey on aquatic larvae of invertebrate Diptera, Ephemeroptera, Corixidae and various Crustacea (Ostracoda, Cladocera, Copepoda), which they catch with the help of long setae (stylets?) on the fore legs, which form a catching net. In their turn, Notonectidae are eaten by other aquatic predators: aquatic scorpions, large Odonata larvae, aquatic birds and also rarely fish.

Males of some Notonectidae, particularly Anisops, make sounds by means of friction of teeth of the comb of tibia around the projection on the third segment of the rostrum. They are differentiated by the positive phototropism which permits catching them in light.

Eggs are laid in the tissue of plants, most often in leaves and stems, rarely are they stuck to them; in some species there are special floats for attachment. The

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[1] Basically, according to Poisson's (1951) data.

egg is oval, oblong, bears two small projections in the anterior pole. Embryonic development takes about two-three weeks on the average; development of nymphs about one month, so that the last stage is of greatest duration. Usually hibernate in the imagal stage, rarely in the egg stage, among vegetative remains, or both in the adult stage and in the egg stage (Rice, 1954); sometimes, if the temperature is not very low, Notonectidae can be encountered swimming actively below the ice.

Comparison. Differ from all families of the superfamily in the strongly elongated torpedo form of body and densely hairy hind legs; from Scaphocoridae, Mesotrephidae and Helotrephidae (except Helotrephinae) in the strongly convex body from above; from Pleidae in the less wide head, larger eyes and presence of well developed membrane.

Composition: Three subfamilies: Clypostemmatinae, Lower Cretaceous of the Transbaikals, fossil Notonectinae from the Upper Jurassic of Kazakhstan, Cainozoic of North America, West Europe and European USSR, Anisopinae of the Paleocene of West Europe, and also fossil remains not determined to subfamily from the Upper Jurassic of West Europe and Liassic of Asian USSR; representatives of living fauna distributed worldwide. In world fauna over 200 species, of which about 15 species are extinct.

Determinant Table of Subfamilies of the Family Notonectidae

1(2) Clypeus has an isolated anterior sector (anteclypeus) Clypostemmatinae
2(1) Clypeus whole, without isolated anteclypeus.
3(4) Tegmen without pits at base of claval suture; mid femora with spurred distal section; antennae four-segmented; male genitalia symmetrical. Notonectinae
4(3) Tegmen with pits, set with hairs; mid femora simple; antennae three-segmented; male genitalia, as a rule, asymmetrical. Anisopinae

SUBFAMILY CLYPOSTEMMATINAE Y. Popov 1964 T. VIII, F. 6

Short Description. Elongated, almost cylindrical; fairly large. Head strongly transverse; eyes of medium size, frons wide, anteclypeus separated by distinct sutures from surrounding sclerites; rostrum four-segmented, reaching four coxae. Projections of meso- and metathorax well expressed. Ventral side with longitudinal central elevation. Tarsi of all pairs of legs two-segmented.

Comparison. Differs from other two subfamilies, Anisopinae and Notonectinae, in distinctly separated anteclypeus.

Composition. Two genera: Clypostemma Y. Popov from Lower Cretaceous of Transbaikals and Clematina Y. Popov from Oligocene of West Europe.

GENUS CLYPOSTEMMA Y. Popov 1964[1]

Clypostemma: Popov, 1964, p. 64.

Genotype. C. xyphiale Y. Popov, 1964; Lower Cretaceous, Baisin series; Transbaikals, Vitim River.

Description. Fairly large, 16-18 mm. Below strongly hairy, especially the thorax, 168 lateral sides and central ine of abdomen from below less hairy. Head almost twice wider than its length. Anterior sector of frons and fused posterior half of clypeus

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[1] I have given a complete review of the Mesozoic Notonectidae in connection with the imago found with well preserved legs and genital segment; originally, the last, fifth stage of the nymph was incorrectly described as an imago (Popov, 1964).

(postclypeus) form a narrow tongue into the anteclypeus. Labrum well expressed, triangular, not less than the length of the first segment of the rostrum. Eyes large, occupy almost half the head surface. Rostrum segments of unequal length. Central projections of mesothorax (mesocyphus) and metathorax (metacyphus) are developed to an identical degree. Ventral surface of abdomen with wide central elevation and small fin. Legs with well developed claws on mid and hind tarsi. Male genital segments symmetrical.

Specific Composition. Monotypic genus.

CLYPOSTEMMA XYPHIALE Y. Popov 1964 T. VIII, Fs. 3-5, F. 110

Clypostemma xyphiale: Popov, 1964, p. 64-66.

Holotype. PIN 1668/1738; positive imprint of body; Buriat ASSR, Eravnin Province, left bank of Vitim River, below mouth of Bais River; Lower Cretaceous, Baisin series, Baisin layers 19, 31 and 35 (Martinson, 1961).

Description. Body narrow, cylindrical with almost parallel sides, length exceeds width 2.5-2.8 times. Head (together with eyes) almost as wide as fore margin of pronotum; posterior half of clypeus runs deeply into anteclypeus by a narrow convex tongue; anteclypeus wide, less convex; labrum with slightly indented lateral sides, apex of which slightly projects in front of first segment; rostrum gradually thins out toward apex, second segment longest and almost twice exceeds other segments, each taken separately. Central projections of hind margin of meso- and metathorax project like a triangular plate. Tegmen long and project beyond apex of abdomen. Abdomen long, approximately 1.5 times longer than its apex; borders of second to sixth segments almost straight; seventh sternite largest, eighth sternite has sides strongly narrowed backward, second and third valves like narrow longitudinal plates, the latter covered from above by the eighth tergite; central elevation longitudinal, on fourth-sixth sternites elevation wide and more or less flattened, on seventh-eighth narrows noticeably and is raised, the longitudinal fin on it more distinct and sharp. Fore and mid legs of similar structure, fore femora somewhat thicker than mid, tarsal segments of uneven length, first segment of fore tarsus twice longer than second, first segment of mid tarsus 1.5 times longer than second. Hind legs natatory, somewhat longer than others; femora thicker and with small talons on inner side from below, somewhat longer than thin tibia; tarsi thin, two-segmented, first segment more than twice longer than second; tibia and tarsi of hind legs covered with dense swimming hairs, especially long on tarsi. Tibia of fore legs barely shorter than femora and longer than tarsi, tibia of mid legs shorter than femora and longer than tarsi. Lower surface of body thickly covered with long hairs, especially thick on thorax, almost completely hiding the sternal-pleural region.

Dimensions. Length of adult bug 17-18 mm, width 6.5 mm.

Material. Besides holotype (nymph) from same locality, six specimens of adult Notonectidae and over 40 paratypes of nymphs of all five stages.

SUBFAMILY NOTONECTINAE Leach 1815 T. IX, Fs.1-2 170

Description. Of medium size (8-16 mm), rarely smaller. Head with large eyes, most strongly developed in Nychia and Martarega, in which the eyes are contiguous on their inner sides; frons convex or slightly indented; antennae four-segmented, rarely three-segmented (Nychia). Lateral margins of pronotum pitted like glands, hind margin always straight or slightly concave. Scutellum large (Notonectini) or weakly developed (Nychiini). Claval suture at base without sensory pit. Tarsi of fore and mid legs two or three-semgneted, mid tarsi usually with two well developed segments and one very small basal (Notonectini) or only with one well developed segment; mid femora often with clear tooth at apex on outer surface. Male genital segment whole (Notonectini) or split in back; genitalia more or less asymmetrical, especially in Nychia; in Notonecta they are almost symmetrical, vary fairly strongly; gonapophyses of female fairly short, in Enithares weakly developed.

Comparison. Differs from Clypostemmatinae in the not isolated anteclypeus, from Anisopinae in the lack of a sensory pit at the base of the claval suture and presence of contiguous large eyes in representatives of some genera (Nychia, Neonychia, Martarega).

Composition. Eight genera: Asionecta Y. Popov, Upper Jurassic of South Kazakhstan; Pelonecta, gen. nov., Upper Jurassic of West Europe; fossil representatives of genus Notonecta Linnaeus from the Paleocene and Neocene of North America and West Europe; other genera not found as fossils; living representatives distributed worldwide.

GENUS PELONECTA Y. Popov, gen. nov.[1]

Genotype. P. solnhofeni, Upper Jurassic, Solnhofen, FRG
Description. Body oval, elongated, widest at base of abdomen. Hind margin of pronotum almost straight. Sternite of metathorax with distinct central fin; episterna and epimeres strongly developed. Hind coxae, contiguous almost along entire line; trochanter strongly elongated; length of thickened hind ribs 3.7-3.8 times exceeds their width; tibia shorter than femora and hind tarsi. Abdomen raised along central line and delimited by laterotergal fissure; reaching genital segment; central fin comes along entire abdomen.

Comparison. Differs from all known genera in structure of hind legs (powerful femora, small thin tibia and very long tarsi, exceeding length of tibia). Very similar in preserved part of body to living genus Notonecta Linnaeus.

Specific Composition. Monotypic genus.

Comments. The body imprint has acquired an oval-elongated body form, characteristic for Naucoridae, as a result of the strain of the rock containing it along the cross axis of the body.

PELONECTA SOLNHOFENI Y. Popov, sp. nov.[1] T. IX, F. 3, F. 111 171

Holotype. Collection of Munich University, Department of Paleontology and Historical Geology, AS V 8, direct and reverse imprints of body; Solnhofen,FRG, lithographic shales, Kimeridge-Titon, Upper Jurassic.

Description. Lateral margins of pronotum straight, gradually narrowing in front. Basi-sternite, apparently, fused with episternum; epimeres strongly developed, almost of same length as episterna. Inner margins of hind femora straight, outer noticeably curved; tibia linear, thin, less than 1.5 times shorter than femora, devoid of hairs; hind tarsi, apparently two-segmented, 1.2 times longer than tibia, their whole surface covered with a dense set of swimming hairs of moderate length. Abdomen in back of third segment gradually narrows toward its apex, second and third segments largest and widest; laterotergal fissures run along entire abdomen, almost reaching its base; central fin well expressed and also reaches base of abdomen.

Dimensions. Length of body, 19.3 mm, width 9.6 mm.

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[1] From the Greek words pelos (silt) and nectos (swimming).

[1] From the locality in Bavaria - Solnhofen.

SUBFAMILY ANISOPINAE Hutchinson 1929 T. IX, F. 4, F. 112

Description. Of medium size, but not more than 12 mm. Head with large, but never contiguous eyes. Frons convex, often in males elongated in front into a triangle; antennae four-segmented. Hind margin of pronotum sometimes curved (Paranisops). Scutellum, as a rule, well developed, except forms with reduced hind wings (Paranisops). Claval suture at base with pit, in which sensor hairs are set. Tarsi of fore and mid legs one or two-segmented; mid femora without teeth at apex. Abdomen with developed ventral longitudinal fin, usually reaching last abdominal segment. male genital segment, as a rule, whole, not split (except Paranisops); genitalia asymmetrical, weakly variable. A system of stridulating combs (plectrum) and 172 fields (pars stridens) is developed on the legs of males.

Comparison. Differs from rest of subfamilies in presence of sensory pit at base of claval suture, system of stridulators in males, and also narrow and elongated body.

Composition. Four genera[1]: Soevenia Statz, Upper Oligocene of West Europe, other genera - Anisops Spinola, Paranisops Hale and Buenoa Kirkaldy not known as fossils; representatives of living fauna distributed worldwide.

NOTONECTIDAE INCERTAE SEDIS

I have placed in the group Incertae Sedis species which for a whole number of characters can be placed into some known genera, the closeness to which is insufficiently valid.

GENUS LIADONECTA Y. Popov, gen. nov.[2]

Genotype. L. tomiensis, sp. nov.; Lower Jurassic (Lias), Siberia.

Description. Of medium size, 4-6 mm. Head slightly narrower than pronotum. Pronotum strongly transverse, width exceeds length not less than 3.5 times; not wider than base of tegmen, with central transverse fissure along entire line; fore margin curved, hind straight. Central longitudinal fin distinct only in posterior half. Wing case well developed, lateral lobes not set apart or slightly set apart. Hind legs somewhat shortened at base at expense of tibia, noticeably condensed, especially tarsi, which are considerably longer than tibia.

Specific Composition. Monotypic genus.

Comments. The described remnant of a larval form is not in very good preservation. However, the very fact of finding the oldest real representative of the family Notonectidae prompted the author to give it a preliminary description.

LIADONECTA TOMIENSIS Y. Popov, sp. nov.[1] T. IX, F. 5, F. 113 173

Holotype. PIN 1068/1; direct imprint of nymph body; Kemerov Provinces, Krapivin District, left bank of Tom River, above village of Cherny Etap II; Upper Liassic.

Description. Body oval-elongated, its greatest width on level of meso- and metathorax. Head (together with eyes) transverse, width exceeds length slightly more than twice; frons wide, more than less convex, syntlipsis almost twice more than diameter of eyes; eyes fairly large, inner margins almost parallel or slightly separating toward apex. Width of pronotum 3.5 times exceeds length; fore margin

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[1] Notonectites elterleini,(Deichm.), from the Upper Jurassic lithographic shales of Bavaria, can also for now be placed conditionally in this family.

[2] For discovery in the Liassic and Greek word for swimming (nectos).

[1] From the name of the Tom River.

slightly concave, almost straight, parallel to hind; lateral sides slightly curved and narrowed in front; hind margin wavily curved, central portion concave; lateral corners sharp, slightly projecting outward. Wing case strongly shortened, lateral lobes spread apart outward and do not reach fore abdominal tergites, their inner sides spread apart, central projection between lateral lobes distinct and noticeably projecting; length of wing case (beginning with apex of central projection) along central line is 1.3 times greater than length of pronotum. Tarsi and tibia of hind legs of same thickness along entire line, femora thicker, weakly project beyond lateral margins of abdomen, tibia shorter than tarsi 1.5 times; tarsi thickly covered with somewhat shortened hairs. 'Abdomen noticeably narrowed toward apex, length slightly more than width; borders of segments straight.

Dimensions. Length of body (holotype) 4 mm, width 2 mm.

Material. Holotype (collected by I. V. Lebedov in 1948).

GENUS NEPIDIUM Westwood 1854, comb. nov. 174

Nepidium: Westwood, 1854, p. 384, 396; Handlirsch, 1906, p. 639.

Genotype. N. stolones Westw.; Upper Jurassic (Malm), England.
Description. Fairly small, about 8-9 mm. Head transverse, two times wider than its length; hind margin of head noticeably projecting; inner margins of eyes not parallel. Eyes very large, occupy greatest portion of dorsal surface of head. Pronotum more or less trapezoid, lateral margins weakly narrowed in front. Sternal region of thorax well developed. Abdomen not transverse, gradually narrowing toward apex, without longitudinal central fin; margins of first sternite reach lateral margins, borders of segments variable; central portion of fourth-seventh sternites distinctly raised; eighth sternite projects beyond seventh.

Specific Composition. Monotypic genus.

Comments. The redescribed remains originally were somewhat distorted by the strain of the rock containing them along the longitudinal axis of the body, giving it a somewhat "naucorid" form. Apparently, thus, Handlirsch (1906) put these remains into the family Naucoridae. Also, he notes the presence on the imprint of traces of a tooth apparatus; however, I have not been able to examine the original. The presence of a central fin and cylindrical parasternites on the ventral side indicates more that Nepidium stolones Westw. belongs to real notonectids.

NEPIDIUM STOLONES Westwood 1854 T. VIII, F. 4, F. 114

Nepidium stolones: Westwood, 1954, p. 384, 396, Pl. 18, F. 9; Handlirsch, 1906, p. 639, Pl. 41, F. 27.

Holotype. British Museum (N.H.), Department of Paleontology, 12480, reverse imprint of body; Ridgeway, Dorset, England; Upper Jurassic, Lower Purbeck.

