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FYLOGENESE A TAXONOMIE ČELEDI ENCYRTIDAE (HYM., CHALCIDOIDEA)

THE PHYLOGENY AND TAXONOMY OF THE FAMILY ENCYRTIDAE

(HYM., CHALCIDOIDEA)

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Fylogeneze a taxonomie čeledi Encyrtidae (Hym. Chalcidoidea).

The Phylogeny and Taxonomy of the Family Encyrtidae (Hym., Chalcidoidea).

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Čeď *Encyrtidae* náleží mezi druhově nejpočetnější čeledi *Chalcidoid* s poměrně velmi vysokým generickým koeficientem; pro značnou hospodářskou důležitost věnuje se jí v současné době velká pozornost, což si vynutilo i sestavení moderních určovacích rodových klíčů (NIKOLSKAJA 1951, FERRIÈRE 1953, HOFFER, v tisku), založených však spíše na znacích nápadnějších, prakticky použitelných, než takových, jež by ukazovaly na vzájemnou příbuznost rodů. Dosud nebylo provedeno definitivní rozdělení této velké a mnohotvárné čeledi na triby a subtriby, které by bylo založeno na fylogenetickém vývoji; příčinou toho jsou velmi nejasné rozdíly mezi těmito systematickými kategoriemi, což neobyčejně ztěžuje jejich ohraničení.

Čeď rozpadá se na tři podčeledi (*Encyrtinae* HOW., *Arrhenophaginae* MERC. a *Antheminae* MERC.), z nichž poslední dvě zastoupeny jsou v palaearktické oblasti po jediném rodu, kdežto veškeré ostatní rody spadají do první podčeledi. O rozdělení podčel. *Encyrtinae* pokusili se nejprve HOWARD (1886, 1892, 1895 a 1908) a ASHMEAD (1900, 1904). Některé HOWARDOVY triby byly později povýšeny na podčeledi (*Bothriothoracinae* a *Tetracneminae*) bez jakéhokoliv oprávnění. Toto rozdělení však zdaleka nevyčerpalo skutečný počet přirozených menších systematických jednotek. O dokonalejší rozčlenění podčeledi zasloužil se teprve MERCET (1921), který stanovil celkem 12 rodových skupin, jež stručně definoval; jeho klasifikace vnesla první světlo do taxonomie *Encyrtinů*, byla však založena na tehdejších ještě kusých a příliš lokálních znalostech a na poměrně malém materiálu, takže nutně vyžadovala dalšího propracování a revise. V nejnovější době ohraničil několik přirozených tribů HOFFER (1953—1954); ke kritické moderní revisi celé podčeledi *Encyrtinae* však dosud nedošlo.

K této práci rozhodl jsem se přistoupit na základě srovnávacího studia vnější morfologie dostupných mi forem této čeledi, při čemž byl

vzat zřetel i na jejich bionomii a parazitický způsob života. Materiál, který se mi podařilo během řady let získat, je zajisté v Evropě nejrozsáhlejší. Jsem si vědom toho, že časem bude nutno soustavu této podčeledi dále zdokonalovat, zejména po podrobnějším prozkoumání fauny Nového světa; nicméně se domnívám, že níže podaným ohraničením tribů a subtribů na podkladě studia fylogenetického vývoje skupiny bude dán základ systematisace hospodářsky tak důležité čeledi, což pokládám v dnešní době za úkol zcela nezbytný.

I. The Phylogenetic Development of the Family.

The family *Encyrtidae* must be regarded as a highly specialised group of the *Chalcidoidea*, which together with the related, more primitive family *Eupelmidae* forms a specific branch without any distinct transitions to the other families. Both families probably split off from the family *Pteromalidae*; but today it is difficult to decide from which group they directly arose.

As subfamilies of the family *Encyrtidae* we can regard with certainty only the subfam. *Encyrtinae* HOW., *Arrhenophaginae* MERC., and *Antheminae* MERC.; the other, higher systematic groups placed by various authors to the fam. *Encyrtidae* cannot be regarded as lower taxonomic units belonging here. This applies especially to the fam. *Signiphoridae*, which has far closer relations to the fam. *Aphelinidae*; nevertheless we must regard it as a taxonomic equivalent to the other families.

Of the three subfamilies mentioned above the subfam. *Encyrtinae* must be regarded as the most primary one; the remaining two are on the contrary indubitably more perfect groups, characterised especially by a reduction of the tarsal segments and by other features which compel us to regard them as separate, more differentiated groups. Though the two subfamilies are both characterised by such an important feature as the four-segmented tarsi, yet they are quite independent, recent groups, which arose from two very distant evolutionary lines. The subfam. *Arrhenophaginae* is with some characters closely linked to the subfam. *Encyrtinae*, whereas the subfam. *Antheminae* represents a group which is isolated to a considerable extent. Both subfamilies show, however, certain relations to more differentiated families standing far in the system; thus it is necessary to place the subfam. *Encyrtinae* at the beginning of the system of the family, the subfam. *Arrhenophaginae* in the second place, and to declare the subfam. *Antheminae* the highest subfamily. Up till now authors have arranged the subfamilies in the reverse order.

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In tracing the evolution of the tribes and subtribes of the widest subfamily we have to take into consideration especially the phylogenetically important characters, none of which proves to be a general criterion for

defining the lower systematic units. On the contrary, each of these characters has in different groups a different generic importance, and sometimes it occurs suddenly also in those generic groups in which we should not have expected it; these are the so-called progressive types, which are either evolutionary mutations or the results of very specific lateral branches. One of the most important characters for judging of the phylogeny of the tribes is the configuration (denticulation) of the mandibulae, though even this character cannot be regarded as a guide criterion and was obviously overestimated by ASHMEAD. The general habit, the structure of the head and other parts of the body, the position and structure of the antennae, the mouth organs, the venation of the wings, the schema of their smokiness, the built of the legs, the sculpture, coloration and degree of differentiation of the two sexes, all these are characters which may be used with advantage when solving these evolutionary questions. But we have always to take into consideration all of these characters and not only one of them.

