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Taxonomy and bionomy of the weevils of the tribe Hyperini (Coleoptera: Curculionidae)

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I declare that I wrote this thesis myself and presented the citation of all papers, which I used.

In Prague, 2nd March 2007 Jiří Skuhrovec

I agree that my publication and results from it are included in this Ph.D. thesis.

In Prague, 2nd March 2007 Prof. RNDr. Pavel Štys, CSc.

I agree that my publication and results from it are included in this Ph.D. thesis.

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At the beginning of this acknowledgement, I have to excuse myself that following text is in Czech. I am not able to express following lines in English.

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INTRODUCTION

The main aim of my study is to present new knowledge about the weevils of the tribe Hyperini. This PhD thesis includes the Introduction of three parts and the Results of nine parts (papers, manuscripts and abstract).

The Introduction reviews recent published information and author's knowledge about weevils, in more detail about weevils from the tribe Hyperini.

The first chapter "*Taxonomy and phylogenetics*" gives information about history and also recent view on higher taxonomy of these interesting beetles. The major part of this chapter is dedicated to the taxonomic position of genera and subgenera in the tribe Hyperini.

In the second chapter "*Morphology of larvae*", the basic information such as history of development of our knowledge of weevil's larvae, and their apomorphies, are given. The part about morphology of weevil's larvae of the tribe Hyperini is more exhaustive. At the end of chapter, there is shown how the chaetotaxy of larvae can be useful in the applied entomology.

The last chapter "*Ecology*" presents basic data about the life strategy and host plants of Curculionoidea. New bionomic data such as host plants, life strategy (monophagy, oligophagy, polyphagy; ectophagy, endophagy) and aggressive behaviour of larvae are discussed in the part *Tribe Hyperini and its allies*.

The Results include nine parts (papers, manuscripts and abstract). These studies were published on the basis of research during master and postgraduate study.

The first two papers are directed to the taxonomy and phylogenetics of the tribe Hyperini.

The first paper (manuscript) is the first known cladistic analysis of the tribe Hyperini. The analysis is based only on external characters of adults and it supports the monophyly of this tribe. The presence of several genera (*Coniatus*, *Coniatrichus*, *Herpes*, *Phaeopholus*) in the tribe Hyperini is challenged.

The second paper was published in the on-line journal *Zootaxa*. The new species, *Hypera* (*Dapalinus*) *kayali*, from Syria is described and illustrated. The paper included also an illustrated key to the species of the subgenus *Dapalinus* Capiomont, 1868 and a summary of the distribution of the members of the subgenus *Dapalinus*.

The aim of the next five papers is the larval morphology and its use in the applied entomology.

In the first three papers, the descriptions of mature larva of the twenty-nine species of the tribe Hyperini are given. The third paper was published in the journal *Acta Societatis Zoologiceae Bohemiae*. The descriptions of mature larvae of nine species of the nominotypical subgenus *Hypera* Germar, 1817 are presented.

The fourth paper was published in the journal *Entomologica Basiliensia et Collectionis Frey*. The descriptions of mature larvae of ten species of of the subgenera *Antidonus* Bedel, 1886; *Eririnomorphus* Capiomont, 1868; *Dapalinus* Capiomont, 1868 and *Boreohypera* Korotyaev, 1999 of the genus *Hypera* Germar, 1817 are given there.

The fifth paper (submitted) was sent to the journal *Zootaxa*. The descriptions of mature larvae of ten species of the genus *Donus* Jekel, 1865 are given. An identification key of described mature larvae is included in all three papers.

The sixth part of my presented results is the abstract of poster from the *VIIIth European Congress of Entomology* in Izmir, Turkey. The taxonomy of the tribe Hyperini based on the larval characters is discussed here. The character of number of teeth on mandible is especially crucial character of larvae for group (*Neoglanis* with three teeth, *Donus* with four teeth and *Hypera* with two teeth). Chaetotaxy provides characters more useful for identification of species rather than genera.

The seventh paper presents a new method for identification of larval instars. This new method is applicable for all larvae of weevils of the tribe Hyperini and it shows the chaetotaxy as applicable method in the applied entomology. The paper was published in the *Journal of Economic Entomology*.

The last two papers were focused on the ecology of weevil of the tribe Hyperini.

The eighth paper is a review of the host plants of the weevils of genus *Hypera* Germar, 1817 from the Czech Republic. The review is based on my own investigation and literature data including previous feeding experiments. In the paper, new observations on larval development for *H. arator* (Linnaeus, 1758) and *H. nigrirostris* (Fabricius, 1775) are described. The larvae of *H. plantaginis* develop on several plant genera from the Fabaceae but not on *Plantago* spp. from the Plantaginaceae, where they only build the cocoon and pupate. The paper was published in the journal *Klapalekiana* in Czech with exhaustive English summary.

Two unusual types of behaviour (wandering and intraspecific agressive behaviour), which have been observed when rearing larvae of the alfalfa weevil, *Hypera* *postica* (Gyllenhal, 1813), are the main topic of the last paper (manuscript) in this Ph.D. thesis. Intraspecific aggressive behaviour of weevil’s larvae has never been described yet. Larvae that develop in aggregations search for better location when food becomes scarce. Mutual encounter between the larvae may result in agonistic behaviour and some larvae may die as a consequence of fighting. The aggressivity increases with food limitation. Agonistic behaviour is artificial and probably does not occur under natural conditions where there is a plenty of food and larval densities are decreased by pathogens or parasitoids.

1. General information

The weevils are beetles of the superfamily Curculionoidea, mostly phythophagous as both adult and larval stages. To date more than 60,000 described species are classified in 6,000 genera (Thompson 1992, Kuschel 1995, Marvaldi & Lanteri 2005). The higher classification of weevils is under continuous revision, due to new characters provided by adult and larval morphology, and the addition of molecular data. The analyses of these data apply a phylogenetic approach, such as those of Thompson (1992), Zimmerman (1993, 1994a, 1994b), Kuschel (1995), Lawrence & Newton (1995), Morrone (1997), Marvaldi & Morrone (2000), Marvaldi et al. (2002), Marvaldi (2003), and Marvaldi & Lanteri (2005). The majority of the recent classificatory schemes agree in the circumscription of the main higher groups of Curculionoidea (Marvaldi et al. 2002), but they differ in the assignment of ranks and/or the evaluation of the monophyletic status of some heterogeneous subfamilies and tribes (see below).

2. Taxonomy and phylogenetics

2.1. Superfamily Curculionoidea

The first comprehensive view on the classification of the Curculionoidea was made by Schoenherr (1823, 1826, 1833-1845, 1847). He divided the weevils into two groups; “Orthoceri” (weevils with straight antennae) and “Gonatoceri” (weevils with geniculate antennae). “Gonatoceri” are divided into two legions: “Brachyrhynchi” (broad-nosed weevils) with nine divisions and “Mecorhynchi” (long-nosed weevils) with six divisions. Schoenherr included here also Bruchidae, and excluded Scolytidae and Platypodidae.

Lacordaire (1863, 1866) recognized five families of weevils: “Curculionides”, “Scolytides”, “Brentides”, “Anthribides”, and “Bruchides”. He divided “Curculionides” into “Adelognatha” (weevils with prementum covering maxillae) with six tribes and “Phanerognatha” (weevils with prementum leaving maxillae exposed) with 76 tribes. Pascoe (1870) gave the 82 Lacordaire’s tribes of Curculionidae subfamily status without any discussion. This artifical system was taken over for weevil’s classification for decades.

Crowson was the first author who had a major influence on weevil classification. In 1955 he transferred Bruchidae to Chrysomeloidea, treated several subfamilies of Curculionidae as distinct families (Oxycorynidae, Belidae, Apionidae, and Attelabidae), and downgraded Scolytinae and Platypodinae to subfamilies of Curculionidae. Crowson (1955) recognized nine families of Curculionoidea; Nemonychidae, Anthribidae, Belidae, Oxycorynidae, Aglycyderidae, Attelabidae, Brentidae, Apionidae and Curculionidae.

Now, we can distinguish two basic classificatory schemes. At first, we recognized seven (Nemonychidae, Anthribidae, Belidae, Attelabidae, Caridae, Brentidae and Curculionidae) families (Fig. 1), according to the phylogenetic proposals of Kuschel (1995), Marvaldi & Morrone (2000), Marvaldi et al. (2002) Marvaldi (2003), and Marvaldi & Lanteri (2005). The alternative classificatory scheme by Alonso-Zarazaga & Lyal (1999) published in the *“A World Catalogue of Families and Genera of Curculionoidea”* recognized 22 families (Nemonychidae, Anthribidae, Belidae, Eobelidae(+), Eccoptarthridae, Oxycorynidae, Obrieniidae(+), Ulyanidae(+), Rhynchitidae, Attelabidae, Brentidae, Ithyceridae, Eurhynchidae, Apionidae, Nanophyidae, Brachyceridae, Dryophthoridae, Platypodidae Erirhinidae, Raymonodionymidae, Cryptolaryngidae and Curculionidae), following the classification of Thompson (1992) and Zimmerman (1993, 1994a, 1994b).

Fig. 1. Strict consensus of four MPTs obtained from the combined 18S rDNA + morphology parsimony analysis. Numbers above and below branches are bootstrap and jackknife values (>50%), respectively. Take over from Marvaldi et al. (2002)

The cladogram of almost all authors shows a close relationship between Nemonychidae and Anthribidae (including Urodontinae), forming a sister group of the monophyletic “Curculionoidea” (Fig. 1), as also suggested by results of the morphological analysis. These two weevil groups share similar ovipositor (Thompson 1992, Howden 1995); antennae of larvae with three or two segments; maxilla of adults with lacinial lobe or spine (Marvaldi et al. 2002); and mandibular pharyngeal process present, shorter than mandible (Morimoto 1962). Fossil Nemonychidae are known from Jurassic beds (Kuschel 1983, Zherikhin & Gratshev 1995), fossils attributable to Anthribidae are known only from the Middle Cretaceous (Zherikhin 1993), consistent with their bond to angiosperms and angiosperm-dependent ascomycetes and basidiomycetes.

Belidae *sensu lato* is another a monophyletic group of relatively basal weevils (Curculionoidea) (Fig. 1), according to evidence from morphology (of larvae and adults) and 18S rDNA sequences (Marvaldi et al. 2002). The fossil evidence shows that Belidae were present in the Jurassic (Zherikhin & Gratshev 1995), which is in accordance with the basal dichotomy of Curculionoidea leading to (Nemonychidae&Anthribidae) x (Belidae&others) (Marvaldi et al. 2002). Kuschel (1995) provided the first cladistic analysis supporting the monophyly of Belidae, and defined three subfamilies: Belinae, Aglycyderinae and Oxycoryninae. These have family rank in other classificatory schemes (i.e. Thompson 1992, Zimmerman 1994, Alonso-Zarazaga & Lyal 1999). The monophyly of each belid subfamily has not yet been tested (Marvaldi 2004).

A monophyletic Attelabidae *sensu lato* (Fig. 1) was recovered in the combined analysis (Marvaldi et al. 2002). The oldest fossils attributable to Attelabidae are from late Lower Cretaceous (Gratshev 1998) to Middle Cretaceous (Kuschel et al. 1994), but the phylogenetic placement of the family would predict that older fossils may be found. The family is divided into two subfamilies; Attelabinae and Rhynchitinae, according to Kuschel (1995), Marvaldi & Morrone (2000), Marvaldi et al. (2002), Marvaldi (2003), and Marvaldi & Lanteri (2005). These have family rank in other classificatory schemes (Thompson 1992; Zimmerman 1994, Alonso-Zarazaga & Lyal 1999).

