REVIEW OF THE WORLD GENERA OF OAK CYNIPID WASPS (HYMENOPTERA: CYNIPIDAE: CYNIPINI)

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Abstract – The current classification of world genera of Cynipini follows Weld (1952a), who divided Cynipini into 39 genera. Later, Monzen (1954) described a new genus, *Neoneuroterus* from Japan; Maisuradze (1961) reported a new genus, *Repentinia* Belizin & Maisuradze from Ciscaucasus (Azerbaijan); Kovalev (1965) described two new genera, *Belizinella* and *Ussuraspis* from the Far East of Russia; Lyon (1993) synonymized *Xystoteras* to *Phylloteras* and described a new genus, *Euxystoteras*; and Melika & Abrahamson (1997b) described a new genus *Eumayriella* from Florida and synonymized *Trisoleniella* to *Eumayria*. Later, Melika, Ros-Farré & Pujade-Villar (2001) synonymized *Fioriella* to *Plagiotrochus*. Recently 41 genera of Cynipini were known to associate with oaks, generic division of which was based on the presence or absence of a basal lobe on the tarsal claws. A reclassification of world genera of oak gall-inducing cynipids of the tribus Cynipini (Hymenoptera: Cynipidae) is given in which 26 genera are proposed as valid, 15 are synonymized, one *Neuroterus* subgenus, *Latuspina* Monzen, 1954 has an uncertain status; 73 **comb. nov.** and 26 **comb. rev.** are made.

Key words: Cynipidae, Cynipini, gall-wasps, taxonomy

Introduction

The clear definition of genera is the primary difficulty in the classification of Cynipidae (Hymenoptera), particularly in the tribus Cynipini (Dailey & Menke 1980). The presence of alternating asexual and sexual generations in many genera creates considerable morphological variation among adults that markedly complicates the assessment of generic limits and hence classification. The assessment of generic limits requires that generic characters be defined that include the character states of both generations.

Burks (1979) listed 485 species of oak gall-inducing cynipids for North America north of Mexico and subsequent to this publication many new species have been described. Although the majority of North American species of oak gall wasps are known from only one generation, there are nearly 150 species from Central America, mainly Mexico, whose lifecycles are not known. Accumulation of controlled rearing data to determine lifecycles of cynipids will take decades. However, we can improve the classification of the Cynipini by using information from the existing literature on cynipid lifecycles and by detailed analysis of type specimens.

The diagnostic features that are used currently in the keys to the world genera of Cynipini frequently include morphological characters that are inconsistent. Consequently these keys frequently are unable to distinguish some genera. For instance, identification of the representatives of *Plagiotrochus* Mayr, *Bassettia* Ashmead, *Eumayria* Ashmead, *Trisoleniella* Rohwer and Fagan, *Xanthoteras* Ashmead, *Sphaeroteras* Ashmead, and some species groups of *Callirhytis* Foerster are especially complicated. The current systematic arrangement of *Bassettia*, for instance, includes several *Callirhytis* and *Andricus* Hartig species, *Eumayria* includes some *Callirhytis* species, and *Trisoleniella* appears to be a synonym of *Eumayria* (Melika & Abrahamson 1997b). These systematic difficulties result from the use of inappropriate diagnostic characters for some genera. Such characters are not useful because they are shared by the representatives of several genera and, thus, are inappropriate to use at the generic level. In some cases, the structure and location of a gall or novel host associations were more heavily weighted in the description of new species, species groups, or even new genera than were morphological peculiarities of adult wasps. For example, the North American genus *Heteroecus* Kinsey was established on the basis that its species associate only with *Quercus chrysolepis* Liebm. with distribution limited to California.

A historical review of Cynipidae classification was given in Melika & Abrahamson (2000b). The current classification of world genera of Cynipini follows Weld (1952a). No corrections to Weld's Cynipidae classification were made in a manuscript Weld prepared later entitled "Supplement to Cynipoidea (Hym.) 1905-1950 (1952)." This manuscript, which is dated 1964, is available at the United States National Museum, Smithsonian Institution. Weld's Cynipini classification needs a substantial alteration. It is important to recognize that very little was known about the alternation of generations in North American cynipids during Weld's time. This alone markedly complicated the task of establishing a more natural classification of Cynipini. Excellent studies of the alternation of generations for USA cynipids have been completed during the past several decades (Doutt 1959, 1960; Dailey 1969; Dailey & Sprenger 1973a, 1973b; Dailey, Perry & Sprenger 1974; Evans 1967, 1972; Lyon 1959, 1963, 1964, 1969, 1970; Melika & Buss 2002). These results have increased our understanding of gall-inducing cynipids and given us a better background to establish a more natural classification of Cynipini, particularly for those restricted to North America.

Materials and Methods

Our study analyzed the type species of genera and also many other species types. Specimens were examined from the following museums and institutions: USNM (United States National Museum of Natural History, Smithsonian Institution, Washington DC, USA, A. Menke), AMNH (American Museum of Natural History, NYC, NY, USA, J. Carpenter), CNCI (Canadian National Collection of Insects, Ottawa, Canada, J.T. Huber), BMNH (British Natural History Museum, London, England, J. Noyes, D. Notton and N.D.M. Fergusson), OUM (Hope Entomological Collections, University Museum, Oxford, UK, C. O'Toole and G. McGaven), NHMW (Naturhistorisches Museum, Vienna, Austria, S. Schödl), NHMH (Hungarian Natural History Museum, Budapest, Hungary, L. Zombori and J. Papp), ZIN (Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia, O.V. Kovalev), IZU (Schmalhausen Institute of Zoology of the Ukrainian Academy of Sciences, Kiev, Ukraine, M.D. Zerova and L.V. Diakontshuk), and MNHN (Muséum National d'Histoire Naturelle, Paris, France, C. Villemant-Ait-Lemkadem). In addition, we examined specimens from different genera that were kindly sent to the authors by J. Pujade-Villar (Universitat de Barcelona, Barcelona, Spain), J.L. Nieves Aldrey (Museo Nacional de Ciencias Naturales, Madrid, Spain), G.N. Stone (Institute of Cell, Animal and Population Biology, University of Edinburgh, Edinburgh, Scotland). Authors express their deepest appreciation to mentioned colleagues for help in obtaining material for research. Also the Cynipidae collection of Systematic Parasitoid Laboratory (Kőszeg, Hungary) was examined.

We use the following terminology: for mesosoma (Gibson 1985; Menke 1993), for head, metasoma, and ovipositor (Fergusson 1988; Ronquist & Nordlander 1989) (Figs 1-4). The surface sculpturing follows Harris (1979). Abbreviations for the forewing venation follow Ronquist & Nordlander (1989). The measurements and abbreviations used herein include: F1-F12, 1^{st} and subsequent flagellomeres; POD (post-ocellar distance), the distance between the inner margins of the posterior ocelli; OOD (ocellar-ocular distance), the distance from the outer edge of a posterior ocellus to the inner margin of the compound eye; LOD, the distance between lateral and frontal ocellus; transfacial line, distance between inner margins of compound eyes measured across antennal sockets (Fig. 1). The width of the radial cell is measured along 2r (Fig. 3). Drawings were made with the aid of a Leica drawing tube or from stereomicroscope photographs, which were scanned into a PC and modified in Adobe Photoshop 6.0.

Results and Discussion

Morphology and current arrangement of genera

The tribus Cynipini (Hymenoptera, Cynipidae) includes species that induce galls on members of Fagaceae, primarily *Quercus* L. with exceptions for only a few species. For instance, *Dryocosmus kuriphilus* (Yasumatsu), the only species of Cynipini known to associate with *Castanea*, threatened the chestnut industry of Japan and Korea and was discovered in Georgia, USA in 1974 (Payne *et al.* 1975). Another species, *Dryocosmus castanopsidis* (Beutenmueller), known from Oregon and California, induces galls on catkins of *Castanopsis chrysophylla* and *C. sempervirens* (Burks 1979).

Three genera, *Liebelia* Kieffer, 1903 *Paraulax* Kieffer, 1904, and *Poncyia* Kieffer, 1903 that were included in Weld's (1952a) Cynipini key belong elsewhere. The genera *Liebelia* and *Diplolepis* Geoffroy, 1762 belong in the Diplolepidini (Ronquist 1999). *Paraulax* possesses some character states (e.g., the structure of the antenna and forewing venation) that indicate the genus should be placed in the Charipinae subfamily (Cynipoidea: Figitidae) (Ronquist 1995). Furthermore, on the basis of its description, *Poncyia* may be a *Plagiotrochus*, or if the description of the pronotum is incorrect, the genus must be placed among inquilines on the basis of its longitudinally striate petiole and long tergum II. Currently it is placed in the Cynipidae, *incertae sedis* (Ronquist 1999). The genus, *Synophrus* Hartig, 1843, with only three known species from Western Palaearctic, *S. pilulae* Giraud in Houard, 1911, *S. politus* Hartig, 1843 (Europe, Asia Minor, North Africa), and *S. olivieri* Kieffer, 1899-1901 (Algeria, Israel, Iran), originally was described as a gall inducer, however, on the basis of the morphological characters of adults, this genus belongs to cynipid inquilines (Ronquist 1994). *Synophrus* has never been a subject to detailed research and, thus, it is quite possible, that *Synophrus* species, in spite of their taxonomic identity with cynipid inquilines, lack gall-inducing capability. This genus is also excluded from the below analysis.

Around 1000 species of Cynipini are known worldwide, all in the Holarctic region, mainly in the Western Palaearctic (around 140 valid species) and America North of Mexico (Burks (1979) listed 485 species of oak gall-inducing cynipids). The taxonomy of Cynipini species have undergone substantial changes: new names, synonymies, new name combinations, and new alternate life forms were experimentally obtained for several gall wasps. Currently 41 genera of Cynipini are known to associate with oaks (Table 1).

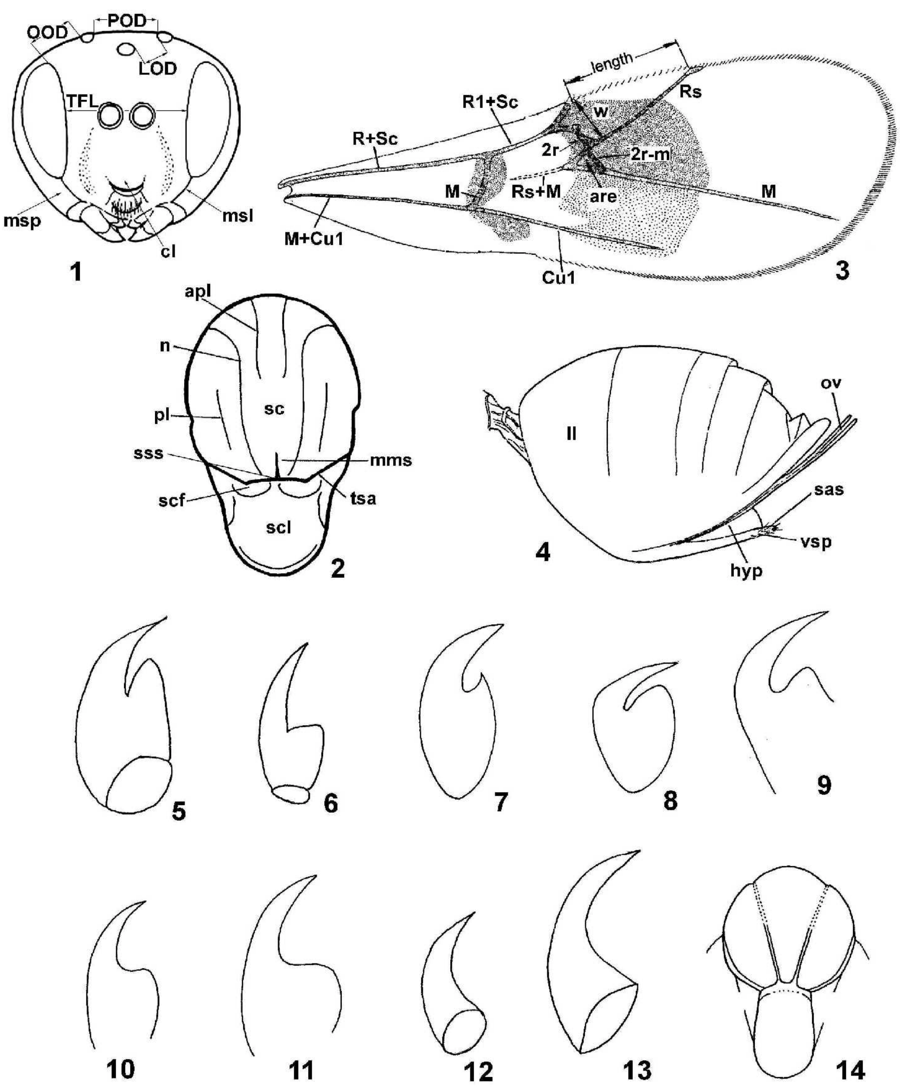
Table 1 Current arrangement of Cynipini genera and their distribution (after Pujade-Villar, Bellido, Segú & Melika 2001, with some changes)

Genus name	Geographic distribution	Number of species
Acraspis Mayr, 1881	Nearctic	probably > 30
Amphibolips Reinhard, 1865	Nearctic	around 30
Andricus Hartig, 1840 (= *Adleria* Rohwer & Fagan, 1917)	Holarctic and Oriental?	probably > 300
Antron Kinsey, 1930	Nearctic	around 40
Aphelonyx Mayr, 1881	Palaearctic	4
Atrusca Kinsey, 1930	Nearctic	uncertain; probably > 40
Bassettia Ashmead, 1887	USA	9
Belizinella Kovalev, 1965	Russia, Far East	2
Belonocnema Mayr, 1881	USA	2
Besbicus Kinsey, 1930	USA	8
Biorhiza Westwood, 1840	Palaearctic	2
Callirhytis Foerster, 1869	Holarctic	around 150
Chilaspis Mayr, 1881	Occidental Palaearctic	3
Cynips Linnaeus, 1758	Palaearctic	around 25
Disholcaspis Dalla Torre & Kieffer, 1910	Nearctic	around 40
Dros Kinsey, 1937	Nearctic	11
Dryocosmus Giraud, 1959	Holarctic	Around 25
Erythres Kinsey, 1937	Mexico	2
Eumayria Ashmead, 1887 (=*Trisoleniella* Rohwer & Fagan, 1917)	USA	5
Eumayriella Melika & Abrahamson, 1997	USA	2
Euxystoteras Lyon, 1993	USA	1
Heteroecus Kinsey, 1922	USA	15
Holocynips Kieffer, 1910	USA	4
Liodora Foerster, 1869	Europe, USA	3
Loxaulus Mayr, 1881	Nearctic	14
Neoneuroterus Monzen, 1954	Russia, Far East and Japan	5
Neuroterus Hartig, 1840	Holarctic	About 100
Odontocynips Kieffer, 1910	USA	1
Paracraspis Weld, 1952	USA	3
Parandricus Kieffer, 1906	China	1
Philonix Fitch, 1859	USA	8
Phylloteras Ashmead, 1897 (= *Xystoteras* Ashmead, 1897)	Nearctic	6
Plagiotrochus Mayr, 1881 (= *Fioriella* Kieffer, 1903)	Western Palaearctic & Himalaya	14
Repentinia Belizin & Maisuradze, 1961	Transcaucasus	1
Sphaeroteras Ashmead, 1897	USA	8
Trichagalma Mayr, 1907	Japan and China	2
Trichoteras Ashmead, 1897	USA	8
Trigonaspis Hartig, 1840	Palaearctic	Around 10
Ussuraspis Kovalev, 1965	Russia, Far East	1
Xanthoteras Ashmead, 1897	USA	12
Zopheroteras Ashmead, 1897	USA	6

With the exception of the genus *Neuroterus* Hartig, 1840 (Fig. 14) the current classification of the world genera of the Cynipini is based on the presence or absence of a basal lobe (tooth) on tarsal claws (Figs 5-13) (Weld 1952a). The use of this character dates to earlier treatments including Ashmead's (1903) key to 33 genera of Cynipini. Earlier, Mayr (1881), Ashmead (1885), Dalla Torre (1893), Kieffer (1897-1901) used this character for subgeneric level to separate *Callirhytis* and *Andricus* as subgenera of *Andricus*. Again with the exception of *Neuroterus*, Weld (1952a) divided all the genera into two groups: (a) those that possess a basal lobe on tarsal claws and (b), those that have simple tarsal claws without a basal lobe (Table 2). Consequently, the number of oak gall-inducing Cynipini genera distinguished by Weld (1952a) was 39. Later, Monzen (1954) described a new genus, *Neoneuroterus* from Japan; Maisuradze (1961) reported a new genus, *Repentinia* Belizin & Maisuradze from Ciscaucasus (Azerbaijan); Kovalev (1965) described two new genera from Far East of Russia, *Belizinella* and *Ussuraspis*; Lyon (1993) synonymized *Xystoteras* to *Phylloteras* and described a new genus, *Euxystoteras*, which differs from *Phylloteras* only by having simple tarsal claws; and Melika & Abrahamson (1997b) described a new genus *Eumayriella* from Florida and synonymized *Trisoleniella* to *Eumayria*. Later, Melika, Ros-Farré & Pujade-Villar (2001) synonymized *Fioriella* to *Plagiotrochus*. We will discuss these new genera and synonymizations below.