Description. Body oval-elongated, its greatest width on level with second abdominal segment; abdomen gradually narrows toward apex. Head with hemispherical convex eyes, which occupy two thirds of head; inner margins of eyes toward base spread apart; frons narrow, smaller than diameter of eyes; vertex and occiput wide, two-three times wider than frons; center of hind margin of head projects like a short and strongly transverse tongue. Pronotum transverse, width exceeds length 2.4 times; fore margin concave, hind straight, lateral margins slightly rounded, almost straight; fore corners distinctly sharpened, hind rounded; pleural region of prothorax without distinct episternal and epimeral sutures; left and right sides of propleura fused in front of coxal cavities; lateral wings of propleura come onto mesothorax. Mesothorax with strongly developed epimeres, partly covering those of metathorax and almost reaching abdomen; inner sides curved, inner corners like tongue-shaped lobes, elongated along fore margin of mesothorax. Epimeres of metathorax triangular, considerably smaller than preceding ones, hind margin of which border upon fore lateral sides of first abdominal sternite. Abdomen widest at the base, its width barely less than length; first sternite concave in central portion of fore margin, hind margin almost straight, central portion slightly concave; fourth to fifth sternites slightly project into previous segments; eighth sternite like two curved plates, separated by seventh sternite and almost closing up under it; 175 borders of fifth to eighth segments evenly curved along entire line; central elevation of fifth-seventh sternites strongly convex and fairly wide, narrowing toward base of fourth segment and like a narrow fin on fourth segment, not reaching third segment and coming into beginning of fifth and second-fourth segments in a weak and wider oval elevation; lateral corners of segments not projecting. Length of body 8 mm, width 4.5 mm.

Episterna

Material. Holotype.

CHAPTER VI

ORIGIN AND BASIC DIRECTIONS OF EVOLUTION OF THE INFRAORDER NEPOMORPHA

Basic directions of morphogeneses in evolution, morphological prototypes of the infraorder and phylogenetic interrelationships with the infraorder Leptopodidomorpha

Generally accepted presently is the opinion that the real Heteroptera, which are connected with water, arose from terrestrial ancestors. Aquatic Heteroptera settled the depths of water (Nepomorpha), its surface (Gerroidea), littoral areas at rivers, lakes, etc. (littoral Ochteridae, Gelastocoridae and Saldidae), and in some cases even the tidal zones of sea shores (Aepophilinae of the Saldidae). Different from representatives of other insect orders (Odonata, Ephemeroptera, Plecoptera, Trichoptera, Diptera), in some, the larval stages are aquatic, and the imaginal terrestrial; real aquatic bugs are in water the whole cycle of development, and in this respect, Heteroptera can be compared only with aquatic beetles. Aquatic bugs spend a great part of their time in water, and the adults abandon water only to fly to other reservoirs or to find cover in winter.

Presently, there is little to raise doubt that all aquatic bugs initially were predators. Popham (1964) has tried to give an answer to the question of why aquatic bugs could have developed only from predatory forms. Bugs which eat plants can procure food material from terrestrial plants and are connected with terrestrial biotypes: vegetarian forms could hardly have succeeded in adapting to life in water and feeding on aquatic plants in connection with the great expenditure of energy in this form of life. It is most likely that ancestral forms of aquatic Heteroptera were multivorous (phytozoophagous - which is the most widely distributed type of feeding in the order); however, they preferred animal food.

Right, in this respect the opinion of Goodchild (1966) is somewhat of an exception. On the basis of Miyamoto's data (1961) on the digestive system of Heteroptera, Goodchild came to the conclusion that the ancestors of bugs were primarily mesophilic sucking insects and sucked out plants like the living thrips (!). Cobben (1968) correctly does not agree with this conclusion, citing the presence among initial (primitive) Heteroptera forms of omnivorous or predatory bugs, a part of which secondarily reverted to phytophagy. This return really occurred (and possibly more than once), but already on a different morphological basis: mobile head, lack of tentorium, etc.; in other words, bugs are bound by their origin in the first instance, i.e., preditoriness. In my opinion, Cobben's suggestion (1965, 1968, p. 376) about the primacy of predatory insects, both for Heteroptera and Homoptera, is contradictory with this point of view and could hardly have occurred.

(of reversion to phyto-phagy)

On the other hand, we can suggest that the surface of reservoirs is visited by or 177 has carried onto it by the wind a large number of insects, which are a rich source of food for Heteroptera which have settled the water. Besides this material, aquatic bugs could have used a large number of small animals, which settled the bottom or thickets of subaquatic vegetation. It is completely natural that nymphs of predatory bugs which lived on littoral vegetation from the beginning accidentally went into the water in search of additional sources of feeding on animal food, and also for protection from drying in drought periods. The large number of animal organisms which they could eat gave a push toward prolonging periods of staying under water both in the larval stage and in the adult state up to the time that now, in the end of ends, their life cycle has become wholly aquatic.

However, one of the groups of aquatic bugs (Corixidae) made good use of the not lesser, if not the greater, the intensification of the vegetative mass of aquatic plants, turning gradually to phytophagy. Representatives of this group of aquatic bugs possess one feature - the presence of functioning odor glands in the nymphs in the 3rd-5th abdominal segments (similar to terrestrial Heteroptera). In all other Nepomorpha there is only one pair of larval abdominal glands. It is necessary to suppose that the presence of these odor glands in any form is connected with phytophagy. Thus, in terrestrial predators of the family Reduviidae, the abdominal odor glands are reduced, as in all predatory, aquatic Heteroptera, Thus, the presence of three pairs of abdominal odor glands is, apparently, an ancestral character preserved in living Corixidae.

Adaptation to life in water corresponds to changes of structure: this process also entails changes in physiology, ecology and etiology. In the first place, the respiratory system underwent radical changes, which is of the most important adaptive significance for constant life in water. The process of carrying on and improving breathing in aquatic surroundings occurred diversely. In this respect, among aquatic bugs of the infraorder Nepomorpha, two basic evolutionary directions are noted: the earlier, with the formation of the respiratory tube (siphon) and the conducting air canal (Nepoidea) and the later, where breathing occurs with the help of air bubbles, the so-called "physical gills" (Naucoroidea, Notonectoidea and Corixoidea).

One of the most important reasons which gave a push toward the settling of aquatic surroundings, from my point of view, in the first place was the pursuit for prey and the finding of new victims, which settled plants partly submerged in water, i.e., active predation; and secondly, the departure from excessive dryness, first to the littoral mesophilic vegetation and later directly into the water onto the submerged plants. The transition directly into the water, according to Popham (1964), promoted hydrophobia of the cuticle of insects, permitting use of the surface tension of the water, and also preventing water from penetrating inside the organism. Nepoidea developed a respiratory tube, which connected the submerged body of the insect in the water with the atmospheric air by an air canal. In all other real aquatic bugs (Naucoroidea, Notonectoidea and Corixoidea), breathing is realized through bubbles of air, with body parts retained especially adapted for this. Subsequently, some representatives of this group (reophilic Aphelocheirinae) acquired more specialized breathing, allowing them to use oxygen exclusively dissolved in water for breathing. An exchange 178 supply is preserved in the spaces between the dorsal surface of the abdomen and the tegmen. Interchange of gases is realized through air bubbles, retained basically by hairs on the body surface and playing the role of "physical gills", which adsorb oxygen from the surrounding water. Nymphs, especially in the early stages, have thin and soft coverings and can carry on exchange of gases along the whole surface of the body and all the easier realize breathing than the adults. From the beginning in Corixidae, and later in Naucoridae, in the course of the evolutionary process, the dorsal-ventral flattening of the body occurred, which visibly permitted the ventral surface bearing the air bubbles (China, 1955; Popham, 1964) to increase, making exchange of gases easier. In Notonectoidea the basic air supply is preserved in the space formed by the flat dorsal surface of the abdomen and the roof-shaped folded wings, and also in the rows formed by the lateral and central rows of dense hairs on the ventral side of the abdomen (f. 59).

Transition to living in water occurred in aquatic Heteroptera of the infraorder Nepomorpha, most likely, through littoral and aquatic vegetation: such an intermediary form of life is characteristic for the littoral Ochteridae and Saldidae. Thus, representatives of living littoral families, for example, Gelastocoridae, were not even once observed visiting plants or other objects semi-submerged or even completely submerged in water (Todd, 1955).

For all aquatic bugs, except Nepoidea, the general process of accretion of the external head sclerites is characteristic, which leads to the complete fusion of both parts of the clypeus without any traces of sutures, the widening of its distal portion - anteclypeus - and also the appearance of a special filtering system in the throat, known under the name of ~~gular or~~ pharyngeal teeth. The process of fusion of head sclerites, most likely, occurred independently and not simultaneously in the

and Corixoidea ?

"cibarial" is better term

various groups of true aquatic and littoral bugs, since we still observe an isolated clypeus in the Jurassic Shurabellidae and Clypostemmatinae, even after the isolation of true aquatic forms from the littoral. In the earlier separating Nepoidea, the isolated clypeus is preserved in the present time. Development of the above-mentioned filtering system is a result of the use of small plant particles as well as living animal food. As a result, detritophagy developed and, finally, based on it, many living Corixidae realized almost complete transition to vegetative food.

anteclyp.
M.C.P.

The appearance of phytophagy among aquatic Heteroptera, like the algo- and detritophagy in Corixidae, did not come from any sudden phenomenon, but was prepared for by the entire path of historical development of the Nepomorpha. The gradual transformation and complication of the filtering apparatus can be traced in the infraorder I have studied. First of all, this was expressed in the appearance of the system of small hairs and knobs on the epipharyngeal and hypopharyngeal sides of the throat, forming the most simply constructed filtering apparatus (Nepoidea and, possibly, ancestral forms of the littoral Gelastocoroidea). The following stage of complication of the filtering system is observed in the living littoral families Ochteridae and Gelastocoridae, in which there is a transversely striated chitinized plate (the "striped" plate) on the epipharyngeal surface of the esophagus. The subsequent improvement of this apparatus occurs in the Notonectoidea, and then the Naucoridae, where it is represented by a system of "striped" plates and teeth (pharyngeal teeth) on both surfaces of the throat which also fulfill the function of pulverizing food particles by grinding them. And, finally, the most complex filtering apparatus is 179 attained by the aquatic phytozoophags of the living family Corixidae. The origin and development of the filtering system in Nepomorpha is a distinctly apomorphic phenomenon, and its development occurred independently at least twice (Nepoidea and all the other groups) or, perhaps, even three times (Nepoidea, Corixoidea and the remaining Nepomorpha), as Parsons (1965) correctly affirms.

cibarium
(M.C.P.)

It seems that the real aquatic Heteroptera arose from littoral forms by at least two independent branches. This, however, is contradicted by the later phylogenetic scheme of aquatic bugs suggested by China (1955), which essentially is a confusion of the typological and phylogenetic principles of the construction of a scheme. The original divergency of the main branches of the infraorder - superfamilies (Nepoidea and, possibly, Corixoidea) or complex of superfamilies (Gelastocoroidea, Naucoroidea and Notonectoidea) - consists of the above-mentioned development of the respiratory apparatus and filtering system of the throat. The first stage of adaptation to an aquatic form of life was made by the littoral ancestors of the nepoid-belostomatid branch (Nepoidea). Some of them in the new for them conditions of aquatic surroundings initially became adapted to swimming, and subsequently development and distribution of the swimming belostomatid forms (Belostomatidae) arose in connection with the increase of speed of movement and final transfer to active predation. In the course of time, some of them came to lead a form of life of lying in wait for prey, moving about slowly on the bottom. In a number of forms, for a closer connection to the ground, arose the serious reconstruction of the sterno-pleural region of the thorax, including lateral divergence of the leg coxae and development of the sternal portion of the thorax (Nepidae).

Representatives of Nepoidea demonstrate a great morphological similarity of the sutures of the head capsule with those in representatives of the family Saldidae, similarity of the basic salivary glands with those of the Ochteridae and have a weakly developed filtering apparatus of the esophagus (at least in Nepidae and Belostomatidae), which is plesiomorphic within the limits of this suborder. An analogous divergence of the coxae and development of the sternopleural region of the thorax we encounter in the other closely related infraorder - Leptopodidomorpha - in representatives of aquatic groups (Gerridae, Veliidae, Hebridae, etc.), but here these phenomena are connected with active movement along the aquatic surface. Examples of secondary

cibarium

divergence of leg coxae occur also in other insects, for example, in the Hymenoptera Chalcididae in connection with parasitism on scales and scale insects in the sinuses. of leaves [?] or in Diptera, ectoparasites of Hipoboscidae for closer attachment to the host; leg coxae are strongly moved apart in many insects which live under bark, for example, in bugs of the family Aradidae, beetles of the family Nitidulidae, etc.

Isolation of the corixid-like forms from the ochterid-like or even from the gelastocorid-like ancestors is the second stage of entry of littoral Heteroptera into water. Development of the corixid branch occurred along the line of intensive specialization of a whole number of organs (flattening of the body, especially the last abdominal segments, strong modification of the mouth parts, development of the throat filtering apparatus, appearance of diversely constructed stridulators, etc.), on the one hand, and preservation of plesiomorphic traits for the whole infraorder (presence of simple eyes in the most primitive forms, presence of three pairs of abdominal odor glands, wide aperture of the basic salivary glands), on the other.

The third stage of entry of the Heteroptera into water occurred somewhat later, after the isolation of the littoral families Ochteridae and Gelastocoridae (or their ancestors), when true Nepidae and the first Corixidae had already finally been formed. 180
Most likely, these were some kind of swimming bugs. They moved actively from the silty and meadow-flooded banks directly into water, also using the submerged aquatic plants and sunken terrestrial plants as a substrate. The active mobile form of life led in many forms to condensing of the tarsi or even the tibia of the hind legs and appearance of long (Notonectidae, some Naucoridae), dense (Scaphocoridae and most of the recent families) swimming hairs.

Later, part of the aquatic Heteroptera naucorid branch, instead of flatly folding wings, acquired a roof-shaped folding, using the formed space as a reservoir of air supply (Notonectoidea).

The most probable ancester of all Nepomorpha, as already mentioned above (see Chapter IV), must be considered the hypothetical ochterid-like form, which possessed the maximal number of plesiomorphic characters, mosaically preserved in the separate families (superfamilies) of the infraorder. In Hennig's opinion (1953, p. 13), according to the principle of deviation and his idea about "sister groups" (Schwestern-Gruppen), the latter is the plesiomorphic sister group, which remains at the point of origin of the othr, apomorphic in respect to it, Nepomorpha sister group.

The hypothetical ancestral form I have suggested would have possessed the following basic plesiomorphic characteristics:

insert: ... (the ochterid-like form) is that representative of the ...

1. Body flattened
2. Head opistognathous.
3. Anteclypeus distinctly separated by external sutures.
4. Rostrum opistognathous, four-segmented, of moderate thickness and reaching at least the base of the abdomen.
5. Eyes large, reaching fore corners of pronotum or projecting beyond them.
6. Two set apart simple eyes present.
7. Antennae four-segmented, long, not hidden under the eyes and visible from above.
8. Mandibular levers of the 4th type, i.e. 4-cornered, directly adjoining the stylet.
9. Hind margin of pronotum indented, scutellum entirely unconcealed; fore cornors widened like a leaf.
10. Tegmen well delimited into three sections: leathery clavus and corium and more or less transparent membrane.
11. Membrane with five closed cells, which do not reach apical portion of wing.
12. Thorax with withdrawn sternal (cryptosternum) and strongly developed pleural regions.
13. Pleural region of meso- and metathorax segmented . Metathorax with openings of odor glands.

14. Leg coxae strongly drawn together, often contiguous, of padiopod type, i.e., move in one plane.
15. The three pairs of legs homonomous, walking; all tarsi three-segmented; tarsal claws apical, symmetrical.
16. Male genital segments and genitalia symmetrical; female genital segments with ovipositor.
17. Ovipositor has the following structure: first gonapophysis long, smooth; second gonapophysis long, its folds not fused; gonoplak well developed; gonangulum developed like a triangular plate.
18. Filtering apparatus of throat consists of a system of knobs and hairs. 131
19. Digestive system possesses the following features: esophagus short, midgut of three sections - stomach, tube and bladder-like sections; pylorus very short, scarcely visible; hind gut of two sections - short ileum with covering and sack-shaped straight gut with rectal covering; main salivary glands two-lobed, simple, smooth, with wide aperture; accessory glands [illegible] - bubble-like and elongated, as long as main glands; malpighian tubes like two pairs of more or less long, weakly curved tubes, apices of which are free.
20. Male reproductive system consists of a two-lobed, spiral-like vasa deferentia, containing not more than 4-5 follicles, a ductus ejaculatorius with a vesicula seminalis at the basal portion and a mesodene at the apex of the ductus ejaculatorius.
21. Female reproductive system consists of a short ovipositor, short bubble-like vagina, long spermatica and long duct of the spermatica.
22. Form of life: littoral.