The phylogenetic position of Caridae (Fig. 1) has been enigmatic for a long time. Different authors have included *Car* and related taxa in different families, e.g., Attelabidae (Crowson 1955), Apionidae (Wibmer & O'Brien 1986), Belidae (Thompson 1992, Zherikhin & Gratshev 1995), Curculionidae (Kuschel et al. 1994), and Brentidae (Kuschel 1995), whereas others considered them to be a distinct family (Zimmerman 1994). Results of the combined cladistic analysis support placement of Caridae as sister taxon of the clade (Brentidae&Curculionidae) (Marlvaldi et al 2002). The Caridae are known from Late Jurassic deposits (Arnoldi 1977, Gratshev & Zherikhin 1999) and were abundant in the Lower Cretaceous (Kuschel et al. 1994).

The original concept of Brentidae *sensu lato* (Fig. 1) was widened by several authors (Morimoto 1976, Kuschel 1990, 1995, Thompson 1992, Marlvaldi et al 2002) to include Eurhynchinae, Antliarhininae, Cyladinae, Apioninae, and Nanophyinae (and also Carinae; Kuschel 1995). These have family rank in other classificatory schemes (Zimmerman 1994, Alonso-Zarazaga & Lyal 1999).

The combined analysis places the monotypic genus *Ithycerus* in the Brentidae, in accordance with Oberprieler (2000), but independent analyses of morphology and molecules do not support this grouping. The some of authors give the family rank (Ithyceridae) for this enigmatic weevil (Morrone 1997, Alonso-Zarazaga & Lyal 1999).

Curculionidae *sensu lato* can be clearly established as the sister group to the Brentidae and permit identification of Curculionidae as a monophyletic group (Fig. 1); larval apomorphies (frontal lines incomplete, not extending to mandibles; sensillum next to dorsoepicranial seta 2 absent; dorsal epicranial seta 3 (*des3*) on frontal line or on frons; thoracic spiracle on prothorax and segments on abdomen with 3 or 4 folds) and adult apomorphies (type of antennae geniculate; antennal club (segments 9–11) - all segments tightly articulated or compact; tibial spurs absent or very rudimentary; tarsal segment 2 rounded at apical angles and spermathecal duct and gland well apart on spermathecal body) defining the Curculionidae (Marvaldi et al. 2002). The oldest described fossil of a curculionid is *Cretulio nucula* from late Lower Cretaceous deposits (Zherikhin 1993). Its tentative placement in Erirhininae is consistent with the placement of erirhinines among the most basal curculionids in cladogram (Marvaldi et al. 2002).

Curculionids classified in Ocladiinae, Erirhininae and Dryophthorinae, which retain the primitive orthocerous type of male genitalia (tectum is present) (Morimoto 1962, Kuschel 1971, Thompson 1992), occupy basal positions (Fig. 1) in the phylogeny estimate (Marvaldi et al. 2002). Although sequences were not available for representatives of two small groups with orthoceroustype genitalia (Brachycerinae and Cryptolarynginae), the morphological characters suggest they are among the basal members of the Curculionidae (Marvaldi et al. 2002). Evidence for a close relationship between Brachycerinae sensu stricto and Ocladiinae is provided by both adult

(Thompson 1992) and larval (Marvaldi 1997) morphology. Larvae of the Cryptolarynginae remain unknown, but adult morphology suggests a close relationship to Ocladiinae or Erirhininae (Marvaldi & Morrone 2000, Oberprieler 2000). Erirhininae in the strict sense of Kuschel (1971, see in Alonso-Zarazaga & Lyal 1999) are difficult to delimit. However, monophyly of the Dryophthorinae is strongly supported, and they probably represent an independent offshoot branch to neighbouring Curculionidae. All its subfamilies (Brachycerinae, Cryprtolarynginae, Erirhininae, Raymondionyminae, Dryophthorinae and Platypodinae) have family rank in other classificatory schemes (Thompson 1992, Zimmerman 1994, Morrone 1997, Alonso-Zarazaga & Lyal 1999).

Curculionidae *sensu stricto* is the largest group of weevils, in agreement (except for the inclusion of Platypodinae) with the restricted concept of Curculionidae proposed by Thompson (1992) and Zimmerman (1993, 1994a, 1994b). They are characterized by the derived gonatocerous type (tectum is absent) of male genitalia (apomorfies): (1) plate of male sternite 8 divided to form paired hemisternites (Thompson 1992); (2) male genitalia: manubrium (apodeme of tegmen) smaller than spiculum gastrale (Thompson 1992, Zimmerman 1994a); (3) aedeagal dorsal plate or tectum absent (dorsal part of the aedeagus entirely membranous and sometimes enfolded by ventral part) (Morimoto 1962, Kuschel 1971, Thompson 1992, Zimmerman 1993, 1994a, 1994b), when the tectum is absent, it is of the gonatocerous type; (4) tegminal dorsal plate (=cap piece or parameral sector of tegmen) vestigial, reduced to a pair of delicate asetose lobes, or absent (Morimoto 1962, Thompson 1992); (5) insertion and relative position of aedeagal apodeme in lateral view lateral or ventral, deflexed from axis of aedeagal body (Marvaldi et al. 2002); and (6) apodemal bridge of aedeagus absent (Morimoto 1962, Zimmerman 1993).

The Platypodinae have been considered by several authors as a distinct family, mainly because unique adult morphological characters (e.g., Calder 1989, 1990, Thompson 1992, Lyal & King 1996, Alonso-Zarazaga & Lyal 1999) were interpreted as providing none or equivocal evidence of relationship to any other group of weevils. However, the larval characters naturally place them within Curculionidae *sensu lato* (May 1993) and suggest a close relationship of Platypodinae with Dryophthorinae (Marvaldi 1997).

The rank of subfamilies in Curculionidae *sensu stricto* is under continuous revision, due to new characters provided by adult and larval morphology, and the addition of molecular data. The majority of cladistic analysis have been still directed to researching higher clades. After solving of this problem, the attention of experts will be directed to this topic. In the *"A World Catalogue of Families and Genera of Curculionoidea (Excepting Scolytidae and Platypodidae)"* (Alonso-Zarazaga & Lyal 1999) Curculionidae *sensu stricto* is divided into 16 subfamilies (excluded Scolytidae); Curculioninae (included Ulomascinae), Bagoinae, Baridinae, Brachyceropsidinae, Ceutorhynchinae, Conoderinae (included Zygopinae), Cossoninae, Cryptorhynchinae, Cyclominae (included Rhytirrhininae, Goniopterinae), Entiminae (included Amycterinae and Thecesterninae), Hyperinae (synonym Phytonominae), Lixinae (synonyms Geomorinae, Cleoninae), Mesoptiliinae (synonym Magdalininae), Molytinae, Orobitidinae, Xiphaspidinae.

Some of curculionids "subfamilies" were recovered in the combined cladogram (30 "subfamilies") (Marvaldi et al. 2002), with high support values found for their monophyly (e.g., Bagoinae, Entiminae, Baridinae, Ceutorhynchinae, Platypodinae) (Fig. 1). Other "subfamilies" appear to be polyphyletic (e.g. Molytinae, Derelominae) (Fig. 1) or paraphyletic (e.g., Cossoninae, Scolytinae) (Fig. 1) in the combined analysis (Marvaldi et al. 2002).

2.2. Tribe Hyperini and its allies

The subfamily Hyperinae is divided into two tribes; Cepurini Capiomont, 1867 and Hyperini Marseul, 1863 (Alonso-Zarazaga & Lyal 1999). Weevils of the first tribe are almost unknown. Tribe Cepurini included 15 genera occurring particularly in the south hemisphere (Alonso-Zarazaga & Lyal 1999). Mainly individual descriptions and almost no facts about immature stages, ecology and/or thier host plants are known. The exception is the Neotropical weevil, *Phelypera distigma* (Boheman, 1842). The ectophagous larvae are one of the most important character of the subfamily Hyperinae. The subfamilies Rhytirrhininae, Goniopterinae and Cyclominae share this character. Morrone (1997) and Alonso-Zarazaga & Lyal (1999) classified Rhytirrhininae and Goniopterinae with tribe rank in the subfamily Cyclominae.

In the literature from second half of the 20th century (Hoffmann 1954, Smreczyński 1968, Kippenberg 1983, Dieckmann & Behne 1994) Hyperinae were classified with tribe rank in the subfamily Hylobiinae. This artifical classificatory scheme has been already left. All new taxonomic papers accepted the new view and differentiate these probably unrelated groups of weevils.

Alonso-Zarazaga & Lyal (1999) recognized 19 genera in the tribe Hyperini (Table 1). Three years later, they published (Alonso-Zarazaga & Lyal 2002) the first *"Addenda and corrigenda to Catalogue"*, where they added three genera into tribe Hyperini (see Table 1).

Table 1. The comparison of two recent check-lists of genera and subgenera in the tribe Hyperini; Alonso-Zarazaga & Lyal 1999 and 2002

Alonso-Zarazaga & Lyal 1999	Alonso-Zarazaga & Lyal 2002
Adonus Zaslavskij, 1999	***Adonus*** Zaslavskij, 1999
Agriochaeta Pascoe, 1872	***Agriochaeta*** Pascoe, 1872
Bubalocephalus Capiomont, 1868	***Bubalocephalus*** Capiomont, 1868
Coniatrichus Reitter, 1901	***Coniatrichus*** Reitter, 1901
Coniatus Germar, 1817 (sbg. ***Coniatus*** s.str.; ***Bagoides*** Capiomont, 1868; ***Pseudogeranorhinus*** Pic, 1914)	***Coniatus*** Germar, 1817 (sbg. ***Coniatus*** s. str.; ***Bagoides*** Capiomont, 1868; ***Pseudogeranorhinus*** Pic, 1914)
Diastrophilus Faust, 1892	***Diastrophilus*** Faust, 1892
Donus Jekel, 1865	***Donus*** Jekel, 1865 (***Donus*** s. str.**;** ***Antidonus*** Capiomont, 1868)
Eremochorus Zaslavskij, 1962	***Eremochorus*** Zaslavskij, 1962
	Herpes Bedel, 1874
Hypera Germar, 1817 (sbg. ***Hypera*** s. str.; ***Antidonus*** Capiomont, 1868; ***Boreohypera*** Korotyaev, 1999; ***Dapalinus*** Capiomont, 1868; ***Eririnomorphus*** Capiomont, 1868; ***Tigrinellus*** Capiomont, 1868)	***Hypera*** Germar, 1817(sbg. ***Hypera*** s. str.; ***Boreohypera*** Korotyaev, 1999; ***Dapalinus*** Capiomont, 1868; ***Eririnomorphus*** Capiomont, 1868; ***Tigrinellus*** Capiomont, 1868;)
Hyperites Zherikhin, 1989 (†)	***Hyperites*** Zherikhin, 1989 (†)
Lamprohypera Heller, 1908	***Lamprohypera*** Heller, 1908
Limobius Schoenherr, 1843	***Limobius*** Schoenherr, 1843
Lycosura Pascoe, 1875**,**	***Lycosura*** Pascoe, 1875
Macrotarrhus Bedel, 1906 (sbg. ***Marcotarrhus*** s. str.; ***Proteromera*** Zaslavskij, 1958; ***Ectomochila*** Zaslavskij, 1958; ***Alexiola*** Suvorov, 1912)	***Macrotarrhus*** Bedel, 1906 (sbg. ***Marcotarrhus*** s. str.; ***Proteromera*** Zaslavskij, 1958; ***Ectomochila*** Zaslavskij, 1958; ***Alexiola*** Suvorov, 1912)
Metadonus Capiomont, 1868	***Metadonus*** Capiomont, 1868
Neoglanis Alonso-Zarazaga & Lyal, 1999 (sbg. ***Neoglanis*** s. str.; ***Altaiodonus*** Legalov, 1999)	***Neoglanis*** Alonso-Zarazaga & Lyal, 1999 (sbg. ***Neoglanis*** s. str.; ***Altaiodonus*** Legalov, 1999)
	Oreochorus Zaslavskij & Korotyaev, 1998
Orthodonus Zaslavskij, 1965	***Orthodonus*** Zaslavskij, 1965
	Pachypera Capiomont, 1868
Parahypera Brancsik, 1914	***Parahypera*** Brancsik, 1914
Phaeopholus Roelofs, 1873	***Phaeopholus*** Roelofs, 1873

In the following text, 22 genera of the tribe Hyperini will be divided in two groups: (1) Relatives of Hyperini, and (2) Hyperini *sensu stricto*; and detailed comments to their taxonomic position, occurence and bionomy are given for every genus.