On the whole it may be said that the normal structure of the body (somewhat elongated, not too much vaulted forms), the broadly ellipsoid head, the simply built antennae with a six-articled funiculus (where the articles are not too short nor unusually elongated), and with a three-segmented club, the mandibles with a fairly minor number of teeth, the hyaline wings with well developed veins, the smooth or only finely coriaceous sculpture, the non-metallic coloration, and the resemblance of the two sexes are characters which fall into the frame of this more primary subfamily. On the contrary the stocky or exceptionally elongated habit, the hemispheric head, or a head with angular connection of frons and face, the strong convexity or considerable flattening of the body, the antennae either with a lesser number of segments or differentiated in a specific manner (e. g. with very short, or with flattened and expanded segments, or sending out lateral branches, etc.), the fusion of the segments of the club, the mandibles with more teeth on the inner side, the wings with some veins reduced or even vanished, the triangular widening of the submarginal vein before the end, the different pattern of the smokiness of the wings, the coarser sculpture, the metallic coloration, and the lesser or greater difference of the two sexes are characters of the more perfect forms.

Nevertheless we must be careful when judging of the significance of the different characters. In answering the questions of the phylogeny we cannot use a fortuitous, purely adaptive character, as e. g. the reduction of the wings; every micropteris or brachypteris species may form under certain conditions a macropteris form. Also it is necessary to examine when judging of so-called „primitive” characters, whether these characters did not arise convergently by adaptation to the special evolutionary conditions of the species. Thus e. g. the short metatarsus (usually with the long spur still preserved) is not a primitive character (genus *Pseudorhopus!*) but only a suppressor of the jumping type of leg in a form which indubitably developed from a normal type. The same applies to some species with parallelly developed segments of the abdomen (when the pygostili are considerably shifted backwards); we can regard such

characters as primary only when most of the other characters likewise indicate the primariness of these forms. The same applies of course also to all forms with very small eyes or with vanished ocelli.

Some features mark in a characteristic manner certain natural groups, even when somewhat farther in the system they may reappear again here and there. Thus some tribes show a specific surface sculpture (e. g. a close longitudinal grooving of the thorax, which is proper only to the tribe *Ageniaspini*; other types of sculpture are shown e. g. by the tribes *Bothriothoracini* or *Copidosomini*), another specific configuration of the antennae (e. g. flattened and expanded antennae in the females of the subtribe *Tetracladii*, or the ramified antennae of the males of the same subtribe, further of the subtribes *Charitopii* and *Tetracnemii*; nevertheless the same characters appear also in individual genera of other tribes); all species of the tribe *Trechnitini* have four-toothed mandibles, but sporadically also genera of other tribes; a peculiar, quite specific configuration of the female antennae belongs to the tribes *Ericydnini*, *Aphycini*, *Homalotylini*, *Cerapterocerini*, *Habrolepini*, etc. An angular separation of the head from the facial part belongs to the tribes *Cerapterocerini*, *Habrolepini*, the subtribe *Hunterellii*, but also some genera of other tribes, as *Apterencyrtus* ASHM., etc. It would be quite incorrect to combine all the genera showing one of these characters into a common tribe, as e. g. HOWARD does in placing all genera with ramified antennae in the males in the one tribe *Tetracnemini*.

The smokiness of the anterior wings is a more or less fortuitous character often also within individual genera, but it is at the same time a very interesting fact that different natural systematic categories have a very expressive character of variability of these spots or bands. Thus the spots appear in a certain specific manner on the wings in the tribe *Ectromini* (see HOFFER 1954), in an entirely different one in the tribe *Mirini* (cp. the smokiness of the wings in the genera *Tetracladia*, *Echthroplexiella*, but also in *Mayridia* and *Hoplopsis!*), differently in the tribe *Ericydnini* (of course in so far as this smokiness is developed), differently in the related tribes *Encyrtini* and *Cheiloneurini*, or quite specifically in the tribes *Cerapterocerini* and *Habrolepini*. Thus also this character, apparently the least important one, may explain some evolutionary roads.

The carriers of the predominant part of important taxonomic characters are the females, on which the system of the family is built; but also the valuable characters of the males, when developed, have to be taken into consideration in solving taxonomic questions and have to be regarded as of equal value as the characters of the females.

The copulation organs of the males are not so different (with the known simplicity of the structures of the penis in the *Chalcidoidea*) that they could be used in systematics with the same success as in evolutionarily older groups. The simplicity of these organs clearly shows the relatively young age of the *Chalcidoidea* which are at present at the maximum of their development.

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The phylogenetic development of the subfamily *Encyrtinae* proceeded in several parallel branches, whose common primary type is not known. Thus we can trace in the palaearctic genera clearly several independent evolutionary lines; the groups of related genera are the resulting recent types of this more or less ramifying evolutionary series.

To the first, relatively considerably primitive branch belongs the group of tribes characterised by a more or less elongated, rather flat body (especially abdomen), an only rarely narrow forehead, long, simple to considerably differentiated antennae (but never with very short or small basal articles of the funiculus), parallel or only slightly expanding towards the end, relatively narrow and long wings with a finely coriaceous sculpture, in the perfect tribes of this series with a scattered punctuation on the head, of a non-metallic to metallic coloration, with two- to three-toothed (quite exceptionally four-toothed) mandibles, where, however, the evolution of these characters did not proceed always conformably and uniformly. Thus we can again record several resulting types of lateral branches manifesting themselves by a more or less striking differentiation in a certain way.

A character of indubitably very primitive forms is the imperfect development of the antennal club, where its basal segment (7th segment of the flagella) is distinctly differentiated from the following segments so that the club is in fact not very markedly indicated only by the approachment of the 8th and 9th segment of the flagella. I place the forms thus characterised (the genera *Anomalicornia* MERC. and *Heterencyrtus* HFFR.) in the separate tribe *Anomalicornini* nov., which stands on the lowest evolutionary rank of the first branch.

The following tribe *Anagyryni* HFFR. comprises already the forms with an antennal club normally formed from the last three segments of the flagella. It is a well characterised group, as it contains a number of considerably uniform genera. From this tribe splits off a separate branch represented by the genus *Quadrencyrtus* HFFR., which is highly specialised in a certain direction, and which forms the separate tribe *Quadrencyrtini* HFFR.; among other characters the specific configuration of the mandibles (4 teeth!) has in this genus a considerable importance.