Table 2 Division of the Cynipini based on the presence or absence of a basal lobe on the tarsal claws (* – genera which include species in both groups)

Genera with toothed claw	Genera with simple claw
Acraspis	*Aphelonyx*
Amphibolips	*Bassettia*
Andricus	*Belizinella* *
Antron	*Belonocnema*
Atrusca	*Biorhiza*
Belizinella *	*Callirhytis* *
Besbicus	*Chilaspis*
Callirhytis *	*Dryocosmus*
Cynips	*Erythres*
Disholcaspis	*Eumayria*
Dros	*Eumayriella*
Liodora	*Euxystoteras*
Neoneuroterus	*Heteroecus*
Paracraspis	*Holocynips*
Parandricus *	*Loxaulus*
Philonix	*Odontocynips*
Phylloteras	*Parandricus* *
Repentinia	*Plagiotrochus*
Trichoteras	*Sphaeroteras*
Trigonaspis *	*Trichagalma*
Xanthoteras	*Trigonaspis* *
	Ussuraspis
	Zopheroteras



Figures 1–14 Cynipidae: Cynipini. 1, Head, front view: cl, clypeus; msl, malar sulcus; msp, malar space; POD, post-ocellar distance; OOD, ocellar-ocular distance; LOD, the distance between lateral and frontal ocellus; TFL, transfacial line. 2, Thorax, dorsal view: apl, anterior parallel line (anteroadmedian line); mms, median mesoscutal sulcus (median mesoscutal line); n, notaulus; pl, parapsidal line; sc, scutum (mesoscutum); scf, scutellar fovea; scl, scutellum; sss, scutoscutellar sulcus; tsa, transscutal articulation. 3, Forewing: length, length of radial cell; w, width of radial cell. 4, Gaster: II, 2nd tergite; hyp, hypopygium; sas, subapical setae; ov, ovipositor; vsp, ventral spine of hypopygium. 5-13, Tarsal claw: 5, *Amphibolips quercuscinerea*. 6, *Andricus quercusfoliatus*. 7, *Cynips quercusfolii*. 8, *Cynips divisa*. 9, *Neuroterus quercusbaccarum*. 10, *Neuroterus tricolor*, asexual female. 11, *N. tricolor*, sexual female. 12, *Belonocnema quercusvirens*. 13, *Sphaeroteras ocala*. 14, *N. tricolor* (scutellar foveae absent)

Thus, classification of the Cynipini has relied on the presence or absence of the tarsal claw (Figs 5-13). Lyon (1993), for example, stated that in cynipid taxonomy “the presence or absence of a tooth on the tarsal claw is considered to be of fundamental importance in separating major genera of the group.” However, this morphological criterion, dividing the Cynipini genera into two major groups, is insufficient for all taxonomic distinctions. There are a number of exceptions to this criterion, including those discussed by Weld (1952a). For instance, the majority of *Neuroterus* species have tarsal claws without a basal lobe, however, *quercusbaccarum* L., *numismalis* Olivier, and *petioliventris* Hartig, have toothed tarsal claws with a basal lobe in the asexual generations but simple claws in the alternate sexual generations. The same is true for *Callirhytis*, in which both generations of the European species *glandium* (Giraud) have toothed tarsal claws as the asexual generation of *bella* (Dettmer) (Nieves Aldrey 1992). One species from *Trigonaspis* genus, *T. megaptera* (Panzer) has a weak tooth on claws, while other species, *T. synaspis* have simple tarsal claws. The sexual generations of the North American genus *Xystoteras* have a very weak tooth on claws, and in *Parandricus mairei* Kieffer, the females have toothed tarsal claws while the males have simple claws without a basal lobe. In the genus *Belizinella*, one species, *B. gibbera* Kovalev, has claws with a basal lobe while another species, *B. vicina* Kovalev, have simple claws (Kovalev 1965). The presence or absence of a basal lobe is a likely homoplasy and probably evolved separately in different cynipine genera. The ancestral condition is a simple tarsal claw without a basal lobe, based on its appearance in the majority of genera from the Aylacini. However, even in this tribe, *Xestophanes* Foerster, *Diastrophus* Hartig and *Gonaspis* Ashmead have a basal lobe. An additional complication is the use of the term “tooth” Given that the term basal lobe would be more precise. In some cases the claws have a strong basal lobe, for example as in *Amphibolips* and many *Andricus* species. However in numerous species, including those that Weld treated as possessing a tooth, no distinct tooth occurs on the claws.

This character has been used for generic separation in other Hymenoptera groups as well, as for example in the Chalcidoidea. However, later works reconsidered the diagnostic value of this character in these groups and subsequently dropped it. Anura Wijesekara (Sri Lanka, *pers. comm*) eliminated the use of this character for the separation genera of Chalcididae and Leucospidae; Eric Grissell (*pers. comm.*) attempted to use this character to separate species (but not genera of Torymidae) and found that this character does not work even at the species level.

The main diagnostic characters for genera separation used by Weld (1952a) and characters that we use in genera separation were discussed earlier (Melika & Abrahamson 2000b) and they are provided below.

Acraspis Mayr, 1881

Acraspis Mayr 1881: 2, 29. Type species: *Acraspis pezomachoides* (Osten Sacken, 1862). Designated by Rohwer & Fagan 1917. Types examined. Ashmead 1903 and Beutenmueller 1909 (synonym of *Philonix*). Weld 1922 (*Acraspis* and *Philonix* distinct genera).

Paracraspis Weld 1952b: 324. Type species: *Callirhytis guadaloupensis* Fullaway, 1911. Designated by Weld 1952b. Types examined. **New synonym.**

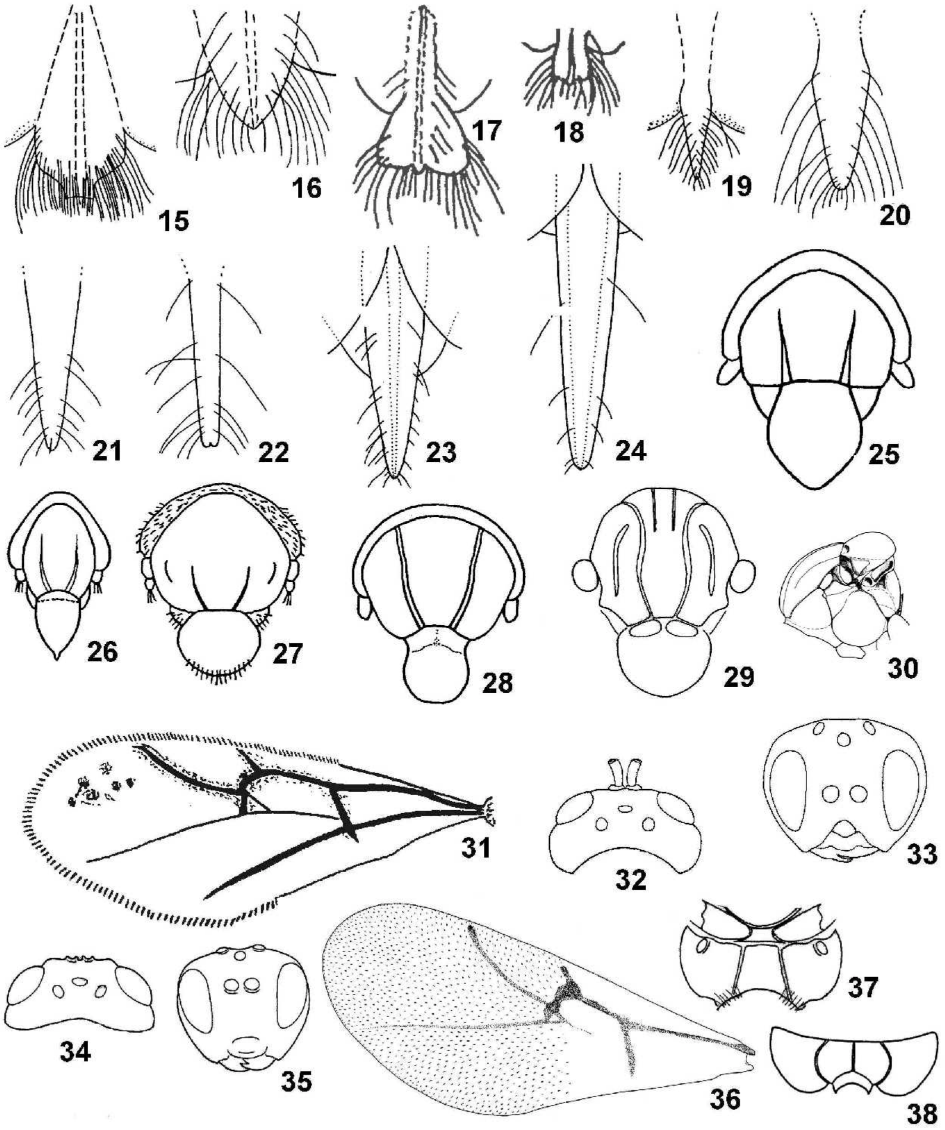
Diagnosis. Similar to *Philonix*, however, the scutellum of asexual *Acraspis* females is elongated and pointed posteriorly (Figs 25, 26), while in *Philonix* it is rounded (Fig. 27); the projecting part of the ventral spine of the hypopygium in *Acraspis* is equally broad through entire length or slightly tapering to a point at the apex, with dense subapical setae (Fig. 18); in *Philonix* the projecting part of the ventral spine is flattened, broadest at the apex, with long dense subapical setae reaching far beyond the apex of the spine to form a broad truncate tuft (Fig. 17). The asexual females of *Acraspis* also resemble *Biorhiza* but differ in having distally elongated and flattened scutellum, which overhangs the metascutellum and hides the propodeum; the latter declines more strongly than in *Biorhiza*.

In sexual *Acraspis* females, the scutum is coriaceous or microreticulate, bare or with very sparse short setae; notauli are incomplete in the anterior one-third or very indistinct. Closely resembling *Disholcaspis* but F1 of the antenna is equal or very slightly shorter than the scapus+pedicellum; the head is more broad from above; the scutum and mesopleuron are coriaceous, while in *Disholcaspis* F1 is 2.0 times as long as scapus+pedicellum; the head is more narrow from above; the scutum and mesopleuron are more densely reticulate. In *Acraspis* males, F1 is straight or only slightly incised, less than 2.0 times as long as scapus+pedicellum; the scutum is shorter; the scutellum is coriaceous, elongated, gradually and slightly depressed toward the transscutal articulation, without scutellar foveae or transversal groove, with white setae. In *Disholcaspis* males, F1 is 2.0 times as long or longer than scapus+pedicellum; the scutum is longer. We are unable to find appreciable diagnostic characters for the precise separation of *Acraspis* males from *Cynips*. It is, however, possible that *Acraspis* forms a brachypterous species-group within *Cynips* as Kinsey (1930, 1936) proposed. Additional biological experimental data on alternation of generations and/or using of molecular techniques are required to solve this problem. See also Diagnosis to *Cynips*.

Comments. The only diagnostic character given by Weld (1952b) for differentiating his newly described *Paracraspis* from *Acraspis* is that it has “less reduced wings, a more robust thorax with a normally rounded scutellum.” However, the scutellum in *Paracraspis* is longer than broad, slightly overhanging the metascutellum; not tapering posteriorly to a point as in a typical *Acraspis* but distinctly elongated, not rounded as in *Philonix*; the scutum is flattened as in *Acraspis* (Fig. 25). For instance, *A. inflata* (Kinsey) and *A. gemula* var. *suspecta* (Kinsey) have an elongated scutellum, which do not taper posteriorly to a point. Some *Acraspis* species are also densely pubescent. Thus, we consider *Paracraspis* as a **syn. nov.** of *Acraspis*. Three *Paracraspis* species must be transferred to *Acraspis*: *guadaloupensis* (Fullaway, 1911), **comb. nov.**, *insolens* Weld, 1926, **comb. rev.**, and *patelloides* Weld, 1926, **comb. rev.**

Biology. The majority of species are known from the asexual generations only and the galls produced by asexual species are very similar, known commonly as “hedgehog” galls. They are usually globular, hard and slightly elongated, detachable leaf galls, with surface reticulate or rough, with points or spines. The sexual generation induces tiny bud galls. The sexual form was described by Bassett (1881) for the first time as *Cynips gemula*. Triggerson (1914) established alternation of generations experimentally for *A. erinacei* (Beutenmueller, 1909).

Distribution. Seventeen species of *Acraspis* were listed for the United States and Canada (Burks 1979), however, two species must be transferred into *Cynips*: *arida* Kinsey, 1930, **comb. rev.** and *conica* Kinsey, 1930, **comb. rev.** Currently the number of known species is 18. Several species were also described from Mexico (Kinsey 1930, 1936), however, the validity of some species is very dubious and must be revised. Several of them are likely synonyms and several other species described in the *Acraspis* genus must be transferred to other genera.



Figures 15–38 15–24, Ventral spine of hypopygium: 15, *Cynips quercusfolii*, asexual female; 16, *Sphaeroteras ocala*; 17, *Philonix fulvicollis*; 18, *Acraspis echini*; 19, *Cynips longiventris*, sexual female; 20, *Neuroterus laeviusculus*, sexual female; 21, *N. quercusbaccarum*, asexual female; 22, *N. numismalis*, sexual female; 23, *Andricus solitarius*; 24, *A. quercusramuli*. 25–29, Thorax, dorsal view: 25, *Acraspis insolens*; 26, *A. echini*; 27, *Philonix fulvicollis*; 28, *Trigonaspis quercusforticorne*; 29, *Andricus askewi*. 30, *Andricus kollari*, asexual female, mesosoma in lateral view. 31, *Atrusca quercuscentricola*, forewing. 32–33, *Bassettia pallida*, head: 32, from above; 33, front view. 34–35, *Plagiotrochus quercusilicis*, head: 34, from above; 35, front view. 36, *B. pallida*, forewing. 37–38, propodeum: 37, *B. pallida*; 38, *P. quercusilicis*

Amphibolips Reinhard, 1865

Amphibolips Reinhard 1865: 10. Type species: *Cynips spongifica* Osten Sacken, 1862. Designated by Rohwer & Fagan 1917. Types examined.