(1) Relatives of Hyperini

The four genera occur in the south hemisphere; the genera *Agriochaeta* Pascoe, 1872 and *Lycosura* Pascoe, 1875 in the Australia, species of the genus *Lamprohypera*

Heller, 1908 in the New Guinea and the genus *Diastrophilus* Faust, 1892 is known from the Neotropical region. In my opinion, these genera do not belong to the tribe Hyperini, but it is only subjective view. All these genera were classified in the tribe Hyperini on the basis of similar scales, or according to only historical view. I think that tribes Hyperini, Cepurini and subfamily Cyclominae sensu lato have very close relationships with each other, and belong to a higher group, but not Hyperini *sensu stricto*.

The genus *Herpes* Bedel, 1874 was transfered into the tribe Hyperini from the subfamily Cyclominae on the basis of similar bionomy (Alonso-Zarazaga & Lyal 2002, Gültekin, 2004). Unfortunately, authors did not consider that the bionomy of Hyperini-species and Cyclominae-species are almost the same. They transfered this genus only according to ectophagous larvae and skill to spin a webby cocoon. We know several species which have identical strategy and they are really not Hyperini, e.g. genus *Phytobius* Schoenherr, 1833 (Ceutorhynchinae). That it is reason why I still do not accept this transfer. The comparison of the morphology of larvae and adults resolve the taxonomic classification of this enigmatic weevil.

The only one species *Parahypera ussurica* Brancsik, 1914 in the genus can not be classified in the tribe Hyperini, because it is a new synonym of *Fronto bimaculatus* Petri, 1901 in the tribe Cepurini (Winkelmann, pers. comm).

The enigmatic genus *Phaeopholus* Roelofs, 1873 occurs in the East-Palaearctic (Hong et al. 2000). At first, it can appear like the representatives of the tribe Cionini or Cepurini. The analysis strongly supports the hypothesis about relationship of genus *Phaeopholus* and tribe Cepurini (Skuhrovec, unpubl. data).

The genera *Coniatus* and the monotypic *Coniatrichus* are the most problematic groups in the tribe Hyperini. The presence of short projecting setae on the body is the only difference between these two genera. The development of *Coniatus*-species is well known, they develop on the plant family Tamaricaeae. The differential diagnosis for both genera are round eyes, round scales on the whole surface of body, coloration of scales (mainly green), and larvae with two setae at the abdominal segement IX. Some characters (round eyes, round scales on the whole surface of body) are also shared by some representatives of the genus *Gronops* Schoenherr, 1823) in the subfamily Cyclominae. The analysis without *Coniatus* and *Coniatrichus* gives us more strict relationships between other genera and subgenera in Hyperini *sensu stricto* (Skuhrovec, unpubl. data). Therefor, these two genera probably belong to other tribe, e.g. Listroderini, in the subafmily Cyclominae.

(2) Hyperini *sensu stricto*

The genus *Hyperites* Zherikhin, 1989 (Alonso-Zarazaga & Lyal 1999) is extinct. The relationship with other genera is unknown.

In the strict consensus (Skuhrovec, unpubl. data), Hyperini *sensu stricto* are divided into four basic clades. The clades are very similar to the groups published by Zaslavskij (1959b).

(A) Clade (*Neoglanis* incl. *Pachypera* + *Oreochorus* + *Adonus*)

The species of the genus *Neoglanis* Alonso-Zarazaga & Lyal, 1999 occur primary in the European and Asian mountains. Their host plant belong to several plant families (polyphagy). This clade corresponds to the second group in Zaslavskij (1959b), who included there only *Neoglanis*-species. Zaslavskij did not recognize the other genera on the genera rank. The existence of the genus *Neoglanis* presents a great problem for the taxonomy of Hyperini large problem. In former (Kippenberg 1983) and in several recent papers (Winkelmann 2001, Skuhrovec, in prep.), *Neoglanis*-species are classified into the genus *Donus* Jekel, 1865. Zaslavskij (1959b) divided *Donus* into two genera;

Neoglanis and *Donus*. The limit between these two genera was not specified well, which is reason why I and my colleague Herbert Winkelmann (both Hyperini-group in CURCULIO-Institut) did not accepte these taxonomic changes in our papers.

The genus *Pachypera* Capiomont, 1868 was described on the basis of enlarged distal part of protibia and sharp inner margin of protibia. Petri (1901) provided these weevils as the first group of the genus *Donus* (respectively "*Neoglanis*") identified by the mentioned characters. The analysis strongly supports *Pachypera*–species as the component of the genus *Neoglanis* (only as well-defined group).

All four known species of the genus *Oreochorus* Zaslavskij & Korotyaev, 1998 occur in the Altai and Mongolia (Krivets & Korotyaev 1998). Bionomy is completely unknown.

Petri (1901) included the unusual species *Hypera tychiodes* (Capiomont, 1868) in the subgenus *Dapalinus* Capiomont, 1868 in the genus *Hypera*. This species was later synonymized with *Tanyrhynchus asiaticus* Schoenherr, 1849 and a new genus, *Adonus* Zaslavskij 1999, was proposed for it, so that its valid name is *Adonus asiaticus* (Schoenherr, 1849). It does not belong in the genus *Hypera* (Alonso-Zarazaga & Lyal 1999).

(B) Clade (*Donus*)

The species of *Donus* Jekel, 1865 occurs especially in the European and Asian lowlands. The representatives of *Donus* are oligophagous, theirs host plants belongs to several plant genera of one plant family (e. g. Fabaceae, Geraniaceae). This clade partially corresponds to the first group in Zaslavskij (1959b), who included there also the genera *Bubalocephalus*, *Eremochorus*, *Macrotarrhus* and *Metadonus* (clade 3 and 4). The taxonomic position of *Donus*-species has not been resolved yet as I present above.

The transfer of the subgenus *Antidonus* Bedel, 1886 from genus *Hypera* Germar, 1817 into genus *Donus* brings another problem. The situation is the same as the previous one (*Neoglanis* versus *Donus*). We did not accepte these chnages without detailed revision of several groups of Hyperini. My results of larval morphology partially correspond with these taxonomic changes, but we must establish the basic groups before making taxonomic changes inside.

(C) Clade (((*Eremochorus*+*Orthodonus*) & *Macrotarrhus*) & *Metadonus*)

The species of this clade occurs especially in the steppes and semideserts in Asia, the several exceptions occur in the Europe and in the northern Africa. Unfortunately, our knowledge about their host plants and bionomy are almost none. Zaslavskij (1959) classified these three genera into his first group, together with genus *Donus*.

All known species (more than 40) of the genus *Eremochorus* Zaslavskij, 1962 occur in the central and northeastern Asia (Kazakhstan, Kyrgyzstan, Turkmenistan, Mongolia, Siberia). The majority of species were described by Zaslavskij (1962, 1978). Several species probably develope on plants of genus *Atraphaxis* from the family Polygonaceae. Zaslavskij (1959b) classified *Eremochorus* in the first group, together with *Donus*-species. The monotypic genus *Orthodonus* Zaslavskij, 1965 occur in Kirgizia on some unidentified plant from the family Chenopodiaceae (Zaslavskij 1965).

The genus *Macrotarrhus* Bedel, 1906 is divided into four subgenera (*Proteromera* Zaslavskij, 1958; *Ectomochila* Zaslavskij, 1958; *Alexiola* Suvorov, 1912 and *Marcotarrhus* s. str.) (Zaslavskij 1962). More than 40 known species occur only in Asia. The majority of species were described by Zaslavskij (1958, 1961, 1965, 1967) and Bajtenov (1975, 1980, 1982). Several species probably develope on plants of genus *Atraphaxis* from the family Polygonaceae.

The genus *Metadonus* Capiomont, 1868, has only 18 species occurring primarily in Asia; the exceptions are *M. gracilentus* (Capiomont, 1868) (Portugal, Spain), *M. vuillefroyanus* (Capiomont, 1868) (Spain, part of the northern Africa) and *M. distinguendus* (Boheman, 1842) (Ukraine, Moldavia, Russia). The taxonomic position of the former two species in the genus *Metadonus* is not very certain.

(D) Clade (*Bubalocephalus*) & (*Hypera* (incl. *Limobius*))

All four described species of the endemic Spanish genus *Bubalocephalus* Capiomont, 1868 have round eyes and long projecting setae on the whole body (Gonzáles 1965). The knowledge about its ecology is scarce. Zaslavskij (1959b) classified this genus in the first group, together with *Donus*-species.

The genus *Hypera* Germar, 1817 currently includes more than 115 Palaearctic species (Smreczyński 1968) and 17 species from North America (Anderson 2002). The genus is divided into six subgenera (*Antidonus* Bedel, 1886; *Eririnomorphus* Capiomont, 1868; *Tigrinellus* Capiomont, 1868; *Dapalinus* Capiomont, 1868; *Boreohypera* Korotyaev, 1999 and *Hypera* s. str.) (Alonso-Zarazaga & Lyal 1999). The *Hypera*-species are mostly oligophagous, but several monophagous are also known (Skuhrovec 2003). Alonso-Zarazaga & Lyal (2002) transfered the subgenus *Antidonus* to the genus *Donus*, but without any discussion of this nomenclatorical change. Alonso-Zarazaga (2005) described a new subgenus *Kippenbergia*. Skuhrovec (2006a) considers it is most probably only a species group of *Hypera arator* (Linné, 1758) within the nominotypical subgenus *Hypera*. Identical presentation is given in the monography by Petri (1901) and/or in the revision of this species group by Kippenberg (1986). We (I and H. Winkelmann, both Hyperini-group in CURCULIO-Institut) do not accept these taxonomic changes in our papers (see above).

The genus *Limobius* with three species is classified in this group also. All known species develope on plants from the family Geraniaceae (Smreczyński 1968). The *Limobius*-species have six funicle segments, which is the only difference from *Hypera*-species, which have seven funicle segments. My cladistic analysis supports that *Limobius* is really the component of the genus *Hypera*, probably relative to group of *Hypera cumana*.

3. Morphology of larvae

3.1. Superfamily Curculionoidea

The descriptions of weevil larvae in the older literature are mostly very schematic and quite useless for identification. Recent important contributions are made by Cotton (1924) on the North American Dryophthoridae, Keifer (1933) on some broad-nosed weevils of the Pacific coast, Gardner (1934) on many Indian species, Anderson (1938-1960) on *Proterrhinus*, *Hypera*, Anthribidae, Dryophthoridae and Cossoninae, Viedma (1963) on the European xylophagous weevils, Emden (1938, 1952) on the primitive families and the broad-nosed subfamilies, Scherf (1964) on all European weevils, Ahmad & Burke (1972) on Anthonomini, May (1966-1993) mostly on New Zealand weevils, Lee & Morimoto (1988-1996) on the Japan weevils, and Marvaldi (1997) and Marvaldi & Lanteri (2005) mostly on the South American weevils.