The described hypothetical proto-ochterid form must have been the initial plesiomorphic group of the infraorder Nepomorpha, consisting exclusively of littiral representatives of the Heteroptera. I have placed this ancestor at the very base of the phylogentic tree of the Nepomorpha, and it must have arisen directly from another hypothetical protosaldid form that belongs to the same group which, in my opinion, in its turn, must stand at the very base of the order Heteroptera.

Thus, the common ancestor of the entire group of the Heteroptera of the infraorder Nepomorpha, or aquatic bugs, can be considered to be the hypothetical primitive protoochterid forms of the ochterid branch and, correspondingly, all aquatic bugs initially were littoral predators. The ancestors of the three superfamilies - Nepoidea, Corixoidea and Naucoroidea, apparently went along this path independently.

The first splitting of the protoochterid stem evidently arose in the early Triassic as a result of the appearance of aquatic protobelostomatid forms (Nepoidea), which possessed a short respiratory tube and more or less walking legs, and their isolation from the less specialized forms of the basic littoral stem. This apomorphic nepid branch is represented presently by the two aquatic families Nepidae and Belostomatidae.

The second, later, splitting occurred apparently at the beginning of the second half of the Triassic. As a result of it, two superfamilies were isolated: the littoral Gelastocoroidea and the aquatic Corixoidea. Representatives of the former superfamily possess a lesser number of apomorphic traits, and living Ochteridae and Gelastocoridae have preserved a whole number of plesiomorphic traits (head with long opistognathous rostrum, simple eyes, 4th type of manidbular levers, venation of tegmen, structure of separate internal organs, etc.). Representatives of the latter corixid-like superfamily, along with some ancestral plesiomorphic characteristics (simple eyes in some forms, wide aperture of salivary glands, presence of abdominal odor glands in nymphs), acquired traits of strong specialization (multivorous, stridulating apparatus as an isolating mechanism, etc.), which permitted a considerable increase in diversity (basically [illegible] species) of the single living family Corixidae.

The strongly specialized forms of this family are the most numerous group of recent fauna of the infraorder (slightly more than half of all true aquatic).

The third large splitting occurred in the remaining littoral stem because of the 182
isolation of new aquatic predator forms (Naucoroidea) from the active littoral predators of the type represented by the living more or less specialized family Gelastocoridae. The final departure of the naucorid aquatic branch (Naucoroidea), which in the present epoch is represented by the one family Naucoridae, apparently occurred not later than the Triassic.

And, finally, the fourth, basic splitting, already the naucorid stem proper, was realized by the isolation of aquatic helotrephoid-like forms with strongly convex body, fore legs weakly adapted for grasping, and strongly shortened thick rostrum, which subsequently was transformed into a group of aquatic bugs with hypognathous head, strongly convex body and roof-shaped folding wings. Thus arose the superfamily Notonectoidea, which evolutionized into the direction of perfection of active predation. Apparently, the connecting link between these superfamily groupings was a fossil aquatic Heteroptera related to the living South American relict subfamily Potamocorinae, which is the most primitive among living Naucoridae (China, 1936, 1940; Usinger, 1941; Hungerford, 1942). These small aquatic bugs, along with basic traits of the superfamily Naucoroidea, demonstrate some similarity to the primitive Helotrephidae of the New World (Paratrephes and Neotrephes), which served as the reason for China (1955) to branch the protohelotrephoid off from the naucorid-like ancestors. The first Notonectoidea separated from the ancient Naucoroidea, most likely, at the border between the Trias and the Jurassic (not later).

A more precise timing of the appearance of the above-discussed superfamily unfortunately for now remains not entirely clear and in each case must be made with reservation, indicating only approximate periods of origin. This lies in the fact that apparently the above-noted splittings of the basic branches had relatively small time hiatuses because of the existing convergent apomorphies of these groups. Judging from the available sparse paleontological finds, the basic processes of divergency of the superfamily groups of Nepomorpha occurred in the early Mesozoic: in the interval of time between the Lower Trias and Lias (f. 115).

As has already been discussed above, the ochterid branch most likely arises directly from the other littoral (protosaldid) group, which at the beginning apparently represented a different, basic direction of evolution of the infraorder Leptopodidomorpha - adaptation to life on the surface of water (Gerroidea). The lack of a single opinion on the solution of the question of the true congeneric interrelationships between living littoral families Ochteridae and Saldidae, placed correspondingly at the bases of the phylogenetic trees of Nepomorpha and Leptopodidomorpha, does not permit me to have a generally accepted point of view regarding their origin. One of the reasons, in my opinion, is the most plesiomorphic condition of both discussed littoral families among the groups of Heteropters of the infraorders Nepomorpha and Leptopodidomorpha, and also the difficulty of determining the character of the adaptive characteristics. Thanks to an analysis of the morphological traits of the most generalized recent littoral families Ochteridae and Saldidae, it became possible to construct the above-mentioned hypothetical initial ancestral protoochterid form, characterized by approximately twenty plesiomorphic characters.

In my opinion, the initial ancestral form for all groups of aquatic bugs (Nepomorpha
and Leptopodidomorpha) of the order Heteroptera basically must be differentiated from
the protoochterid form by the more distinct segmentation of the external sclerites of 183
the head, the more drawn together simple eyes, the distinctly reduced membrane and character of structure of the separate structures of the digestive system (mid gut consists only of two sections, the malpighian tubes of two or possible even three pairs of fairly short almost straight tubes).

However, the most difficult problem remains the origin of the amphibial Gerroidea and, in connection with this, the taxonomic position of the Saldidae. For a long time the opinion existed (Bueno, 1923; Ekblom, 1929; China 1965a, Carayon, 1962, Parsons, 1965, 1966a) that the most probable ancestors of the above-water bugs can be hypothetical protosaldid forms. Recently, on the basis of thorough investigations of the digestive organs of Heteroptera, this point of view has come into doubt (Miyamoto, 1961). This study showed that the greatest differences of the Saldidae from the Gerridae are contained in the structure of the basic salivary glands, which are unique among Leptopodidomorpha, and also the malpighian tubes. The constancy of structure of the salivary glands is strictly sustained for each infraorder of bugs which I have established; on this basis, Miyamoto has shown the similarity of these groups in the structure of basic glands (same width of aperture of glands) and the malpighian tubes (two pairs of short, weakly developed tubes) of the Saldidae with those of Cimicomorpha, assessing this as proof, on the one hand, of their relation- 184 ship and, on the other, of the great primitiveness of the family Saldidae.

However, as my analysis has shown, these characters in no way are synapomorphic and, consequently, hardly have significance for explaining the degree of the phylogenetic relationship of the littoral Saldidae and the terrestrial Cimicomorpha. The unclear structure of the basic salivary glands (simple two or one-segmented with wide aperture) in the Saldidae (Leptopodidomorpha) and Cimicomorpha (and, also, consequently, in the Pentatomomorpha) is different and indicates only the plesiomorphic condition of the Saldidae and the apomorphic condition of the latter infraordinal groups of terrestrial Heteroptera.

Actually, in the course ofthe historical development of the order Heteroptera, the smooth covering of the basic salivary glands, consisting of numerous flat cells, came to acquire a different structure, represented by large high cells, and the aperture of the glands correspondingly became narrow. This apomorphic process arose both in overwhelming majority of representatives of the aquatic groups of bugs (Leptopodidomorpha, except Saldidae, and Nepomorpha, except Corixidae), and in a small part of the terrestrial Heteroptera (Enicocephalomorpha), i.e., bore a definite divergent character and, thus, also cannot be used as a definitive indicator of their phylogenetic relationship.

In the basic mass of terrestrial Heteroptera (Cimicomorpha and Pentatomomorpha), the development of structures of the basic salivary glands followed the line of decrease of the size of cells and increase of their number, which led to a secondary (autapomorphy) increase of the aperture of the glands. For Cimicomorpha and Pentatomomorpha, the result of this process was synapomorphy and, consequently, excludes their phylogenetic closeness.

In the infraordinal groups of aquatic bugs (Nepomorpha and Leptopodidomorpha), in the recent families Saldidae and Corixidae, the plesiomorphic condition was preserved of the structure of these glands - smooth covering of flat cells with wide aperture. Such a symplesiomorphy for these families, of course, cannot serve as an indicator of close phylogenetic relationship. It can indicate the Saldidae as the most primitive group of Heteroptera, and for Corixidae serve as an indicator of the very early isolation of the latter from the basic stem of the Nepomorpha.

The similarity of the Saldidae and the terrestrial Heteroptera in the structure of the malphigian tubes, which are shortened and weakly curved in both groups, from my point of view, must be considered as definite symplesiomorphy. The study of the structure of the head capsule conducted by Parsons (1962) also puts in doubt the possibility of the Gerroidea actually branching off from the Saldidae. An analysis of a great number of characters of the external and internal morphology of Saldidae and Gerroidea conducted by Gupta (1963b) led him to the definite conclusion of the impossibility of including the Saldidae in the Gerroidea (Amphibiocorisae s. Gupta). Recognizing the separate identity of the Nepomorpha and the Cimicomorpha, this investigator, on the basis of

the similarity of the structure of a number of structures, suggests joining the Saldidae either with the Cimicomorpha (labrum, additional salivary glands, distal fusion of the veins R and M of the hind wings, and oval odor reservoir od the odor apparatus) or with the Pentatomomorpha (structure of male genitalie and eggs), proposing two variants, which are illustrated in the two schemes. Gupta, recognizing parallelism in the evolution of the eggs and the male genitalia as the most probable variant, in the end, is inclined to consider the Saldidae as the Cimicomorpha line. In my opinion, such a similarity of a number of characters to the basic groups of Heteroptera (Cimicomorpha, Nepomorpha, Pentatomomorpha and also, correspondingly, to Leptodidomorpha) indicates first the most primitive condition of the Saldidae and 185
the necessity of putting them at the base of the heteropterous phylogenetic stem within the infraorder Leptopodidomorpha, where the Gerroidea are clearly an apomorphic branch of bugs, adapted to life on the surface of water and isolated, apparently, from some kind of saldid-like ancient forms. Secondly, the little similarity in structures having great convergency (eggs and genitalia) characterizes the Pentatomomorpha as the most isolated group of bugs, representing a special evolutionary branch of the Heteroptera. Nonetheless, a similar phylogenetic analysis is needed of leading characters with a precise explanation of their ano- and plesiomorphology, and it is on this basis, proceeding from the presence of synapomorphy, that it will be possible to establish the true phylogenetic relationship.

Most recently, Cobben (1968) again called into serious question the existence of proto-saldid forms as the supposed ancestors of both the Nepomorpha and the Leptopodidomorpha. Cobben considers the Gerroidea (Amphibiocorisae s. Cobben) as the initial primitive group of Heteroptera which, in his opinion, possess a primitive type of embriogenesis, egg structure and phallic structures. However, he for some reason completely ignored such a morphological indicator of clearly apomorphic character as the set apart position of the coxae and, in connection with this, the secondary change of the sterno-pleural region of the thorax. In connection with the transition to life on the water surface, the set apart leg position was a consequent adaptation to new conditions; this indicates that all Gerroidea arose from some littoral saldid-like form and are undoubtedly a secondary group. We run across an analogous situation in the family Nepidae, in the presence of many preserving plesiomorphy, where the strongly set apart legs serve as an important adaptation to a benthid form of life. The strongly specialized wing venation also testifies against considering the Gerroidea as the initial group. Such a variable indicator as the structure of the reproductive organs (in this case, phallic structures), which is applied a gread deal for differentiating species and even genera, can hardly serve as a criterion for such relatively large taxons as family, and even more so, superfamily or infraorder. In this connection, demonstrative are the erroneous phylogenetic conclusions of Kumar (1961) regarding the supposed closely related connections of Coreidae and Notonectidae, which supposedly have a common terrestrial ancestor, or the Reduviidae and Belostomatidae, also not connected by a common origin, and, besides, the necessity of separating the Nepidae and Belostomatidae as one group. A similar solution to phylogenetic problems, based only on some one morphological indicator and especially on such superficial and limited structures as genital, can hardly be accepted.

? opinion of Popov, not Kumar?

Cobben places great significance on the embrionic development of bugs, considering the relations between the features of development of embryos as independent adaptations. Thus, he considers that a comparison of the embriogenetic types furnishes the truest data for the phylogeny in comparison with other indicators used for classification. Determining the primitive type of embriogenesis as the invagination of the embryos under conditions of preservation of connection of head parts with the serosa and rotation of the embryo 180° before the basic complete turnover, Cobben came to the conclusion a similar type of embriogenesis occurs only in the Gerroidea (especially in Hebridae) and the Cimicomorpha and, consequently, the Gerroidea can be considered as the most primitive group. Sticking to his last assertion, Cobben shows the gradual

revolution?

re rotation?

loss of such an embryonic rotation before the complete turnover of the embryo in all Pentatomomorpha and Reduviidae. However, from my point of view, this circumstance 186 can harly serve to show the actual primitiveness of the Gerroidea, all the more since in Nepomorpha such a "180° rotation" is preserved.

Furthermore, Cobben differentiates two basic types of ruptures (realized by four methods) of the embryonic cuticle of the head as a result of the evolutionary development of the egg structures: transverse ruptures in the region of the clypeus (clypeal) and longitudinal in the region of the frons (frontal). Thus the transverse ruptures are considered as a plesiomorphic condition, and the longitudinal as apomorphic. In some Gerroidea, Cobben considers the transverse type of rupture as initial (Hebridae and Veliidae), which later changed into longitudinal (Gerridae, Hydrometridae, Mesoveliidae). In the Saldidae there are both frontal and clypeal ruptures. In this case, the question is not asked whethr the presence of transverse and longitudinal sutures simultaneously is a plesiomorphic condition in the case of the Saldidae. Thus, in the course of historical development in some Heteroptera was preserved the transverse nature of the embryonic factor of the head capsule (Leptopodidae, some Gerroidea), in others longitudinal (some Gerroidea and all other Heteroptera). The realization of longitudinal rupture in various groups arises differently. If the transverse (clypeal) rupture is considered primary, then its position in the Saldidae (not like in the Leptopodidae) is more "beginning", i.e., occupies a lower position than in Hebridae and Veliidae, or is identical to the initial suggested archetype (Cobben, 1968, f. 278). Cobben himself perceives something strange in this fact, explaining this as an increase of the anteclypeal region and the simultaneous shortening of the vertex.

In the laying and orientation of the laid eggs, Cobben also distinguishes three basic types, of which the surface horizontal position of the egg (Type I) is considered to be the initial primary one different from Type II (surface vertical position of the egg) and Type III (egg basically intruded into the plant tissue). However this scheme of evolution of ovipositing shows that the primary horizontal type has representatives of all families and that between the other two types there are a number of transitions. Besides, the questions of the primariness of the character of egg laying, apparently, must be considered solved, since in Homoptera Type III is most common, i.e., insertion of the egg into the plant tissue. The position ofthe embryionic region also does not provide proof of primitiveness for many groups. Thus, besides the Saldidae, which have a primitive central position of the embryo, we find an analogous orientation in Miridae, Cimicidae, Coreidae, a fairly close position in Hebridae, Reduviidae and Nabidae. However, in Gerroidea the embryo distinctly occupies a lateral position like the majority.

And, finally, all schemes of closeness of groups, based on similarities of some stages of ontogenetic development, usually do not correspond with their actual congeneric ties and the evolutionary paths of the basic groups of taxons (approximately in the rank of infraorder), established on morphological and paleontological data.