Trissandricus Kieffer 1910: 115. Type species: *T. maculipennis* Kieffer, 1910. Original designation. Monotypic. Weld 1931 (synonym of *Amphibolips quercusspongifica*).

Diagnosis. The head and mesosoma are dull, coarsely rugose. The mesosoma is robust, highly arched, broader than the head; the scutum is broader than long; the scutellum is subquadrate or cushion-shaped, slightly broader than long, with large, deep and sometimes wrinkled scutellar foveae. The projecting part of the ventral spine of the hypopygium is narrow, needle-like, long, usually more robust and broader than in closely related *Andricus.* The forewing has distinct or less distinct smoky spot(s). Tarsal claws have strong basal lobes. The genus is very uniform in the characteristics of adults and the galls that they induce. The morphology of the asexual and sexual females is identical.

Comments. On the basis of diagnostic characters given above, 6 species from the genus *Andricus* herein are transferred to *Amphibolips*: *A. ellipsoidalis* Weld, 1926, **comb. rev.**, *A. femoratus* Ashmead, 1887, **comb. nov.**, *A. quercusostensackenii* (Bassett, 1863), **comb. nov. (=** *Andricus quercussingularis* (Bassett, 1863), **syn. nov.**), *A. ruginosus* (Bassett, 1890), **comb. nov.**, *A. vernus* Bassett, 1900, **comb. rev.** Galls of these six species structurally are also typical *Amphibolips* galls.

Méhes (1953) described *Amphibolips mernyensis* on the basis of one gall, collected from *Quercus cerris* in Hungary, however it appears to be a nomen nudum (Melika, Csóka & Pujade-Villar 2000).

Biology. Both asexual and sexual generations induce stem, bud and leaf galls, the majority of which are uniform in their structure: the larval chamber occurs in the center of the gall and supported by radiating filaments.

Distribution. North and Central America. With the species transferred herein, 40 species are known: 30 from America north of Mexico (Burks 1979) and 10 from Mexico (Beutenmueller 1911; Kinsey 1937b).

Andricus Hartig, 1840

Andricus Hartig 1840a: 185. Type species: *A. noduli* Hartig, 1840 (= *A. trilineatus* Hartig). Designated by Foerster 1869.

Aphilotrix Foerster 1869: 331, 336. Type species: *Cynips corticis* Linnaeus, 1758. Original designation. Mayr 1881 (synonym of *Andricus*).

Manderstjernia Radoskowsky 1866: 304. Type species: *M. paradoxa* Radoszkowski. Original designation. Later, the name was determined to be the elder synonym of *Cynips albopunctatus* Schlechtendal.

Oncaspis Dettmer 1925: 123. Type species: *O. filigranata* Dettmer. Original designation. Dettmer 1928 (*O. filigranata* is the sexual generation of *Andricus solitarius* (Fonsc.) and, thus synonym of *Andricus*. Weld 1930 (synonym of *Andricus*).

Euschmitzia Dettmer 1925: 122. Type species: *E. rara* Dettmer. Original designation. Later, the author thought it was the sexual generation of *Andricus nudus* Adler and asked Weld to publish it. Weld 1930 (synonym of *Andricus*).

Femuros Kinsey 1937a: 65. Type species: *F. repandae* Kinsey. Original designation. Weld 1952a (synonym of *Andricus*).

Feron Kinsey 1937a: 69. Type species: *F. verutum* Kinsey. Original designation. Weld 1952a (synonym of *Andricus*).

Druon Kinsey 1937a: 56. Type species: *D. protagion* Kinsey. Original designation. Weld 1952a (synonym of *Andricus*).

Conobius Kinsey 1938: 262. Type species: *C. strues* Kinsey. Original designation. Weld 1952a (synonym of *Andricus*).

Adleria Rohwer and Fagan 1917: 359. Type species: *Cynips kollari* Hartig, 1843. Original designation. Benson in Marsden-Jones 1953 (synonym of *Andricus*).

Dros Kinsey 1937a: 49. Type species: *D. petasum* Kinsey. Original designation. Types examined. **New synonym.**

Erythres Kinsey 1937b: 461. Type species: *E. hastata* Kinsey. Original designation. Types examined. **New synonym.**

Liodora Foerster 1869: 331, 334. Type species: *L. sulcata* Foerster. Original designation. Mayr 1881 (synonym of *Dryophanta*). Dalla Torre 1893 (treated as a separate genus). Dalla Torre & Kieffer 1910 (synonym of their "*Diplolepis* L. Geoffr."). Mayr 1903 (restored its generic status). Types of North American species examined. **New synonym.**

Parandricus Kieffer 1906: 102. Type species: *P. mairei* Kieffer. Original designation. Monotypic. Types examined. **New synonym.**

Trichoteras Ashmead 1897a: 67. Type species: *T. coquilletti* Ashmead. Original designation. Types examined. **New synonym.**

Diagnosis. Projecting portion of the ventral spine of the hypopygium is needle-like, long, with subapical setae that do not reach beyond the apex of the spine; if short then slender and thin, tapering to point at the apex, at least 2.0 times as long as broad, with short sparse subapical setae which if reaching beyond the apex of the spine then never dense and they do not form a truncate tuft (Figs 23, 24). Mesosoma is arched, notauli usually complete, sometimes absent or indistinct in the anterior 1/3-1/4; scutum is usually as long as broad or subequal, subquadrate; scutellar foveae usually distinct, separated by a median carina (Figs 29, 30).

Comments. Mayr (1881) treated *Callirhytis* as a subgenus of *Andricus*. Dalla Torre & Kieffer (1910) erroneously synonymized *Trisoleniella* Rohwer & Fagan to *Andricus*.

Adleria. Rohwer & Fagan (1917) proposed *Adleria* instead of *Cynips* sensu Authors, which they did not accept along with the type designations. The European species of the former *Cynips* sensu Authors [not *Cynips* Linnaeus!] were transferred to *Andricus* after the sexual generations were discovered and found to have the diagnostic characteristics typical of the sexual *Andricus* (Benson in Marsden-Jones 1953). Zerova, Diakontshuk & Ermolenko (1988), in their review of the gall-inducing insects of the European portion of the former Soviet Union, removed 11 species from *Andricus* and transferred them again to reestablished *Adleria*. Their decision was based solely on the analysis of the adults of the asexual generations. The diagnostic characteristics given by these authors to separate *Adleria* from *Andricus* are the same as those in Weld (1952a). Kovalev (1965) described two other *Adleria* species from south of Far East of Russia, which were synonymized later to *Andricus* (Abe 1986). Currently the genus *Adleria* with 6 species is listed as a valid genus in Burks (1979) for America north of Mexico. Five of these species must be transferred to *Andricus*: *A. dimorphus* (Beutenmueller), **comb. nov.**, *A. flavicollis* (Ashmead), **comb. nov.**, *A. nigricens* (Gillette), **comb. nov.**, *A. quercusstrobilanus* (Osten Sacken), **comb. nov.**, *A. vacciniiformis* (Beutenmueller), **comb. nov.**, and *A. weldi* (Beutenmueller), **comb. nov.**, while one species, *A. arizonica* (Cockerell) must be transferred to *Disholcaspis*: *D. arizonicus* (Cockerell), **comb. nov.** (the projecting part of the ventral spine of the hypopygium is shorter with very long setae reaching far beyond the apex of the spine, see *Disholcaspis*).

Weld (1951) synonymized *Andricus ashmeadii* Bassett to *Adleria nigricens* (Gillette). However, examination of the types showed an appreciable difference: in *A. ashmeadii* the ratio of antennal segments 1:3:4 is 20:20:11; the gena are only slightly broadened behind the eye; anterior tentorial pits are much deeper; the frons punctate; the scutum is bare with fine sculpture; scutellar foveae are larger with sculptured bottom; the transscutal articulation continuous, while in *A. nigricens* the ratio of antennal segments 1:3:4 is 15:20:13; the gena are much broader behind the eye; the frons is dull, transversely rugose; the scutum is densely pubescent, with more dull sculpture; scutellar foveae are smaller with smooth shiny bottom; the transscutal articulation is interrupted medially; the areolet of the forewing is twice shorter than in *A. ashmeadii*. We believe that these are distinct species and consequently we restore species status for *Andricus ashmeadii* Bassett, **comb. rev.**, **status nova**.

Erythres. The only character separating this genus from *Andricus* is the simple tarsal claw. Both known species, *E. hastata* Kinsey and *E. jaculi* Kinsey occur on red oaks and induce cone-like galls inside enlarged bud scales and form terminal clusters of aborted leaves and bracts that enclose a small, seed-like cell. Galls resemble those of *Dryocosmus floridensis* (Beutenmueller), *Andricus stropus* Ashmead, *A. quercusfoliatus* (Ashmead), and *A. fecundator* (Hartig). Thus, *A. hastata* (Kinsey) and *A. jaculi* (Kinsey) are **comb. nov**.

***Liodora* and *Dros*.** Dalla Torre & Kieffer (1910) treated *Liodora sulcata* Foerster as the sexual generation of *Cynips quercusfolii* (Linnaeus), however, Weld (1930, 1951, 1952a) considered *Liodora* as a distinct genus. Kinsey (1937a) stated that *Dros* "includes some species which have previously been assigned to "Andricus", "Driophanta" [sic], etc. Its further limitation must await a monographic revision of the whole group". He also mentioned that the genus may be related to *Feron* and *Druon* which were synonymized by Weld (1952a) to *Andricus*. *Dros*, according to Kinsey (1937a), is most readily distinguished from these "other genera" by a head which is narrowed behind eyes, by a 14- or 15-segmented antenna, entirely smooth scutum and mesopleuron, widely separated, pear-shaped scutellar foveae, and by distinctive vase or urn-shaped galls. The only difference between *Liodora* and *Dros* is that the head in *Dros* is narrower than the thorax while in *Liodora* it is equal to the thorax (Weld 1952a). However, this character is insufficient to distinguish *Liodora* from *Dros*. *Dros viscidum* (Weld), for example, differs from *Liodora* only by having a polished scutum, while *D. sessile* (Weld) has an alutaceous and polished scutum. The two genera were also confusing for Weld. Weld (1952a) considered *caepula* (Weld) and *discale* (Weld) as *Dros* species, but later moved them to *Andricus*; *viscida* was described by Weld (1944) in *Liodora*, but later was transferred to *Dros*. *Dros atrimentum* (Kinsey) and *D. pedicellatum* (Kinsey) originally were described in *Andricus*. Dailey & Sprenger (1973a) moved *atrimentum* (Kinsey) from *Dros* to *Andricus.* The same character states found in *Dros* and *Liodora* are encountered in many European *Andricus* species as in for instance, *inflator* Hartig, and *gallaeurnaeformis* (Fonscolombe). The latter species induces urn-shape galls as well.

Evans (1972) determined that *Liodora dumosae* Weld is the sexual generation of *Andricus pattersonae* Fullaway. Rosenthal & Koehler (1971) were incorrect when they concluded that this species was the bisexual generation of *Andricus kingi* Bassett, the latter was described by Dailey & Menke (1980). Probably Rosenthal and Koehler had the sexual generation of *A. kingi*.

Liodora and *Dros* are distinguished easily from the sexual *Cynips* by the presence of a long ventral spine of the hypopygium, with short sparse setae, which never reach beyond the apex of the spine.

Consequently, three *Liodora* and 11 *Dros* species known from North America must be transferred to *Andricus*: *apiarum* (Weld), **comb. nov.**, *clarkei* (Bassett), **comb. nov.**, *comata* (Weld), **comb. nov.**, *amphorus* (Weld), **comb. nov.**, *atrimentus* Kinsey, **comb. rev.**, *moreliensis* (Kinsey) (Mexico), **comb. nov.**, *pedicellatus* Kinsey, **comb. rev.**, *periscellus* (Kinsey) (Mexico), **comb. nov.**, *perlentus* (Kinsey) (Mexico), **comb. nov.**, *petasus* (Kinsey) (Mexico), **comb. nov.**, *picatus* (Kinsey) (Mexico), **comb. nov.**, *repicatus* (Kinsey) (Mexico), **comb. nov.**, *sessilum* (Weld), **comb. nov.**, and *viscidus* (Weld), **comb. nov.**

Parandricus. The genus is known from one species, *P. mairei* Kieffer, 1906, described from China, and is known to induce catkin galls on oaks (Kieffer 1906). The location of types is unknown. We examined one male and one female labelled as "Hankow" which are deposited at the USNM, Washington, DC and are originated from the type series. Weld (1952a) differentiated *Parandricus* from *Andricus* in that females have an "abdomen in side view longer than high, ... and hind femur stout". In many sexual *Andricus* species, which induce catkin galls, both females and males have "stout" hind femur. In males, except that the hind femur is very short and stout, metatarsus is equal 2+3+4 tarsomeres; 5th is equal 1st in length (Weld 1952a). However, several *Andricus* males, e.g., *A. quercuscalicis* (Burgsdorf), *A. burgundus* Giraud, *Callirhytis blastophaga* (Ashmead) and others, have the same proportions of hind tarsomeres and are "stout." Consequently, the proportions of hind tarsomeres and length of hind femur vary markedly in the sexual *Andricus*. Thus, the diagnostic characters given for *Parandricus* are insufficient to treat it as a separate genus and, thus *Parandricus* is a **syn. nova** of *Andricus*, and *Andricus mairei* (Kieffer) is a **comb. nov.**

Trichoteras. One of the diagnostic characters offered to separate *Trichoteras* (for the type species *T. coquilletti* Ashmead) from *Andricus* is a 12-segmented antenna, F2 is equal or slightly longer than F1. *Andricus formosalis* Weld, for example, has F2 longer than F1, has enlarged gaster as in *coquilletti*; in *A. pattoni* (Bassett) F2=F1; the shape and proportions of the head, scutum, scutellum, central area of propodeum, the forewing venation, the ventral spine of the hypopygium are the same as in *coquilletti*. The females of the sexual generation of the European *A. gallaeurnaeformis* (Fonscolombe) have F2=F1, the head is slightly broader than the mesosoma, the scutum is same as in *Trichoteras*. Three species are known as brachypterous: *coquilletti* (fully winged females known also), *frondeum* (Weld), and *tubifaciens* (Weld). Consequently, all 8 known species must be transferred to *Andricus*: *burnetti* Dailey & Sprenger (1983), **comb. nov.**, *californicum* (Beutenmueller), **comb. nov.**, *coquilletti* (Ashmead), **comb. nov.**, *frondeum* (Weld), **comb. nov.**, *perfulvum* (Weld), **comb. nov.**, *rotundula* (Weld), **comb. nov.**, *tubifaciens* (Weld), **comb. nov.**, and *vacciniifoliae* (Ashmead), **comb. nov.**

Biology. Alternation of generations is known. These species induce galls on all organs of oak trees, and the shapes and sizes of galls vary markedly. Life-cycles are known for numerous European species, however, we know little about the life-cycles of the American and Asian species.

Distribution. Holarctic.