A morphological characterization of the weevils' larvae is as follows: comma-shaped grubs; with soft (usually whitish) abdominal segments, the first seven or eight transversely divided into two to four dorsal folds or plicae; legs absent or greatly reduced to 2 or fewer segments; head hypognathous, with reduced antennae (usually one-segmented, rarely two-segmented, plus the sensorium); hypopharyngeal bracon present (except in some leaf-miners and platypodines); maxilla with a single apical lobe or mala; abdominal tergum IX without urogonphi or a terminal spine; spiracles annular, with or without airtubes (Stehr 1991, Marvaldi & Lanteri 2005). Comparative notes: larvae of some Chrysomeloidea (Cerambycidae, Megalopodidae, and Chrysomelidae (including Bruchinae)) can be confused with weevil larvae, but all of the former differ in lacking a hypopharyngeal bracon and most of them differ in having legs (Marvaldi & Lanteri 2005). Legless larvae of Cerambycidae, as well as those of Buprestidae, can be separated from weevil larvae by their straight body and enlarged prothorax (Stehr 1991, Marvaldi & Lanteri 2005). Larvae of Scarabaeoidea can be differentiated from weevil larvae on the basis of their strongly curved body, well-developed legs, and cribriform and reniform spiracles (Stehr 1991, Marvaldi & Lanteri 2005).

3.2. Tribe Hyperini and its allies

Differential morphological characters of larvae of the tribe Hyperini were published by Lee & Morimoto (1988), May (1993), and Marvaldi & Lanteri (2005); epipharynx and maxilla with simple setae, epipharynx with two anterolateral (*als*) and four anteromedian (*ams*) setae, the third dorsal seta (*des3*) on epicranium, the fifth frontal seta (*fs5*) longer than the fourth one (*fs4*), one-segment labial palpus, mandible with sharp teeth, labral rods absent, postoccipital condyles present, pedal areas swollen to form prolegs or large lobes, head maculate and body pigmented. Larvae of these weevils are mainly ectophagy, feeding on leaves and sometimes on flowers. Two morphological characters (pedal areas swollen to form prolegs or large lobes and body pigmented) are probably the adaptation to ectophagy, which could be apomorphy of the tribe Hyperini / subfamily Hyperinae or of the clade (Hyperinae & Cyclominae). Mature larvae of Hyperini weevils form cocoons, in which they pupate, and the adults hatch after one (*Hypera*-species) or two (*Donus*-species) weeks (Skuhrovec, unpubl. data).

Table 2. Check-list of Hyperini-species (36) whose larvae are described more than ten years ago

***Coniatus*–species**
C. splendidulus (Fabricius, 1781)
C. wenckeri Capimiont, 1868

***Donus*–species**
D. arnoldii (Zaslavskij 1967)
D. comatus (Boheman, 1842)
D. crinitus (Boheman, 1834)
D. elegans (Boheman, 1842)
D. gemina (Zaslavskij 1967)
D. intermedius (Boheman, 1842)
D. oxalidis (Herbst, 1795)
D. ovalis (Boheman, 1842)
D. palumbarius (Germar, 1821)
D. segnis (Capiomont, 1867)
D. rubi (Krauss, 1900)
D. tesselatus (Herbst, 1795)
D. velutinus (Boheman, 1842)

***Hypera*–species**
H. (*Antidonus*) *dauci* (Olivier, 1807)
H. (*Antidonus*) *subfasciculata* (Zaslavskij 1967)
H. (*Antidonus*) *vidua* Gené, 1837
H. (*Antidonus*) *zoila* (Scopoli, 1763)
H. (*Eririnomorphus*) *adspersa* (Fabricius, 1792)
H. (*Eririnomorphus*) *arundinis* (Paykull, 1792)
H. (*Eririnomorphus*) *rumicis* (Linné, 1758)
H. (*Dapalinus*) *contaminata* (Herbst, 1795)
H. (*Dapalinus*) *meles* (Fabricius, 1792)
H. (*Tigrinellus*) *pastinacae* Rossi, 1790
H. (s. str.) *arator* (Linné, 1758)
H. (s. str.) *fuscocinerea* (Marsham, 1802)
H. (s. str.) *nigrirostris* (Fabricius, 1775)
H. (s. str.) *ononidis* (Chevrolat, 1863)
H. (s. str.) *pandellei folwacznyi* Dieckmann, 1975
H. (s. str.) *plantaginis* (De Geer, 1775)
H. (s. str.) *postica* (Gyllenhal, 1813)
H. (s. str.) *suspiciosa* (Herbst, 1795)

Limobius borealis (Paykull, 1792)
Macrotarrhus arachnoidea (Suvorov, 1912)
Metadonus distinguendus (Capiomont, 1868)
Orthodonus pilosus Zaslavskij, 1965

Descriptions of larvae of Hyperini-species are relatively scarce with the exception of last decade. Only 36 Hyperini-species (Table 2) were known ten years ago (Goureau 1844, Heeger 1851, Perris 1851, Laboulbène 1862, Rupertsberger 1872, Rosenhauer 1882, Titus 1911, Servadei 1944, Anderson 1947, Anderson 1948, Peterson 1951, Zaslavskij 1959a, Scherf 1964, Zaslavskij 1965, 1967, Dieckmann 1975, Bland 1983, Strejček & Dieckmann 1987, Lee & Morimoto 1988, Dieckmann 1989, Stehr 1991, May 1994). Majority of papers (Goureau 1844, Heeger 1851, Perris 1851, Laboulbène 1862, Rupertsberger 1872, Rosenhauer 1882, Titus 1911, Peterson 1951, Scherf 1964 (majority of descriptions), Dieckmann 1975, Strejček & Dieckmann 1987, Dieckmann 1989) include only descriptions of body colouration, and size and lack precise data on the morphology and chaetotaxy. The important papers were written by Anderson (1948) and Zaslavskij (1959a). They include some basic descriptions (not detail) and an identification key and can still be used to identify larvae. Only the recent paper by Lee & Morimoto (1988) contained detailed drawings and descriptions of the chaetotaxy based on the general chaetotaxy plan proposed by May (1994).

In the last ten years, several detailed descriptions of 31 Hyperini-species were Publisher (Nazarenko 1998, 2000a, 2000b; Skuhrovec 2003, 2005a, 2006c, submitted). Larvae of 14 species (Table 3) were described for the first time, larvae of 10 species (Table 3) were described for the first time in detail and larvae of 7 species (Table 3) were redescribed.

Table 3. Check-list of Hyperini-species (31) whose the describtions of larvae were published in the last ten years

Status of description	**Check-list of species**
First description (14)	*Hypera* (s. str.) *denominanda* (Capiomont, 1868); *H.* (s. str.) *jucunda* (Capiomont, 1868); *H.* (s. str.) *venusta* (Fabricius, 1781); *H.* (s. str.) *viciae* (Gyllenhal, 1813); *H.* (*Antidonus*) *lunata* Wollaston, 1854; *H.* (*Dapalinus*) *kayali* Skuhrovec, 2006; *H.* (*Dapalinus*) *striata* (Boheman, 1834); *H.* (*Boreohypera*) *diversipunctata* (Schrank, 1798); *Donus austerus* (Boheman, 1834); *D. bucovinenis* (Penecke, 1928); *D. cyrtus* (Germar, 1821); *D. nidensis* Mazur and Petryszak, 1981; *D. osellai* Winkelmann, 2001 and *D. reichei* (Capiomont, 1868)
First description in detail (10)	*Hypera* (s. str.) *arator*; *H.* (s. str.) *plantaginis*; *H.* (*Antidonus*) *dauci*; *H.* (*Antidonus*) *vidua*; *H.* (*Eririnomorphus*) *arundinis*; *H.* (*Dapalinus*) *contaminata*; *Donus comatus*; *D. oxalidis*; *D. palumbarius* and *D. tesselatus*
Redescribtion (7)	*Hypera* (s. str.) *nigrirostris*; *H.* (s. str.) *postica*; *H.* (s. str.) *suspiciosa*; *H.* (*Antidonus*) *zoila*; *H.* (*Eririnomorphus*) *rumicis*; *Donus crinitus* and *D. intermedius*

Descriptions of larvae of three species (*Donus bucovinensis*, *D. intermedius* and *D. nidensis*) by Nazarenko (1998, 2000a, 2000b) are detailed, but unfortunately different nomenclature of chaetotaxy is used. In one of his papers, Nazarenko (2000a) used the combination of two nomenclatures (Emden 1952 and Scherf 1964). Skuhrovec (2003, 2005a, 2006c, submitted) used for the detailed descriptions of larvae the nomenclature of Curculionoidea, which is listed in May (1994). Unfortunately, her nomenclature is not corresponding to those used for other groups of beetles.

Larval characters of Hyperini-species seem to correspond well with the preliminary results of phylogenetic analysis based on adults (Skuhrovec, unpubl. data). Number of teeth of mandible is especially crucial character of larvae for group. Larvae of all known *Neoglanis*-species (Table 4) have three teeth on mandible, *Donus*-species (Table 4) have four teeth on mandible and *Hypera*-species (Table 4) have only two teeth on mandible. Zaslavskij (1959b) divided the genus *Donus* into two genera; *Neoglanis* and *Donus*. Alonso-Zarazaga & Lyal (2002) transfered the subgenus *Antidonus* from the genus *Hypera* to the genus *Donus*, but without any discussion of this nomenclatorical change. The limits between these three genera were not specified well, which is the reason why I and my colleague Herbert Winkelmann (Hyperini-group in CURCULIO-Institut) still accept only two genera, *Donus* and *Hypera*.

Table 4. The groups of Hyperini-species, whose larva was described in last ten years, based on number of teeth on mandible of larvae

Genus / Group	**Number of teeth on mandible**	**Check-list of species**
"*Donus*-species"	**4**	*Donus crinitus*, *D. reichei*, *Hypera* (*Antidonus*) *dauci*, *H.* (*Antidonus*) *lunata*, *H.* (*Antidonus*) *vidua* and *H.* (*Antidonus*) *zoila*
"*Neoglanis*-species"	**3**	*Donus austerus*, *D. bucovinenis*, *D. comatus* , *D. cyrtus*, *D. intermedius*, *D. nidensis*, *D. osellai*, *D. oxalidis*, *D. palumbarius* and *D. tesselatus*
"*Hypera*-species"	**2**	*Hypera* (*Eririnomorphus*) *arundinis*, *H.* (*Eririnomorphus*) *rumicis*, *H.* (*Boreohypera*) *diversipunctata*, *H.* (*Dapalinus*) *contaminata*, *H.* (*Dapalinus*) *kayali*, *H.* (*Dapalinus*) *striata*, *H.* (s.str.) *arator*, *H.* (s.str.) *denominanda*, *H.* (s.str.) *jucunda*, *H.* (s.str.) *nigrirostris*, *H.* (s.str.) *plantaginis*, *H.* (s.str.) *postica*, *H.* (s.str.) *suspiciosa*, *H.* (s.str.) *venusta* and *H.* (s.str.) *viciae*

Chaetotaxy of the Hyperini-species provides characters more useful for identification of species than genera (Skuhrovec, unpubl. data). An identification key for the mature larvae of all twenty-nine Hyperini-species is presented by Skuhrovec (in prep). Several characters, however, are specific for identification of genus, e. g.

presence of setae on abdominal segment IX. Two setae are present only by *Coniatus*-species, while all other larvae of Hyperini, and Curculionidae in general have no setae on this abdominal segment.

Larval chaetotaxy can be also used for applied entomology. Skuhrovec (2006b) presented new easy identification of instars by using chaetotaxy. This new method is quick and accurate. The previous methods are more slowly and inaccurate. The best method of instar identification is the combination of two methods (visual inspection and new method). At first, we differentiate small (the first and the second instar) and large (the third and the fourth instar) larvae by visual inspection, and then to use a stereomicroscope for exact differentiation between L1 versus L2 and L3 versus L4. Such knowledge enables us to refine the timing of control decisions in the pest management.

This new method has been also helpful during breeding of larvae. The quick and accurate identification of instars is necessary for the observations of the larval development at several different temperatures (Skuhrovec & Honěk, unpubl. data). Manipulation with larvae during the breeding is unadvisable beacuse of the possibility of increased mortality.