The tribe *Ectromini* ASHM. forms another natural link of the first evolutionary branch, characterised habitually and in most cases also by the characteristic pattern of the smokiness of the wings. A separate type, not in direct evolutionary connection with the preceding type, is the tribe *Ericydnini* nov., expressively characterised by a typical venation and by the special form of the antennae. I believe that this tribe has a quite different origin, not too remote from the strange genus *Prionomastix* MAYR.

The tribe *Prionomasticini* nov. is represented by the one genus *Prionomastix* MAYR., placed by ASHMEAD and MERCET to the genus *Encyrtus* LATR., because of the similar structure of the mandibles. In my opinion these two distinct genera must not on any account be combined into one tribe; the genus *Prionomastix* represents rather an archaic type of a separate branch whose only recent representative it is. The tribe

Ericydnini nov. is probably a lateral branch formerly separated from the common stem and preserved to this day.

Also this tribe is represented by only the one genus *Ericydnus* WALK., and represents a quite specific group with typically configured antennae in both sexes, a quite unique venation and a peculiar habit. Scutellum terminated by a hyaline membrane. Also the pattern of smokiness of the wings in the darker forms is unique in the system of the family. By the coarser scattered punctation it is distinguished also from the lower groups.

The tribus *Mirini* ASHM. in the new definition is linked in many respects directly to the tribe *Anagyrini* and forms a further evolutionary link of the first branch. The definition of this tribe is, however, because of the considerable manifoldness of the shapes of the forms, rather difficult. We include in it the forms with two- to three-toothed mandibles, from the genera with simply arranged antennae to the genera in which one of the sexes is very differentiated in this respect. From the higher tribes it can be distinguished very easily habitually [elongated, only slightly vaulted forms with a sharp ending of the relatively long and flattened abdomen, usually relatively longer antennae (we must take into account, that some genera have in the females the club fused into one whole, which reminds of tribe *Copidosomini*) and a not too marked sculpture, as said already above]. Relatively more difficult is it to distinguish this group from the tribe *Anagyrini* (especially the most primitive subtribes belonging here). *Anagyrini* has to be regarded as the most primary, little variable tribe, from which the *Mirini* gradually arose; the non-metallic coloration proper to the *Anagyrini* was replaced in the tribe *Mirini* (with the exception of some forms of the subtribe *Echthroplexiellii*) by metallic colours. The genus *Mira* SCHELL., after which ASHMEAD named the tribe, is not exactly a suitable type of this group because of its singular morphological structure.

The development within this tribe proceeds, as said above, from subtribes with simple antennae to subtribes with the antennae differentiated in various ways, and from forms with two-toothed mandibles to three-toothed forms. The pattern of the smokiness of the wings (as far as it is developed) is very typical, with one medial and one distal transverse band (the latter often connected in the central part with the first band); often only the medial band is developed (or outlined).

The subtribe *Mayridii* n. has a still enigmatic origin and systematic position; in some features (the smokiness of the wings and the general aspect) it approaches considerably the tribe *Mirini*; the antennae are, however, more reminiscent of the tribe *Microteryni*. It is still an open question whether we can regard this tribe as a transition group between the tribes *Mirini* and *Microteryni* or not.

The genus *Encyrtus* LATR. is a further archaic type, interesting especially by the primitive build of the mandibles; it is the only representative of the tribe *Encyrtini* ASHM. This tribe is the representative of a separate branch, which has in the recent fauna no related generic groups except the tribe *Cheiloneurini* nov., which I believe to be an only,

if already considerably differentiated, lateral branch starting from the common stem and having with the preceding tribe a number of similar characters (habit, in some genera a similar shape of the antennae, similarity of the venation and in the smokiness of the wings, presence of a peculiar brush of long hairs at the end of the scutellum); it would be difficult to ascribe this resemblance to a fortuitous convergence of the characters, called forth by outer conditions.

Two very different branches start from the tribe *Mirini*; one of them is represented by the forms with a head, often short in upper view, with a rounded anterior margin (broadly lying to the thorax), with short antennae, with the articles of the funiculus moderately rounded at the base, of which especially the basal articles are very short, the distal ones more considerably expanded and lengthened, and with an ovoid clava; the habit of these forms is rather sturdy, rather short than long, wings relatively broad, abdomen usually shorter than thorax. The second branch consists of the forms with the body more vaulted, with a transversally ellipsoid head or subquadratic, with a more or less elongated, and more pointed abdomen, with the antennal segments more parallel, most often lengthened, and usually with a coarse punctation or with a specifically longitudinally grooved sculpture of the thorax.

The former branch is represented in the recent fauna especially by the tribe *Aphycini* HFFR., which, however, is not the most primitive type of this evolutionary line. It comprises the non-metallic, mostly light coloured forms with a characteristic configuration of the antennae (the first three basal segments are as compared with the following ones very small); exceptionally the antennae are strikingly transformed (genus *Paraphycus* GIR.). The wings are only exceptionally smoky and in this case the pattern of the tribe *Mirini* has been preserved here; sex dimorphism on the whole trifling. The tribe is divided into 4 subtribes, of which the subtribe *Aphycii* n. is the most primary one, the others (*Pseudaphycii* n., *Stemmatosterii* n. and *Paraphycii* n.) are gradually more differentiated. A quite peculiar type is *Pseudorhopus* TIMB., for which MERCET established a special systematic group at the beginning of the system of the whole subfamily. I have only one specimen mounted as permanent microscopic preparation so that I cannot examine some important characters, especially the denticulation of the mandibles, which the authors do not, however, mention. I believe, however, that this genus is not so different that we could not reckon it to the tribe *Aphycini*, even though some striking characters, as the very short metatarsus and the undivided clava, make it very remarkable. Therefore I place it in the separate subtribe *Pseudorhopii* n., which I join provisionally to this tribe. But in no case can this highly differentiated type with a five-articled funiculus and undivided clava be placed at the beginning of the system of the subfamily as its lowest recent evolutionary stage.