Aphelonyx Mayr, 1881

Aphelonyx Mayr 1881: 29. Type species: *Cynips cerricola* Giraud, 1859. Type designated by Mayr (1881).

Diagnosis. Very closely resembles asexual *Andricus*, differs in antennae 2.0 times as long as head+mesosoma, notauli incomplete in the anterior 1/3, tarsal claws are simple, while in asexual

Andricus notauli usually complete, antennae are less than 2.0 times as long as head+mesosoma, tarsal claws are usually toothed.

Biology. Only the asexual generation is known.

Distribution. Four species are known: *Aphelonyx cerricola* (Giraud, 1859) from Western Palaearctic, *A. crispulae* Matsumura, 1920, *A. glanduliferae* Matsumura, 1920, and *A. acutissimae* Monzen, 1953 from Japan (Monzen 1953), however, the last three Japanese species must be revised.

Atrusca Kinsey, 1929

Cynips (*Atrusca*) Kinsey 1930: 276. Type species: *Cynips* (*Atrusca*) *dugesi* var. *simulatrix* Kinsey. Original designation. Weld (1952a) gave it genus status.

Diagnosis. The malar space lacks sulcus; the scutum is reticulate; the forewing possesses dark spots and/or dark stripes along veins, the radial cell is 2.0-2.5 times as long as broad, the 4th abscissa of Rs is strongly angulate (Fig. 31). The scutum and the pronotum laterally have dense setae; the projecting part of the ventral spine of the hypopygium is at least 3-4 times as long as broad, subapical setae always long and dense, reaching far beyond the apex of the spine. Most closely resembles *Cynips* (= *Antron* and *Besbicus*), however, differs in diagnostic characters given above. See also Diagnosis to *Cynips*.

Comments. On the basis of a short radial cell and the absence of a malar sulcus, five species from the *Sphaeroteras* genus herein are transferred into *Atrusca*: *A. carolina* (Ashmead), **comb. nov.**, *A. rydbergiana* (Cockerell), **comb. nov.**, *A. texana* (Ashmead), **comb. nov.**, *A. trimaculosa* (McCracken and Egbert), **comb. nov.**, and *A. unica* (Weld), **comb. nov.**; one *Xanthoteras* species, *A. pulchripenne* (Ashmead), **comb. nov.** Dailey and Menke (1980) indicated that *Antron clavuloides* Kinsey must be placed in *Xanthoteras*. In our opinion, it must be transferred to *Atrusca*: *A. clavuloides* (Kinsey), **comb. nov.** because the ventral spine of the hypopygium is long and the radial cell is short, the 2nd abscissa of Rs is strongly angulate.

Biology. Only asexual generations are known currently that induce rounded detachable leaf galls.

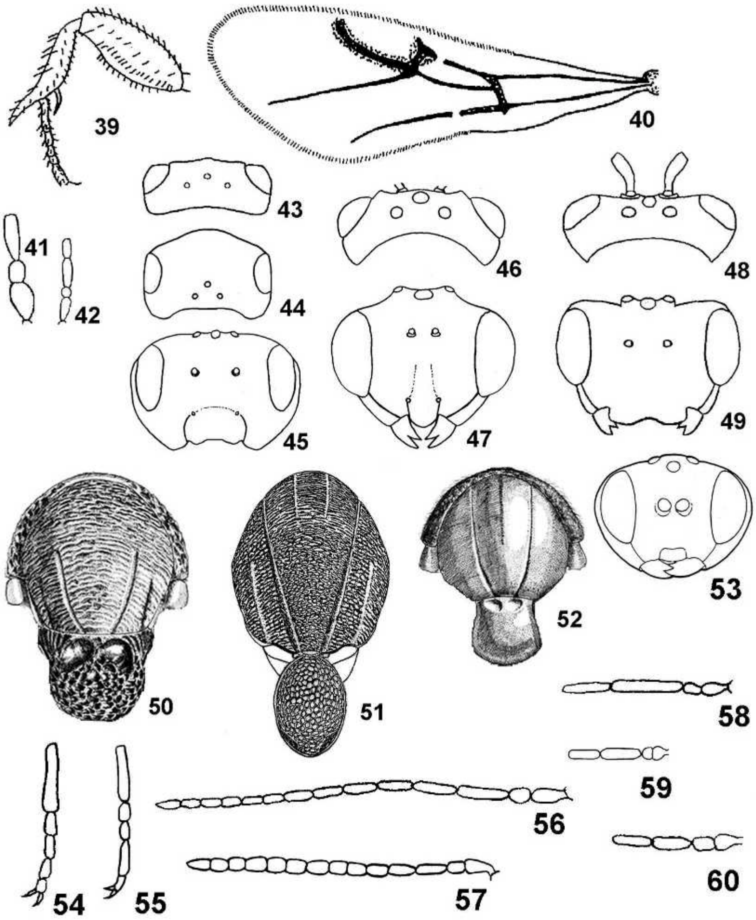
Distribution. North and Central America.

Bassettia Ashmead, 1887

Bassettia Ashmead 1887: 146. Type species: *Bassettia floridana* Ashmead, designated by Ashmead (1903). Types examined.

Diagnosis. Closely resembles *Plagiotrochus*, however, the head is 2.0-2.5 times as broad as long from above (Fig. 32), higher or equal to width in front view; the malar space lacks radiating striae (Fig. 33); the female forewing margin lacks cilia (Fig. 36); the median propodeal area is narrow, limited by nearly straight or slightly outward bent lateral propodeal carina, without or with fragmented median longitudinal carina (Fig. 37); F1 of the male antenna is nearly straight, not incised. In *Plagiotrochus*, the head is less than 2.0 times as broad as long from above (Fig. 34); as broad as high, or broader than high (transverse), but it is never higher than broad in front view; the malar space has radiating striae (Fig. 35); the female forewing margin has cilia; the central propodeal area is broad, limited by a strongly outward bent lateral propodeal carina, with complete or partially complete median longitudinal carina (Fig. 38); F1 of the male antenna is strongly incised and broadened distally. The asexual females of two *Bassettia* species (*B. ligni* Kinsey and *B. pallida* Ashmead) and one *Plagiotrochus* species (*Plagiotrochus australis* (Mayr)) share a unique character within the Cynipini: the vertex has a deep longitudinal depression from the median ocellus to the antennal sockets, with or without a carina at the bottom.

Another closely related genus is *Loxaulus* Mayr, which can be easily distinguished from *Bassettia* by the structure of the propodeum similar to *Plagiotrochus* and the scutum is very finely transversely sculptured (Melika & Abrahamson 2000a).



Figures 39–60 39–40, *Belonocnema quercusvirens*: 39, fore leg, 40, forewing. 41–42, antenna, asexual female: 41, *Biorhiza pallida*; 42, *Trigonaspis quercusforticorne*. 43, *Cynips quercusfolii*, asexual female, head from above. 44–45, *B. pallida*, asexual female, head: 44, from above; 45, front view, asexual female. 46–49, *Trigonaspis megaptera*, sexual generation, head: 46, female, from above; 47, female, front view; 48, male, from above; 49, male, front view. 50–52, thorax, dorsal view: 50, *Callirhytis glandium*; 51, *Bassettia pallida*, 52, *Plagiotrochus quercusilicis*. 53, *C. glandium*, head, front view. 54–55, Hind tarsus: 54, *C. quercusfolii*, asexual female; 55, *B. pallida*, asexual female. 56–57, Antenna: 56, *C. quercusfolii*; 57, *B. pallida*. 58–59, first four segments of antenna: 58, *Disholcaspis quercusmamma*, female 59, *D. quercusmamma*, male; 60, *Acraspis gemula*

Bassettia also resembles some *Callirhytis* species, however, the head is greater or equal to its width; the mesosoma is compressed dorso-laterally, usually 1.3-1.5 times as long as high in lateral view; the scutum 1.5-2.0 times as long as broad (Figs 32-33), while in *Callirhytis* the head is transverse, broader than high (Fig. 53); the mesosoma is arched, if slightly compressed dorso-laterally, then less than 1.2-1.3 times as long as high in lateral view; the scutum equal or only slightly longer than broad.

Comments. Four species from *Bassettia* must be transferred to *Callirhytis*: *C. aquaticae* (Ashmead), **comb. nov.**, *C. ceropteroides* (Bassett), **comb. rev.**, *herberti* (Weld), **comb. nov.**, and *C. quercuscatesbaei* (Ashmead), **comb. nov.**

Biology. Alternate asexual and sexual generations are known. Rosenthal & Koehler (1971) and Evans (1972) described the sexual generation of *B. ligni* Kinsey. The present authors also found sexual *Bassettia* in Florida. The asexual generation induces stem galls with cells hidden under the bark of twigs. The sexual generation induces small oval swellings on leaves, which protrude both sides.

Distribution. Currently five *Bassettia* species are known, all from North America north of Mexico.

Belonocnema Mayr, 1881

Belonocnema Mayr 1881: 16. Type species: *B. Treatae* Mayr. Original designation. Types examined. Ashmead 1885 (synonym of *Dryorhizoxenus*).

Dryorhizoxenus Ashmead 1881: xxv. Type species: *D. floridanus* Ashmead. Original designation. Monotypic. Types examined. Ashmead 1886 (synonym of *Belonocnema*).

Diagnosis. Readily distinguished from all other Cynipini genera by the apex of the foretibia extending far beyond the base of the foretarsomere I (Fig. 39); 4th abscissa of Rs is strongly angulate, the forewing possess a short radial cell and narrow dark stripes prolong veins (Fig. 40).

Comments. It appears that *B. kinseyi* Weld, known to induce detachable pea-like leaf galls on *Q. virginiana* and distributed in Texas only, is the alternate generation of *B. treatae*, known to induce root galls on *Q. virginiana* and distributed from Florida and Georgia to Texas. Thus, *B. kinseyi* is a synonym of *B. treatae* (Lund, Ott & Lyon 1998). A congeneric species, *B. quercusvirens* (Osten Sacken) is known from Florida and Georgia only. Both species, *B. quercusvirens* and *B. treatae* (asexual generations) induce pea-like leaf galls on *Q. virginiana*, which are indistinguishable. However, in *B. quercusvirens* females, the spur on the foretibia is as long as the metatarsus, 2.0 times as long as the furcula; the midtibia possess a distinct spur, while in *B. treatae* the spur on the foretibia is 0.25 times as long as the metatarsus and is not longer than the furcula; the midtibia lacks a spur. So, it is questionable, if *B. quercusvirens* and *B. treatae* are distinct species or only different geographical races of the same species.

Biology. Recently alternation of generations for *B. treatae* Mayr was established experimentally (Lund, Ott & Lyon 1998).

Distribution. USA only (Florida, Georgia and Texas). Only two species are known.

Biorhiza Westwood, 1840

Biorhiza Westwood 1840: 56. Type species: *Cynips aptera* Fabricius, 1793. Designated by Westwood (1840).

Apophyllus Hartig 1840a: 185, 193. Type species: *Cynips aptera* Fabricius. Designated by Hartig (1840a). Mayr 1881 (synonym of *Biorhiza*). Monotypic.

Teras Hartig 1840a: 185, 193. Type species: *Cynips quercus terminalis* Fabricius, 1798. Designated by Hartig (1840a). Monotypic. Mayr 1881 (synonym of *Biorhiza*).

Heterobius Guerin-Meneville 1865: 138. Dalla Torre (1893), Dalla Torre & Kieffer (1910), Rohwer & Fagan (1917) (synonym of *Biorhiza*).

Dryoteras Foerster 1869: 331, 334. Type species: *Cynips quercus terminalis* Fabricius, 1798. Designated by Foerster (1869). Mayr 1881 (synonym of *Biorhiza*).

Sphaeroteras Ashmead 1897a: 67. Type species: *Biorhiza mellea* Ashmead, 1887. Designated by Ashmead (1897a). Mayr (1902), Beutenmueller (1909), Dalla Torre & Kieffer (1910) treated *Sphaeroteras* as a synonym of *Biorhiza*. Weld (1951) reestablished the validity of this genus. Types examined. **New synonym.**

Beutenmueller (1909) erroneously treated *Xanthoteras* and *Phylloteras* also as synonyms of *Biorhiza*, while Dalla Torre (1893) and later Dalla Torre & Kieffer (1910) erroneously treated also *Philonix* Fitch as a synonym of *Biorhiza*.

Diagnosis. The asexual generation of *Biorhiza* most closely resembles *Trigonaspis*. Differs in having a more dorso-ventrally flattened mesosoma, the frons has longitudinal carina or elevation which reach between antennal sockets; F1 is only 1.2-1.5 times as long as F2 (Fig. 41); the scutellum does not or slightly overhangs the metascutellum; the dorsal median part of the pronotum is longer and more pronounced; the propodeum is nearly in the same plane as the rest of the mesosoma or only slightly declined; the projecting part of the ventral spine of the hypopygium is 1.0-1.5 times as long as broad, while in *Trigonaspis* the mesosoma is strongly arched anteriorly; the frons lacks elevation; F1 is 1.6-2.0 times as long as F2 (Fig. 42); the scutellum strongly overhangs the metascutellum; the pronotum is shorter in dorsal median line, the propodeum declines strongly, the projecting part of the ventral spine of the hypopygium is 2.0-2.5 times as long as broad.

The sexual generation of *Biorhiza* differs from *Trigonaspis* in that the head is straight between eyes from above, not lunate, ocelli smaller, the malar space without sulcus (Figs 43–45); scutellar foveae is absent, only a transverse groove is present anteriorly, while in *Trigonaspis* the head is lunate between eyes from above; ocelli larger; the malar space with deep sulcus (Figs 46–49); an indistinct ridge separates scutellar foveae, the bottom of which is smooth and shiny.

Some sexual *Andricus* females are very similar to *Biorhiza* but differ in that the hind tarsomer II is equal or longer than tarsomer V; the scutellum is smooth or delicately reticulate; antennae are filiform, antenna nearly equally broad through entire length, while in *Biorhiza* the hind tarsomere II is nearly 2.0 times as short as tarsomere V; the scutellum is dull rugose; antennae shorter, subsequent flagellomeres broadento the apex.

Comments. *Sphaeroteras*. Ashmead (1897a) distinguished his newly described *Sphaeroteras* genus from "the true *Biorhiza* in having no carina on the frons between the antennae, in having only 13-jointed antennae, by the scutellum being rounded, and finally by the hind tarsi being much shorter than the tibiae." In the asexual generation of *Biorhiza pallida* Olivier, the first character varies extraordinarily from a distinct strong carina to a delicate elevation only. *Biorhiza nawai* (Ashmead, 1904) (= *B. weldi* Yasumatsu & Matsuda, 1955, synonym in Pujade-Villar, Ros-Farré & Melika 2002, *in press*) described from Japan also has a weak elevation only. *Biorhiza pallida* and *B. nawai* have 14-segmented antenna. However, even the type specimen of *S. melleum* has an indistinct suture that separates F11 from F12; antenna of one of the syntypes of Ashmead's *melleum* has a distinct suture that separates F12. *Sphaeroteras caepuliforme* (Beutenmueller) has 14-segmented antenna. In *Biorhiza*, the shape of the scutellum varies from rounded to slightly elongated posteriorly; in some specimens the scutellum is more rounded than in the type specimen of *melleum*. In the majority of examined *S. caepuliforme* specimens, scutellum is slightly elongated posteriorly. The hind tarsus in the asexual *B. pallida* females is shorter than tibia; in the sexual females, which may be also apterous, the length of hind tarsus is nearly equal to the tibia. Weld (1951, 1952a) and later Burks (1979) placed 8 species into the genus *Sphaeroteras*. Only two of them belong to *Biorhiza*: *B. mellea* Ashmead, **comb. rev.** and *B. caepuliformis* Beutenmueller, **comb. rev.**, all other species must be transferred into *Atrusca*, based on the absence of the malar sulcus, short radial cell and strongly angulate Rs (see *Atrusca* above).