4. Ecology

4.1. Superfamily Curculionoidea

Weevils have colonized virtually every plant group and every plant part, but particular lineages often show strong conservatism in the evolution of host use. Weevil lineages that are classified at ranks from subfamilies to groups of genera are primarily associated with one of the major vascular plant groups: cycads, conifers, monocots, or "dicots" (Marvaldi et al. 2002).

The larvae of Curculionoidea are primitively endophagous, feeding inside host tissues. Like the endophagous longhorn beetle family Cerambycidae, weevil larvae have lost the development of legs (Crowson 1955, Stehr 1991, Marvaldi 1997, Farrell 1998a). Larval endophagy is associated with adult rostrum development and oviposition behavior (Marvaldi et al. 2002). Most weevils use the rostrum to place eggs inside larval substrates, but the adults of Scolytinae and Platypodinae tunnel deep inside tree trunks and branches for adult feeding and oviposition (Marvaldi et al. 2002).

Adults of broad-nosed weevils, such as those in the large subfamily Entiminae, do not use the rostrum for oviposition and the larvae feed on roots from adjacent positions in the soil (Marvaldi et al. 2002). Construction of earthen cells for feeding has also been reported for other broadnosed weevils in Thecesterninae (McClay & Anderson 1985), in some Rhytirrhininae (Scott & Way 1989), and in Lixinae (O'Brien & Marshall 1987).

Thus, even the external root feeders are still endophagous in the sense that they live concealed inside the substratum (Marvaldi 1997). Being totally legless, larvae of Curculionidae are mostly endophagous feeders, although some instances of larval ectophagy have evolved, e.g., as exposed external feeders on leaves in Cyclominae (*Gonipterus*, *Oxyops* and *Listroderes*), or Hyperinae (*Hypera*) (Marvaldi et al. 2002). Predicted consequences of leaf feeding are higher overall rates of parasitism (Hawkins 1994), and external feeding insects show fewer instances of interspecific or intraspecific competition than do internal feeders (Denno et al. 1995, Skuhrovec et al, in prep.).

Although most curculionoids feed on tissues of vascular plants, dependence on fungi, fungus-modified host tissues, or fungusriddled wood has evolved in the Anthribidae, Attelabidae, in some Brentidae, and in Scolytinae and Platypodinae, typically enabling use of a broad array of host-plant groups (Holloway 1982, Beaver 1989, May 1993, Oberprieler 1999, Farrell et al. 2001). Compared to specialists on conifer and cycads, the angiosperm feeding weevils occupy a larger array of larval niches, including stem/trunk boring, root feeding, folivory, leaf mining, and seed and fruit feeding, although it is not clear whether these differences reflect greater average disparity (i.e., given the greater numbers of both hosts and weevils) (Marvaldi et al. 2002). Larval feeding habits clearly are highly conservative; species with similar habits (strobilus feeders, root feeders, leaf miners, aerial leaf eaters = ectophagous, seed feeders) usually appear grouped together or in close proximity. Some of these feeding habits are apparently irreversible (e.g., feeding on leaves or seeds), whereas stem and trunk boring frequently give rise to use of other tissues (Marvaldi et al. 2002).

Larvae in several groups of weevils develop on host tissues that are not living, raising the issue of whether such associations should be expected to evolve as associations with obviously living, and thus defended, plant parts (Anderson 1995). Our phylogeny estimate shows that development in dying tissues characterizes most basal weevils except Nemonychidae (Marvaldi et al. 2002). This finding suggests that angiosperm colonization by these weevils is coupled with breeding in decaying tissues, whereas consumption of living tissues of angiosperms occurrs remarkably in the brentid–curculionid clade (Marvaldi et al. 2002).

4.2. Tribe Hyperini and its allies

To date only one paper was focused on primarily host plants of the tribe Hyperini (Skuhrovec 2005b). All published data about host plants of the genus *Hypera* are summarized and subjected to critical view of author. The host plants are dividend into two categories; (1) those verified by rearings and from the original literature data, and

(2) notes on incorrectly cited host plants (Skuhrovec 2005b). In the literature we can find many incorrect records of host plants, e.g. doubtful and clearly incorrect records for the genus *Hypera* belong to nine families: Brassicaceae, Chenopodiaceae, Lamiaceae, Malvaceae, Plantaginaceae, Poaceae, Punicaceae, Rosaceae and Solanaceae. This is partly due to the lack of distinction between host plants on which the larvae develop, and other plants on which the adults feed (Skuhrovec 2005b). Feeding on related plants is particularly frequent in immature specimens and the autumn generation (Miller 1956). In some cases (see Skuhrovec 2005b), the larvae also seek other plants for suitable pupation places. Unfortunately, Skuhrovec (2005b) provides information only about host plants of the *Hypera*-species occuring in the Czech Republic.

Hyperini-species can be categorized by their general ecology. Phytophagy can be divided into three classes; monophagy, oligophagy and polyphagy. The monophagous development occurs on one or several closely related plants, e.g. some sibling species or species from one group / subgenus. Oligophagous develope on various plants from one family. I differentiate it into the two subclasses, i.e. strictly oligophagous (sensu stricto) and broadly oligophagous (sensu lato). Strictly oligophagous (sensu stricto) develops on less than 3 related genera of one plant family and broadly oligophagous (sensu lato) develops on more than 3 related genera of one plant family. Polyphagous species can develop on plants from more than one plant family. Of course, all these terms are not strict.

Another problematic issue for the weevils of the tribe Hyperini could be ectophagy and endophagy. The definition of ectophagy means that development takes place on the surface of plant, but we know several Hyperini-species (Skuhrovec 2005b, unpubl. data) which have larvae inside the inflorescences (i.e. *Hypera nigrirostris*).

Therefor, the development is outside of the plant tissue, but the closed blossom still provides the protection to larvae from parasites, predators or unfavourable conditions. Such return to „endophagy" is not unique for weevils in the tribe Hyperini. Skuhrovec (2005b) published it for *Hypera nigrirostris* and *H. arator*. The same life strategy was observed by *Limobius borealis* at the inflorescences of the *Geranium*-species and *Metadonus gracilentus* at the unidentified species of Apiaceae in southern Portugal (Skuhrovec, unpubl. data). Endophagy is plesiomorphic for superfamily Curculionoidea according to phylogenetic analysis (Marvaldi et al., 2002). Several ectophagous weevils return to their original life strategy (endophagy) due to coevolution.

Data about host plant can help us with future observations and gain the new data about this insect. Forthemore, it can be applied into the general framework of ecology, e.g. two unusual types of behaviour: wandering and intraspecific agressive behaviour, were observed when rearing larvae of the alfalfa weevil, *Hypera postica* (Gyllenhal, 1813) (Skuhrovec et al, in prep.).

Wandering in search for food was observed in L1, L2, L3 and young L4 larvae. L1 larvae disperse in response to crowding. The female lay eggs in batches of 3-30 and the newly hatched disperse and thus escape competition. The dispersal of L1 larvae is known also in other beetle species. Wandering of L2 to young L4 instars was a response to food shortage. Wandering of late L4 larva ("prepupa") occurs because of searching place for spinning the cocoon and pupation.

Intraspecific aggressive behaviour of larvae has not been known as yet (Skuhrovec et al, in prep.). Larvae that develop in aggregations search for better location when food becomes scarce. Mutual encounter between the larvae may result in agonistic behaviour and some larvae may die as a consequence of fighting. The aggressivity increases with food limitation. Agonistic behaviour is artificial and probably does not occur under natural conditions where there is a plenty of food, and larval densities are decreased by pathogens (fungi *Zoopthora phytonomi* (Arthur)) or parasitoids (e.g. hymenopteran *Bathyplectes anurus* (Thomson)).

This new observation is just example of numerous interesting characters that have not been previously recognized even in a well characterized species such as alfalfa weevil. Future studies are required to achieve a complex picture of its ecology.

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RESULTS

1. Papers on taxonomy and phylogenetics

1.1. Preliminary cladistic analysis of the tribe Hyperini (Coleoptera: Curculionidae) based on external morphological characters of adults [prepared for *Systematic entomology*]

Preliminary cladistic analysis of the tribe Hyperini (Coleoptera: Curculionidae) based on external morphological characters of adults

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Abstract. The cladistic analysis based on external morphological characters of adults brings the first complex view on relationships among genera and subgenera in the tribe Hyperini. I used 53 ingroup taxa (Hyperini) and 6 outgroup taxa (tribe Cepurini and Cionini). Based on this analysis, the representatives of the Cepurini were confirmed as a sister group to Hyperini *sensu stricto* and the genus *Phaeopholus* is more closely related to the Cepurini than to the Hyperini. Hyperini *sensu stricto* forms a clearly monophyleric group subdivided into four clades ((*Neoglanis*, *Oreochorus Adonus*) + (*Donus*) + (*Eremochorus*, *Orthodonus*, *Macrotarrhus*, *Metadonus*) + (*Bubalocephalus*, *Hypera*, *Limobius*)). The genus *Pachypera* is demoted to the *Neoglanis* species group. The results of analysis supports the taxonomic position of three essential genera (*Neoglanis*, *Donus*, *Hypera*) in the tribe Hyperini, but its nomenclature must be resloved before using of these names.

Introduction

The subfamily Hyperinae is divided into two tribes; Cepurini Capiomont, 1867 and Hyperini Marseul, 1863 (Alonso-Zarazaga & Lyal 1999). Representatives of this subfamily are characterized by ectophagous larvae and skill to spin a webby cocoon. Identical characters have are known also for some representatives of the former subfamilies Rhytirrhininae, Goniopterinae and Cyclominae which are currently classified as tribes within the subfamily Cyclominae according to Morrone (1997) and Alonso-Zarazaga & Lyal (1999).

In his papers representing the first comprehensive view on the classification of the Hyperini, Capiomont (1867, 1868) divided Hyperini into six genera. The most important paper on the taxonomy of the tribe Hyperini was written by Petri (1901). His monograph has been the first and also for the present still is the last taxonomic revision of the tribe Hyperini. In contrast to Capimiont (1867, 1868), Petri recognized seven genera (recently used names are given in parentheses): *Bubalocephalus* Capiomont, 1868; *Coniatus* Germar, 1817; *Hypera* Capiomont, 1868 [= *Donus* Jekel, 1865 (Hoffmann 1954)]; *Phytonomus* Schoenherr, 1843 [= *Hypera* Germar, 1817 (Hoffmann 1954)]; *Lepidophorus* Kirby, 1837; *Limobius* Schoenherr, 1843 and *Macrotarsus* Schoenherr, 1843 [= *Macrotarrhus* Bedel, 1906, nomen novum for *Macrotarsus* preoccupied by *Macrotarsus* Lacépède, 1799 in Mammalia]. The genus *Lepidophorus* is recently classified in the subfamily Cyclominae (Alonso-Zarazaga & Lyal 1999).

Zaslavskij (1959) divided the tribe into four groups on the basis of female genitales and their bionomy. The first group included *Donus* Jekel, 1865, *Bubalocephalus*, *Metadonus* Capiomont, 1868, *Macrotarrhus* Bedel, 1906 and *Alexiola* Suvorov, 1912 [subgenus of *Macrotarrhus* Bedel, 1906 (Zaslavskij 1962)]; the second group included only the mountain genus *Glanis* Jekel, 1864 [= *Neoglanis* Alonso-Zarazaga & Lyal, 1999, nomen novum for *Glanis* Jekel, 1864 preoccupied by *Glanis* Agassiz, 1857 in Pisces); the third group included genera *Hypera* Germar, 1817 and *Limobius*; and the last group included the genera *Coniatus* and *Coniatrichus* Reitter, 1901.

Alonso-Zarazaga & Lyal (1999) recognized 19 genera in the tribe Hyperini occurring chiefly in the Palaearctic Region. Three years later, Alonso-Zarazaga & Lyal (2002) published the first *"Addenda and corrigenda"* to Catalogue, where they added three other genera into the tribe Hyperini.