Without belittling the great significance of Cobben's excellent embryological book, which still is one important step in the matter of the study of the evolution of bugs, I, however, can in no way agree with his idea about the Gerroidea (Amphibiocorisae s. Cobben) as the initial group of all Heteroptera and in this case return to the last opinions of China (1955) and Carayon (1962) about the origin of the Gerroidea from a saldid-like ancestor.

I have examined in somewhat greater detail the basic stages of embryogenesis and egg structures of Heteroptera, since many of them can be interpreted simply indepen- 187 dently from the established point of view.

In connection with the problem of the position of the littoral families Ochteridae and Saldidae in the system of aquatic groups of Heteroptera (Nepomorpha and Leptopodidomorpha) as supposed initial taxons and connected with this question of their origin, not without interest also is an explanation ofthe congeneric interrelationships of the superfamilies Gerroidea and Leptopodoidea. In the course of recent years, great interest has been drawn to the amphibious family Mesoveliidae. The fact is that representatives of this family, apart from the basic characteristics of Gerroidea, also possess those of Leptopodoidea (Scudder, 1959; Gupta, 1963ab; Kumar, 1961, 1964): a number of related traits of head, abdomen, to a lesser degree thorax, distal fusion of the veins R and M of the tegmen, structure of female genitalia - particularly similar is the weakly concave, hard ovipositor and the correlatively connected with it method of egg laying (Type III according to Cobben), and also the separate stages of embryogenesis. All of this raised doubt in some authors regarding its taxonomic position, and attempts were even made to put the Mesoveliidae into the Leptopodoidea (Scudder, 1959). The lack of a gonoplak in the female genitalia of the Gerroidea and the presence of the latter in one of the members of this superfamily, Mesoveliidae, served as the basis, as Gupta (1963b) correctly explained, to consider the Mesoveliidae as a primitive group or a separate branch, which separated before the time that all its other members lost the gonoplak. It is probable that this also served as one of the reasons for Cobben to put the Gerroidea at the base of the entire Heteroptera stem. In connection with this, I have come to the conviction that, in view of a whole number of such means (apomorphic and plesiomorphic), Mesoveliidae evidence a true, although possible a separate, relationship with the family Saldidae, and apparently are one of the real connecting links between the amphibial Gerroidea and the littoral Leptopodoidea. It is also possible that all Gerroidea arose from some mesoveliid ancestor common to Gerridae+Veliidae and Hebridae (?), isolated in their time directly from the basic protosaldid stem (it is also not excluded that this was possibly the common ancestor of the Ochteridae and Saldidae). Since an explanation of the phylogenesis of the closely related infraorder Leptopodidomorpha is not basically part of the problem of my investigation, just as I am limited in scope, I am limited only by this preliminary opinion.

Interesting also for the Saldidae as the most primitive group among living Heteroptera is the fact of the existence of the cross veins rm and m-cu on the hind wing. This is a unique chracter for Heteroptera, and we find it only in the closely related order Homoptera, namely in the suborder Auchenorrhyncha. Apparently, this phenomenon bears a purely convergent character.

The infraorder Leptopodidomorpha (together with the Nepomorpha), which is one of the four[1] main evolutionary directions of the order of real Heteroptera, in its phylogenetic roots goes back deep into the Triassic and possibly even the Permian. However, the Permian with respect to Heteroptera fauna for now remains for us an absolutely blank spot and we can only assume that the infraorders of aquatic and terrestrial bugs had common ancestors. It is possible that these are the early Mesozoic Actinoscytinidae, which apparently arise directly from the Homoptera or even from a common ancestor of the latter and the Heteroptera.

The phylogenetic schemes which I have suggested are to a considerable degree pre- 188
liminary and in the future, probably, will be essentially supplemented and changed.

PHYLOGENY OF THE SUPERFAMILY NEPOIDEA F. 116

The isolation of the apomorphic group of the nepid-like bugs from the plesiomorphic protochterid ancestors must have occurred approximately in the early Triassic. In intering the water in search of food, the first nepids gradually began to conquer littoral areas: shore or semiaquatic plants which grew in the shallows of various closed basins, of estuary type, backwaters, flood plains, etc. With the development of a respiratory tube, the ancient aquatic scorpions began to transfer to gradual

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[1] The three other evolutionary directions are represented by the infraorders Enicocephalomorpha+Cimicomorpha, Pentatomorpha and Actinoscytinomorpha.

habitation in water. In these new places of habitation, they crossed over to a new source of feeding: fish roe, young, small crustacea and molluscs and also aquatic insects.

The first nepoids were small in size and apparently still had weakly developed leg coxae, not very different from the plesiomorphic condition of those in the protoochterid ancestors, and also a more or less distinctly developed respiratory siphon. It seems to me that the other characteristics are as follows: body became wholly flat, not convex from above (apomorphy), weakly sculptured (plesiomorphy), head prognathous, with distinctly separated anteclypeus (plesiomorphy) and 4-segmented more or less long rostrum, eyes large, but smaller than in ancestral littoral form and do not project beyond fore corners of the pronotum (apomorphy), ocelli missing (apomorphy), antennae 4-segmented, shortened and almost wholly hidden in the lower side of the body (apomorphy), pronotum without leaflike widening at fore corners (apomorphy) and with indented hind margin, rest of scutellum completely open (plesiomorphy), membrane of tegmen with more than five cells (apomorphy), fore legs directed forward and more or less grasping with unevenly developed tarsal segments, mid and hind legs became more flattened and somewhat longer than fore (apomorphy), ovipositor basically similar to that of protoochterids, digestive system with more or less long esophagus, divided mid gut (apomorphy), short pylorus, twice-dividing hind gut (plesiomorphy), salivary glands elongated, malpighian tubes of two pairs of long curved tubes, apices of which free (apomorphy), male and female reproductive system, apparently, analogous to that of protoochterids.

Subsequently, the ancestral forms of the nepoids became larger (by a few centimeters) and basically mastered the deep waters as a result of activization of pursuit of prey and, in the appearance of adaptation to swimming, nektonic forms served to develop the second basic direction - Belostomatidae. The establishment of the belostomatid group was accompanied first of all by the acquisition of maximal body size for all nepoids (up to 6 cm in fossils and to 11 cm in living forms), some increase of the convex eyes, acquiring ellipsoid form and reaching the fore corners of the pronotum; shortening of the clavus (except Stygeonepinae) and ,correspondingly, the claval suture (commissura clavi) approximately to the length of the scutellum; transformation of the cells of the membrane of the tegmen into parallel veins and flattened mid and hind legs in most forms.

In the second half of the Jurassic, among nepoids of belostomatid direction, the 189
quickly swimming Stygeonepinae became isolated with clearly expressed traits of extreme specialization: strongly flattened oar-shaped hind legs, thin and long mid legs, adapted apparently for attachment to the substrate, similar to living Corixidae, and also strongly developed original grasping fore legs and original elongated drop-like body. Together with this, this form preserved an amount of plesiomorphy: such as the long claval suture and relatively small convex eyes. Apparently, one of the basic reasons for the extinction of the Stygeonepinae was the unsolved inner contradiction between locomotion and predatory form of feeding; i.e., on the one hand, ~~the~~ need to overtake quick-swimming (sustained for a long time) prey. Actually, in Stygeonepa foersteri, sp.n., the long hind swimming legs with elongated femora and oar-shaped tarsi with very shortened tibia did not permit operation with great frequency and did not provide sufficient progressive movement according to the principle of resistibility.

Later, the development of the belostomatid branch followed the line of formation of quick-swimming forms like the separate and extensive family Belostomatidae through the preservation of less mobile and slowly-swimming forms of the sea genus Mesonepa, which had weakly flattened and fairly long mid and hind legs (particularly the tibia), strongly developed fore grasping legs and less developed venation (nepid type). In connection with quick swimming, the mid and hind terminalia in most Belostomatidae became shortened and more flattened, basically due to the appearance and development

legs?

insert: ... the possibility of relatively quick (but short-lived) swimming and, on the other hand, the ...

of the longitudinal rib along the whole line of the tibia from outside (which we can well observe in the Jurassic Mesonepa primordialis Germ. of the subfamily Belostomatinae) and the direct widening of the tarsi with the formation of swimming hairs like a thick short brush on the inner side of the tibia and tarsi. However, later in representatives of Mesobelostomum deperditum Germ. - another Jurassic subfamily of the Lethocerinae, which was isolated, apparently, from some Belostomatinae - a strong roughness was preserved and in places even an uneven dorsal surface of the body, which apparently made quick swimming very difficult, and they became extinct in the Mesozoic.

The Cainozoic Belostomatidae (Lethocerinae, Horvathiniinae and Belostomatinae) achieved a more successful development, in which along with gradual development of swimming legs arose a hydrodynamic terminal development of the body with acquisition of a smooth surface, comfortable for quick swimming.

Especially interesting for the morphogenesis and phylogeny of the nepoids is the center fissure on the sternites of the abdomen, which demarcates the parasternites and laterotergites. In many living forms a fold occurs at this place (Nepinae), which disappears in the most specialized representatives (Ranatrinae) due to the protrusion of the parasternite under the laterotergite (f. 53b). A different path occurred in the disappearance of the above-mentioned fissure in living Belostomatidae: as a result of gradual fusion of the parasternites with the sternites proper, on the one hand, and the strong widening on the other.

Recent Belostomatidae are represented by three different in size subfamilies: Lethocerinae, Belostomatinae and Horvathiniinae, of which Lethocerinae are recognized as initial, and the Horvathiniinae occupy an intermediate position between them and the Belostomatinae (Menke, Lauck, 1961). An analysis of the characters which characterize these subfamilies showed that the Lethocerinae and Horvathiniinae together with the Belostomatinae are not connected with each other directly and only come, apparently, from a common ancestor, which had distinctly expressed central fissures the whole length of the abdomen and fairly narrow laterotergites.

Actually, in Lethocerinae and Horvathiniinae practically missing is distinct synapomorphy (except the single apomorphic character - finger-shaped projections on the 2nd and 3rd segments of the antennae, which, most probably, is convergency). At the same time, many of the analyzed characters are either symplesiomorphic (4-segmented antennae, presence of central fold on ventral side of abdomen, position of spiracles on laterotergites, length of siphon), or are autapomorphic, both for Lethocerinae (4th segment of antennae with projections, hind tibia and tarsi flattened and widened, folds of laterotergites come to apex of genital plate), and for Horvathiniinae (2-segmented tarsi, fused ventral diverticulum and phallus, wide laterotergites, etc.).

The central fold on the ventral side of the abdomen, which serves as a basis for drawing the Lethocerinae and Horvathiniinae close to each other, is itself plesiomorphic. At the same time, the existing synapomorphy connects the Horvathiniinae with the Belostomatinae, and not with the Lethocerinae. Synapomorphies of the Belostomatinae and Horvathiniinae are distinct and definite (2-segmented tarsi, dorsally fused with each other, wide laterotergites, projections of 8th segment, forming the breathing siphon, strongly shortened and moved apart, ventral diverticulum and phallus fused). However, Horvathinia in structure of fore tarsi is very similar to Diplonychus (Belostomatinae), in structure of male genitalia to the most primitive African genera of the subfamily Belostomatinae, Limnogeton and Hydrocyrius.

Thus, two basic branches of the belostomatids arose from the common ancestral form: 191
the belostomatids proper (Lethocerinae), characterized by the partial fusion (beginning with the first sternites) of the paratergites and laterotergites, in the preservation of narrow laterotergites with spiracles situated along the borders, and general
transl. -> ok
belostomatidness (Horvathiniinae+Belostomatinae), which also has partially fusing para- and laterotergites, but with a considerable widening of the latter (spiracles occupy primitive position - at the border). Subsequently occurred the isolation of the Belostomatinae because of the great widening of the laterotergites and fusion of the

borders of the latter with the partially reduced central fissure (Limnogeton, Hydrocyris) or, probably, by means of its simple reduction.(Diplonychus).

Along with the origin and development of nekton forms in the Mesozoic occurred also mastery of the ground surface. These forms basically led a benthic form of life in new deeper and often running water, where a more stable position of the body was required with dependable attachment to the substrate. In some Nepoids this led to a gradual increase of the ventral surface of the body, contiguous with the bottom of the reservoirs, because of the gradual divergence of the leg coxae and, as a consequence of this process, the protrusion of the sternal region of the thorax outward. Such a large rebuilding of the organism, apparently, took up the entire Liassic period, in the course of which these ancient Mesozoic nepids led a more or less predatory lie-in-wait form of life, falling mainly upon not very mobile animal organisms. They are characaerized by smaller eyes with their acquisition of spherical shape; in some, besides, arose a reduction of the venation of the tegmen and a cellular netting on the membrane was formed. This evolutionary direction led to representatives of the family Nepidae, the earliest forms of which apparently appered in the Liassic. In the Jurassic period, in connection with the increase of aquatic expanses and development of aquatic vegetation, in the nepids, which by this time had already developed a whole benthic group, arose the opportunity to master new, often much deeper places. In the nepid group, this led to further elongation of the walking mid and hind legs, the final acquisition in most forms of grasping fore legs, and the subsequent development of the respiratory system.

The descendents of the ancient aquatic scorpions survived to the present time as relatively equal in size subfamilies: the apomorphic Nepinae and the still more apomorphic Ranatrinae. The morphological process of transition from the former to the latter can be observed in living genera which comprise these subfamilies. The development of aquatic scorpions of the subfamily Ranatrinae followed the line of the narrowing of the body and the acquisition of the present drumstick form, accompanied by the further process of fusion of the sterno-pleural regions of the thorax, the unusual elongation and development of the trochanters and femora of the first pair of legs through the undifferentiated condition of the abdominal sternites. As a result of such a transformation, the fore legs were brought far forward beyond the head, so that the movement of the legs in catching prey became similar to the movement of the fore legs of Mantoidea. The initial forms of the living specialized subfamilies of aquatic Ranatrinae must be considered the Australian Austronepini, which undoubtedly arose from the more specialized synapomorphic aquatic scorpions (Nepinae) of the tribe Curictini. These tribes hardly differ at all from each other, and the differences in the characteristics which separate the two subfamilies - the correlation of the width of the head and the fore margin of the pronotum, the length of the leg coxae, the structure of the fore legs, the sternal part of the abdominal segments and the form of the body - are the least sharp.

misprint in book? → meant "thoracic"?

The oldest known true fossil insect representing real aquatic scorpions (Nepinae) 192 must now be considered the Upper Jurassic Laccotrephes incertus Y. Pop. from the Solnhofen shales of West Europe. Representatives of the other subfamily, Ranatrinae, are not known in fossil form.

PHYLOGENY OF THE SUPERFAMILY GELASTOCOROIDEA

After the aquatic nepids branched off from the common ancestral protoochterids, a new closely related littoral group separated from the latter - the superfamily Gelastocoroidea.

Presently, this small group of littoral bugs is known to us only from two living families, Ochteridae and Gelastocoridae. Despite their presumed great antiquity, up to now real fossil representatives of Ochteridae have not been found.

The process of the isolation of the littoral superfamily Gelastocoroidea is included in the appearance of the following apomorphy: partial fusion of the anteclypeal sclerites with the other cranial parts, diminishing of number of tarsal segments to two, first [illegible] on the forelegs, later on the hind legs [illegible]; asymmetry of male genital segments and genitalia, diminished size of the aperture of the basic salivary glands, final loss of the inner coverings of sectors of the hind gut, elongation and greater curving of the malphigian tubes, loss of vesiculum seminalis in the male reproductive system.

The living family Ochteridae basically has preserved all traits of the ancestral forms of this superfamily: prognathous head, 4-segmented rostrum and antennae, free antennae, walking fore legs, tarsi of legs 2-2-3, spread apart ocelli, and also the almost unchanged basic structure of the digestive system. Reduction of the antennae had already partially originated, apparently, in the ancient ochterid forms and was noted for living representatives by Reuter (1910) even. However, reduction here was insignficant and led to the shortening of the first and second segments. Simultaneously, the place of attachment of the antennae was moved under the eyes. The ancient ochterids continued to remain purely littoral forms and subsequently did not form any branches, except the Gelastocorids which have been preserved up to the present time without essential changes in the tropical and subtropical regions of the earth.