Sphaeroteras ocala **(Weld)** is known from Florida only and from the bisexual generation known to induce root galls on white oaks. It closely resembles asexual *Atrusca* because the forewing possesses dark stripes along veins, the radial cell is only 2.0-2.5 times as long as broad, the 2nd abscissa of Rs is strongly angulate. However, the ventral spine of the hypopygium is very short, less than 2.5 times as long as broad, which resembles the sexual *Cynips*. Thus, the status of this species is currently uncertain.

Also two species from ***Xanthoteras*** must be transferred to *Biorhiza*: *eburnea* (Bassett), **comb. nov.** and *emoryi* (Ashmead), **comb. nov.** (see also in *Trigonaspis* below).

Biology. Alternation of asexual and sexual generations is known.

Distribution. Holarctic. Six species are currently known: 4 from North America north of Mexico (herein transferred *Sphaeroteras* and *Xanthoteras* species), one species from Western Palaearctic and one species from Japan and Far East of Russia.

Callirhytis Foerster, 1869

Callirhytis Foerster 1869: 331, 335. Type species: *C. hartigi* Foerster. Original designation. Monotypic.

Eusymphagus Dettmer 1930: 54, 55, 56, 57. Type species: *E. bellus* Dettmer. Original designation. Dettmer 1933 (synonym of *Callirhytis*). Weld 1952a (synonym of *Andricus*, because tarsal claws with basal lobe). Nieves Aldrey 1992 (revision of the European species).

Diagnosis. A transversely rugose scutum characterizes only three Cynipini genera, *Bassettia*, *Callirhytis*, and *Plagiotrochus* (Figs 50–52). The diagnostic characters that separate *Callirhytis* from *Bassettia* and *Plagiotrochus* are discussed above (see Diagnosis to *Bassettia*). Additionally *Callirhytis* differs from *Plagiotrochus* in having a transverse head (front view), the malar space with a sulcus (Fig. 53); and forewing margins lack cilia. In *Plagiotrochus*, the head in front view is higher than broad, the malar space with radiating striae but without distinct malar sulcus (Fig. 35), and forewing margins are ciliate. The central propodeal area in *Callirhytis* is usually narrower than in *Plagiotrochus*, the latter in both generations has a very broad central propodeal area with strongly bent lateral longitudinal carinae, the area is usually smooth and delicately striate, except *P. marianii*, in which the central median area has strong parallel striae, but the area is large, broad.

Comments. Mayr (1881), Ashmead (1885), Cameron (1893), Dalla Torre (1893), Kieffer (1897-1901) and many others treated *Callirhytis* as a subgenus of *Andricus*, which differed in possessing simple tarsal claws, while the subgenus *Andricus* (*Andricus*) had tarsal claws with basal lobe. Mayr (1902) restored the generic status of *Callirhytis* and Dalla Torre & Kieffer (1910) followed this convention. The main diagnostic character for the reestablished *Callirhytis* genus was the simple tarsal claw. Weld (1930) wrote "in the original description of the genotype, *Callirhytis hartigi* Foerster, it is not stated whether the tarsal claws are toothed." It is puzzling why no attention was given to the transversely rugose scutum; a diagnostic character of *Callirhytis* described by Foerster as the main diagnostic feature of the genus. As a consequence of misunderstanding the character's importance, the North American *Callirhytis* genus, in our opinion, currently includes more *Andricus* than *Callirhytis* species. Presence or absence of the basal lobes on tarsal claws is a specific nor a generic character. Nieves Aldrey (1992) in his revision of the European *Callirhytis* genus showed that different species vary in the presence or absence of toothed tarsal claws; for instance, both generations of *C. glandium* (Giraud) and the asexual *C. bella* (Dettmer) have tarsal claws with basal lobes, while other species have simple tarsal claws.

Of the 115 species placed into *Callirhytis* in North America north of Mexico (Burks 1979), only 15 species have the scutum transversely sculptured as in the typical Western Palaearctic *Callirhytis* species: *cedrosensis* Dailey & Sprenger, *corrugis* (Bassett) (= *defecta* Kinsey), *eldoradensis* (Beutenmueller), *electrea* Weld, *flora* Weld (= *C. milleri*, the asexual generation (Dailey, Perry and Sprenger 1974), *fructicola* Ashmead, *fructuosa* Weld, *intersita* Weld, *lapillula* Weld, *medularis* Weld, *morrisoni* (Ashmead), *perrugosa* Weld, *petrina* Weld, *petrosa* Weld, *quercusmedullae* (Ashmead).

Two *Callirhytis* species, *quercuspomiformis* (Bassett) and *quercusrugosa* (Ashmead), herein are transferred to the *Amphibolips* genus (see *Amphibolips* above); all other species in our opinion belong to the genus *Andricus*.

Seven species of *Andricus* known from North America north of Mexico have the scutum transversely sculptured and, thus must be transferred into *Callirhytis* genus: *albobalani* (Weld), **comb. nov.**, *chrysobalani* (Weld), **comb. nov.**, *coortus* (Weld), **comb. nov.**, *coronus* (Beutenmueller), **comb. nov.**, *montezuma* (Beutenmueller), **comb. nov.**, *rhizoxenus* Ashmead, **comd. rev.**, and *wheeleri* (Beutenmueller), **comb. nov.**

Two species of *Bassettia* are transferred to *Callirhytis*: *ceropteroides* Bassett and *herberti* (Weld) (see *Bassettia* above).

Biology. Alternate asexual and sexual generations are known. The asexual generations are known to induce galls on/in acorns, while the sexual generations develop in stem swelling-like galls in young twigs or in cells hidden under the bark in twigs.

Distribution. Holarctic.

Chilaspis Mayr, 1881

Chilaspis Mayr 1881: 6, 32. Type species: *Andricus nitida* Giraud, 1882. Designated by Mayr (1881). Pujade-Villar, Ros-Farré & Melika (2002, *in press*) (revision of the genus).

Diagnosis. The genera *Cynips* and *Biorhiza* resemble *Chilaspis* in having a smooth mesoscutum and mesopleuron, but they possess malar sulcus, and the malar space lacks striae at the base of the clypeus. *Chilaspis* also resembles *Plagiotrochus*, however, it differs in possessing a smooth scutum and mesopleuron. *Chilaspis* is very closely related to *Dryocosmus*. In *Chilaspis*, striae on the frons are indistinct or weak, radiating from the clypeus in the malar space and in the lower face only; the vertex and occiput are smooth or very weakly coriaceous; the scutellum usually is uniformly smooth or weakly sculptured in the central part and occasionally with some wrinkles that prolong the marginal carina; scutellar foveae are separated by a distinct carina; the pronotum is smooth in females, sometimes with indistinct striae in males, while in *Dryocosmus* striae radiate from the clypeus to one half of the eye height, some reaching the antennal foramina; the vertex and occiput are sculptured, sometimes strongly coriaceous or rugose; the scutellum is uniformly wrinkled; scutellar foveae are separated or not by a weak carina; the pronotum, especially in females, has long and distinct striae in the posterior lateral portion.

Closely related also to the genus *Cynips*, *Clilaspis* differs in the head, the scutum and scutellum are smooth and shiny, without reticulation, while in *Cynips* the scutellum and/or the head are reticulate or coriaceous.

Biology. Alternate asexual and sexual generations are known. The asexual generation emerges from rounded detachable leaf galls, while the bisexual generation develops in catkin galls.

Distribution. Three species are known from the Western Palaearctic only (Pujade-Villar, Ros-Farré & Melika 2002, *in press*). Known from Europe, North Africa, Israel, and Iran.

Cynips Linnaeus, 1758

Cynips Linnaeus 1758: 553. Type species: *Cynips quercus-folii* Linnaeus, 1758. Designated by Westwood (1840).

Dryophanta Foerster 1869: 331, 335. Type species: *Cynips quercus-folii* L. Designated by Foerster (1869). Monotypic. Rohwer & Fagan 1917 (synonym of *Cynips*).

Antron Kinsey 1930: 180. Type species: *Cynips* (*Antron*) *echinus* var. *schulthessae* form *schulthessae* Kinsey. Original designation. Weld (1952a) gave the genus status. Kinsey (1930) proposed as a subgenus of *Cynips*. Types examined. **New synonym**.

Besbicus Kinsey 1930: 222. Type species: *Cynips* (*Besbicus*) *multipunctata* var. *conspicua* Kinsey. Original designation. Weld (1952a) gave the genus status. Kinsey (1930) proposed as a subgenus of *Cynips*. Types examined. **New synonym**.

Diagnosis. Asexual females are fully winged; the ventral spine of the hypopygium is short, broadened at the apex, with dense, long subapical setae that reach far beyond the apex of the spine and form a dense truncate tuft (Fig. 15). Sexual females resemble those of *Biorhiza*, but differs in that the hind tarsomere II is equal or only slightly shorter than tarsomere V (Fig. 54); the head is narrower from above (Fig. 43), antennae filiform, subsequent flagellomeres of the same width (Fig. 56); the transscutal articulation is bent; the scutellum is longer, while in *Biorhiza* females the hind tarsomere II is shorter than V (Fig. 55); the head is broader from above (Fig. 44), antennae are shorter, subsequent flagellomeres broadento the apex (Fig. 57); the transscutal articulation is straight; the scutellum is shorter. Males differ from *Biorhiza* in that they have F1 straight, not incised, while in *Biorhiza* F1 is strongly incised and enlarged distally. Males are also very similar to *Acraspis* and we are unable to find characters to distinguish them. See also Diagnosis to *Acraspis* and *Biorhiza*.

Comments. Mayr (1881) synonymized *Liodora* Foerster to *Dryophanta*. Dalla Torre (1893) treated it as a separate genus with one species, *L. sulcata* Foerster. Dalla Torre & Kieffer (1910) synonymized it with their "*Diplolepis* L. Geoffr." After revising Foerster's types of *L. sulcata*, Weld (1930) concluded that they are "not congeneric with the sexual generation of *Diplolepis folii* (L.)" and he restored it to generic status. See *Liodora* also above in *Andricus*.

Kinsey (1936) in his revision of the genus *Cynips* divided it into six subgenera: *Cynips* (European species), *Antron*, *Besbicus*, *Atrusca*, *Philonix*, and *Acraspis*. Under the "*mellea*" species-complex in the *Acraspis* subgenus, he included also all known *Sphaeroteras* species. It is possible that *Acraspis* and *Philonix* might be synonyms of *Cynips*, however, more information on the alternation of generations is necessary. See also Diagnosis to *Acraspis* and *Atrusca*.

***Antron* and *Besbicus*.** Weld's (1952a) key is incorrect in separating *Besbicus* from *Cynips* on the basis of structural differences in the ventral spine of the hypopygium (couplet 59). The structure of the ventral spine of both genera is identical (Fig. 19). The only diagnostic character given by Weld (1952a) for separation asexual generations of *Antron* and *Cynips* is the presence of smoky spots on forewing in *Antron* and their absence in *Cynips*. Kinsey (1936) described that the darker spotting on the forewings of *Cynips* (in his understanding of the genus) can vary strongly from no spots to numerous fused spots. Dark stripes along veins are typical for the European *Cynips* species. The peculiarities of Rs configuration, carinae on propodeum, width of genae, notauli completeness, and pubescence of the scutum, given by Weld (1952a) are specific rather than generic -level characters.

Alternation of generations occurs in *Antron* and *Besbicus*, however, the only *Besbicus* species known to have an alternate sexual generation is *B. mirabilis* (Kinsey) (Evans 1967). The adults of sexual *B. mirabilis* are entirely congeneric with the sexual generations of *Cynips*. Two species of *Antron* were listed among those with alternating asexual and sexual generations, *A. douglasii* (Ashmead) and *A. quercusechinus* (Osten Sacken). *Andricus ribes* Kinsey was listed as the sexual generation of *A. quercusechinus* (Weld 1951; Burks 1979). Weld (1952a) described for this species that "on circumstantial evidence this is considered the alternating generation of *echinus*". There is no evidence for this. Kinsey (1922a) did not mention that *A. ribes* might be the sexual generation of any other cynipid wasp in the original description. Kinsey (1930) gave no acceptable evidence for the synonymization of *A. ribes* to *A. quercusechinus*. However, *A. ribes* is entirely congeneric with sexual *Cynips* and, of course, is the sexual generation of one of the Californian *Cynips* (*Antron*) species. However, it is too early to state that it is the sexual generation of *A. quercusechinus*; this must be proved.

Weld (1951) and Burks (1979) listed *Dryophanta lobata* as the sexual generation of *Antron douglasii* (Ashmead), although, it was not mentioned in the original description (McCracken & Egbert 1922). Kinsey (1930) synonymized *A. lobata* to *A. douglasii* on circumstantial grounds. An examination of paratypes of females and a male [Paratype No. 53990, USNM] as well as the original description (McCracken & Egbert 1922) indicates that it is not a bisexual *Cynips*. There are no other bisexual cynipids known that have such broad, short ventral spines of the hypopygium. Consequently, the status of *D. lobata* is uncertain.

The following species must be transferred from *Besbicus* to *Cynips*: *conspicuus* Kinsey, **comb. rev.**, *heldae* Fullaway, **comb. rev.**, *indictus* Kinsey, **comb. rev.**, *leachii* Kinsey, **comb. rev.**, *maculosus* Weld, **comb. rev.**, *mirabilis* Kinsey, **comb. rev.**, *multipunctatus* (Beutenmueller), **comb. nov.**, *tritior* Kinsey, **comb. rev.**, as well as the following *Antron* species: *acraspiformis* (Weld), **comb. nov.**, *douglasii* (Ashmead), **comb. nov.**, *dumosae* Kinsey, **comb. rev.**, *magdalenae* (Weld), **comb. nov.**, *plumbeum* Weld, **comb. rev.**, *quercusechinus* Osten Sacken, **comb. rev.**, *quercusnubila* Bassett, **comb. rev.**, *russus* Kinsey, **comb. rev.** These species are known from North America north of Mexico. We have not analyzed *Besbicus* and *Antron* species mainly described from Mexico by Kinsey. They require a detailed revision.

We also transfer one species from the genus *Xanthoteras* to *Cynips*: *C. pulchellum* (Beutenmueller), **comb. nov.**

Biology. Alternation of asexual and sexual generations is known. The bisexual generation induces detachable leaf galls, while the asexual generation induces tiny small bud galls.

Distribution. Holarctic. One species, *Cynips staminobia* Kovalev, 1965, was described on the basis of males reared from catkin galls on *Quercus mongolica* from Far East of Russia (Kovalev 1965).

Disholcaspis Dalla Torre & Kieffer, 1910

Disholcaspis Dalla Torre & Kieffer 1910: 371. Type species: *Callaspidia quercus-globulus* Fitch, 1858. Designated by Ashmead (1903). Types examined.

Holcaspis Mayr 1881: 35. Name preoccupied by Chaudoir in Coleoptera.