An unclear position in the system occupies the tribe *Homalotylini* HFFR., which is well defined (almost imperceptible sex dimorphism, quite specifically formed antennae with the segments placed to each other in the whole width, and with the clava in the females as a rule undivided.) In contradistinction to the two preceding tribes the antennae

are distinctly longer. Some forms, especially of the genus *Homalotyloidea*, are very reminiscent of the *Aphycini*; also the genus *Isodromus* approaches in some characters this tribe, especially the genus *Paraphycus* GIR.

Parallely with the tribe *Aphycini*, from the same stem, developed the tribe *Microteryni* nov., of which the more primitive subtribe has still the head longer, subquadratic and the antennae more slender. This tribe comprises a huge number of genera and is the largest tribe of the family. This complex of genera is divided into a number of smaller generic groups (subtribes), as whose guide types we may regard the genera *Metaprionomitus* MERC., *Microterys* THOMS., *Hunterellus* HOW., *Pentacnemus* HOW. and *Adelencyrtus* ASHM.

A rather primary tribe, developed directly from the unpreserved basic stem of the broad-winged, short-antennal tribes, is the tribe *Discodini* HFFR., where even the most primitive genera have two mandibular teeth developed. One cannot connect with it the perhaps parallelly formed branch which is represented by the tribe *Bothriothoracini* HOW. in its narrower definition; the coarse sculpture often occurring in both tribes does not entitle us to connect two morphologically so distinguished groups as MERCET believes. The true *Discodini* are in many respects more similar to the subtribe of *Microterysi* (tribe *Microteryni*), while *Bothriothoracini* again to subtribe of *Metaprionomitii* of the same tribe.

As the more differentiated types, developed from the stem of the short-antennal *Encyrtidi*, can be regarded the related tribes *Carapterocerini* nov. and *Habrolepini* nov., whose definition is very clear.

The second large branch which split off from the tribe *Mirini* is represented in our fauna especially by the tribes *Copidosomini* nov. and *Ageniaspini* nov. Contrary to the tribes developed from the preceding branch the head is always transversally subquadratic, the body more vaulted (but for a few exceptions), the antennae with longer and parallel segments, not too much expanding towards the end, clava often fused into one whole, cylindrical or truncate; wings usually hyaline. The originally coriaceous sculpture passes into a more or less punctate sculpture; the tribe *Ageniaspini* has a quite specific sculpture closely and finely longitudinally grooved, which perfectly characterises this generically related group. The metallic coloured forms (with the exception of the predominantly black coloured *Ageniaspini*) with the sex dimorphism not too much marked (differences only in the form of the antennae) are parasites of the *Lepidoptera*.

A group with a set of quite individual characters is the tribe *Trechmitini* nov. In all known species of our genus *Trechmites* Thoms the funiculus is five-articled and the mandibles are four-toothed; the post-marginal vein has disappeared without trace. This tribe formed probably from the tribe *Copidosomini*.

The most differentiated tribe of the subfamily Encyrtinae is the tribe *Cercobelini* HFFR., characterised by four articles of the funiculus and also four-toothed mandibles. Originated probably from the tribe *Trechmitini*. To it belong the genera *Cercobelus* WALK. and *Plagiomerus* GRAWF.

The division which I propose above on the basis of my study of the palaeartic genera of the *Encyrtidae* is the first attempt to solve the taxonomy of this family. Nevertheless the definition of the natural generic groups causes just here unusual difficulties. It will be necessary to carry out a supplementation or also correction especially on the basis of a study of exotic material, which unfortunately is not accessible to us; this applies especially to the fauna of *Encyrtidi* of the New World. The considerable economic importance of this family of the *Chalcidoidea* has placed it in recent years in the foreground of the interest of European hymenopterologists and thus forces us already now to establish a firm systematic foundation which would correspond to the natural evolution of this group.

II. Survey of the System of the Family

(with the descriptions of the newly established tribes and subtribes).

Familia *ENCYRTIDAE* WALKER (1837)

I. Subfamilia *ENCYRTINAE* HOWARD (1886)

1. Tribus *Anomalicornini* nov.

Habit fairly elongated, somewhat flattened; configuration of the head and thorax normal. Frons wide. Antennae of both sexes with relatively short scapus and pedicel with articles of the funiculus in the number of seven, all elongated, parallel, and with a short clava of two segments of the same shape as the preceding segments. Mandibles two-toothed or with one sharp tooth and a broad knob. Wings hyaline, narrow, with a short submarginal vein, the other veins short or indistinctly developed; speculum either lacking or only faintly indicated; sometimes the wings are rudimentary. Legs thin. Abdomen oval, pygostyli shifted considerably forward; ovipositor hidden or long-projecting. Sculpture, the abdomen included, smooth to strongly shagreened. Coloration non-metallic. Sex dimorphism only slightly developed. (Parasites of *Homopt.*: *Coccoidea*).

Genera: *Anomalicornia* MERC., *Heterencyrtus* HFFR.

2. Tribus *Anagyrini* HOFFER (1953).

Genera: *Xanthoectroma* MERC., *Paraenasioidea* HFFR., *Leptomastidea* MERC., *Callipteroma* MOTSCH., *Leptomastix* FOERST., *Ana-*

gyrus HOW., *Gyranusa* MERC., *Thomsonisca* GHESQ., *Doliphoceras* MERC., *Rhopus* FOERST., *Anusia* FOERST., *Xanthoencyrtus* ASHM., *Clausenia* ISHII, *Heterarthrellus* HOW. (?)

- a) Subtribus *Anagyrii* n.
Antennae not strongly flattened and expanded in the females.
All genera of *Anagyriini* except the g. *Anusia* FOERST.
- b) Subtribus *Anusii* n.
Female antennae strongly flattened and expanded. Male not yet known.
Genus *Anusia* FOERST.

3. Tribus *Quadrencyrtini* HOFFER (1953).

Genus *Quadrencyrtus* HFFR.

4. Tribus *Ectromini* ASHMEAD (1900). (= *Dinocarsini* HFFR. 1954).

Genera: *Dinocarsis* FOERST., *Dicarnosis* MERC., *Dinocarsiella* MERC., *Ectroma* WESTW., *Dusmetia* MERC., *Aquaencyrtus* HFFR.