The family Gelastocoridae is undoubtedly related to the Ochteridae and represents a specialized branch of the ochterids. There is no doubt among most hemipterologists of their direct origin from the latter (Reuter, 1910; China, 1933, 1935; Miyamoto, 1961; Parsons, 1959, 1966). The first Gelastocoridae were isolated, apparently, at the end of the Triassic - beginning of the Jurassic and were more closely connected with water, frequenting very wet soil and littoral pools. In connection with this, they acquired their characteristic external appearance with strongly knobby structure. The predatory form of life promoted the appearance of such apomorphic characters as the acquisition of the more hypognathous position of the rostrum, its strong and thickened shortening, reaching only the fore coxae, transformation of the walking fore legs into grasping with fusion of the tarsi with the tibia. There arose also a drawing together of the ocelli, some changes in the digestive system, and also the fusion of the second pair of gonapophyses of the female ovipositor. Reduction of the antennae, or, more precisely, their shortening, went further in the Gelastocoridae; here all four segments became shortened and in a state of rest entirely concealed in the antennal pit under the eyes. Todd (1955) suggested that the reason for this 193 shortening and position in a special pit of the antennae is either an adaptation to in the soil or adaptation to the aquatic conditions. For the latter suggestion, he presents the single species Nerthra martini Todd, which was found both along the shores of a reservoir and directly in the water. However, the overwhelming majority of Gelastocoridae prefer life along rivers and streams and other similar places. The residence of the above-mentioned species in water (Nerthra) must be considered an accidental phenomenon and not permanent.

Presently the family Gelastocoridae is represented by two monotypic subfamilies, which are widely distributed in tropical and subtropical zones: Gelastocorinae and Nerthrinae. Analyses which I conducted ofthe subfamily characteristics do not confirm Todd's (1955) opinion about the great primitiveness of the subfamily Gelastocorinae. One of the basic characters differentiating the subfamilies - structure of the rostrum - is apomorphic for Gelastocorinae (short and thick rostrum), and is closer to the ancestral in Nerthrinae (longer and thinner, slightly curved forward). This permits suggesting that most probably a common ancestral form existed in which the rostrum was as long as wide as in Nerthrinae, but entirely straight, free and directed backward. Autapomorphy occurs both in Gelastocorinae (modified antennae ,especially their third segment, withdrawn ninth abdominal male sternite, asymmetrical male genitalia), and in Nerthrinae, although in a somewhat greater degree (fore legs with fused tibia and tarsi, furnished with one claw, asymmetry in a number of cases of the female abdominal segments, separate structures of the digestive system). In number of species, the Nerthrinae more than twice (75 species) exceed the Gelastocorinae (fewer than 30 species). The present distribution of the two subfamilies does not permit making a determination about the original distribution of the Gelastocorinae and the Nerthrinae, and also about the probable geographic habitation of the ancestral forms.

PHYLOGENY OF THE SUPERFAMILY CORIXOIDEA F. 117

A most difficult and now still practically not solved problem is the problem of the phylogenetic relationships of the corixids. Corixidae evolved from the Notonectidae (Handlirsch, 1906–1908; Reuter, 1910; China, 1933), from the common hydrocorid stem (Esaki, China, 1928; Ekblom, 1929), directly from the littoral stem (Parsons, 1965), from the Nepoidea (Parsons, 1959), and even directly from terrestrial groups of Heteroptera (Spooner, 1938); many hemipterologists have connected them with the naucorid stem (Kirkaldy, 1909; Sutton, 1951).

In my opinion, the most acceptable variant is the great phylogenetic similarity of the Corixidae with the littoral group of bugs. A whole number of plesiomorphic characters in the Corixoidea testify to this. For example, both in the Nepidae and Belostomatidae, as also in the Corixidae, the histological structure of the epithelia of the mid gut is identical, on the basis of which an attempt was even made to derive the latter from the Nepoidea (Parsons, 1959). The extremely primitive structure of the basic salivary glands (wide opening with flat covering cells), besides the Corixidae, occurs only in the Saldidae, which stand at the base of the phylogenetic tree of the entire suborder. Besides, the presence of three pairs of abdominal odor glands in the numphs of the Corixidae is inherent only to the suborder of terrestrial bugs Cimicoidea. The unusually specialized structure of the separate organs of the Corixoidea (strongly developed filtering system of the throat, mouth apparatus and stri- 194
dulating system) indicates the very early separation of the Corixoidea from the basic mass of the aquatic Heteroptera. The earliest isolation of the Corixidae is corroborated also by paleontological finds of the latter from the Liassic deposits of Asiatic USSR (Shurabellidae).

The history of the family Corixidae begins with the ancient Jurassic representatives of the family Shurabellidae and the subfamily Ijanectinae. Separating from the littoral protoochterid ancestors, the first corixids were still fairly strongly differentiated from living Corixidae. In this respect, very interesting are the oldest and, apparently, most primitive Central Asiatic Shurabellidae from the Lower Jurassic. In these bugs, the anteclypeus was still not fused with the sclerites surrounding it and was widened like the recent Corixinae and Micronectinae, the venation of their tegmen was partially preserved, and the hind legs were not flattened and were covered with very long swimming hairs. In external appearance, they resemble living Micronectinae. However, the phylogenetic interrelationships of the Jurassic corixid family with true Corixidae is presently problematical and at the present moment there is hardly any detailed discussion about them. The only thing that can be said with certainty is that, in the presence of a general plesiomorphic structure of representatives of this family, the widened part of the fore margin of the tegmen in Shurabellidae is an apomorphic condition.

'AC → never fused in Corixids M.C.P.

In the same way, it is possible to discuss the other early Jurassic corixid subfamily of true Corixidae, Ijanectinae. Like the Shurabellidae, representatives of the Ijanectinae also had a strongly widened fore margin of the tegmen, but already with a distinct nodal fissure. Apparently, such a strongly widened and flattened fore margin of the wing in the most ancient representatives of the Corixoidea must be considered as one of the prototypes of the embolium rim of the later Corixidae, particularly the 195
Micronectinae. Such a structure of the tegmen, in the further activization of swimming and the corresponding transformation of the entirely not flattened hind rowing legs (Shurabellidae) with long brush of swimming hairs and the strongly

Lipnectidae ?
& Shurabellidae ?

condensed legs with short brush of hairs, apparently, served as one of the reasons for their extinction.

No!

In the most specialized living Corixidae, the anteclypeus is unusually strongly widened and completely fused with the head sclerites surrounding it; besides, in them is observed a reduction of the venation and development of stridulating organs. At the present time, the Corixidae are represented only by two rich in species ~~subfamilies~~ (Corixinae and Micronectinae). Known to us from the early Jurassic are the ancient Jurassic representatives of the primitive subfamilies Archaecorixinae and Diaprepocorinae; a few forms of the latter have survived up to our day in the southernmost Australian region as the single genus Diaprepocoris. However, in the geological past several genera existed of which two are known to us: Gazimuria from the Lower Jurassic of East Transbaikals and Karataviella from the Upper Jurassic of South Kazakhstan. Corixidae of the subfamily Archaecorixinae existed only into the Mesozoic era (beginning with the Upper Jurassic) and are known to us only from four genera: Archaecorixa from the Upper Jurassic of South Kazakhstan, Diapherinus and Baissocorixa from the Lower Cretaceous of the Transbaikals and Mesosigara from the Upper Cretaceous of the Kabarov territory. Representatives of the Corixinae proper are known only beginning with the Paleocene.

subfamilies which are

On the basis of the taxonomic study of the fossil corixids, a morphological study of a whole number of living forms, and also from literature data, I have tried to isolate some basic morphological processes, which originated in the course of the historical development of the Corixidae.

Corixidae occupy a somewhat isolated position among the other living aquatic bugs of the infraorder Nepomorpha. This is connected, in the first place, with the special method of feeding: algophagy and detritophagy along with predation. The adaptation to feeding on waterplants and detritus (basically in the soil) served the great reconstruction of the separate body parts - first the head and fore pair of legs. As is known, Heteroptera possess a hypognathous type of head, i.e., mouth organs directed forward through the horizontal or slightly fallen below position of the head. However, in connection with catching food from the bottom of reservoirs in the process of evolution the position of the head acquired another direction: mouth and rostrum from the beginning turned vertically downward (hypognathous type), and then in the process of the further development, these parts, together with the head, became turned slantingly backward and downward, i.e., acquired an opistognathous position. In the preservation of a general plan of structure of the mouth organs in Corixidae, the rostrum was strongly shortened and in a state of rest hidden under the labrum. In its turn, the labrum developed strongly and was covered inside with hairs and setae, the significance of which relates to the filtration of diverse particles which fell into the throat. The unusual for aquatic bugs method of feeding is in line also with the modification of the fore legs, namely: fusion of tarsal segments into one, development of a system of hairs and setae on them, and flattening of the legs as a whole. When procuring food, Corixidae stick close to the ground like an anchor with the mid legs, maintain the body in a horizontal position with the hind legs, and quickly make rotary movements with the fore legs, perching on the substrate itself and catching rising particles and small organisms (Benwitz, 1956).

No! "Rostrum" should be labrum; "labrum" should be labium
MCP

Original for aquatic bugs, and for the whole order of bugs, must be considered 196
zoophagy (predation), and transition to any other method of feeding is undoubtedly a secondary phenomenon (apomorphic). In this case, transition to feeding on aquatic plants and organic remains sharply widened the realm of feeding in comparison with obligatory predation and maximally lowered competition on the part of other predatory aquatic bugs. This, in its turn, gave impetus to the powerful development and distribution of the corixids, the seizure of new ecological niches and the appearance of numerous new forms. Presently, this is the most numerous and flourishing group among living aquatic Heteroptera, numbering over 500 species; the separate genera in size

represent some of the largest genera among all Heteroptera. For example, the genus Micronecta has more than 100 species, and the genus Sigara (sensu lato) several hundreds of species.

The presence of such a large number of species in one genus was conditioned by the appearance of a special isolating mechanism. In the male Corixidae the characteristic system of stridulators on the sixth tergite of the abdomen (strigils) and on the fore legs, which arose independently of each other, reached wide distribution. In the author's opinion (Popov, 1963), the stridulating organ on the abdomen appeared considerably earlier and represents a system of combs which move against each other, the friction of which creates the varied frequency of sound. The form, number and dimensions of the combs vary greatly. Especially different in structure of strigils is the relict subfamily Diaprepocorinae, where they consist of two simple toothed plates (f. 118b). Two other subfamilies of Corixidae, Corixinae and Micronectinae, have a similar (to each other) structure of strigils on the abdomen (f. 118a). In the process of historical development, representatives of the most numerous subfamily of the Corixidae, Corixinae, have developed an additional stridulating mechanism on the fore femora and tarsi, consisting of numerous teeth. The process of the formation of teeth on the fore tarsi, which look like little blades (f. 119), in the process of historical development, went through the beginning of a system of hairs and setae, which gradually were transformed into small stridulating teeth, situated in one row. This single row of teeth, in its turn, became two rows by means of a sharp curve at its central portion as the first step, and the disappearance of teeth at the site of the curve. The two forming rows bifurcated later (f. 119de) [д + е →]. Apparently, another method of formation existed by a second means of elongation of the existing row of stridulating teeth along the distal margin of the blade (f. 119 zh, z) [Ж, З →] and the loss of part of the teeth at its apical end. The variability of size, number, form and distribution of the stridulating teeth on the tarsi and femora, even in the case of a single genus, is practically inexhaustible and much greater than of the strigils on the abdomen. The advantage of this type of stridulators over the abdominal strigils is evident. In the development of foot stridulators in some living genera, the strigils on the abdomen have become partly reduced, as, for example, in the subgenus Vermicorixa (Sigara) or in the genus Morphocorixa. Strigils are represented here only like the so-called strigil stem. In this case, the strigil is completely missing, as, for example, in Callicorixa, Neocorixa , or partly in Neosigara. There are also cases of loss of both types of stridulators, for example, in the relatively primitive among Corixinae genus Cymatia. It is not excluded that in this case the abdominal strigil, and even more so the leg stridulators, may not have arisen at all. The basic mass of true living Corixidae has preserved some kind of stridulator. Also to be considered is the fact of the possible participation of the genital apparatus of the males in the stridulating work. Thus, Mitis (1935) shows that separate parts of the male 197 genitalia can participate in stridulation, particularly the parameres and the penis, for example in the genera Sigara and Micronecta. Thus, in Sigara the parameres appear in the role of plectrum, and in Micronecta (in connection with the great distance of the strigils from the genitalia) the parameres directly bear the function of additional strigils. As can be seen in the figures in this paper, and also according to numerous observations of Prof. A. Vrublevsky, there are small fields with very fine chitinized teeth on the left paramere (sometimes even at the base of the right paramere) of Corixidae. Thus, in Micronecta such fields are sometimes also found on the sternites of the eighth segment. Apparently, this entire system (left paramere with toothed section, right hooked paramere, sector of ninth segment with scaly apical margin and toothed fields of eighth segment) actually bears a stridulating function also. This is particularly correct, evidently, for the very small Micronectinae with a large number of species in the genus and relatively weakly developed stridulating system.

Thus, the basic process of sexual isolation of species in the subfamily Corixinae followed the path of development and perfection of the stridulating apparatus of the fore pair of legs. In the other subfamily, Micronectinae, this process of developing means of isolation was arrested at the level of the existence of abdominal strigils, and also, apparently, with the help of the separate parts of the male genital apparatus. Micronectinae consist of four genera: three close genera are distributed in the Old World and one isolated genus in the New World. The main feature of the single American genus Tenagobia is the lack of a stridulating mechanism on the abdomen, which is so characteristic for the three other genera (Micronecta, Synaptonecta and Micronectella).

reword (below)

The probability of secondary disappearance of strigils, which arose already as an isolating sexual mechanism without any analogous compensation, for example, the stridulating system of teeth, as has occurred in the above-mentioned Callicorixa, Neocorixa and some other genera in the subfamily Corixinae, could hardly have been possible. Thus we must consider the lack of strigils as a plesiomorphic condition in the American genus Tenagobia. Besides, only in this genus is the scutellum 198 strongly developed and almost entirely not covered by the pronotum, like the primitive living Corixidae of the Australian subfamily Diaprepocorinae, which are considered as one of the possible initial forms of all living Corixidae. The lack of an abdominal strigil in one genus of Micronectinae permits making very important conclusions for the history of the development of the family Corixidae. In the first place, all of the above discussion testifies to the fact that the isolation of representatives of Micronectinae from the ancestral forms of the basic stem of the Corixidae occurred very long ago at the time of the existence, at the beginning of the Mesozoic, of a land connection with the American continent, when the resettling ancestral forms of Micronectinae still had no stridulating mechanisms. Secondly, representatives of the genus Tenagobia are remains of the ancient Micronectinae, which were isolated in the course of the Mesozoic and the entire Cainozoic, and also had not developed any kind of stridulating apparatus different from the micronectids of the Old World. The geographic distribution of most living species of the genus Tenagobia on the American continent (14 species, of 16 in South America and only two in the Sonor subregion of North America), apparently, reflects their ancestral condition. Finally, in the third relict subfamily, Diaprepocorinae, the abdominal strigil is of differmt structure and consists of a pair of mobile plates (f. 118b) apparently able to issue sounds highly limited in amplitude.

The presence of asymmetry of the male abdominal segments so characteristic for Corixidae, in the first place, is connected with the development of the abdominal strigil. In the Australian relict Corixidae of the genus Diaprepocoris, abdominal asymmetry is very insignificant, along with a very simplified structure of strigil.

Of definite interest also is the problem of the perception of sound waves in Heteroptera, particularly in the aquatic bugs, which, undoubtedly, in the future will help explain the evolutionary paths of the development of the bugs as a whole. Thus, in the Corixidae, the probable perceptory site of sound vibrations in both sexes must be the space filled with air under the epimeres of the mesothorax (epm2). In many Corixidae this pleural region is the thinnest, often almost transparent and very supple. Apparently, in undulating vibrations, the epimeres can vibrate like a flexible membrane. However, this still requires experimental corroboration.