Diagnosis. Asexual females. Robust specimens, the ventral spine of the hypopygium is short, the projecting part is a maximum of 2.0-3.5 times as long as broad or much shorter, subapical setae are long, dense, reaching far beyond the apex, but never forming a dense truncate tuft; notauli incomplete; usually scutellum has a transverse impression anteriorly, scutellar foveae absent, if present then indistinct. See also Diagnosis to asexual *Andricus*. Sexual generation. The mesosoma is bare, with setae on the pronotum laterally only; the head is narrower than the mesosoma; the scutum anteriorly is microreticulate or coriaceous; the scutellum is elongated, gradually and very slightly depressed toward the transscutal articulation, without foveae or transversal groove; in females, F1 is 1.6-1.8 times as long as scapus+pedicellum, in males, F1 is 2.0 times as long as scapus+pedicellum (Figs 58-60). See also Diagnosis to sexual *Acraspis* and *Cynips*.

Comments. There are seven known species of *Disholcaspis* from the western United States: *D. chrysolepidis* (Beutenmueller), *conalis* Weld, *corallina* (Bassett), *plumbella* Kinsey, *sulcata* (Ashmead), *truckeensis* (Ashmead), and *washingtonensis* (Gillette), which differs from other species of this genus by the ventral spine of the hypopygium that is broad throughout its entire length, not tapering to a point at the apex; length of the projecting part of the spine is less or equal to its width; Rs is slightly curved in the apical one third and slightly expanded, median propodeal carinae bent, lyre-shaped, while in all other *Disholcaspis* species, the ventral spine is longer, needle-like, the projecting part at least 2.0-3.5 times as long as broad, Rs is straight, the radial cell is slightly longer; propodeal carinae are fragmented or lacking entirely.

Examination of types of some North American asexual *Andricus* species showed that there are three species: *lasius* (Ashmead), *reniformis* McCracken & Egbert, and *spectabilis* Kinsey; and also one *Adleria* species known from Mexico, *lapiei* (Kieffer) (= *Holcaspis weldi* Beutenmueller, 1911, not *Cynips weldi* Beutenmueller, 1918), which differs from "typical" *Disholcaspis*, *Andricus*, and *Adleria*. They agree in their morphology with the mentioned seven *Disholcaspis* species and form the same species-group.

This group of 11 species has caused problems in their placement. Weld (1952a) "provisionally placed in *Disholcaspis*" the seven *Disholcaspis* species mentioned above and wrote that "these species might well form a new genus if the life cycle of any one of them were known." Three *Andricus* species: *lasius*, *reniformis*, and *spectabilis* were "placed" in *Andricus*. Burnett (1977) placed 5 species (*conalis*, *corallina*, *plumbella*, *sulcata*, *washingtonensis*) in his new genus *Weldia* and described a new species, *californicus* (the name is not valid, since it was not published and the name *Weldia* was preoccupied by Yoshimoto (1962) for Eucoilidae). On the basis of the presence of complete notauli, Dailey & Menke (1980) moved *truckeensis* to *Andricus*. Examination of a series of this species at the USNM indicated that notauli vary, notauli can reach the pronotum but also can disappear in anterior one third of scutum. *Andricus truckeensis* is similar to *lasius*, *reniformis*, and *spectabilis* in possessing a very short ventral spine of the hypopygium and all the species occur on oaks of the subgenus *Protobalanus*. McCracken & Egbert (1922) suggested that *reniformis* might be a variety of *truckeensis*. Dailey & Menke (1980) stated "additional studies may indicate that these four species should be placed in a new genus." Burnett (1977) considered *chrysolepidis* and *truckeensis* as a distinct monophyletic group that forms a separate genus differing from the above mentioned seven *Disholcaspis* species. *Adleria lapiei* (Kieffer, 1911) originally was described in *Disholcaspis* (Kieffer 1911), but later Weld (1952a) "placed" it in *Adleria*. Kinsey (1937a) suggested that *D. lapiei* Kieffer was "probably a synonym of *D. weldi* (Beutenmueller)". A Weld note in the general collection of USNM included in a box containing *lapiei* Kieffer (= *Holcaspis weldi* Beut.), offers "Not a true *Disholcaspis*. Test Weld 1936" and later Weld (1952a) treated them as synonyms. Burnett (1977) provisionally treated *lapiei* as *Adleria*.

Consequently, the following species are transferred to *Disholcaspis*: *lasius* (Ashmead), **comb. nov.**, *reniformis* McCracken & Egbert, **comb. nov.**, *spectabilis* Kinsey; **comb. nov.**, and *lapiei* (Kieffer), **comb. nov.**

One species from the current North American *Adleria* is transferred herein to *Disholcaspis*: *arizonicus* (Cockerell), **comb. nov.** (see in *Andricus*).

Biology. Alternation of asexual and sexual generations is known. The sexual generation usually produces detachable, woody bullet-like stem and subterranean or root galls; the asexual generation induces small thin-walled bud galls of the same shape and structure as those of *Cynips*, *Acraspis* and many *Andricus*. For a long time only the asexual generation was known. Evans (1972) experimentally discovered the sexual generation of *D. eldoradensis* (Beutenmueller). We reared females and males from tiny pale grayish-white bud galls on *Quercus bicolor* Willd. collected in Pennsylvania (Bucknell Natural Area, Northumberland County, spring, 1996). Trees were heavily infested with galls of *D. quercusmamma* (Walsh) while other *Disholcaspis* species were not found in this area. The morphologies of these reared females and males agree with those of sexual *D. eldoradensis*. We believe these individuals represent the sexual generation of *D. quercusmamma*.

Distribution. North and Central America.

***Dryocosmus* Giraud, 1859**

Dryocosmus Giraud 1859: 353. Type species: *D. cerriphillus* Giraud. Original designation. Monotypic. Pujade 1985 (revision of the Western Palaearctic species).

Entropa Foerster 1869: 330, 334. Type species: *E. lissonota* Foerster. Original designation. Monotypic. Mayr 1881 (synonym of *Dryocosmus*).

Diagnosis. Most closely resembles *Chilaspis*. Diagnostic characters for separation of *Dryocosmus* from *Chilaspis* are given in Diagnosis to *Chilaspis* above.

Comments. This genus needs a revision, especially the Nearctic and Eastern Palaearctic species; more precise and strict diagnostic generic limits must be established (Pujade-Villar, Ros-Farré & Melika 2002, *in press*).

Biology. The North American *Dryocosmus* species are morphologically uniform with the two known European species and with species described from Asia: *D. japonica* (Ashmead), *D. hakonensis* (Ashmead), *D. nawaii* (Ashmead), *D. mitsukurii* (Ashmead), and *D. kuriphilus* (Yasumatsu). The latter species threatened the chestnut industry of Japan and Korea and was discovered in Georgia, USA in 1974 (Payne 1978; Payne *et al.* 1975). This is the only species of

Cynipini known to associate with *Castanea*. Another species, known from Oregon and California, *Dryocosmus castanopsidis* (Beutenmueller) induces galls on catkins of *Castanopsis chrysophylla* and *C. sempervirens*. Several Eastern Palaearctic species are known only from either asexual or sexual generation and probably some could be paired in alternate generations (Pujade-Villar 1985). Life cycles of these species must be identified in order to know the exact number of species and their limits.

Distribution. Holarctic distribution with 16 known Nearctic (Burks 1979), 2 Western Palaearctic and 6 Eastern Palaearctic species.

Eumayria Ashmead, 1887

Eumayria Ashmead 1887: 147. Type species: *E. floridana* Ashmead, 1887. Designated by Ashmead (1903).

Trisolenia Ashmead 1887: 142. Type species: *T. saltata* Ashmead, 1887. Designated by Ashmead (1903). Rohwer & Fagan 1917 (name preoccupied by Ehrenberg in 1861 for Protozoa). Dalla Torre & Kieffer 1910 (synonym of *Andricus*).

Trisoleniella Rohwer & Fagan 1917: 377. New name for *Trisolenia*. Melika & Abrahamson 1997b (synonym of *Eumayria*).

Diagnosis. Head is 1.5-1.7 times broader than long from above in the sexual generation and is 2.5-2.8 times as broad as long in asexual females; malar sulcus absent (Figs 61-64); thorax is flattened dorso-ventrally, not arching in the anterior part; scutum is slightly longer than broad (Fig. 65), finely coriaceous or macroscopically punctate, never transversely sculptured; base of tergum II has pale felt-like ring of dense short setae, interrupted dorsally (in males dense short pale setae present only ventrally and ventro-laterally). See also the Diagnosis to *Eumayriella* Melika & Abrahamson below.

Comments. In Burks (1979), 4 species of *Eumayria* were listed, from which *Eumayria eldoradensis* was transferred into *Callirhytis* (Dailey *et al*. 1974) and *E. longipennis* to *Andricus*, as well as four species of *Trisoleniella* were transferred to *Eumayria* (Melika & Abrahamson 1997b).

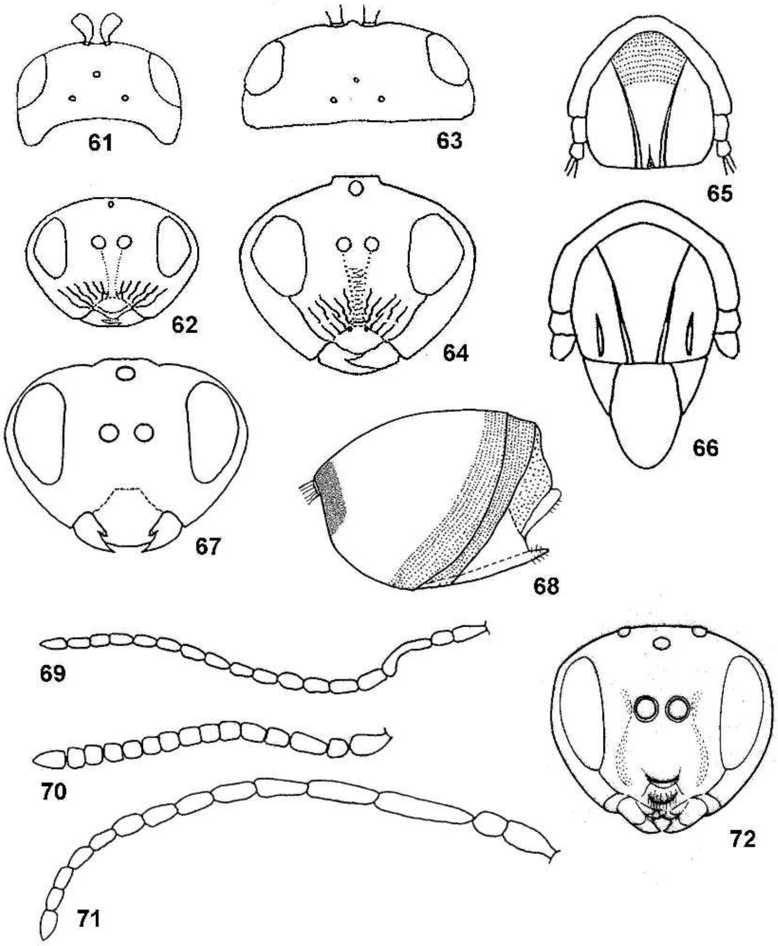
Biology. Five species are known. *Eumayria floridana* Ashmead is known only from a bisexual generation and induces stem swelling-like galls, while the four other species have only asexual generations.

Distribution. Eastern and midwestern United States.

Eumayriella Melika & Abrahamson, 1997

Eumayriella Melika & Abrahamson 1997b: 672. Type species: *Eumayria invisa* Weld, 1952. Original designation.

Diagnosis. Closely resembles the brachypterous species of the former genus *Trichoteras* (*Andricus*, part, after authors, see *Andricus*). In *Eumayriella*, thorax is flattened dorso-ventrally; pronotum is dorsally much longer, placed in the same plane as scutum; scutum and scutellum are pubescent, each longer than broad, scutoscutellar suture distinct, scutellum without foveae; head is broader than thorax from above, 2.3-3.0 times broader than high; antenna filiform, F2 shorter than F1; while in *Trichoteras* thorax is arched in anterior one-third; pronotum is much shorter dorsally and placed in a different plane than scutum; each scutum and scutellum is as long as broad; head is narrower or equal to thorax; antennae are short, F2 nearly equal F1. *Eumayriella* also closely resembles *Eumayria*, but the head is more transverse in front view and from above (2.3-3.0 times broader than high, while in bisexual *Eumayria* it is only 1.5-1.7 times and in unisexual *Eumayria* – 2.5-2.8 times; malar space lacks radiating striae (Figs. 61-64, 67); antenna is filiform, long, 14-segmented, F1 substantially longer than pedicel and scape together; all flagellomeres are much longer than broad (Figs. 69-71).



Figures 61–72 61–62, *Eumayria floridana*, head: 61, from above; 62, dorsal view. 63–64, *E. enigma*, head: 63, from above; 64, dorsal view. 65–66, Scutum, dorsal view: 65, *E. floridana*; 66, *Eumayriella archboldi*. 67, *E. archboldi*, head, front view. 68, *E. floridana*, gaster. 69–71, Antenna: 69, *E. floridana*, male; 70, *E. enigma*, female; 71, *E. archboldi*. 72, *Loxaulus huberi*, head, front view

Scutum and scutellum are longer than broad, with dense white setae, without median and anterior parallel lines (Fig. 66); distinctly emarginated laterally and partially posteriorly as well; scutellum lacks foveae, with transverse depression along scutoscutellar suture; apical one third of scutellum is gradually depressed toward apex and narrowed to a point that joins scutum along median dorsal part; posterior one third of scutellar disk is the highest part, strongly convex; sculpture of scutellar disk is very finely punctate, posterior one-fourth rugose. In *Eumayria*, head is nearly as high as broad, malar space and partially frons with radiating striae; antennae are much shorter, F1 as long as pedicel, scape as broad as long; F2 to F4 is slightly longer than broad, subsequent flagellomeres, except last one, subequal, nearly as broad as long; scutellum with foveae, posterior part of disk never convex; posteriorly rounded and has a dull rugose sculpture; scutum and scutellum are bare, without dense white setae. Second abdominal segment in *Eumayriella* lacks pale felt-like ring of dense short setae at base, while *Eumayria* has such a ring (Fig. 68). The latter character is used also to separate several genera of Eucoilidae (Quinlan 1986) and Figitinae (Figitidae) (Fergusson 1986).

Biology. Only asexual females are known. Galls are cell clusters, hidden under the bark of twigs. Two species, *E. archboldi* Melika & Abrahamson and *E. invisa* (Weld, 1952) represent this genus.

Distribution. Florida, USA.

Heteroecus Kinsey, 1922

Heteroecus Kinsey 1922b: 81. Type species: *Andricus dasydactyli* Ashmead, 1896. Designated by Kinsey (1922b).

Diagnosis. The only diagnostic character provided by Kinsey (1922b), to differentiate this genus from *Andricus* is the tarsal claws without lobe. Discovery of the alternation of generations in this genus (Lyon 1963, 1984) furnished more evidence to synonymize *Heteroecus* to *Andricus* or North American "*Callirhytis*" (sensu Weld 1952a).

Comments. Kinsey (1922b) wrote "Whether to interpret this group as a species or a genus is largely a matter of individual opinion and convenience." The validity of this genus is very dubious and might be synonym of *Andricus*, if the presence or absence of tooth on the tarsal claw is regarded as a non-generic character.

Biology. The other peculiarity of this genus is that the representatives of this genus are distributed in California only and are associated only with *Quercus chrysolepidicola*.

Distribution. California, USA. Twelve species were listed by Burks (1979). Later few new species were described, all from California (Dailey & Sprenger 1983; Lyon 1984). Thus, currently 16 species are known.