The main intention of this paper is to analyze the relationships of the Hyperini genera using the cladistic analysis. Even though the analysis is based only on external morphological characters of adults, it is the first step to resolve the complicate taxomonic and nomenclatoric situation within the tribe.

Material and methods

Specimen's depository

Specimens are deposited in the following museums and private collections (acronyms according to Arnett et al. 1993): DEI – Deutsches Entomologisches Institut, Müncheberg (L. Zerche, L. Behne); HNHM – Hungarian Natural History Museum, Budapest (O. Merkl); HWIC – private collection of Herbert Winkelmann, Berlin; JSKC

– private collection of Jiří Skuhrovec, Praha; MNHN – Muséum National d'Histoire Naturelle, Paris (N. Berti); MNMS - Museo Nacional de Ciencias Naturales, Madrid (M. Alonso-Zarazaga); MTD – Museum für Tierkunde, Dresden (O. Jaeger); MZMB – Moravské Zemské Muzeum, Brno (V. Kubáň); NHRS – Naturhistoriska riksmuseet, Stockholm (B. Viklund); NMW – Naturhistorisches Museum, Wien (H. Schoenmann); ZIN – Russian Academy of Science, Zoological Institute, Sankt Petersburg (B. Korotyaev, N. Yunakov).

The majority of species examined were represented by the type material, especially for the eastern Palaearctic species. All non-type specimens examined were identificated by author and revised by Herbert Winkelmann.

Specimen preparation and terminology

All examined material was examined under OLYMPUS SZ X9 (binocular microscope) and/or OLYMPUS BX 40 (light microscope). Measurements were taken using calibrated oculars. Terminology of morphology follows Kuschel (1995), Marvaldi et al. (2002) and Skuhrovec (2006).

Ingroup taxa

I used 53 species representing 13 genera (Table 1) as ingroup taxa for the performed cladistic analysis. Nine genera classified within the Hyperini by Alonso-Zarazaga & Lyal (2002) were not included for the following reasons:

The extinct genus *Hyperites* Zherikhin, 1989 is inapplicable for the cladistic analysis based on external morphological characters of adults as most of the characters used are not preserved in the fossil.

The next four genera occur in the south hemisphere; the genera *Agriochaeta* Pascoe, 1872 and *Lycosura* Pascoe, 1875 in the Australia, species of the genus *Lamprohypera* Heller, 1908 in the New Guinea and the genus *Diastrophilus* Faust, 1892 is known from the Neotropical region. All of them were classified in the tribe Hyperini on the basis of similar scales, or according to historical view. In my opinion, the tribes Hyperini, Cepurini and subfamily Cyclominae sensu lato have very close relationships with each other. The mentioned four genera probably belong to tribe Cepurini or subfamily Cylominae on the basis of similar scales.

The genus *Herpes* Bedel, 1874 was transfered into the tribe Hyperini from the subfamily Cyclominae on the basis of ectophagous larvae and skill to spin a webby cocoon (Alonso-Zarazaga & Lyal 2002, Gültekin 2004). Unfortunately, authors did not consider that the bionomy of Hyperini-species and Cyclominae-species are almost the same. It is also known several species with identical life strategy and these weevils have not any relationships with the weevils from the tribe Hyperini, e.g. *Phytobius* Schoenherr, 1833 (Ceutorhynchinae). That it is reason why I have already not accept this change. The comparison of the morphology of larvae and adults resolve the taxonomic position of the genus *Herpes*. The position of this genus will be resolve in the near future.

The genera *Coniatus* and the monotypic *Coniatrichus* are the most problematic groups in the tribe Hyperini. Differential characters between these two genera are follows: the presence of short projecting setae on the body. The differential diagnosis for both genera are round eyes, round scales on the whole surface of body, coloration of scales (mainly green), and larvae with two setae at the abdominal segement IX. The representatives of the genus *Gronops* Schoenherr, 1823 (subfamily Cyclominae) have some identical characters (round eyes, round scales on the whole surface of body) as *Coniatus*-species. Cyclominae-species have also ectophagous larvae as Hyperinae-species, but this similarity is not taken in account. These two genera probably belong to other tribe on the basis of identical scales on the whole surface of body and round eyes, e.g. some Listroderini, in the subafmily Cyclominae, and that it is reason for excluding them from the analysis. In my opinion, the relationships between Cyclominae- and Hyperinae-species is more closed than it is presuppose. These problems could be resolved only with the phylogentics analysis of both subfamilies.

Monotypic species *Parahypera ussurica* Brancsik, 1914 can not be classified in the tribe Hyperini, because it is a synonym of *Fronto bimaculatus* Petri, 1901 of the tribe Cepurini (Winkelmann, pers. comm).

Outgroup taxa

I used 6 species representing 5 genera (Table 1) as outgroup taxa in the performed cladistic analysis. The reasons for selecting of these taxa are as follows:

Tribe Cepurini is classified as sister group of the tribe Hyperini by both old and recent authors (Csiki 1934, Alonso-Zarazaga & Lyal 1999, 2002). Cepurini included 15 genera occuring particularly in the south hemisphere (Alonso-Zarazaga & Lyal 1999). For the cladistic, I have chosen 5 species representing 4 genera (Table 1).

Cionus tuberculosus (Scopoli, 1763) is classified into tribe Cionini in the subfamily Curculioninae. Its would be the least related curculionid used in this cladistic analysis (Marvladi et al. 2002), even though it has also ectophagous larvae as Hyperini-species. The habitus shape of *Cionus*–species is very similar to habitus of *Phaeopholus*–species, whose taxonomic position seems unlikely in the tribe Hyperini, e.g. the shape of scales and/or ratio of interval between eyes / width of base of rostrum.

Phylogenetic analysis

Reconstruction of the phylogeny of the studied taxa was performed based on a matrix comprising eighty-nine adults characters concerning external morphology, compiled in WINCLADA version 1.00.08 (Nixon 2002), and then spawned in NONA (Golloboff 1993) with the 1000 replicates and 20 starting Wagner trees to search for the shortest trees. Character state distributions were examined with WINCLADA (Nixon 2002). Characters treated as nonadditive, unless otherwise indicated.

Characters

Morphological characters

Surface = Vestiture

1. Setae on rostrum: (0) absent; (1) present.
2. Scales on rostrum: (0) absent; (1) present.
3. Shape of scales on rostrum: (0) round scales; (1) bifid scales not reaching base; (2) bifid scales reaching base; (–) scales absent.
4. Projecting setae on rostrum: (0) absent; (1) present.
5. Lenght of projecting setae on rostrum: (0) short; (1) long; (–) absent.
6. Setae on cranium: (0) absent; (1) present.
7. Scales on cranium: (0) absent; (1) present.
8. Shape of scales on cranium: (0) round scales; (1) bifid scales not reaching base; (2) bifid scales reaching base; (–) scales absent.
9. Projecting setae on cranium: (0) absent; (1) present.
10. Lenght of projecting setae on cranium: (0) short; (1) long; (–) absent.
11. Setae on middle of pronotum: (0) absent; (1) present.
12. Scales on middle of pronotum: (0) absent; (1) present.

13. Shape of scales on middle of pronotum: (0) round scales; (1) bifid scales not reaching base; (2) bifid scales reaching base; (–) scales absent.
14. Projecting setae on middle of pronotum: (0) absent; (1) present.
15. Lenght of projecting setae on middle of pronotum: (0) short; (1) long; (–) absent.
16. Setae on sides of pronotum: (0) absent; (1) present.
17. Scales on sides of pronotum: (0) absent; (1) present.
18. Shape of scales on sides of pronotum: (0) round scales; (1) bifid scales not reaching base; (2) bifid scales reaching base; (–) scales absent.
19. Projecting setae on sides of pronotum: (0) absent; (1) present.
20. Lenght of projecting setae on sides of pronotum: (0) short; (1) long; (–) absent.
21. Setae on elytra: (0) absent; (1) present.
22. Scales on elytra: (0) absent; (1) present.
23. Shape of scales on elytra: (0) round scales; (1) bifid scales not reaching base; (2) bifid scales reaching base; (–) scales absent.
24. Projecting setae on elytra: (0) absent; (1) present.
25. Lenght of projecting setae on elytra: (0) short; (1) long; (–) absent.
26. Setae on mesosternal sclerite: (0) absent; (1) present.
27. Scales on mesosternal sclerite: (0) absent; (1) present.
28. Shape of scales on mesosternal sclerite: (0) round scales; (1) bifid scales not reaching base; (2) bifid scales reaching base; (–) scales absent.
29. Projecting setae on mesosternal sclerite: (0) absent; (1) present.
30. Lenght of projecting setae on mesosternal sclerite: (0) short; (1) long; (–) absent.
31. Setae on ventrite: (0) absent; (1) present.
32. Scales on ventrite: (0) absent; (1) present.
33. Shape of scales on ventrite: (0) round scales; (1) bifid scales not reaching base; (2) bifid scales reaching base; (–) scales absent.
34. Projecting setae on ventrite: (0) absent; (1) present.
35. Lenght of projecting setae on ventrite: (0) short; (1) long; (–) absent.
36. Setae on coxa: (0) absent; (1) present.
37. Scales on coxa: (0) absent; (1) present.
38. Shape of scales on coxa: (0) round scales; (1) bifid scales not reaching base; (2) bifid scales reaching base; (–) scales absent.
39. Projecting setae on coxa: (0) absent; (1) present.
40. Lenght of projecting setae on coxa: (0) short; (1) long; (–) absent.

41. Setae on femur: (0) absent; (1) present.

42. Scales on femur: (0) absent; (1) present.

43. Shape of scales on femur: (0) round scales; (1) bifid scales not reaching base; (2) bifid scales reaching base; (–) scales absent.

44. Projecting setae on femur: (0) absent; (1) present.

45. Lenght of projecting setae on femur: (0) short; (1) long; (–) absent.

46. Setae on tibia: (0) absent; (1) present.

47. Presence of scales on tibia: (0) absent; (1) present.

48. Shape of scales on tibia: (0) round scales; (1) bifid scales not reaching base; (2) bifid scales reaching base; (–) scales absent.

49. Projecting setae on tibia: (0) absent; (1) present.

50. Lenght of projecting setae on tibia: (0) short; (1) long; (–) absent.

51. Setae on dorsal side of tarsus: (0) absent; (1) present.

52. Scales on dorsal side of tarsus: (0) absent; (1) present.

53. Shape of scales on dorsal side of tarsus: (0) round scales; (1) bifid scales not reaching base; (2) bifid scales reaching base; (–) scales absent.

54. Projecting setae on dorsal side of tarsus: (0) absent; (1) present.

55. Lenght of projecting setae on dorsal side of tarsus: (0) short; (1) long; (–) absent.

56. Ventral side of protarsus: (0) without bristles; (1) with bristles.

57. Ventral side of mesotarus: (0) without bristles; (1) with bristles.

58. Ventral side of metatarsus: (0) without bristles; (1) with bristles.

59. Ventral side of protarsus: (0) without spines; (1) with spines.

60. Ventral side of mesotarus: (0) without spines; (1) with spines.

61. Ventral side of metatarsus: (0) without spines; (1) with spines.

62. Coloration of spines on ventral side of pro,- meso- and metatarsus: (0) pale spines; (1) dark spines; (–) without spines.

Eyes

63. Shape of eyes: (0) oval; (1) round.

Antennae

64. Insertion of antennae: (0) in front of scrobe; (1) in the proximal third of scrobe; (2) in the middle of scrobe; (3) anteriorly of middle of scrobe.

65. Number of funicle segments of antenna: (0) 7; (1) 6.

66. Ratio between the first and the second funicle segments: (0) the first funcile segment distinctly longer than the second one; (1) the lenght of both funcile segments approximately the same; (2) the second funcile segment distinctly longer than the first one.

67. Shape of the seventh funicle segment of antenna (or the last funicle segment in the species with reduced number of funicle segments): (0) spherical; (1) the upper part enlarged.