In many aquatic Heteroptera, the venation of the tegmen is strongly reduced: particularly strongly in Corixinae. By means of a taxonomic survey of the fossil Corixidae preserved in the Paleontological Institute, and also a review of a whole number of living forms from various regions of the world, I succeeded in tracing the process of relative variability and reduction of the basic veins of the tegmen and constructing their morphological sequence, beginning with the Jurassic forms.

The appearance and particularly the formation of the embolium rim and the embolium of the tegmen is accompanied by the gradual disappearance of venation by means of

Par 2, begin: Strigils arose primarily as an isolating mechanism. The probability of their secondary dissappearance without any such compensation as, for example, the stridulating system of teeth (as has occurred in the above-mentioned Callicorixa, Neocorixa, and some other genera in the subfamily Corixinae) could hardly have been possible.

the movement of the basic veins R and M forward toward Sc (Archaecorixa) and later the evolutionary process of their fusion with the latter, and also in a number of cases partial reduction. In one of the oldest Jurassic fossil Corixidae of the true corixid branch - Archaecorixa lata Y. Pop. (Archaecorixinae) and another branch - Gazimuria scutellata Y. Pop. (Diaprepocorinae), the basic veins are situated fan-like and do not approach the fore margin of the tegmen. However, in the later Mesozoic (Cretaceous) - Baissocorixa jaczewskii Y. Pop., Diapherinus ornatipennis Y. Pop., and Mesosigara kryshtofovichi Y. Pop. (Archaecorixinae), the venation is already somewhat moved forward with partial fusion and reduction of R and M with Sc. Thus, in each genus the process of gradual fusion of the basic veins occurred individually as in Baissocorixa jaczewskii Y. Pop. (f. 81b) Sc and R are fused at the basal part 200
of the tegmen, M and Cu are divided only after the leaving of a single branch from the basic stem Sc+R, and later M fuses with R in the distal half. In Diapherinus ornatipennis Y. Pop. (f. 81a), an isolated vein, R and M fused at the distal half of the tegmen, M simultaneously remains fused with Cu at the basal portion, turning into a common stem at the very base of the tegmen. What appear to be the anal veins A1 and A2 in both of these species are not yet completely preserved, although in Baissocorixa these veins are less distinct. In the Upper Cretaceous corixid Mesosigara kryshtofovichi Y. Pop. (f. 82a), Sc and R are fused their entire extent, the fusion of the vein M is analogous to that in Baissocorixa, the anal veins are already completely missing. However, already in the Jurassic specialized forms existed with almost completely reduced venation, as, for example, Karataviella brachyptera B-M. The evolution of these Corixidae, which I have placed in the subfamily Diaprepocorinae, followed the path only of reduction of venation, which excluded the appearance of an embolium rim and the corresponding development of the embolium. This type of morphogenesis of the tegmen for Corixidae, apparently, turned out to be not entirely advantageous hydrodynamically and these and forms analogous to them devoid of an embolium ceased to exist.

And so, in the Mesozoic Corixidae (Archaecorixinae), beginning with the Upper Jurassic, the process of the movement of the basic veins R and M to the fore margin of the tegmen occurred almost simultaneously for the whole group, with the gradual development of the embolium rim. However, the real embolium or embolium rim had not yet appeared, although in Diapherinus ornatipennis Y. Pop. there is already noted the longitudinal fissure like a weak transverse fracture. Thus, in the basic corixid stem (Archaecorixinae and Corixinae), the embolium was not entirely expressed in most representatives of Mesozoic forms (Baissocorixa, Mesosigara), the nodal fissure appeared initially in Diapherinus. The subsequent process of the formation of the embolium rim of the tegmen can be traced into the Cainozoic corixids Diacorixa miocaenica Y. Pop. from Central Asia and Sigaretta florissantella Cock. from North America. In the former, the veins R and M already definitely have fused and together with Sc occupy a section in the formation of the embolium rim. However, the nodal fissure is still missing. Cu is weakly expressed and is represented like a residual vein. In the North American corixid from Florissant, the curve and reduction of the vein has already practically been formed into a well expressed embolium rim. The postcubital field is already well expressed in the Mesozoic Baissocorixa jaczewskii Y. Pop. Together with this, in the West European corixid Corixa rhenana Statz from the Upper Oligocene of Rott, the embolium rim has finally formed and the venation is maximally reduced like the living form. The nodal fissure is also missing, along with the still preserved anal vein on the clavus.

Thus, in aquatic bugs of the family Corixidae, the process of reduction of the venation leads to the formation of the embolium or embolium rim, which arose because of both the transformation of the basic veins R and M with the latter fusing with Sc into a single vein (rib of the embolium rim), and partial reduction. Thanks to this process, the sharp isolation of the costal field and the changing of its position into vertical in the fore portion of the tegmen occurred. The appearance of a nodal fissure (embolium) in the basic corixid stem was a later occurrence, i.e., at the beginning the embolium rim was formed and later the nodal fissure, which in various groups appeared at different times. In the diaprepocorid stem the process of fusion of the basic veins remained incomplete and kept this state still into the Mesozoic, 201 apparently also because of the very early appearance of the nodal fissure in this period. The cubital vein disappears later, the precubital field also occupies a partly vertical position, so that at the base of the tegmen it is widest.

An appraisal with respect to synapomorphy of the basic distinctive characters of the subfamilies is very difficult, since the speed of these processes for each subfamily can be different, a similar condition may not be reached simultaneously, and correspondingly any synapomorphy can be convergent. Thus, if we assume that in the process of historical development the speed of the formation of the embolium rim in the Corixinae and Micronectinae is different and of different periods, then this character can hardly be useful for determining the phylogenetic relationship. The same could have occurred with respect to the hidden position of the scutellum, the appearance of the strigil, and the lack of a distinct membrane of the tegmen. The difficulty is made greater by the lack of true paleontological finds of real Micronectinae.

Despite this, we all the same can try to provide an approximate map of the phylogenetic development of the family Corixidae. The evolution of the Corixidae is based, mainly, on the activization of swimming, and also on the appearance and development of phytophagy. The formation and development of the Corixidae followed two basic directions, connected with the different, in my opinion, formation of the embolium rim.

The first direction is characterized by the significant widening of the fore margin of the tegmen with its preservation of a flattened condition in the early forms (Shurabellidae and Ijanectinae). Subsequently, some forms, separating from the common stem of this direction (Shurabellidae+Ijanectinae) gradually transformed the widened sector of the wing into a narrower margin, occupying a more or less vertical position with respect to the whole plane of the tegmen, i.e., forming the real embolium rim. Through this process occurred the gradual reduction of the basic veins, leading in the final count to their complete disappearance. At the same time, the pronotum remained very transverse, keeping the scutellum completely open. Thus appeared the living Micronectinae. Thus, the representatives of the Western Hemisphere (Tenagobia) preserved basically the same appearance, whereas the Micronectinae of the Eastern Hemisphere (Micronecta) acquired a more changed appearance - isolated nodal suture of the embolium by a more or less overgrown pronotum, development of a special stridulating system (strigils) on the abdominal tergites. All of this verifies my point of view on the early isolation of the Micronectinae still during the existence of the Gondwana landmass, the more primitive condition of the American members of this subfamily and the similarity of the latter with the Australian representatives of the relict Diaprepocorinae, which have preserved an undeveloped embolium rim.

The second evolutionary direction was developed along the line of the formation of the embolium rim (process of formation, see above), and also, apparently, the abdominal strigil, by which some forms, evidently, in the course of the Jurassic, were isolated into the independent subfamilies Archaecorixinae and Diaprepocorinae. Thus one section of the corixids had only begun (Archaecorixa) or had continued (Diapherinus, Baissocorixa) this process, which ended, evidently, at the very end of the Cretaceous Period (Mesosigara) - beginning of the Paleocene. Thus along with this occurred the process of the growth of the pronotum and the scutellum hidden by its hind end, and also the appearance of male abdominal asymmetry in connection with the development of abdominal strigils. In the Paleocene, most probably, also occurred the isolation of the subfamily Corixinae, one of the first representatives of which (Diacorixa) still had a not strongly developed embolium rim. The subsequent development of the stridulating system on the fore tarsi as a basic sexual isolating mechanism, and also the perfection of the embolium rim (see above), the hydrodynamic refinement of the surface of the tegmen, promoted the quick increase of the diversification of this subfamily and, along with the development of phytozoophagy, promoted the whole subsequent rapid flourishing of this subfamily. The other sector of the Corixidae of this direction preserved more or less the ancestral condition of body structure: entirely not developed pronotum and because of this a completely free scutellum, incomplete although considerable reduction of venation and correspondingly practically entirely undeveloped embolium rim like a very narrow margin, almost symmetrical male abdomen, and, finally, simple eyes on the vertex. At the same time, representatives of the Diaprepocorinae developed individually, in the differently constructed apparatus on the abdominal tergites (see above) which, along with adaptation to phygophagy, permitted their preservation to the present time.

PHYLOGENY OF THE SUPERFAMILY NAUCOROIDEA F. 120

The naucorid branch, as shown above, separated from the basic ochterid-naucorid littoral stem after the isolation of the nepid and corixid. This evolutionary direction of the aquatic bugs is represented by the single family Naucoridae, fossil representatives of which are known already from the early Jurassic.

In structure of digestive organs, the naucoroids resemble littoral living families of Nepomorpha, particularly the Gelastocoridae. However, the structure of the basic salivary glands of Aphelocheirinae indicates the intermediary position of the latter between the Ochteridae, on the one hand, and the Gelastocoridae, on the other.

The systematics of the family Naucoridae, living representatives of which are basically distributed in tropical regions, has been weakly developed, and paleontological material on it is so sparse and fragmentary that now it is very difficult to estimate accurately the similarity and differences between some subfamilies. Apomorphic and plesiomorphic characters are unevenly and extremely mosaically distributed and usually are characteristic only for one subfamily. For example, for Aphelocheirinae, the strongly overgrown anteclypeus (apomorphy) and the long, opistognathous rostrum (plesiomorphy) are characteristic. In Cryphocricinae, on the other hand, the anteclypeus is small, plesiomorphic, and the rostrum is apomorphic, strongly shortened and thickened. Thus our description of their phylogeny must of necessity turn out to be preliminary and incomplete. However, I have made a preliminary attempt to form an approximate map of the interrelationships and path of development of the separate groups in the rank of subfamily and tribe.

In number of separate subfamilies, this is one of the largest in size families of the infraorder Nepomorpha; according to the classification given above it numbers five subfamilies, which differ basically in the structure of the head capsule and degree of development of the rostrum. One of them - Sphaerodemopsinae, is represented only by fossil forms and four are living, the subfamily Naucorinae known from the Lower Jurassic.

All Naucoridae form one more or less single conglomerate of aquatic bugs, in which it is possible preliminarily to isolate four groups of genetically close forms: naucoroid, cryphocoroid, potamocoroid and aphelocheiroid stems. To the first belong the subfamilies Naucorinae and the Mesozoic Sphaerodemopsinae, to the second, Cryphocricinae, to the third, Potamocorinae and to the fourth the slightly isolatedly 203
standing Aphelocheirinae. Unfortunately, the presently available extremely fragmentary paleontological data do not permit accurately suggesting their ancestral group. All the more so since one of their basic characteristics, the head capsule, in the overwhelming majority of cases is not preserved in a fossil state. The basic directions of the phylogenetic development are determined, in the first place, by the

development of the head capsule, degree of development of the rostrum, and also the sternopleural region of the thorax and abdomen in connection with adaptation to a different type of respiration.

The most clearly expressed plesiomorphic characteristics are possessed by the Mesozoic Aidiini and Angaronectini in the subfamily Naucorinae, and also the living South American Potomocorinae, and the Aphelocheirinae, distributed in the Eastern Hemisphere. These subfamilies possess an opistognathous long rostrum, which attains greatest length in the Angaronectini (Naucorinae) and Aphelocheirinae. I was not able to observe a direct synapomorphic connection between these groups and must assume that they do not form a monotypic group. Each of these subfamilies has its own peculiar apomorphy: in Aidiini (Naucorinae) are the unusually strongly widened epineres of the metathorax, in Angaronectini (Naucorinae) are the strongly thickened and elongated rostrum, the shortened grasping fore legs with thickened femora and one-segmented tarsus fused with the tibia, considerably flattened hind swimming legs, in Potamocorinae are the long rostrum, relatively weakly developed, but already adapted for grasping, fore legs with one-segmented tarsi, scutellum very large (Potamocorini), tegmen strongly chitinized like elytra (Coleopterocorini), and in Aphelocheirinae the unusually long rostrum, lack of distinctly differentiated embolium, asymmetrical genital segments, strongly developed brachyptery and specific plastronic breathing. A special type of transpiration, which resembles somewhat the plastronic in Aphelo- 204 cheirinae, is possessed by some members of the subfamily Cryphocricinae (Cryphocricini).

episterna

The ancient fossil Naucoroidae are fairly diversified; their representatives belong to at least two subfamilies and tribes: Sphaerodemopsinae and Naucoridae - Liadonaucorini, Aidiini and Angaronectini and Naucorini. Basically these groups, which were isolated in the Mesozoic, are characterized by the definite number of plesiomorphic characters (fairly long rostrum, which reaches at least the fore coxae, the weakly adapted for grasping fore legs, etc.). They, however, had already developed a whole number of apomorphic traits, noted partly above.

misprint in book? → Naucorinae?

Between the fossil and living subfamilies, according to known distinctive characters, there is a definite break because of their autapomorphy. In character of segmentation of the pleural region of the thorax, living Aphelocheirinae somewhat resemble the Upper Jurassic Aidiini (Naucorinae) and also the Cryphocricinae. On the other hand, some common traits exist between them, for example, in Liadonaucorinae, as also in Aphelocheirinae, the embolium is missing, the wide and flat head of the Mesozoic Angaronectini is similar to that of all living Naucorinae. However, the Mesozoic naucorids are known to us so fragmentarily that it is presently difficult to determine their similarity and difference correctly.

With the development of adaptation to predation, the changes of the morphology of the head capsule consisted of the outgrowth, from outside, of the anteclypeus, the shortened and thickened rostrum and the acquisition of a hypognathous position in most living Naucorinae, Laccocorini, Limnocorini, Ambrysinae and Naucorini. In the Cheirocheilini, the partial shortening of the rostrum was accompanied by its original curving. In the specialized Cryphocricinae the rostrum takes an extremely prognathous position (entailing the reduction of the labrum), directed forward and slightly below like the living nepid Ranatrinae (Nepidae). However, the growth of the anteclypeus is the least among living naucorids. In most representatives of the subfamily which have a short rostrum, the genopont has acquired a central fin (Naucorini, Limnocorini, and Cryphocricinae) or has been transformed into a very convex elevation (Ambrysini). In Laccocorini the genopont is very short and without a rib, which is, apparently, an extreme degree of specialization.

The perfection of the fore legs, adapted for seizing and holding prey, occurred gradually, and apparently not simultaneously in the various subfamilies. The transformation of walking legs into grasping was accompanied by a thickening of the femora and preservation of two-segmented tarsi (Laccocorini); afterward the tarsi in most naucorids was reduced to one segment and fused with the tibia. Apparently, there existed other paths of transformation of the fore legs into a predatory type, beginning with the reduction of the tarsi (Potamocorinae).

Naucoridae are the single true aquatic family, some representatives of which have free antennae visible from above (Potamocorinae and Aphelocheirinae). Apparently, the ancestral forms, and also representatives of some extinct subfamilies, had long antennae, which in the course of evolution of the families shortened and came to fold into special deepenings on the head under the eyes and partly on the prothorax. Although the possibility of secondary elongation of the antennae in Aphelocheirinae should not be excluded.