Holocynips Kieffer, 1910

Holocynips Kieffer 1910: 114. Type species: *H. emarginata* Kieffer. Original designation.

Diagnosis. The only distinction of *Holocynips* from many species of *Andricus* is the simple tarsal claw. All other diagnostic characters are found in many *Andricus* species.

Comments. The validity of this genus is very dubious and might be a synonym of *Andricus*, if the presence or absence of tooth on the tarsal claw is regarded as a non-generic character.

Biology. The asexual generation only is known. Galls are on roots or at the base of young sprouts on white oaks only.

Distribution. Four species are known: two from the Eastern and 2 from Western Coast of the USA.

Loxaulus Mayr, 1881

Loxaulus Mayr 1881: 9, 12, 33. Type species: *Cynips quercus-mammula* Bassett, 1881. Designated by Ashmead (1903). Monotypic. Melika & Abrahamson 2000a (revision of the genus).

Solenozopheria Ashmead 1887: 149. Type species: *S. vaccinii* Ashmead. Original designation. Monotypic. Weld 1951 (synonym of *Loxaulus*).

Compsodryoxenus Ashmead 1896: 128. Type species: *C. maculipennis* Ashmead, 1896. Designated by Ashmead (1903). Weld 1951 (synonym of *Loxaulus*).

Diagnosis. The head from above is broader than the mesosoma; the gena possess a malar sulcus (Fig. 72). The scutum is usually finely transversely coriaceous; the scutellum lacks foveae, with a transverse shallow depression (Fig. 74). The central portion of the propodeum is narrow, limited by parallel or slightly outward bent lateral carinae and with a median longitudinal carina and/or longitudinal striae; the median longitudinal carina in some species is indistinct, fragmented but always present at least in anterior half (Fig. 75). The radial cell of the forewing is short and broad, not more than 2.5 times as long as broad (except *L. quercusmammula* with the radial cell 2.6–2.7 times as long as broad), the forewing margin of female with or without cilia, with brown, smoky spots (or stripes) along the areolet, 2r, Rs, and M. (Fig. 76). Tarsal claws lack tooth. The ventral spine of the hypopygium is short, slender or needle-like; subapical setae are short and sparse, do not reach beyond the apex of the spine and the prominent part is never more than 3.0–3.5 times as long as broad (Fig. 73). The propodeum is similar to that of the Mediterranean genus *Plagiotrochus* Mayr. However, in the latter, the central portion of the propodeum is much broader, and is limited by the strongly outward-bending lateral carinae (Fig. 38).

Biology. The genus includes 14 species (Melika & Abrahamson 2000a). Alternate asexual and bisexual generations are known only for *L. trizonalis* Weld.

Distribution. North America only.

Neuroterus Hartig, 1840

Neuroterus Hartig 1840a: 185, 192. Type species: *Neuroterus politus* Hartig, 1840. Designated by Ashmead (1903).

Spathegaster Hartig 1840a: 186. Type species: *S. petioliventris* Hartig. Original designation. Monotypic. Mayr 1881 (synonym of *Neuroterus*).

Ameristus Foerster 1869: 333. Type species: *Neuroterus politus* Hartig. Designated by Rohwer & Fagan (1917). Mayr 1881 (synonym of *Neuroterus*).

Dolichostrophus Ashmead 1887: 129. Type species: *Cynips quercusirregularis* Osten Sacken, 1861. Designated by Ashmead (1887). Dalla Torre 1893 (synonym to *Neuroterus*).

Neuroterus subgenus *Diplobius* Kinsey 1923: 27, 28-31, 35. Type species: *Cynips floccosa* Bassett, 1881. Original designation.

Neuroterus subgenus *Dolichostrophus* Kinsey 1923: 25, 28, 32, 78. Type species: *Cynips irregularis* Osten Sacken Original designation.

Neuroterus subgenus *Neospathegaster* Kinsey 1923: 28, 35, 121. Type species: *Cynips vesicula* Bassett, 1881. Original designation.

Neuroterus subgenus *Neuroterus* Kinsey 1923: 27, 128. The nominal subgenus of *Neuroterus*.

Neuroterus subgenus *Pseudoneuroterus* Kinsey 1923: 130. Type species: *Cynips macroptera* Hartig, 1843. Original designation.

Neuroterus subgenus *Spathegaster* Kinsey 1923: 28, 131. Type species: *Spathegaster petioliventris* Hartig, 1840. Original designation.

Neoneuroterus Monzen 1954: 33. Type species: *N. kashiyamai* Monzen. Original designation. **New synonym.**

Repentinia Belizin & Maisuradze, 1961. In Maisuradze 1961: 28. Type species: *R. lencoranica* Belizin & Maisuradze. Monotypic. Original designation. **New synonym.**

Diagnosis. The scutum is smooth, microreticulate, or alutaceous, shiny, emarginated posteriorly along dorso-axillar surface; transscutal articulation is strongly emarginated laterally, if uninterrupted then strongly curved, never straight (Fig. 14); the scutoscutellar suture is deep, the scutellum lacks separated foveae; fully winged, the radial cell of forewing is elongated, narrow. Usually notauli are absent or only barely traceable, however, some European species have distinct notauli, at least in the posterior half, and one species, *N. lanuginosus* Giraud, has deep notauli reaching the pronotum. The main diagnostic character that separates *Neuroterus* from all other genera of Cynipini is the absence of the scutoscutellar suture. See also in Melika, Stone & Csóka (1999).

Comments. Kinsey (1923) divided the genus into 6 subgenera. Subdivision is appropriate since the genus includes morphologically diverse species, however, some subgenera are hardly distinguishable. The genus *Neuroterus* requires revision, particularly of the North American and Eastern Palaearctic species (particularly described from Japan). A number of new *Neuroterus* species and synonymizations were made recently on the North American species (Melika & Abrahamson 1997a).

Neoneuroterus. The only diagnostic characters given by Monzen (1954) for separation *Neoneuroterus* from *Neuroterus* were: antennae are 14-segmented in females and 15-segmented in males; notauli distinct and complete; head and mesosoma glabrous and smooth; the ventral spine of the hypopygium is long and pointed. However, all these characters occur in Western Palaearctic *Neuroterus* species as well (see the recent key to the Western Palaearctic *Neuroterus* species in Melika, Stone & Csóka 1999). We also examined the types of *Neoneuroterus boni-henrici* (Dettmer, 1934) and found no substantial characters to separate this species from other *Neuroterus* species. Thus, two *Neoneuroterus* species are transferred to *Neuroterus*: *N. kashiyamai* (Monzen, 1954), **comb. nov.** and *N. bonihenrici* Dettmer, 1934, **comb. rev.** Later, Kovalev (1965) described other *Neoneuroterus* species from Far East of Russia: *N. spumeus* Kovalev, 1965 (sexual gen., galls on leaves), *N. nephroideus* Kovalev, 1965 (sexual gen., galls in buds), and *N. vernicosus* (asexual gen., galls unknown). The latter species must be transferred into *Trigonaspis*: *T. vernicosus*, **comb. nov.** Two other species, *N. spumeus* and *N. nephroideus* must be revised, their placement in *Neoneuroterus*, and thus in *Neuroterus*, is questionable.

Repentinia. Maisuradze (1961) described this species from Azerbaijan and placed it near *Neuroterus.* The asexual females are known to induce stem swelling-like galls on twigs of *Quercus castaneifolia* CAM. Maisuradze (1961) mentioned that the new genus closely resembles *Neuroterus* and differs in that the head and mesosoma have a dense white pubescence, F1 is very short, nearly equal F2; lateral propodeal carinae are absent. Weld (1964, ms.) wrote, “Genus can not be placed in key – perhaps near *Trichagalma.*” We examined the types of this species at the Zoological Institute in St. Petersburg (Russia) and found no substantial characters to separate it from *Neuroterus*. Moreover, all the diagnostic characters given by Maisuradze (1961) for *Repentinia* occur in some *Neuroterus* species, particularly in *N. macropterus* (Hartig, 1843). Analysis of type series of *Repentinia lencoranica* showed that it is a **syn. nova** of *N. macropterus*. This species is widespread in Europe on *Q. cerris* only, but it also has been found in Israel on *Q. ithaburensis* (Sternlicht 1968), and is known from Bulgaria (Vassileva-Samnalieva 1974), Romania (Ionescu 1973), and we identified large series collected from Turkey and Iran (Lorestan). Thus, it is apparent that the distribution of this species includes a large distribution within the Western Palaearctic.

Neuroterus (***Latuspina***) Monzen, 1954: 35. Type species: *Neuroterus* (*Latuspina*) *stirps* Monzen, 1954: 35. Original designation. The only character given by Monzen (1954) to differentiate this subgenus and species from *Neuroterus* is that the projecting part of the ventral spine of the hypopygium is not normally pointed at the apex, but dilated "like a spatula". No *Neuroterus* species are known to have distally broadened ventral spine. Consequently, *Latuspina* cannot be placed into *Neuroterus*. Weld (1964, ms.) stated that he was unable to obtain the types and that Dr. Yasumatsu, whom he asked to look for types, didn't find them in Monzen collection. Until the types are revised, the status of *Neuroterus* (*Latuspina*) Monzen will remain uncertain.

Biology. Nearly 100 described species, many are known to have alternate generations. Usually induce tiny integral or detachable leaf galls, mono- or polythalamous, or integral stem and catkin galls. Some species have polymorphic galls.

Distribution. Holarctic.

***Odontocynips* Kieffer, 1910**

Odontocynips Kieffer 1910: 112. Type species: *O. nebulosa* Kieffer. Original designation. Monotypic.

Diagnosis. Easily distinguished from all other Cynipini by the presence of a strong apical lobe on the hind tibia (Fig. 77). Otherwise, it is closely allied to *Andricus* and *Holocynips*.

Biology. One species, *O. nebulosa* Kieffer, 1910 is known from the asexual generation only. It induces root galls on white oaks. Recently details of the biology were described (Wilson, Lester & Edmonson 2000).

Distribution. USA.

***Philonix* Fitch, 1859**

Philonix Fitch 1859: 783. Type species: *P. fulvicollis* Fitch, 1859. Designated by Ashmead (1903). Types examined. Ashmead 1903 and Beutenmueller 1909 (*Acraspis* is a synonym of *Philonix*). Dalla Torre & Kieffer 1910 (synonym of *Biorhiza*). Weld 1922 (*Acraspis* and *Philonix* distinct genera).

Diagnosis. Closely resembles *Acraspis*, see **Diagnosis** to *Acraspis*.

Comments. Kinsey (1930) transferred *Dryophanta pallipes* Bassett into *Philonix* and considered it as the sexual generation of *P. fulvicollis*. However, Kinsey provided no justification for this synonymy. Weld (1959) wrote that *P. pallipes* was "perhaps a synonym of *Acraspis gemula* (Bassett)". We compared the three specimens of *P. pallipes* (from Beutenmueller collection, USNM, Washington, DC) with the paratypes of the sexual generation of *A. gemula* and found no differences. *Philonix pallipes* is a **syn. nov.** of *A. gemula.* If *P. pallipes* (Bass.) is treated as an *Acraspis* species, there is no evidence that species of *Philonix* have alternate sexual generations. Several species of *Philonix*, described by Kinsey (1930, 1936) from Mexico must be revised.

Biology. *Philonix* species are associated with white oaks only. Galls induced by *Philonix* species differ from those of *Acraspis*. They are fleshy, soft, and globular, attached to the leaves, usually the undersides, with a thick wall covered with a short very dense, felt-like pubescence.

Distribution. North America and Mexico.

Phylloteras Ashmead, 1897

Phylloteras Ashmead 1897a: 67. Type species: *Biorhiza rubinus* Gillette, 1888. Designated by Ashmead (1897a). Monotypic. Dalla Torre & Kieffer 1910 (synonym of *Trigonaspis*). Beutenmueller 1909 (synonym of *Biorhiza*). Types examined.

Xystoteras Ashmead 1897b: 260. Type species: *X. volutellae* Ashmead, 1897. Original designation. Monotypic. Lyon 1993 (synonym of *Phylloteras*). Types examined.

Euxystoteras Lyon 1993: 138. Type species: *E. campanulatum* Lyon. Original designation. Types examined. **New synonym.**

Diagnosis. Ant-like, apterous or brachypterous but the forewing is not longer than the mesosoma. Similar to *Zopheroteras*, however, the scutellum is not knobbed; the head is equal or even higher than broad in front view. *Phylloteras poculum* (Osten Sacken) has a slightly elevated scutellum similar to *Zopheroteras*, but not nearly as strongly elevated. See also *Diagnosis* to *Zopheroteras*. Closely related to *Trigonaspis* but has a longer, needle-like ventral spine of the hypopygium, the propodeum is placed in the same plane as the rest of thorax or only slightly declined, while in *Trigonaspis* the projecting part of the ventral spine is nearly 3.0 times as long as broad, the propodeum declines strongly.

Comments. Lyon (1993) separated *Euxystoteras* from *Phylloteras* “by its simple tarsal claws”. The inadequacy of this generic character argues that *Euxystoteras* must be a synonym of *Phylloteras*. Thus, *Euxystoteras campanulatum* (Lyon 1993) must be transferred to *Phylloteras*, *P. campanulatum* (Lyon), **comb. nov.** If data are obtained on the alternate bisexual generations of *Phylloteras*, it is possible that it will join *Trigonaspis*, forming only a group of species rather than a separate genus.

Biology. Asexual generation is only known. Induces small detachable leaf galls.

Distribution. Eight species are known from North America.

Plagiotrochus Mayr, 1881

Plagiotrochus Mayr 1881: 32. Type species: *Cynips quercus-ilicis* Fabricius, 1798. Designated by Ashmead (1903).

Fioria Kieffer 1903a: 31. Type species: *Callirhytis marianii* Kieffer, 1903. Original designation. Kieffer 1903b (name preoccupied by Silvestri in 1869 for Myriapoda).

Fioriella Kieffer 1903b: 95. Melika, Ros-Farré & Pujade-Villar 2001 (synonym of *Plagiotrochus*).

Diagnosis. The gena in the asexual female is broadened behind the eye; the clypeus with radiating striae, do not project as a distinct lamella between mandibles, the malar sulcus is absent; the mesopleuron is shiny, flat in the postero-dorsal margin and ventral area; the metasoma is compressed laterally; the scutellum is equal or only slightly longer than the metascutellum; the propodeum forms an obtuse angle with the scutellum; the lateral propodeal carinae are strongly bent outwards, with a more or less impressed median carina; the ventral spine of the hypopygium is thin, with short sparse white setae not forming an apical tuft. See also Diagnosis to *Bassettia*, *Callirhytis*, and *Loxaulus*. *Plagiotrochus* also resembles *Chilaspis*, however, the latter differs from the former by a smooth scutum and mesopleuron.

Comments. All the mentioned characters are not exclusive to the genus *Plagiotrochus* but the above combination does define this genus. Homoplasies are very common in Cynipini and it is very difficult to find an exclusive diagnostic character for a given genus of Cynipidae, which is not shared with another genus or other genera. For example, the main diagnostic character for recognizing *Plagiotrochus* in the Palaearctic area is the presence of a median propodeal carina, which, however, is also present in some species of the Nearctic *Loxaulus* and *Bassettia* (Melika & Abrahamson 2000a). Another character, the longitudinal depression on the vertex with a median longitudinal carina, is present in some asexual females of *Plagiotrochus* but also in some North American species, e.g., *Bassettia ligni* Kinsey and *B. pallida* Ashmead.