- a) Subtribus *Ectromii* nov. nom. (= *Dinocarsii* HFFR. 1954).
Genera: *Dinocarsis* FOERST., *Dicarnosis* MERC., *Dinocarsiella* MERC., *Ectroma* WESTW.
- b) Subtribus *Dusmetii* HOFFER (1954).
Genera: *Dusmetia* MERC., *Aquaencyrtus* HFFR.

5. Tribus *Prionomasticini* nov.

Habit elongated. Head short, wide, frons very wide. Antennae of the female with cylindrical scapus, short pedicel, six-articled funiculus with flattened, quadratic articles lying with their whole width against each other, with a clava without distinct segmentation. Mandibles broad, truncate at the end. Wings of the females without marginal ciliation, smoky in the apical part, in the males with a short marginal ciliation; marginal vein dot-like, postmarginal vein very long. Tibiae and tarsi of the posterior pairs of legs flattened and expanded. Abdomen triangular, strongly constricted at the sides, ovipositor projecting from the 5th abdom. sternite. Sculpture finely shagreened, with a coarse scattered punctation on the head. Coloration non-metallic. Sex dimorphism slightly developed.

Genus *Prionomastic* MAYR.

6. Tribus *Ericydnini* nov.

Habit more or less elongated. Head transversally subquadratic; frons as a rule very wide. Antennae with 6-articled funiculus, the articles more or less elongated, flattened, quadratic, lying against each

other with their whole width so that their limits appear little distinct; clava 3-segmented, similarly configurated. Mandibles 2-toothed. Thorax normally developed; scutellum terminated by a hyaline membrane. Wings hyaline or more or less smoky, especially along their anterior margin; marginal vein always long, stigmal vein of approximately equal length, sinuate, postmarginal vein unusually long; reduction of the wings very frequent. Tibiae and tarsi of the posterior pairs of legs expanded. Abdomen triangular, in the females often strikingly pointed, shorter in the males; ovipositor only sporadically long-projecting. Sculpture finely shagreened with scattered coarse punctation on the head, more rarely on the thorax. Coloration either non-metallic or with a faint metallic tinge. Sex dimorphism very slightly developed. (Parasites of *Coccoidea* of the fam. *Pseudococcidae* and *Lecaniidae*).

Genus *Ericydnus* WALK.

7. Tribus *Mirini* ASHMEAD 1900).

New definition: Habit elongated. Head transversally oval. Antennae with 6-articled funiculus, sporadically 5-articled, either elongated or very long, of the type of the *Anagyrini* or variously differentiated (in the females strongly flattened and expanded, in the males with lateral ramifications). Mandibles 2- to 3-toothed. Thorax usually rather flat, mesoscutum exceptionally with developed parapsidal furrows. Wings narrow, hyaline or with two transversal smoky bands, one medial and one apical; often only the medial band is developed. Basic venation always developed; the marginal vein always longer than wide; reduction of the wings frequent. Legs thin, long. Abdomen always elongated, flat, pointedly terminated; ovipositor very often long projecting. Sculpture shagreened, head often with a scattered fine punctation. Mostly metallic coloured forms. Sex dimorphism strongly developed except in the subtribus *Ecthroplexiellii*. Very variable tribus, comprising a number of subtribes. (Parasites of *Coccoidea*.)

Subtribes with 2-toothed mandibles:

a) Subtribus *Ceballosii* n.

Antennae in both sexes normally developed. Wings hyaline, venation very short. Ovipositor projecting.

Genus *Ceballosia* MERC.

b) Subtribus *Lykii* n.

Antennae of the female normally built, very long, in the male flattened, with the articles of the funiculus on one side expanded. Wings hyaline, venation rather long.

Genus *Lyka* MERC.

c) Subtribus *Tricladii* n.

Female antennae normally built with elongated segments, clava undivided; in the male the funiculus has 3 lateral branches on segments

1—3. Females with hyaline wings, with short marginal vein; ovipositor long projecting.

Genus: *Tricladia* MERC.

d) Subtribus *Tetracnemii* HOWARD (1892).

New definition: Antennae in both sexes with 5-articled funiculus, in the male with long lateral ramifications in the 1.—4. segment, in the females of simple built, elongated. Wings hyaline, with reduced postmarginal vein. Abdomen of the female strongly constricted on the sides; ovipositor hidden.

Genera: *Tetracnemus* WESTW., *Hungariella* ERD.

e) Subtribus *Tetracladii* nov. nom. (= *Masiini* HFFR. 1953 partim).

Antennae of the females strongly flattened and expanded, in the males with lateral branches on the 2.—5. article of the funiculus. Mesoscutum without parapsidal furrows. Wings with a shorter, straight stigmal vein, with one or two dark transversal bands; sometimes rudimentary. Abdomen either triangular or elongated into a point, but most often with a very long projecting ovipositor.

Genera: *Tetracladia* HOW., *Anusiella* MERC., *Calocerinus* GIR., *Tetralophidea* MERC., *Ramalia* MERC. (?).

Subtribi with three-toothed mandibles:

f) Subtribus *Charitopii* n. (= *Masiini* HFFR. 1953 partim).

Body flat, parallel; head strongly transversal. Antennae in the female thin, strongly elongated, in the male of the same configuration as in the preceding tribus. Mandibles with 2 teeth and one knob. Mesoscutum with parapsidal furrows strongly divergent. Wings faintly yellowish without dark bands, with a bent, rather long, always well developed stigmal vein. Abdomen parallel; ovipositor hidden.

Genus *Charitopus* FOERST.

g) Subtribus *Boučekiellii* n.

Body flattened. Female with shorter antennae, clava undivided. Mandibles with two teeth and one knob. Frons wide, eyes small. Wings narrow, with quadratic marg. vein, the smoky bands faintly perceptible. Ovipositor long projecting. Male not known.

Genus *Boučekiella* HFFR.

h) Subtribus *Echthroplexiellii* HOFFER (1954).

Genera: *Echthroplexiella* MERC., *Baeocharis* MAYR, *Metanotalia* MERC., *Metallon* WALK.

i) Subtribus *Mirii* s. str.