In Naucoridae there is also the tendency to fusion of the coriaceous parts of the tegmen (clavus and corium), which we see in Coleopterocoris Hung. (Potamocorinae), Melloiella De Carlo (Naucorinae), and also in the fossil Sphaerodemopsis Handl. (Sphaerodemopsinae). Besides, there is a widely distributed tendency toward brachyp- 205
tery, connected, most probably, with the special "plastron" type of breathing, so characteristic for Aphelocheirinae and partly for Cryphocricinae (Cryphocricini).

In degree of segmentation of the head capsule, bugs of this family can be separated into two groups. The first group, to which belongs the subfamily Cryphocricinae with the two tribes Cryphocricini and Cataractocorini, has the greatest segmentation of the head capsule into sclerites with strongly developed convex eyes and distinctly differentiated and strongly moved forward genal plates. With this character is correlated also the rough, like small granules, surface of the dorsal side of the body. To the second group with strongly integrated head capsule belong all the other Naucoridae. The latter, in its turn, in degree of development of the rostrum falls into two more groups: with the long opistognathous rostrum - Aphelocheirinae, Potamocorinae and the Mesozoic Angaronectini (Naucorinae), and with the short, directed below, most of the remaining Naucoridae. Thus, in the subfamily Naucorinae we find practically an uninterrupted transition of changing of the position of the rostrum from opistognathous - Laccocorini, Limnocorini, through hypognathous - Cheirochelini, to slightly prognathous condition - Naucorini, Ambrysini. The position of the rostrum, and also the degree of development of the frons and labrum, in the subfamily Naucorinae well indicate the phylogenetic directions of development of the groups of genera in the rank of the above-mentioned tribes.

ie, max. plates

Great variability also appears in the structure of the ventral side of the body, together with the positioning of the abdominal spiracles on the sternites of the abdomen. Here we have also a series of transitions in the structure of the sternopleural regions of the thorax. Among these characters, from the point of view of phylogenetic ties, the structural data in the tribes of the subfamilies Cryphocricinae and tribe Ambrysini in the subfamily Naucorinae interest us. ~~Variants of similar structure of the sternopleural regions of the thorax~~ in Ambrysini (for example, the lateral margin of the pronotum not turned onto the ventral side, the strongly developed sternal region of the prothorax, and the degree of development of the epimeres of the mesothorax) ~~we see both in Cryphocricini and in Cataractocorini.~~ Apparently, only representatives of Ambrysini of the real Naucorinae have a true relationship with representatives of the subfamily Cryphocricinae through the common hypothetical ancestor, one of the descendents of which became clearly specialized (Cryphocricos). In its turn, the Ambrysini, evidently, are connected with the other members of the subfamily Naucorinae through representatives of the tribe Cheirochelini - some similarity, for example, appears in the common structure of the head. All these data are still not sufficient to classify them validly and for now allow only discussions of some views about their phylogeny.

reword (below)

These groups of aquatic bugs, apparently, were widely distributed still in the Mesozoic (beginning with the Jurassic), as testified by their paleontological finds in localities which are very diverse and far from each other. They actively settled

In both Cryphocricini and Cataractorini we see variations of the structure of the sternopleural regions of the thorax which are similar to those in Ambrysini (for example, the lateral margin of the pronotum ....).

various fresh water reservoirs thanks to good flight and swimming ability, relatively large dimensions and quickly perfecting prodation. However, presently only some genera have a large number of species, widely distributed in geographic regions, for example, in the genus Ambrysus they number about 70, in the genus Limnocoris about 35, and in the genus Aphelocheirus about 30.

PHYLOGENY OF THE SUPERFAMILY NOTONECTOIDEA F. 121 206

The development of this branch of aquatic bugs, as the study of the morphology of relict families and fossil representatives shows, followed two basic directions: notonectid proper and helotrephoid.

The isolation of these two branches, reflecting the above-discussed direction of evolution of the Notonectoidea, occurred no later than the second half of the Jurassic Period, in which the first, the notonectid direction, more specialized and progressive, attained real flourishment in the present epoch. The weakly swimming helotrephoids, with a fairly wide body, having the following characteristic indicators, must be considered initial for Heteroptera of this superfamily: head hypognathous with relatively small eyes, four-segmented rostrum and antennae, pronotum of moderate size, not covering the moderately developed scutellum, tegmen with weakly developed veins, dividing into clavus, corium, embolium and well developed membrane, fore legs grasping, but little perfected, tarsi in all pairs of legs three-segmented, male genitalia symmetrical, odor glands in adult form developed on metathorax and on second abdominal tergite in nymphs.

The first direction in the present time is represented by the single family Notonectoidea, the first representatives of which are known from the Lower (Liadonecta) and Upper (Asionecta) Jurassic of Asian parts of the USSR; in the process of evolution, bugs of this family acquired a strongly elongated torpedo-shaped body form, strongly narrowed at the sides, and swimming hind legs, thickly covered with hairs, and also a stridulting system. The structure of the ovipositor and its appendages indicates their still weakly specialized condition, with the exception of the appearance of serration on the apex of the first gonapophyses and well developed gonangulum. The condition of the digestive system of living Notonectidae is also the least apomorphic among notonectids and only two distinct apomorphies are observed: weakly developed bubble-like section of the mid gut and adjoining apices of the malphigian tubes. In the living fauna this is one of the most numerous groups of aquatic bugs, second only to the Corixidae.

The first Notonectidae still possessed an anteclypeus segemented from the outside and consisted of the independent subfamily Clypostemmatinae, separate representatives of which existed in the Cretaceous (Clypostemma) and Paleocene (Clematina). However, in the basic mass of Notonectidae, the widening of the anteclypeus and its fusion with the sclerites bordering it (loral, maxillary, mandibular, genal) occurred fairly early, and also the diminishing in a number of cases of the number of segments of the antennae, excessive increase of the eyes and integration of parts of the genital segment in living forms.

fuses only with loral (mandibular), not with maxillary M.C.P.

↖ singular in Russian

Already from the late Jurassic in Kazakhstan (Asionecta), true representatives of a subfamily of real Notonectinae are known to us. In the Paleocene and Neocene, Notonectinae occupy a predominant position and most of the known paleontological finds of the Cainozoic Notonectidae (see Ch. II) belong to this subfamily.

The loss of some plesiomorphic characters (sensor pits at the apex of the clavus, some details of the digestive system) and acquisition of new apomorphic ones (reduction of number of segments of the tarsi to one, further distribution among members of the family of integration of genital segments and their symmetry, and also formation of the stridulating system) conditioned the isolation of the more apomorphic subfamily

Anisopinae. The most remarkable adaptive acquisition of this group of notonectids must be considered the system of the stridulating combs (plectrum) and fields (pars 207 stridens) on the male legs (f. 51e), which allowed the similar living Corixidae to isolate a great number of closely related species (over 120 species in the genus Anisops). In connection with this, it is interesting to note that in the subfamily Notonectinae isolation of numerous species of the genus Notonecta (about 100 species) occurred basically because of the unusually large variability of the male genitalia and in the features of their parameres. The second direction of development of the notonectids is characterized by a wider and in some cases even slightly flattened body (in Idiocorinae in the family Helotrephidae flattening is undoubtedly a secondary charactr) with not flattened thin, hind legs, thickly covered with swimming hairs, and also the loss of a clearly expressed embolium. The first helotrephoids arose, apparently, from the above-mentioned helotrephoid-like ancestor; some of the Helotrephidae have preserved to the present time a more or less flattened body, not raised roof-shaped from above (Neotrephinae and Idiocorinae, Helotrephidae).

The earliest helotrephoids are known from the Upper Triassic of Kazakhstan, such as the independent apomorphic family Scaphocoridae, which stands somewhat by itself among notonectids of this direction (strongly developed pronotum, completely covering a very small scutellum and the shortened swimming legs with one-segmented tarsi). In the late Cretaceous one more specialized extinct family, Mesotrephidae, exists, which also has no distinct connection with living forms, but somewhat resembles the above-mentioned Jurassic family (strongly developed pronotum and small scutellum). The Cretaceous Mesotrephidae differ essentially from the Scaphocoridae in the less roof-shaped body, free scutellum and unusually long thin hind legs. The lack of dis- 208 tinct synapomorphy does not allow connecting these Mesozoic families directly, so that in some characters (completely reduced venation of the tegmen, free scutellum) the Cretaceous Mesotrephidae turn out to be more plesiomorphic than the Jurassic Scaphocoridae, and in other characteristics more apomorphic (strongly opistognathous head, with is not visible from above, weakly expressed sclerotized membrane of the tegmen).

Then follows a long break in the paleontological chronicle of the Notonectoidea, and right up to the present time no finds of these bugs have been made. Two living families of this direction, Helotrephidae and Pleidae, in external characters (morphological) also have little connection with each other. Helotrephidae, in many characters (fusion of head capsule with the prothorax, fusion of clavus and corium of the tegmen, reduction in a number of cases of tarsal segments to one, structure of ovipositor, and its appendages), are undoubtedly more specialized than the Pleidae, so that the specialization of the Helotrephidae is autapomorphic. In structure of the digestive system, Helotrephidae show greater apomorphy also (long esophagus, mid gut divided into only two sectors and unusual structure of the basic salivary glands) than the Pleidae (straight gut with diverticulum and somewhat original structure of the basic salivary glands).

The Pleidae are a monotypic family, species of which (about 20) are widely distributed in all zoogeographic regions. The family Helotrephidae consists of three subfamilies: Helotrephinae, Neotrephinae and Idiocorinae. The last of these is clearly the most apomorphic (strongly flattened body, complete fusion of head with prothorax, one-segmented and strongly shortened antennae, not differentiated into sections tegmen, etc.). Of the two other subfamilies, the first, apparently, is somewhat plesiomorphic (presence of ovipositor, the least fusion of the head with the prothorax); however, the reduced leg tarsi analogous to the Idiocorinae (1-1-2) and roof-shaped body, and also lack of other data common for all three subfamilies makes it difficult to estimate the phylogenetic condition of the Helotrephinae and Neotrephinae more or less definitely. It is possible that the Helotrephidae represent a heterogeneous group of aquatic bugs, where the Idiocorinae, apparently, are an independent family. and are subdivided only into two subfamilies: Neotrephinae and Helotrephinae, Translation of Russian bibliog. only

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LIST OF WORD DESIGNATIONS TO FIGURES

A, A1,A2	Anal veins
acl	Anteclypeus (proclypeus)
ae	Aedeagus
aepm	Anepimere
ag	Accessory salivary gland
Ax1,Ax2, Ax3	axillary plates
bc	
bl	bubble-like section of midgut
bst1-bst3	basisternites of pro-, meso- and metathorax
cb	thickening on comb of transverse plate of epipharyn
cg	comb of genopont
CL	clavus
cl	clypeus
clep	longitudinal comb of epipharynx
CR	corium
CuA	fore cubital vein
CuP	hind cubital vein
cs	secretory cell
cx	coxa
d	disc of egg stalk
ds	stridulating teeth
EM	embolium
ep	epipharynx
epd	toothlike projections of epipharynx
epm1-epm3	epimeres of pro-,meso- and metathorax
eps1-eps3	episternites of pro-, meso- and metathorax
epso	epipharyngeal sense organ
f	femora
fc	food canal
fllb	fleshy part of labium
fo	occipital opening
fp	foodpump
fr	frons
fst	furcasternite
fta	fore tentorial pits
ftp	hind tentorial pits
g	genopont
ga	gonangulum
gpl	gonoplak
gpo1,gpo2	1st and 2nd gonapophyses (1st and 2nd valvules)
gx1,gx2	1st and 2nd gonacoxae (1st and 2nd valvifers)
hml	(tegmen)- hemelytron
hyp	hypopharynx
hypd	toothlike projections of hypopharyhx
~~ils~~	ileum
is	inserted? sclerite
J	jugal vein

A, A_1, A_2 — анальные жилки
acl — антеклипеус (предналичник)
ae — эдеагус
aepm — анэпимер
ag — придаточная слюнная железа
Ax_1, Ax_2, Ax_3 — аксиллярные пластинки
bc — буккула
bl — пузыревидный отдел средней кишки
bst_1, bst_2, bst_3 — базистерниты передне-, средне- и заднегруди
cb — утолщения на гребнях поперечной пластинки эпифаринкса
cg — гребень генопонта
CL — клавус
cl — наличник
clep — продольный гребень эпифаринкса
CR — кориум
CuA — передняя кубитальная жилка
CuP — задняя кубитальная жилка
cs — секреторные клетки
cx — тазик
d — диск ножки яйца
ds — стридуляционные зубцы
EM — эмболиум
ep — эпифаринкс
epd — зубцеобразные выросты эпифаринкса
epm_1, epm_2, epm_3 — эпимеры передне-, средне- и заднегруди.
eps_1, eps_2, eps_3 — эпистерны передне-, средне- и заднегруди
epso — эпифарингеальный чувствительный орган
f — бедро
fc — пищевой канал
fllb — мясистая часть нижней губы
fo — затылочное отверстие
fp — пищевой насос
fr — лоб
fst — фуркастернит
fta — передние тенториальные ямки
ftp — задние тенториальные ямки
g — генопонт
ga — гонангулум
gpl — гоноплак
gpo_1, gpo_2 — первые и вторые гонапофизы (первые и вторые вальвулы)
gx_1, gx_2 — первые и вторые гонакоксы (первые и вторые вальвиферы)
hml — надкрылья
hyp — гипофаринкс
hypd — зубцеобразные выросты гипофаринкса
il — илеум
is — вставочный склерит
J — югальная жилка

kepm — катэпимер
kr — респираторные каналы вентральной стороны брюшка
la — латеральная аподема
lap — вершинная пластинка
lb — нижняя губа
lbas — базальная пластинка генитальной капсулы
lbg — верхнегубной желобок
lbr — верхняя губа
lep — эпифарингеальная пластинка
lepa — передняя часть эпифаринкса
lha — передняя часть гипофаринкса
lhp — задняя часть гипофаринкса
lhst — гипостомальная пластинка
lhyp — гипофарингеальная лопасть
llor — лоральная пластинка
lmx — максиллярная пластинка
lor — лора
ls — суспензорная пластинка
lt — поперечная пластинка эпифаринкса
lt I, *lt* II, *lt* III, *lt* IV — зоны поперечной пластинки
ltla — передняя доля поперечной пластинки
ltlp — задняя доля поперечной пластинки
ltst — поперечная борозда поперечной пластинки
lv — вентральная пластинка генитальной капсулы
m — мышца
M — медиальная жилка
Mb — мембрана
mdfp — дилататорная мышца пищевого насоса
mdm — мандибулярные рычажки
*Med*₁ — внутренняя первая медиальная пластинка
*Med*₂ — вторая медиальная пластинка
mg — максиллярные железы
mlb — нижнегубная мембрана
mt — мальпигиевы сосуды
mx — максиллы
mxm — максиллярные рычажки
o — сложный глаз
oc — затылочный мыщелок
ocl — глазки
oe — пищевод
p — глотка
pa — анальная складка
paa — преданальная складка
pcl — постклипеус

kerm	katepimere
kr	respiratory canal of ventral side of abdomen
la	lateral apodeme
lap	apical plate
lb	labium
lbas	basal plate of genital capsule
lbg	labrum groove
lbr	labrum
lep	epipharyngeal plate
lepa	foremost part of epipharynx
lha	foremost part of hypopharynx
lhp	hindmost part of hypopharynx
lhst	hypostomal plate
lhyp	hypopharyngeal lobe
llor	loral plate
lmx	maxillary plate
lor	lora
ls	suspensory plate
lt	cross plate of epipharynx
lt I-IV	zones of cross plates
ltla	fore field of cross plate
ltlp	hind field of cross plate
ltst	cross fissure of cross plate
lv	ventral plate of genital capsule
m	muscle
M	medial vein
Mb	membrane
mdfp	dilatory muscle of food pump
mdm	mandibular levers
Med1	inner first medial plate
Med2	2nd medial plate
mg	maxillary glands
mlb	labial membrane
mt	malpighian tubes
mx	maxillae
mxm	maxillary levers
o	compound eyes
oc	occipital muscle
ocl	eyes
oe	oesophagus
p	throat
pa	anal fold
paa	preanal fold
pcl	postclypeus

pd — ножка яйца
pg — основная слюнная железа
ph — гипофарингеальные крылья
pj — югальная складка
pl — пилорус
po — постокципут
pr — парамеры
prst — парастерниты (латеростерниты)
prt — паратергиты (латеротергиты)
ps — стридуляционное поле
pst — простернум
R — радиальная жилка
r — прямая кишка
rt — дыхательная трубка
s — шов
sb — связка
sc — копулятивная сумка
scll — клипеолоральный шов
sd — сперматекальный проток
slb — нижнегубной шов
slg — лорогенальный шов
smx — максиллярный шов
sn — нодальный шов
sp — слюнный насос
spl — плевральный шов
spt — сперматека
sstpl — стерноплевральный шов
st — стернит
stg — стигма (дыхальце)
stl — боковой семепроток
stm — желудок
stmd — медиальный семепроток
str — стридуляционный гребешок
t — тергит
tb — голень
tg — место прикрепления мышц эпифаринкса
tr — лапка
ts — семенник
vs — семенной пузырек
vx — темя
I—IX — стерниты брюшка

pd	egg cover
pg	basal salivery gland
ph	phypopharyngeal wings
pj	jugal fold
pl	pylorus
po	postocciput
pr	paramere
prst	paresternite (laterosternite)
prt	paratergite (laterotergite)
R	radial vein
r	straight gut
rt	respiratory tube
s	suture (cleft?)
sb	sheaf (bunch?)
sc	copulatory pouch
scll	clypeo-oral suture (cleft?)
sd	sperm duct
slb	labial suture (cleft?)
slg	lorogenal suture (cleft?)
smx	maxillary suture (cleft?)
sn	nodal suture (cleft?)
sp	salivary pump
spl	pleural suture (cleft?)
spt	spermateka
sstpl	sterno-pleural suture (cleft?)
st	sternite
stg	stigma (respiratory)
stl	lateral semeduct
stm	stomach
stmd	medial semeduct
str	stridulatory comb
t	tergite
tb	tibia
tg	place of attachment of muscles of epipharynx
tr	tarsus
ts	testicle
vs	semen bubble
vx	vertex
I-IX	abdominal sternites