Rostrum

68. Lenght of rostrum: (0) very broad, ratio of length / width ca 1:1; (1) broad, ratio ca 1,5-2:1;(2) long, ratio ca 2,5-3:1.

69. Ratio of interval between eyes / width of base of rostrum: (0) >0.5; (1) 0.75 - 1.25; (2) >1.5.

70. Shape of rostrum in lateral view: (0) straight; (1) hooked.

71. Posterior part of scrobe on the rostrum: (0) not enlarged, reduced; (1) slightly enlarged; (2) enlarged into the half of the height width of rostrum; (3) enlarged into the whole of the height of rostrum.

72. Ventral part of rostrum: (0) straight; (1) with process.

73. Ratio of width of base and apex of rostrum: (0) identical; (1) apex appreciably enlarged.

74. Ratio of height of base and apex of rostrum from ventral view: (0) identical; (1) apex appreciably enlarged.

75. Longitudinal groove in the middle of rostrum: (0) present; (1) absent.

76. Distinct rim between base of rostrum and interocular interval: (0) present; (1) absent.

77. Ratio of the length of rostrum and length of pronotum: (0) the length of rostrum shorter than length of pronotum, ratio: 0.5<; (1) the length of rostrum ca identical as length of pronotum, ratio: 0.75 to 1.25; (2) the length of rostrum longer than length of pronotum, ratio: >1.5.

Pronotum

78. Shape of pronotum: (0) cylindrical; (1) orbiculate; (2) heart-shaped.

79. Shape of pronotal margins: (0) straight; (1) orbiculate.

80. Ratio of length of anterior and posterior margins of pronotum: (0) approxiametly the same length; (1) the length of posterior margin longer than the length of anterior margin of pronotum; (2) the length of posterior margin distinctly longer than the length of anterior margin of pronotum.

Elytra

81. Shape of elytra: (0) rounded; (1) oblong; (2) ovaled.
82. Humeral angels: (0) absent; (1) featureless humeral angels; (2) distinct humeral angels.

Mesosternum

83. Mesosternal projection: (0) blended with mescoxae; (1) distinctly extended from the join of mesocoxae.

Legs

84. Inner margin of protibia: (0) rounded; (1) shraply surrounded.
85. Hook on protibia of males: (0) absent; (1) present.
86. Distal margin of protibia: (0) rounded; (1) distinctly enlarged.
87. Location of procoxa on ventral side of prothorax: (0) situated closely to posterior margin; (1) situated ca. in the middle of the prosternal length.
88. Distal margin of protibia: (0) without spine; (1) one spine; (2) two spines.
89. Ratio of length of the fifth tarsomere and length of the third tarsomere: (0) 1.0-1.5; (1) 1.7-2.9; (2) 3.0-4.0; (3) 4.0-more.

Results and Discussion

The cladistic analysis resulted in 90 most-parsimonious trees (tree length (TL)=341, consistency index (CI)=0.29, retention index (RI)=0.78). Strict consensus of these trees is shown in Fig. 1.

In the strict consensus (Fig. 1), Hyperini *sensu stricto* are divided into four basic clades: *Neoglanis* incl. *Pachypera* + *Oreochorus* + *Adonus* (clade A), *Donus* (clade B), *Eremochorus* + *Orthodonus* + *Macrotarrhus* + *Metadonus* (clade C), and *Bubalocephalus* + *Hypera* + *Limobius* (clade D). The clades are very similar to the groups published by Zaslavskij (1959), the differences from the latter paper are commented for each clade below.

Monophyly of Hyperini sensu stricto

The analysis strongly supports the monophyly of 13 genera presented in Alonso-Zarazaga & Lyal (2002) with 7 unambiguous and unique synapomorphies (Fig. 1): 24(1). Projecting setae on elytra present; 49(1). Projecting setae on tibia present; 55(1). Long projecting setae on dorsal side of tarsus; 69(1). Ratio of interval between eyes / width of base of rostrum: 0.75 - 1.25; 73(1). Ratio of width of base and apex of rostrum (apex appreciably enlarged); 80(0). Length of anterior and posterior margin of pronotum approxiametly the same; 89(1). Ratio of length of the fifth tarsomera and length of the third tarsomera: 1.7-2.9.

(A) Clade (*Neoglanis* incl. *Pachypera* + (*Oreochorus* + *Adonus*)

The monophyly of this clade is supported by 2 unambiguous and unique synapomorphies (Fig. 1): 12(0). Scales on middle of pronotum absent; 82(0). Humeral angels absent.

This clade partly corresponds to the *Neoglanis* group in Zaslavskij (1959) who however include only the genus *Neoglanis* into this group and did not recognize other genera (*Pachypera*, *Oreochorus* and *Adonus*) as separate genera. The genus *Neoglanis* have been divided from the genus *Donus* by Zaslavskij (1959) only on the basis of vague differential characters. For these reasons, *Neoglanis*-species were classified as a part of the genus *Donus* Jekel, 1865 by some recent authors (Kippenberg 1983, Winkelmann 2001, 2006, Skuhrovec 2006). The taxonomic position of *Neoglanis*-species will be resolve only by the their detailed revison.

The genus *Pachypera* was described on the basis of enlarged distal part of protibia and sharp inner margin of protibia and classified also as a part of *Donus* by Petri (1901). The results of the presented phylogenetic analysis clearly results that the generic status of *Pachypera* is unjustified and should be classified as a part of the genus *Neoglanis*.

Both genera *Neoglanis* and *Oreochorus* occur in mountain areas of both Europe and Asia (*Neoglanis*) or only in Altai and Mongolia (*Oreochorus*). The host plants of *Neoglanis*–species belongs to several plant families (polyphagy).

(B) Clade (*Donus*)

The monophyly of this clade is supported by 2 unambiguous and unique synapomorphies (Fig. 1): 50(1). Long of projecting setae on tibia; 70(1). Shape of rostrum in lateral view: hooked.

Zaslavskij (1959) included in this clade also the genera *Bubalocephalus*, *Eremochorus*, *Macrotarrhus* and *Metadonus* (clade C and D). The taxonomic position of *Donus*-species has not been resloved yet as I present above (clade A).

The transfer of the subgenus *Antidonus* Bedel, 1886 from genus *Hypera* Germar, 1817 into genus *Donus* (Alonso-Zarazaga & Lyal 1999) brings following problem. The situation is the same as the previous one (*Neoglanis* versus *Donus*). Skuhrovec (2006) and Winkelmann (2001, 2006) did not accept these changes without detailed revision of several groups of Hyperini. My results of larval morphology partially correspond to these taxonomic changes, but we must establish the basic groups before makeing taxonomic changes inside.

The species of *Donus* Jekel, 1865 occurs especially in the European and Asian lowlands. The representatives of *Donus* are oligophagous, their host plants belong to several plant genera of one plant family (e. g. Fabaceae, Geraniaceae).

(C) Clade (((*Eremochorus* + *Orthodonus*) & *Macrotarrhus*) & *Metadonus*)

The monophyly of this clade is by 2 unambiguous and synapomorphies (Fig. 1): 66(1). The lenght of the first and the second funicle segment approximately the same; 80(1). The length of posterior margin longer than the length of anterior margin of pronotum.

Zaslavskij (1959) classified these three genera into his first group, including genus *Donus*.

The monophyly of the first group (*Eremochorus* + *Orthodonus*) is by 10 unambiguous and synapomorphies (Fig. 1): 19(0). Projecting setae on sides of pronotum absent; 28(1). Mesosternal sclerite with bifid scales not reaching base; 30(1). Long projecting setae on mesosternal sclerite; 33(1). Ventrite with bifid scales not reaching base; 35(1). Long projecting setae on ventrite; 38(1). Coxa with bifid scales not reaching base; 43(1). Femur with bifid scales not reaching base; 62(1). Dark spines on ventral side of pro,- meso- and metatarsus; 67(0). The seventh funicle segment in the antennae spherical; 70(1). Rostrum hooked.

All known species (more than 40) of the genus *Eremochorus* Zaslavskij, 1962 occur in the central and northeastern Asia (Kazakhstan, Kyrgyzstan, Turkmenistan, Mongolia, Siberia). The majority of species were described by Zaslavskij (1962, 1978). Several species develope on plants of genus *Atraphaxis* from the family Polygonaceae (Zaslavskij 1962, 1978). The monotypic genus *Orthodonus* Zaslavskij, 1965 occur in Kirgizia on some unidentified plant from the family Chenopodiaceae (Zaslavskij 1965).

The monophyly of the genus *Macrotarrhus* Bedel, 1906 is by 8 unambiguous and synapomorphies (Fig. 1): 39(0). Projecting setae on coxa absent; 44(0). Projecting setae on femur absent; 68(1). Ratio of length / width of rostrum ca 1,5-2:1; 75(1). Longitudinal groove in the middle of rostrum absent; 80(0). Length of anterior and posterior margin of pronotum approxiametly the same length; 81(2). Elytra oval; 83(1). Mesosternal projection distinctly extended from the join of mesocoxae; 88(0). Distal margin of protibia without spine.

The genus is subdivided into four subgenera (Zaslavskij 1962). More than 40 known species occur only in Asia. The majority of species were described by Zaslavskij (1958, 1961, 1965, 1967) and Bajtenov (1975, 1980, 1982). Several species have the development on the plant from genus *Atraphaxis* from the family Polygonaceae (Zaslavskij 1965, 1967).

The genus *Metadonus* Capiomont, 1868, has only 18 known species occurring primarily in Asia; the exceptions are *M. gracilentus* (Capiomont, 1868) (Portugal, Spain), *M. vuillefroyanus* (Capiomont, 1868) (Spain, part of the northern Africa) and *M. distinguendus* (Boheman, 1842) (Ukraine, Moldavia, Russia). The taxonomic classification of the former two species in the genus *Metadonus* is not very certain.

(D) Clade ((*Bubalocephalus*) & (*Hypera* + *Limobius*))

The monophyly of this clade is by 10 unambiguous and synapomorphies (Fig. 1): 2(0). Scales on rostrum absent; 3(1). Rostrum with bifid scales not reaching base; 8(1). Cranium with bifid scales not reaching base; 13(1). Middle of pronotum with bifid scales not reaching base; 18(1). Sides of pronotum with bifid scales not reaching base; 23(1). Elytra with bifid scales not reaching base; 28(1). Mesosternal sclerite with bifid scales not reaching base; 33(1). Ventrite with bifid scales not reaching base; 38(1). Coxa with bifid scales not reaching base; 43(1). Femur with bifid scales not reaching base; with the exception of two taxons *Hypera adspersa* (Fabricius, 1792) and *Limobius mixtus* (Boheman, 1834).

All four described species of the endemic Spanish genus *Bubalocephalus* Capiomont, 1868 have round eyes and long projecting setae on the whole body (Gonzáles 1965). Bionomy is completely unknown. Zaslavskij (1959) classified this genus in the first group, including *Donus*-species.

The group (*Hypera* + *Limobius*) correspond with the third group in Zaslavskij (1959).

The genus *Hypera* Germar, 1817 currently includes more than 115 Palaearctic species (Smreczyński 1968) and 17 species from North America (Anderson 2002). The genus is divided into six subgenera (Alonso-Zarazaga & Lyal 1999). The *Hypera*-species are mostly oligophagous, but several monophagous are also known (Skuhrovec 2003). Alonso-Zarazaga & Lyal (2002) transfered the subgenus *Antidonus* to the genus *Donus*, but without any discussion of this nomenclatorical change. Alonso-Zarazaga (2005) described a new subgenus *Kippenbergia*. Skuhrovec (2006) considers it is most probably only a species group of *Hypera arator* (Linné, 1758) within the nominotypical subgenus *Hypera* as it is also presented by Petri (1901) and/or by Kippenberg (1986). Skuhrovec (2006) and Winkelmann (2001, 2006) did not accepte these changes without detail revision of several groups of Hyperini.