Related to the preceding tribe, from which it is distinguished by the huge, strongly flattened and expanded antennae in the females and one-sidedly expanded segments of the flagellum in the male. Pronotum posteriorly triangularly indented. Abdomen relat. short; ovipositor not projecting.

Genus *Mira* SCHELL.

k) Subtribus (incertae sedis) *Mayridii* nov.

Wings smoky as in subtr. *Tetracladii*; margin. vein short; female antennae with short, quadratic segments; in the male the first article of the funiculus is particularly long. Abdomen shorter than the thorax; ovipositor never long projecting. This subtribus shows close relations to the tribus *Microteryni*.

Genera: *Mayridia* MERC., *Hoplopsis* HINCKS, *Parasyrrophagus* GIR.

8. Tribus *Encyrtini* ASHMEAD (1900).

New definition: Forms mostly of considerable size and sturdy habit. Head wide, sitting with the whole width of the posterior margin to the thorax. Antennae with cylindrical scapus, 6-articled funiculus, segments cylindrical, in the females somewhat more flattened, towards the end of the antenna strikingly expanding, and with 3-segmented, truncate clava; male antennae either similar to the female ones, or much thinner and longer, erectly villous. Mandibles broad, pointed, without inner teeth. Scutellum in the female with a tuft of long hairs at the end. Anterior wings in the female intensively smoky in the apical half, besides with smaller, triangular dark spot anterior to the end of the marginal vein; male either with similar wings as the female or with hyaline wings; marginal vein dot-like, postmarginal and stigmal veins long, the latter sinuate. Legs sturdy, posterior 2 pairs flattened. Abdomen oval; ovipositor hidden. Sculpture coriaceous or rugulose. Coloration non-metallic. (Parasites of *Coccoidea* of the fam. *Lecaniidae*).

Genus: *Encyrtus* LATR.

9. Tribus *Cheiloneurini* nov.

More slender forms. Head large, hemispheric, frons more or less angularly separated from the facial part. Eyes usually large, strongly convex. Antennae in the female with the scapus often more slightly expanded, with the pedicel fairly long, with 6-articled funiculus more or less expanding towards the end of the antenna, and with 3-segmented, sometimes broadly truncate clava; male antennae always longer, thin, long-villous. Mandibles 3-toothed. Mesoscutum with striking, tough, light, more or less dense, short bristles; scutellum considerably convex, in the females often with a tuft of long hairs at the end. Anterior wings of the females rarely hyaline, rather narrow, usually in the apical half with a large dark spot often expanded to the distal margin of the wing; smaller triangular spot anterior to the end of the submarginal vein; wings of the male hyaline; with the marginal vein usually very long, more rarely short, and with the postmarginal and stigmal veins short; wings only exceptionally rudimentary. Legs long, the two posterior pairs somewhat flattened. Abdomen elongated into a point, often with more or less projecting ovipositor. Sculpture shagreened, on the head with a scattered shallow punctation. Coloration yellowish brown or metallic bluish green. Sex dimorphism considerably developed. (Parasites of *Coccoidea*).

Genera: *Apterencyrtus* ASHM., *Achrysopophagus* GIR., *Cheilonurus* WESTW., *Lepidoneurus* HFFR. in litt., *Prochiloneurus* SILV., *Metacheilonurus* HFFR. in litt., *Tineophoctonus* ASHM., *Mayrencyrtus* HINCKS (?). *Protyndarichus* MERC. (?).

10. Tribus *Aphycini* HOFFER (1954).

Genera: *Aphycus* MAYR, *Metaphycus* MERC., *Waterstonia* MERC., *Aenasioidea* GIR., *Paraphycus* GIR., *Pseudaphycus* CLAUS., *Pezaphycus* NOV., *Timberlakia* MERC., *Aphyculus* HFFR., *Stemmatosteres* TIMB., *Pseudorhopus* TIMB. (?).

a) Subtribus *Aphycii* n.

Antenna normally configured, with 6-articled funiculus and 3-segmented clava.

Genera: *Aphycus* MAYR, *Metaphycus* MERC., *Waterstonia* MERC., *Aenasioidea* GIR., *Pezaphycus* NOV.

b) Subtribus *Pseudaphycii* n.

Antennae with 5-articled funiculus and 3-segmented clava.

Genera: *Pseudaphycus* CLAUS.

c) Subtribus *Stemmatosterii* n.

Antennae with 5-articled funiculus and 2-segmented clava.

Genera: *Timberlakia* MERC., *Aphyculus* HFFR., *Stemmatosteres* TIMB.

d) Subtribus *Paraphycii* n.

Antennae with quadratic, equal segments, without marking of the clava; flagellum 9-articled.

Genus *Paraphycus* GIR.

e) Subtribus (incertae sedis) *Pseudorhopii* n.

Antennae with 5. articled funiculus in the female 6. articled in the male, clava undivided in both sexes. Submarginal vein short, marginal, postmarginal and stigmal veins considerably reduced. Metatarsus of the middle legs relatively short. — Very differentiated type placed provisionally; the other characters have still to be investigated.

Genus *Pseudorhopus* TIMB.

11. Tribus *Homalotylini* HOFFER (1954, nom., fig.).

Forms mostly of medium to more considerable size, sturdy, parallel, with transversally subquadratic head. Antennae composed of the cylindrical to leaf-like expanded scapus, the rather short pedicellus, the 6-articled funiculus, quadratic, rarely elongated segments lying with the whole width against each other, and the not too long, at the end pointed, usually also in the female undivided, often light coloured clava. Eyes large. Mandibles strong, 3-toothed. Thorax normally developed; anterior wings wide, with a very short marginal ciliation, usually in the central

part with a smoky spot of different shapes; marginal vein dot-like; postmarginal and stigmal veins always developed, not too long; posterior wings relatively large; only quite exceptionally the wings are shortened. Legs strong, long, posterior two pairs somewhat flattened. Pygostili only a little shifted forward; ovipositor hidden or more or less projecting. Sculpture coriaceous, sometimes scattered punctate, coarser pit only on the head. Coloration in the light forms non-metallic, in the dark forms with a not too intensive metallic lustre. Sex dimorphism quite slight. (Parasites primarily of *Coccoidea*, but more often of *Coleoptera* of the fam. *Coccinellidae* and *Chrysomelidae* and of *Neuroptera*, fam. *Chrysopidae*.)