EXPLANATION OF TABLES

Table 1
fig. 1 Shurab, Tadzik SSR; Lias. Clearly visible longitudinal section of body
2 same locality. Clearly visible cross section of body
3 Holotype p. 151. Specimen of Munich University Eichstatt FRG Upper Jurassic
4 Paratype (p. 173). Specimen from Munich Univ. same locality

Table 2
1 Spec. from Munich Univ. Eichstatt FRG, Upper Jurassic
2 Original Oppenheim 1888, p.164. Coll. Munich Univ, Eichstatt, FRG, Upper Jurassi
2 a. direct imprint; b. reverse imprint
3 p. 164. Coll. British Mus. Solnhofen, FRG, Upper Jurassic
4 p 185-6, Shurab, Tadzhik SSR, Lias, Wing.

Table 3
1 Holotype p. 156. Coll. Munich Univ. Langenaltheim FRG, Upper Jurassic
2 Holotype p. 168. Tara, West Siberia, Miocene
3 Shurab, Tadzhik SSR, Lias
4 Nymph, same locality.

Table 4
1 Paratype Bais, Transbaikals, Lower Cretaceous
2 Holotype same locality
3 Holotype Karatau, South Kazakhstan, Jurassic
4 Holotype Cagayan, PriAmur, Upper Cretaceous. Imprint of insect body lying on side
5 Holotype Tegmen, Bais, Transbaikals. Lower Cretaceous

Table 5
1 Living, New Zealand
2 Holotype Borov, Transbaikals, Liassic
3 Karatau, South Kazakhstan, Jurassic
4 Nymph same locality
5 Holotype Vladimirovka, East Siberia
6 Nymph same loality

Table 6
1 Col. British Mus. Florissant, USA, Oligocene
2 Col. British Mus. same locality
3 Paratype Chon-Tuz, Tian-Shan, Miocene
4 Holotype same locality

Table 7
1 Holotype Kizil-Ki, Kirghiz SSR ,Lias
2 Holotype Karatau, South Kazakhstan, Jurassic
3 Holotype Col. Munich Univ. Eichstatt, Upper Jurassic
4 Paratype Col. Munich Univ. same locality
5 Holotype Bais, Transbaikals, Lower Cretaceous
6 Holotype Karatau, South Kazakhstan Jurassic

Table 8
1 Holotype Karatau South Kazakhstan Jurassic
2 Holotype Kizil-Dzhar, Karatau, Upper Cretaceous
3 Bais, Transbaikals, Lower Cretaceous
4 Holotype Coll. British Museum, Ridgeway, England, Upper Jurassic
5 same locality
6 Rott, FRG, Oligocene

Table 9

1 Karatau, South Kazakhstan, Jurassic
2 same locality
3 Holotype. Coll. Munich Univ. Solnhofen FRG, Upper Jurassic
4 Rott, FRG, Oligocene
5 Holotype Tom River, Black Stop, West Siberia, Lias

Figures:

P. 31	F.1	Fore part of trunk Weber 30
32	2	Labium. a. general scheme. z. Parsons 66 For designations for this and all following figures see p. 225.
33	3-6	3. ondoskeletal head structure Parsons 59 4. Cross section of base of rostrum Parsons 59 5. Stylets of rostrum - a. mandibular stylet, b. maxillary stylet, B. apex of mandibular stylet, g. apex of l-r maxillary stylets Parsons 59 6. Types of Het mandibular levers. (type V - Spooner 38)
34	7	Scheme of head structure Parsons 65
36-40	8-17	Head. (orig.) a. from the front, b. from below, c. from the side.
42	18-20	18. Salivary pump and epipharynx Parsons 59 19-20 Epipharyngeal surface of throat - a. gen. view, b. transverse plates P66a
43	21-23	21. Epipharyngeal surface of throat - a. gen. view, b. transverse plates P66b 22-23. Epipharyngeal surface of throat Parsons 66a
44	24-26	24. Longitudinal section of throat - a. 5th nymphal stage, b. image Pars.66a 25. Epipharyngeal surface of throat Parsons 66a 26. Cross section of throat in 5th nymphal stage Parsons 66a
45	27	Maxillary glands Puchkova 65
46	28-34	Antennae - Kirichenko 51, Weber 30, Poisson 51, Lauck, Menke 61, Poisson 51, Esaki, China 28, Poisson 57
47-49	35-39	Ventral side of body (orig)
50	40	Ventral side of body (orig) a. famale, b. male
51-55	41-45	Ventral side of body (orig)
56-57	46	Fore legs H-stridulating comb of the same species (a Weber 30) (e,z Poisson 57, K Hungerford 41, m-H Lansbury 62, b,B,g,d,i,l orig)
59	47	Drawn out plate of pretarsus Dashman 53
60	48	Mid legs a-d original g. Hungerford 41
61	49	Hind legs a-d original g. Hungerford 41
64	50	Tegmen a Parsons 59, b,g Lundblad 33, B,d Poisson 57
65	51	Basal part of hind wing Puchkova 61
66	52	Hind wings a-B, d-z Puchkova 61, g-Davis 61, u Esaki, China 28
69	53	Abdomen of Nepidae (schematic cross section of abdomen) (b-ventral side of abdomen) Mencke, Steinge 64
70-71	54	Digestive system
73	55	Male genitalia a,b genital capsule; B,g copulatory organs Poisson 51
74	56	Internal male copulatory organs Pendergrast 57
P. 76-77	F. 57.	Female genital and anal appendates u-f Scudder 59
78	58	Female internal copulatory organs Pendergrast 57
79	59.	Ventral side of abdomen Poisson 51
80	60	Eggs z cover? of egg Poisson 57
80	61	Hatching of nymph from egg Weber 30
81	62	Laying of eggs Jordan 50
81	63	Maturing of eggs on back of male Poisson 51
82	64	Nymphs a-zh, i Poisson 57, z Esaki + China 28
85	65	Couplings of fore and hind wings Weber 30

Text abbreviations:

Het	-	Heteroptera
H	-	Helotrephidae
B	-	Belostomatidae
C	-	Corixidae
G	-	Gelastocoridae
O	-	Ochteridae
P	-	Pleidae
Na	-	Naucoridae
Ne	-	Nepidae
No	-	Notonectidae
S	-	Scaphocoridae (fossil)

CHAPTER V: FIGURES

p. 100 f. 66 Ochterus marginatus latr., living (orig.)
p. 101 f. 67 Gelastocoris vicinus Champ., living (Poisson, 1951)
p. 102 f. 68 Family Gelastocoridae, living a- head of Gelastocorinae; b- head Nerthrinae; B- male copulatory organ; g- female last abdominal segments (Todd, 1955)
p. 105 f.69 Nepa cinerea L., living (Poisson, 1951)
p. 105 f. 70 Laccotrephes incertus sp. nov.; paratype, Munich Univ. collection, 1965 III 21, Eichstatt FRG, Up. Jur.
p. 105 f. 71 Ranatra linearis L., living (Poisson, 1951)
p. 110 f. 72 Family Belostomatidae; living a-d- fore tarsi; e-z- ventral part of abdomen; i-k- genitalia of male (Lauck and Menke, 1961)
p. 111 f. 73 Mesobelostomum deperditum (Germ.) original (Oppenheim, 1888); Coll. Munich Univ.; AS I 583; Eichstatt FRG; Up. Jur.
p. 114 f. 74 Lethocerus turgaicus sp. nov.; holotype. a- foreleg; PIN specimen 1096/9; Ekaterinoslavsk, W. Siberia; Miocene. b- holotype, foreleg, Coll. of Dechin Museum; Northern Bohemia, CSSR, Oligo-Miocene.
p. 115 f. 75 Abedus indentatus (Hald.); living (Menke, 1960)
p. 117 f. 76 Mesonepa primordialis (Germ.) a- original (Oppenheim 1888); Coll. Munich Univ. AS VI 9, Solnhofen FRG; Up. Jur; b- reconstruction
p. 120 f. 77 Stygeonepa foersteri sp. nov. a- holotype, Coll. Munich Univ., 1952/183; Langenaltheim, FRG; Up. Jur. b- reconstruction
p. 123 f. 78 Shurabella lepyroniopsis B.-M; specimen PIN imago a- insect body 2032/255; b- insect body 2032/261; B- wing, 2038/256; g- nymph, 2032/244; Shurab III, Kirghiz SSR, Lias
p. 124 f. 79 Shurabella lepyroniopsis B.-M; reconstruction
p. 128 f. 80 Archaecorixa lata Y. Pop.; Karatae, S. Kazakhstan, Jur.
p. 128 f. 81 Forewings of lower Cretaceous Corixidae (Archaecorixinae) a- Diapherinus ornatipennis Y. Pop.; b- Baissocorixa jaczewskii Y. Pop.
p. 130 f. 82 Mesosigara kryshtofovichi sp. n.; holotype; specimen PIN 324/2a; Cagayan, Priamur ; Up. Cretaceous a- insect body; b- middle leg; B- hind leg
p. 131 f. 83 Gazimuria scutellata sp. nov., holotype; specimen PIN 1328/4; Borovsk, Transbaikals, Lias
p. 131 f. 84 Karataviella brachyptera B.-M. Karatau, S. Kazakhstan, Jur. a, b- reconstruction
p. 133 f. 85 Ijanecta angarica sp. nov.; holotype; Coll. PIN 1437/111 a- imago; b-nymph; Vladimirovka, E. Siberia, Lias
p. 134 f. 86 Micronecta minutissima L.; living (Lundblad, 1927)
p. 135 f. 87 Sigara mayri Fieb. living (original)
p. 137 f. 88 Sigaretta florissantella (Cock.) Coll. British Mus., Florissant, Colorado, USA, Oligocene
p. 138 f. 89 Diacorixa miocaenica sp. n. holotype; Specimen PIN 372/16 a- insect body; b- imprint of hind leg, paratype 372/19; Chon-Tuz, Tian-Shan
p. 142 f. 90 Sphaerodemopsis jurassica (Opp.); holotype, Coll. Munich Univ., AS V2V; Eichstatt, FRG, Up. Jur.
p. 145 f. 91 Liadonaucoris rohdendorfi sp. nov.; holotype, specimen PIN 166/2 3, Kizil-Kia, Lias
p. 146 f. 92 Aidium pleurale Y. Pop.; Karatae, S. Kazakhstan, Jur. a- from above; b- from below

p. 147	f. 93	Angaronecta longirostris sp. nov.; holotype, specimen PIN 1668/1742; Bais R., Transbaikals, L. Cretaceous
p. 150	f. 94	Heleonaucoris maculipennis sp. nov; holotype, PIN specimen 2066/3680; Michailovka, Karatau, S. Kazakhstan, U. Jur.
p. 151	f. 95	Ambrysus mormon F.; living (original)
p. 151	f. 96	Asthenocoris luzonensis Using.; living (Usinger, 1938)
p. 153	f. 97	Laccocoris limicola Stål.; living (original)
p. 153	f. 98	Limnocoris signoreti Mont.; living (original)
p. 155	f. 99	Cryphocricos barozzi Sign.; living (original)
p. 155	f. 100	Cataractocoris macrocephalis Mont.; living (original)
p. 157	f. 101	Aphelocheirus aestivalis F.; living (original)
p. 158	f. 102	Potamocoris parvus Hung.; living (Hungerford, 1941)
p. 158	f. 103	Coleopterocoris kleerekoperi Hung.; living (Hungerford, 1942)
p. 160	f. 104	Scaphocoris notatus Y. Pop. a- holotype; PIN specimen 2254/406; Michailovka, Karatau, S. Kazakhstan, Jur. b- reconstruction
p. 161 p.	f. 105	Mesotrephes striata sp. nov.; holotype; PIN specimen 2383/133; Kizil-Dzhar, Karatau, S. Kazakhstan; Up. Cret.
p. 163	f. 106	Limnotrephes campbelli es. et Ch.; living (Poisson, 1951)
p. 163	f. 107	Neotrephes usingeri Ch.; living (Poisson, 1951)
p. 164	f. 108	Paskia minutissima Es., Ch.; living (Esaki, China, 1928)
p. 164	f. 109	Plea minutissima L. a- species from above; b- species from side; living (Poisson, 1957)
p. 169	f. 110	Clypostemma xyphiale Y. Pop. a- specimen PIN 1989/3480; Bais R., Transbaikals, Low. Cretaceous; b- specimen PIN 1668/1843; Bais R., Transbaikals, Low. Cretaceous
p. 171	f. 111	Pelonecta solnhofeni sp. n.; holotype, Coll. Munich Univ., AS V 8; Solnhofen, FRG, Up. Jur.
p. 172	f. 112	Anisops sardea H.-S.; living (Poisson, 1957)
p. 173	f. 113	Liadonecta tomiensis sp. nov.; holotype; Coll. Munich Univ., 1068/1; nymph, Tom R., Black Stop; Lias
p. 173	f. 114	Nepidium stolones Westw.; holotype; Coll. British Mus. 12480; Ridgeway, England; Up. Jur.

CHAPTER VI

FIGURES

115 p. 183 Geological distribution and sceme of the suggested Phylogenetic relationships of the aquatic groups of Heteroptera of the Infraordera Nepomorpha and Leptopodidomorpha.

Superfams: L - Leptopodoidea
G - Gerroidea
C - Corixoidea
O - Ochteroidea
N - Naucoroidea
Nt- Notonectoidea
Np- Nepoidea

116 189 Geological distribution and scheme of suggested phylogenetic relationships of the superfamily Nepoidea

117 194 Geological distribution and scheme of suggested phylogenetic relationships of the superfamily Corixoidea

118 197 Strigils of living Corixoidea a Poisson 57, b Young 62

119 199 Fore tarsi of Corixidae(Corixinae) with the system of stridulating teeth

120 203 Geological distribution and scheme of suggested phylogenetic relationships of the superfamily Naucoroidea

121 207 Geological distribution and scheme of suggested phylogenetic relationships of the superfamily Notonectoidea.