Plesiomorphic traits of *P. semicarpifoliae* (Cameron) known from the Himalayan area suggest a Southeast Asian origin for *Plagiotrochus* and all the species known from the Mediterranean region are derived forms (Bellido, Ros-Farré, Kovalev & Pujade-Villar 2000).

Weld (1926) described one species, *P. suberi* from California, which induces stem galls on the introduced European cork oak, *Quercus suber*. Later, Esquivel & De Santis (1953) described another asexual species, *P. abdominalis*, from Argentina, which is also known to induce stem galls. Nieves-Aldrey (2001) in his Fauna Iberica suggested that both, *P. suberi* and *P. abdominalis* are synonyms of *P. amenti* Kieffer (asexual generation, described as *P. pardoi* Nieves-Aldrey, 1985). However, Pujade-Villar (1998) regarded *P. pardoi* as a distinct species from *P. amenti* and, thus decided that *P. suberi* Weld, 1926 is a valid name, while *P. abdominalis* Esquivel & De Santis, 1953 and *P. pardoi* Nieves-Aldrey, 1985 are synonyms. Bailey & Stange (1966) wrote of *P. suberi*, “the insect has been found in Switzerland and Portugal (where it probably originated) only in the past few years.” This species life cycle has changed and its population occurs as asexual females only. A failure in a genetic regulatory switch from thelyotoky to bisexuality may have resulted in the deletion of the sexual generation in geographic isolation. Geographic parthenogenesis, for example, is present in *Andricus mukaigawae* (Mukaigawa) and *A. targionii* Kieffer in Japan (Abe 1986).

Biology. Alternation of generations is known. The asexual generation usually induces stem galls, the cells of which are hidden under the bark of twigs, while the sexual generation usually induces catkin galls. Some species induce leaf galls.

Distribution. Mediterranean region (Southern Europe and North Africa) – 7 sexual and 7 asexual *Plagiotrochus* forms are known (Bellido, Ros-Farré, Kovalev & Pujade-Villar 2000). Nieves Aldrey (2001) listed 10 *Plagiotrochus* species for the Iberian Peninsula, one species, *P. vilageliui* Pujade-Villar, 2000 was described from Corsica (France) (Pujade-Villar, Villemant & Andrei-Ruiz 2000). One species, *P. marianii* (Kieffer) was recorded from Slovakia and Hungary (Ambrus 1974; Melika, Ros-Farré & Pujade-Villar 2001), one species, *P. semicarpifoliae* is known from the Himalayan area. Introduced to California and Argentina.

Trichagalma Mayr, 1907

Trichagalma Mayr 1907: 3. Type species: *T. drouardi* Mayr. Original designation. Monotypic.

Diagnosis. The ventral spine of the hypopygium is slender and very short, the projecting part broader than long, with sparse subapical setae, reaching beyond the apex of the spine; the metasoma is strongly compressed laterally to a knife-edge dorsally; the forewing is 1.7 times as long as the body, with dark spots, Rs straight, the radial cell very long and narrow, (Fig. 78); the mesosoma is densely pubescent; the propodeum is very short, without carinae. No other Cynipini is known to have such strongly compressed metasoma laterally. In general, the head and mesosoma resemble asexual *Cynips*, however, the absence of notauli, scutellar foveae and propodeal carinae and the laterally strongly compressed metasoma clearly differentiate

Trichagalma from *Cynips*. Absence of notauli and scutellar foveae; smooth mesosoma, strongly laterally compressed gaster, the short ventral spine of the hypopygium also resemble *Neuroterus*. However, the robust size, strongly arched and densely pubescent mesosoma differentiates the genus from *Neuroterus*.

Comments. Ashmead (1904) described *Dryophanta serratae* from Japan (Sapporo) on the basis of one female, reared by Dr. Matsumura from the gall collected from *Quercus serrata*. Later Mayr (1907) described his *T. drouardi*, which appeared to be a synonym of *D. serratae* Ashmead (Monzen 1954). Thus, the genus is known from only one robust species, *T. serratae* (Ashmead, 1904).

Biology. Asexual females only are known to induce detachable stem galls, similar to those of the European *Andricus serotinus* (Giraud).

Distribution. Known from Japan only.

Trigonaspis Hartig, 1840

Trigonaspis Hartig 1840a: 186. Type species: *T. crustalis* Hartig, 1840. Original designation. Monotypic.

Xanthoteras Ashmead 1897b: 262. Type species: *Biorhiza forticornis* Walsh, 1864. Designated by Ashmead (1897b). Specimens from the original Walsh's series examined. **New synonym.**

Belizinella Kovalev 1965: 49. Type species: *B. gibbera* Kovalev. Original designation. Types examined. **New synonym.**

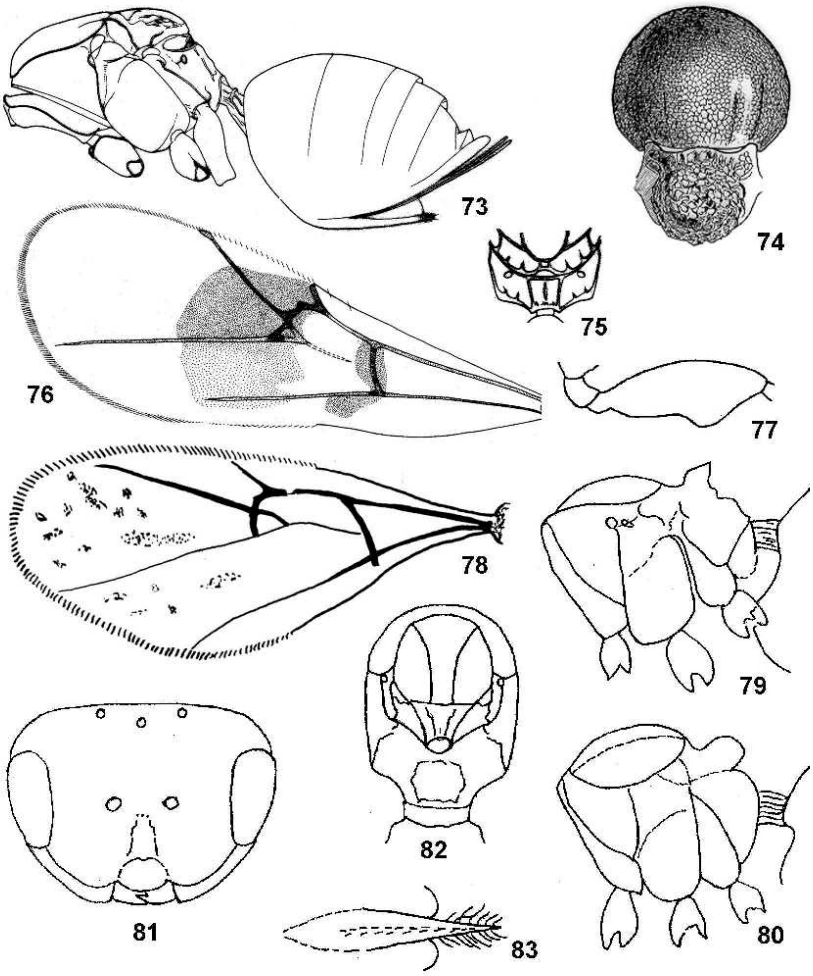
Ussuraspis Kovalev, 1965: 53. Type species: *U. nervosus* Kovalev. Original designation. Types examined. **New synonym.**

Diagnosis. *Trigonaspis* closely resembles *Biorhiza*, however, it differs in the presence of arched mesosoma and shorter pronotum. *Phylloteras* and *Zopheroteras* are also very similar to *Trigonaspis*, however they differ in having longer ventral spines in both genera, knobbed scutellum in *Zopheroteras*, and less arched mesosoma in *Phylloteras*. See also Diagnosis to *Biorhiza*, *Phylloteras* and *Zopheroteras*.

Comments. Dalla Torre & Kieffer (1910) treated *Zopheroteras* as a synonym to *Trigonaspis*. Beutenmueller (1909) placed *Xanthoteras* into *Biorhiza*, while Mayr (1902) considered *Xanthoteras* as a separate genus from *Biorhiza* (= *Sphaeroteras*) because of the strongly arched mesosoma and toothed tarsal claws. The original description of *Xanthoteras* (Ashmead 1897b) does not include substantial diagnostic characters to separate it from *Trigonaspis*. *Xanthoteras fumosum* (Weld), *X. pumiliventre* (Bassett), *X. radicola* (Ashmead) were described and are known from the sexual generations only. Although placed into *Xanthoteras*, they are congeneric with the European species, *T. megaptera* (Panzer). The sexual generation of *Trigonaspis* is quite different from that of *Biorhiza*, which earlier workers had synonymized as *Xanthoteras* (see Diagnosis to *Biorhiza*). Weld (1921) treated these three *Xanthoteras* species as *Trigonaspis* and only later transferred them to *Xanthoteras*.

Weld (1951, 1952a) and Burks (1979) placed 13 North American species into *Xanthoteras*. Dailey & Menke (1980) synonymized *X. obconicum* (Weld) to *X. pulchellum* (Beutenmueller) Seven *Xanthoteras* species here are transferred to *Trigonaspis*: *fumosa* Weld, **comb. rev.**, *mediocre* (Weld), **comb. nov.**, *ornata* Kinsey, **comb. rev.**, *pumiliventre* (Bassett), **comb. nov.**, *quercusforticorne* (Walsh), **comb. nov.**, *radicola* (Ashmead), **comb. nov.**, and *teres* (Weld), **comb. nov.** Two species, *X. eburneum* (Bassett) and *X. emoryi* (Ashmead) herein transferred to *Biorhiza*; *X. pulchellum* (Beutenmueller) is transferred to *Cynips*; *X. pulchripenne* (Ashmead) transferred to *Atrusca*.

Belizinella. Kovalev (1965) mentioned that his new genus is closely related to *Xanthoteras*, *Xystoteras* and *Trigonaspis* and from the latter, it differs in having a 14-segmented antennae, while in *Trigonaspis* antennae are 13-segmented (however, in *T. synaspis* antennae are 14-segmented). He mentioned also that in *Belizinella* notauli are absent, however, in *B. gibbera* the notauli are distinct and complete, reaching the pronotum. The galls of two newly described species *B. gibbera* and *B. vicina* are identical in their shape, location and inner structure as the gall of *T. synaspis*. Without doubt, it is a synonym of *Trigonaspis* and, thus, *Trigonaspis gibbera* Kovalev, **comb. nov.** and *T. vicina* Kovalev, **comb. nov.**



Figures 73–83 73, *Loxaulus huberi*, female, lateral view; 74, *L. masneri*, female, thorax, dorsal view; 75–76, *L. huberi*, female: 75, propodeum; 76, forewing. 77, *Odontocynips nebulosa*, hind tibia. 78, *Trichagalma serratae*, forewing. 79–80, Mesosoma, lateral view: 79, *Zopheroteras guttatum*; 80, *Z. sphaerula*. 81–82, *Z. guttatum*: 81, Head, front view; 82, mesosoma, dorsal view. 83, *Z. sphaerula*, ventral spine of hypopygium

***Ussuraspis*.** The diagnostic characters given by Kovalev (1965) for the separation of his newly described genus from *Trigonaspis* and *Xanthoteras* are not satisfactory – they are identical with those for *Trigonaspis*. So, *Ussuraspis nervosa* Kovalev, 1965 must be transferred to *Trigonaspis*: *T. nervosus*, **comb. nova.**

If data are obtained on the alternate sexual generations of *Phylloteras* and *Zopheroteras*, it may be that both genera will join *Trigonaspis* and will form only a distinct species groups rather than separate genera.

Biology. Alternation of asexual and sexual generations is known. Induces detachable leaf and root galls.

Distribution. Holarctic. We found undescribed *Trigonaspis* species from the material collected in China and Malaysia.

Zopheroteras Ashmead, 1897

Zopheroteras Ashmead 1897b: 261. Type species: *Acraspis vaccinii* Ashmead, 1887. Designated by Ashmead (1903). Dalla Torre & Kieffer 1910 (synonym of *Trigonaspis*).

Parateras Ashmead 1897b: 262. Type species: *P. hubbardi* Ashmead. Original designation. Monotypic. Weld 1922 (synonym of *Zopheroteras*).

Diagnosis. Ant-like, apterous or brachypterous species. Closely resembles *Phylloteras*, differs in that the scutellum is knobbed (Figs 79-80) and the head is transverse in front view (Fig. 81); the scutellum is elevated, with knobbed disk; notauli complete, strongly curving inward posteriorly (Fig. 82); the ventral spine of the hypopygium is narrow, needle-like, the projecting part is never less than 4-5 times as long as broad, subapical setae never reach beyond the apex of the spine (Fig. 83). Species are difficult to distinguish on the basis of the galls only. The adults are required for precise identification of the species.

Comments. If data are obtained on the alternate bisexual generations of *Zopheroteras*, it may be that it will join *Trigonaspis* and will form only a distinct group of species rather than a separate genus.

Biology. Only the asexual generation is known. It induces small, usually rounded or elliptic detachable leaf galls on both red and white oaks.

Distribution. Six species are known from North America (eastern and midwestern United States only).

Conclusions

From 41 currently valid genera 15 are synonymized. Thus, 26 genera in Cynipini are valid (Table 3). As the result, 73 **comb. nov.** and 26 **comb. rev.** are made.

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Table 3 Current arrangement of world genera of oak cynipid wasps (Cynipidae: Cynipini)

	Proposed valid genera	**New synonymic genera**
1.	***Acraspis* Mayr, 1881**	*Paracraspis* Weld, 1952
2.	***Amphibolips* Reinhard, 1865**	
3.	***Andricus* Hartig, 1840**	*Dros* Kinsey, 1937, *Erythres* Kinsey, 1937, *Liodora* Foerster, 1869, *Parandricus* Kieffer, 1906, *Trichoteras* Ashmead, 1897
4.	***Aphelonyx* Mayr, 1881**	
5.	***Atrusca* Kinsey, 1929**	
6.	***Bassettia* Ashmead, 1887**	
7.	***Belonocnema* Mayr, 1881**	
8.	***Biorhiza* Westwood, 1840**	*Sphaeroteras* Ashmead, 1897
9.	***Callirhytis* Foerster, 1869**	
10.	***Chilaspis* Mayr, 1881**	
11.	***Cynips* Linnaeus, 1758**	*Antron* Kinsey, 1930, *Besbicus* Kinsey, 1930
12.	***Disholcaspis* Dalla Torre & Kieffer, 1910**	
13.	***Dryocosmus* Giraud, 1859**	
14.	***Eumayria* Ashmead, 1887**	
15.	***Eumayriella* Melika & Abrahamson, 1997**	
16.	***Heteroecus* Kinsey, 1922**	
17.	***Holocynips* Kieffer, 1910**	
18.	***Loxaulus* Mayr, 1881**	
19.	***Neuroterus* Hartig, 1840**	*Neoneuroterus* Monzen, 1954, *Repentinia* Belizin & Maisuradze, 1961
20.	***Odontocynips* Kieffer, 1910**	
21.	***Philonix* Fitch, 1859**	
22.	***Phylloteras* Ashmead, 1897**	*Euxystoteras* Lyon, 1993
23.	***Plagiotrochus* Mayr, 1881**	
24.	***Trichagalma* Mayr, 1907**	
25.	***Trigonaspis* Hartig, 1840**	*Belizinella* Kovalev, 1965, *Ussuraspis* Kovalev, 1965, *Xanthoteras* Ashmead, 1897
26.	***Zopheroteras* Ashmead, 1897**	

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