Genera: *Homalotylus* MAYR, *Echthroplexis* FOERST., *Isodromus* HOW., *Eupoecilopoda* NOV. et HFFR., *Psilophrys* MAYR, *Homalotylodea* MERC.

12. Tribus *Microteryxi* nov.

Largest tribus. Habit moderately elongated or short. Head either short in the front rounded, seen from above, sitting broadly to the thorax or longer often transversally subquadratic; sporadically the frons is angularly separated from the face. Antennae with 6-articled funiculus, in the female either short, often expanding towards the end, or somewhat elongated, in the male always longer and erect villous, exceptionally with lateral branches. Mandibles three-toothed; some of the teeth may be developed in the form of knobs only. Thorax without special modifications, more or less vaulted. Wings broad with the marginal vein either dot-like or elongated, but never very long; postmarginal vein usually short; smokiness of the wings more often developed in some genera and consisting in one large dark spot which is often in disintegration in the apical part; micropteris or brachipteric forms occur on the whole rarely. Legs long, medium strong. Abdomen with triangular termination; ovipositor never long projecting. Sculpture shagreened, in a number of genera with variously developed scattered punctation. Coloration metallic, more rarely non-metallic. Considerable sex dimorphism. [Parasites of *Homoptera* (*Coccoidea*, *Aphidoidea*, *Psylloidea*), *Lepidoptera*, especially also *Coleoptera*, *Diptera* and *Acarida* of the fam. *Ixodidae*.]

a) Subtribus *Metaprionomiti* n.

Head not too short, hemispherical or subquadratic. Antennae in the females often rather long. Marginal vein usually dot-like.

Genera: *Ooencyrtus* ASHM., *Schedius* HOW., *Schedioides* MERC., *Hazburkia* HFFR., *Coccidencyrtus* ASHM., *Neococcidencyrtus* COMP., *Prionomitus* MAYR, *Subprionomitus* MERC. (?), *Metaprionomitus* MERC., *Superprionomitus* MERC. (?), *Psyllaephagus* ASHM., *Psylladontus* GRAWF., *Blastothrix* MAYR (?).

b) Subtribus *Microteryxi* n.

Head usually short, strongly rounded anteriorly. Antennae shorter, stronger. Marginal vein elongated.

Genera: *Microterys* THOMS., *Trichomasthus* THOMS., *Aphidencyrtus* ASHM., *Paraphaenodiscooides* MERC., *Paraschediella* HFFR., *Syrphophagus* ASHM., *Epiencyrtus* ASHM., *Tyndarichus* HOW.

c) Subtribus *Ixodiphagii* HOWARD (1908).

Genera: *Hunterellus* HOW., *Ixodiphagus* HOW.

d) Subtribus *Pentacnemii* n.

Antennae of the female with moderately elongated segments, large, broadly truncate clava; antennae of the male with lateral branches on articles 1—4 or 1—5 of the funiculus; last article of the funiculus and clava short. Frons very wide. Marginal vein dot-like.

Genera: *Parablastothrix* MAYR, *Calometopia* MERC., *Pentacnemus* HOW.

e) Subtribus *Adelencyrtii* n.

First 4 articles of the funiculus very short, clava huge. Mandibles 4-toothed. Wings very narrow, with the marginal vein dot-like.

Genus: *Adelencyrtus* ASHM.

13. Tribus *Discodini* HOFFER (1954).

Redescription: Medium to considerably large forms with a relatively very broad habit, dorsally more or less flat, only rarely strongly convex. Head short, broad, sitting with the posterior whole margin to the thorax; frons usually considerably wide. Antennae normally built, usually short, only rarely long, not showing any special modifications apart from the more often expanded scapus; clava relatively short, usually three-segmented also in the males. Mandibles 2- to 3-toothed. Thorax broad, most often flat (with the exception of the genus *Amincelus masi*), with the pronotum often distinctly developed, transversally lamellar, with the mesoscutum usually short and transversal, with a triangular, sometimes posteriorly truncated scutellum. Anterior wings in the females broad, as a rule more or less connectedly smoky, sometimes only in the basal part. Cellula costalis broad and arcuate forming at its apical end a more or less striking break of the anterior margin of the wing; marginal vein as a rule distinctly longer than wide, not distinguished in thickness from the submarginal vein, only in some more differentiated subtribes considerably reduced. Strong tendency to reduction of the wings. Abdomen short, ending triangularly. Sculpture either shagreened or with coarse punctation of the head, often also of the thorax. Coloration non-metallic or with not too intensive metallic lustre. Sex dimorphism in the more primitive forms slight, in others up to very considerable. (Parasites of *Coccoidea*.)

Genera: *Eugahania* MERC., *Monodiscodes* HFFR., *Discodes* FOERST., *Choreaspis* HFFR., *Choreia* WESTW., *Semen* HFFR., *Metaphaenodiscus* MERC., *Paraphaenodiscus* GIR., *Coenocercus* THOMS (?), *Rhinoencyrtus* MERC., *Aminellus* MASI.

a) Subtribus *Discodii* s. str.

Marginal vein well developed. Head and antennae of normal shape.

All genera of the tribe except those which are the types of the following subtribes.

b) Subtribus *Rhinoencyrtii* n.

Mandibles 2-toothed. Stigmal vein connected directly to the submarginal vein anterior to the place where it touches the margin of the wing. Antennae of the female with elongated, quadratic articles of the funiculus, antennae of the males thin and erectly villous. Head below the facial part running out in a projecting tubercle.

Genus: *Rhinoencyrtus* MERC.

c) Subtribus *Aminellii* n.

Body very strongly vaulted. Antennae of the female with the articles of the funiculus quadratic, expanding towards the end of the antennae, with truncate clava; antennae of the male flattened, with a 3-segmented clava as wide as the preceding segments. Mandibles with 2 teeth and one knob. Scutellum with a tuft of long hairs at the end. Wings broad, marginal vein dot-like.

Genus *Aminellus* MASI.