The genus *Limobius* with three species is classified in this group also. All known species develope on plants from the family Geraniaceae (Smreczyński 1968). The *Limobius*-species have six funicle segments, which is the only difference from *Hypera*-species, which have seven funicle segments. The analysis supports that *Limobius* is really the member of the genus *Hypera* (Fig. 1), probably relative to group of *Hypera cumana*.

Outgroups + Phaeopholus

All used outgroup taxons – Cepurini-species and *Cionus tuberculosus* were easily differentiate from Hyperini in the strict consensus (Fig. 1).

The analysis strongly supports the monophyly of tribe Cepurini and genus *Phaeopholus* with 9 unambiguous and unique synapomorphies (Fig. 1): 11(0). Setae on middle of pronotum absent; 16(0). Setae on sides of pronotum absent; 21(0). Setae on elytra absent; 26(0). Setae on mesosternal sclerite absent; 31(0). Setae on ventrite absent; 36(0). Setae on coxa absent; 41(0). Setae on femur absent; 47(1). Scales on tibia present; 87(0). Procoxa on ventral side of prothorax situated closely to posterior margin.

Concluding remarks

It has to be noted that the results of my analysis depicted in Figure 1 should be considered as preliminary. The members of the genus *Phaeopholus* are more closely related to the tribe Cepurini than to Hyperini *sensu stricto*. This result was expected. Several unclearness (e.g. the taxonomic position of *Coniatus*-species) still complicate the resolving of the relationships of Hyperinae and Cyclominae. This problems has to be solved by a detailed analysis of both groups. The presented analysis strongly supports the monophyly of Hyperini *sensu stricto*, including 12 genera of 22 published genera (Alonso-Zarazaga & Lyal 2002). This monophyletic group is subdivided into four clades which resemble the groups recognized by Zaslavskij (1959). The descriptions of Zaslavskij (1958, 1961, 1962, 1967, 1978) are difficult to interpret in many cases, but I must admit that his separation of the tribe Hyperini into the four groups is probably correct. Zaslavskij does several errors, in spite of them the knowledges about Hyperini-species are huge in his papers, especially in the ecology and in the morphological characters (Zaslavskij 1959). The results of the analysis supports the genus *Pachypera* as species group of *Neoglanis* as it is also presented in the monograph by Petri (1901). These results supports the taxonomic position of three essential genera (*Neoglanis*, *Donus*, *Hypera*) in the tribe Hyperini, but the nomenclature in these groups must be resloved before using of these results.

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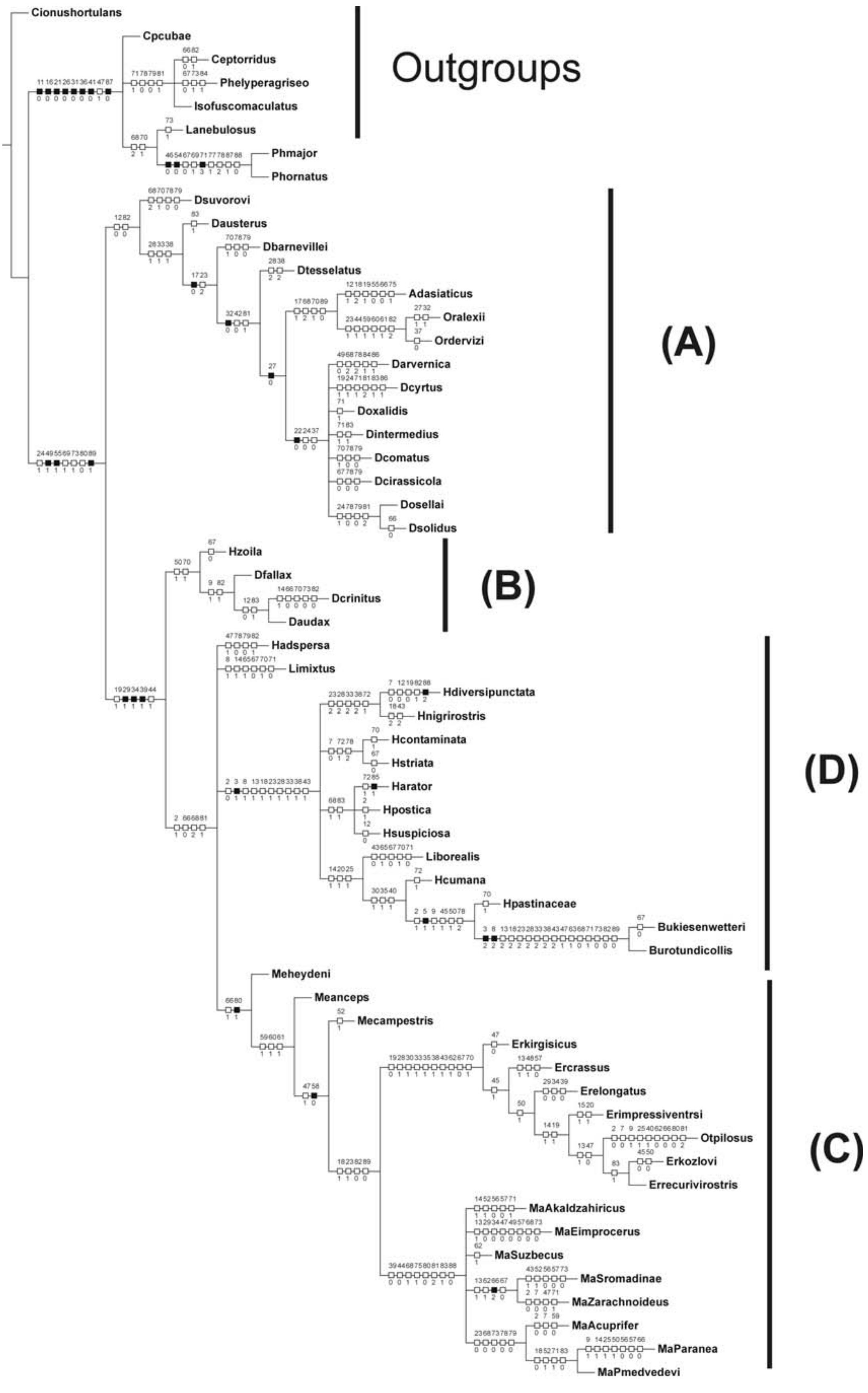

Figure 1. Strict consensus of 90 most parsimonious trees with displayes unambiguous characters; length Ľ341 steps, consistency index Ľ0.29 and retention index Ľ0.75.

Table 1. Check-list of species used in the cladistic analysis. Rows in table interpret the following: (1) taxonomic classification of taxon, (2) genus of taxon, (3) species, (4) country of origin of the studying specimens and (5) collection where the studying specimens are housed.

Taxonomic classification	**Genus**	**Species**	**Country of origin**	**Coll.**
Curculioninae: *Cionini*	*Cionus*	*tuberculosus* (Scopoli, 1763)	Rumania	JSCP
Hyperinae: Cepurini	*Cepurus*	*torridus* (Olivier, 1807)	Senegal	JSCP
	Cephalages	*cubae* (Chevrolat, 1838)	Cuba	NMW
	Isorhinus	*fuscomaculatus* (Capiomiont, 1867)	Mexico	NMW
	Phelypera	*griseofasciata* (Capiomiont, 1867)	Brasil	NMW
	Larinosomus	*nebulosus* (Capiomiont, 1867)	Brasil	NMW
Hyperinae: Hyperini	*Bubalocephalus*	*kiesenwetteri* (Capiomiont, 1867)	Spain	HWCB
		rotundicollis (Capiomiont, 1867)	Spain	HWCB
	Adonus	*asiaticus* (Schoenherr, 1849)	Ukraine	ZIN
	Metadonus	*anceps* (Boheman, 1842).	Ukraine	HWCB
		campestris (Petri, 1901).	Tadshikistan	JSCP
		heydeni (Capiomont, 1868)	Mongolia	HWCB
	Phaeopholus	*ornatus* Roelofs, 1873	Japan	JSCP
		major Roelofs, 1879	Japan	JSCP
	Hypera (*Antidonus*)	*zoila* (Scopoli, 1763)	Turkey	JSCP
	Hypera (*Erirhinomorphus*)	*adspersa* (Fabricius, 1792)	Slovakia	JSCP
	Hypera (*Boreohypera*)	*diversipunctata* (Schrank, 1798)	Germany	JSCP
	Hypera (*Tigrinellus*)	*pastinacae* (Rossi, 1790)	France	JSCP
	Hypera (*Dapalinus*)	*contaminata* (Herbst, 1795)	Greece	JSCP
		striata (Boheman, 1834)	Hungary	JSCP
	Hypera (s.str.)	*cumana* (Petri, 1901)	Turkey	JSCP
		arator (Linné, 1758)	Czech Republic	JSCP
		postica (Gyllenhal, 1813)	Turkey	JSCP
		Suspiciosa (Herbst, 1795)	Czech Republic	JSCP
		nigrirostris (Fabricius, 1775)	Slovakia	JSCP
	Limobius	*borealis* (Paykull, 1792)	Slovakia	JSCP
		mixtus (Boheman, 1834)	Holland	JSCP
	Pachypera	*arvernica* (Capiomont, 1867)	France	ZIN

Neoglanis	*cyrtus* (Germar, 1821)	Greece	JSCP
	oxalidis (Herbst, 1795)	Slovakia	JSCP
	intermedius (Boheman, 1842)	Slovakia	JSCP
	comatus (Boheman, 1842)	Czech Republic	JSCP
	circassicolus (Reitter, 1888)	Caucasus	JSCP
	osellai Winkelamann, 2001	Italy	JSCP
	solidus (Petri, 1901)	Kazakhstan	JSCP
	tesselatus (Herbst, 1795)	Slovakia	JSCP
	barnevillei (Capiomont, 1868)	France	ZIN
	austerus (Boheman, 1834)	Portugal	JSCP
	souvorovi (Fleischer, 1909)	Kazakhstan	JSCP
Donus	*crinitus* (Boheman, 1834)	Tunis	JSCP
	fallax (Capiomont, 1868)	Marocco	JSCP
	audax (Faust, 1887)	Greece	JSCP
Eremochorus	*crassus* Zaslavskij, 1962	Kazakhstan	ZIN
	elongatus (Petri, 1901)	Altaj	ZIN
	impressiventris Zaslavskij, 1962	Tjan-Shan	ZIN
	kirghisicus Zaslavskij, 1967	Altaj (Kirgizia)	ZIN
	kozlovi (Suvorov, 1912)	Kirgizia	ZIN
	recurvirostris Zaslavskij, 1967	Mongolia	ZIN
Oreochorus	*alexii* Korotyaev, 1998	Kazakhstan	ZIN
	dervizii Korotyaev, 1998	Mongolia	ZIN
Orthodonus	*pilosus* Zaslavskij, 1965	Kirgizia	ZIN
Macrotarrhus (*Proteromera*)	*aranae* (Suvorov, 1912)	Altaj	ZIN
	Medvedevi Zaslavskij, 1964	Kazakhstan	ZIN
Macrotarrhus (*Ectomochila*)	*Improcera* Zaslavskij, 1958	Russia	ZIN
Macrotarrhus (*Alexiola*)	*cuprifer* Kindermann, 1901	Mongolia	ZIN
	kaldshiricus (Suvorov, 1912)	Russia	ZIN
Macrotarrhus (s. str. – *Zaisania*)	*arachnoidea* (Suvorov, 1912)	Russia	ZIN
Macrotarrhus (s. str.)	*romadina* Zaslavskij, 1958	Kirgizia	ZIN
	uzbecus Zaslavskij, 1958	Uzbekistan	ZIN

1.2. *Hypera kayali* sp. nov. (Coleoptera: Curculionidae) from Syria with bionomic data [published in *Zootaxa*, **1282**: 17-28]