14. Tribus *Bothriothoracini* HOWARD (1895).

New definition: Medium to very large, parallel forms, dorsally flat, with a very coarse punctate sculpture on head and thorax, usually metallic green coloured. Head short, transversal, semielliptic to elongated quadratic with a flattened frons. Antennae with 6-articled funiculus, relatively long, often moderately flattened, expanding towards the end. Wings relatively narrow, always hyaline; marginal vein dot-like. Sex dimorphism not too marked. (Parasites of *Diptera*, *Coleoptera* and *Homoptera*).

Genera: *Bothriothorax* RATZB., *Eucantabria* MERC., *Agromyzaephagus* Gah., *Zeteticontus* SILV., *Euzkadiella* MERC., *Moraviella* HFFR., *Scaptrophorus* FOERST., *Coccidoxenus* CRAWF.

15. Tribus *Cerapterocerini* nov.

Habit moderately elongated. Head transversally subquadratic, frons angularly separated more or less distinctly from the facial part. Antennae of the female with 6-articled funiculus, either strongly flattened and expanded or otherwise configured, male antennae thin, elongated, with longer villosity. Mandibles 2- to 3-toothed. Thorax normally configured, dorsal side only slightly convex. Wings long, relatively narrow, with the marginal vein distinctly longer than wide, postmarginal vein suppressed, stigmal vein very short; smokiness of the wings in the female either compact or broken up into radial bands; male wings hyaline. Abdomen not long, pointed. Sculpture shagreened, often with a coarser punctation especially on the head. Coloration dark or metallic. Sex dimorphism very marked. (Parasites of *Coccoidea* or Hyperparasites.)

Genera: *Eusemion* DAHLB., *Anicetus* HOW., *Pareusemion* ISHII, *Cerapterocerus* WESTW., *Comperiella* HOW.

a) Subtribus *Eusemionii* nov.

Antennae of the female with lamellar expansion of the scapus, short funiculus and large clava. The smokiness of the wings is not divided into radial bands.

Genera: *Eusemion* DAHLB., *Anicetus* HOW., *Pareusemion* ISHII.

b) Subtribus *Cerapterocerii* s. str.

Antennae of the female strongly flattened, the whole lamellarly expanded. Smokiness of the wings divided into radial bands.

Genera: *Cerapterocerus* WESTW., *Comperiella* HOW.

16. Tribus *Habrolepini* nov.

Related to the preceding one, with which it agrees in habit, shape of the head, and configuration of the venation and smokiness of the wings. Head and thorax sometimes with peculiar squamae. Antennae of the female normally built, but the flagellum of the male is composed only of two anella and a huge clava distinctly longer than the remaining part of the antenna. Sculpture as in the preceding tribus. Coloration intensively metallic green to blue. Sex dimorphosm highly developed. (Parasites of *Homopt*: *Coccoidea*.)

Genera: *Habrolepis* FOERST., *Anabrolepis* TIMB.

17. Tribus *Copidosomini* nov.

Habit medium (in the genus *Copidosoma* to very strongly) elongated; body strongly convex. Head most often subquadratic, more or less transversal, never anteriorly strikingly rounded. Antennae usually elongated, with the articles of the funiculus expanding only slightly in the direction towards the end of the antennae, parallel, in the number of 6, basal one never especially short and small; clava often undivided also in the females. Thorax, especially scutellum, strongly convex. Wings long, hyaline, with the marginal vein usually dot-like or short; sometimes the stigmal vein sets in directly on the submarginal one still before the place where the latter touches the margin of the wing (*Sectiliclava* HFFR.), Legs thin, long. Abdomen variously long, always pointed, often with a long projecting ovipositor. Sculpture passing from shagreened forms to punctate forms (where the punctae touch each other). Coloration always metallic, as a rule green black forms occur only quite exceptionally. Sex dimorphism more faintly developed, chiefly in the form of the antennae. (Most often parasites of *Lepidoptera*, some species propagate polyembryologically.)

Genera: *Litomastix* THOMS., *Paralitomastix* MERC., *Sectiliclava* HFFR. (in litt.), *Copidosoma* RATZB., *Verdunia* MERC., *Cerchysius* WESTW.

18. Tribus *Ageniaspidini* nov.

Habit subelongate, strongly convex. Head transversal, subquadratic, frons wide. Mandibles 3-toothed. Articles of the flagellum of different

shape; funiculus 5 or 6-articled. Related to the preceding tribus, from which it is distinguished chiefly by the very characteristic dense, longitudinally grooved sculpture of the thorax which does not occur anywhere else in the *Encyrtidae*. Wings always hyaline, marginal vein dot-like or short. Ground coloration velvety black, often head or posterior margin of the mesoscutum metallic green or greenish blue shiny; legs black with yellowish portions. Sex dimorphism only in the form of the antennae. (Polyembryonic parasites of the *Lepidoptera*.)

Genera: *Ageniaspis* DAHLB., *Holcothorax* MAYR, *Eustrinus* HFFR. (in litt.), *Geniaspidius* MASI, *Parageniaspis* MASI (?).

19. Tribus *Trechnitini* nov.

Habit subelongate. Head transversally oval. Antennae with 5-articled funiculus and 3-segmented clava. Mandibles 4-toothed. Thorax not too convex, of normal shape. Wings relatively large, hyaline; marginal vein dot-like, stigmal vein relatively short, postmarginal vein entirely reduced. Legs fairly strong. Abdomen triangular. Sculpture shagreened, sometimes with scattered punctation. Coloration metallic. (Parasites of *Homopt.*: *Coccoidea* and *Psyllodea*.)

Genus *Trechnites* THOMS.

20. Tribus *Cercobelini* HOFFER (1953)

Genus *Cercobelus* WALK., *Plagiomerus* GRAWF.

II. Subfamilia *ARRHENOPHAGINAE* MERCET (1921)

III. Subfamilia *ANTHEMINAE* MERCET (1922)

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THE PHYLOGENY AND TAXONOMY OF THE FAMILY ENCYRTIDAE
(HYM., CHALCIDOIDEA)

V únoru 1955 vydalo svým nákladem v počtu 600 výtisků Národní museum v Praze
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