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# Державного природознавчого музею

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# НАУКОВІ ЗАПИСКИ ДЕРЖАВНОГО ПРИРОДОЗНАВЧОГО МУЗЕЮ

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**Наукові записки Державного природознавчого музею. – Львів, 2021. – Вип. 37. – 280 с.**

До 37-го випуску періодичного видання «Наукові записки Державного природознавчого музею» увійшли статті та короткі повідомлення з музеології, екології, ентомології, а також інформація про діяльність музею у 2020 році.

Для екологів, зоологів, ботаніків, працівників музеїв природничого профілю, заповідників, національних природних парків та інших природоохоронних установ і організацій.

**Proceedings of the State Natural History Museum. – Lviv, 2021. – Issue 37. – 280 p.**

The 37th issue of the periodical «Scientific Notes of the State Museum of Natural History» includes articles and short reports on museology, ecology, entomology, as well as information about the activities of the museum in 2020.

For ecologists, zoologists, botanists, employees of museums of natural profile, reserves, national nature parks and other environmental institutions and organizations.

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## ***Ентомологія***

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# IS CLYTINI MONOPHYLETIC? THE EVIDENCE FROM FIVE-GENE PHYLOGENETIC ANALYSIS.

*Tribe Clytini (Coleoptera: Cerambycidae) is one of the largest within the long horn beetles, having over 1500 species. Until now, the tribe was considered monophyletic, despite the fact that it combines several different morphological groups. Morphological data alone could not shed enough light on the taxonomy and phylogeny of Clytini. The data for the last decade on molecular phylogenetics have challenged the Clytini monophyletic hypothesis. In this study, I conducted a comprehensive phylogenetic analysis of Clytini based on the three mitochondrial genes 12S rRNA 16S rRNA COI and two nuclear genes 18S rRNA 28S rRNA. The results of the analysis with high reliability confirmed the hypothesis of polyphyly of Clytini. The tribe includes two phylogenetically different and morphologically distinct evolutionary branches, which gave me reason to conduct a taxonomic revision of Clytini. I proposed new nomenclature acts including 1 new supertribe, 1 new tribe, 4 new subtribes, 3 new genera, 4 new subgenera, 3 new statuses, 22 new combinations, 2 new synonyms. In addition, I redescribed 1 tribe and 3 genera.*

***Key words:*** *Cerambycidae, phylogeny, new taxa.*

Tribe Clytini Mulsant, 1839 belongs to Cerambycinae subfamily within the long horn beetles. It includes around 80 genera and over 1,500 species. Dozens of new species of Clytini are described annually, and their actual number may exceed 2,000 species. The largest genera are *Demonax* Thomson, 1861 (≈465 species), *Chlorophorus* Chevrolat, 1863 (≈279 species), *Xylotrechus* Chevrolat, 1860 (≈270 species), *Rhaphuma* Pascoe, 1858 (≈223 species), *Perissus* Chevrolat, 1863 (≈92 species) [65]. The enormous diversity of the tribe complicates its taxonomy, which needs to be revised, especially in the light of the recent studies [25, 39]. Intra- and extratribal phylogenies of the current Clytini are intricate and unclear.

Mulsant established tribe Clytini [Clytaires], dividing it on three morphological groups: *Plagionotus* Mulsant, 1839, *Clytus* Mulsant, 1839 and *Anaglyptus* Mulsant, 1839 [46]. Essentially, he used two key morphological features for separating mentioned groups. These include 1) shape of pronotum and 2) sculpture of elytra. Accordingly, *Plagionotus* differs from *Clytus* and *Anaglyptus* in transverse pronotum. And the last two differ from each other in the sculpture of elytra. *Clytus* elytra without basal depression. In contrast, *Anaglyptus* elytra with basal depression. In fact, Mulsant believed that *Clytus* and *Anaglyptus* were more related each other than to *Plagionotus*. According to his ideas, *Clytus* and *Anaglyptus* had a common feature – subspherical or subovoidal pronotal shape [46]. Contrary to Mulsant, Leconte & Horn emphasized the relations between two groups "Cyllenes" and "Clity" [37]. They stated that metepimera of both groups extend over hind angles of the 1st ventrite. In contrast, "Anaglypti" metepimera do not reach the hind angles of the 1st ventrite. All three groups of genera were placed in the tribe Clytini [37]. This system was widespread during the first half of XX century [28, 29, 57, 58] until Knull separated tribe Anaglyptini from Clytini [32].

Molecular phylogeny studies of the longhorn beetles from the early 2000s challenged the idea that Clytini is monophyletic. In particular, Yoon and al. [74], on the basis of COI and 16S rRNA studies, demonstrated non-monophyly of Clytini in many cases. Although only three species were included in their analysis *Chlorophorus diadema* Motschulsky, 1853, *Demonax transilis* Bates, 1884, *Plagionotus christophi* (Kraatz, 1879). Grebennikov and al. also indicated that Clytini is non-monophyletic [25]. Their study based on sequences of COI from 11 species. In contrast, Nie et al. considered monophyly of Clytini based on complete mitochondrial sequences of three species (*Clytobius davidis* (Fairmaire, 1878), *Xylotrechus magnicollis* (Fairmaire, 1888), *Chlorophorus diadema*) [50]. However, deep branching of Clytini clade on their tree indicates paraphyly. Phylogenetic analysis of Clytini with the most comprehensive sample of taxa (27 species) is presented in Lee & Lee [39]. Their tree, based on six genes (2 mitochondrial COI and 16S r RNA; 4 nuclear 18S rRNA, 28S rRNA, wingless and CAD), clearly showed that Clytini is a paraphyletic group. It should be noted that the group of genera *Plagionotus* – *Chlorophorus* – *Demonax* is well separated from another group of genera *Neoclytus* – *Perissus* – *Clytus* – *Xylotrechus* on their tree. In general, Clytini and Anaglyptini form a monophyletic clade that is well separated from other Cerambycinae clades. However, Lee & Lee indicate that to resolve intergeneric relationships within Clytini and Anaglyptini it needs to be tested with broader taxon sampling [39].

In the current study, I performed a five genes phylogenetic analysis of the most comprehensive sample of taxa (79 species) of Clytini and Anaglyptini. My findings clearly showed that Clytini is nonmonophyletic, but consists of two evolutionary lineages, which could be recognized as separate tribes Clytini, **trib. sensu nov.** and Chlorophorini, **trib. nov.** The monophyly of the large clade of Anaglyptini, Clytini and Chlorophorini, for which the status of supertribe Chlorophoritae, **supetrib. nov**. is proposed, was confirmed. I proposed new nomenclature acts including 1 new supertribe, 1 new tribe, 4 new subtribes, 3 new genera, 4 new subgenera, 3 new statuses, 22 new combinations, 2 new synonyms. In addition, I redescribed 1 tribe and 3 genera.

## Materials and methods

I used publicly available DNA partial sequences of five genes (79 species of target group and 4 species of outgroup) including three mitochondrial genes: 12S ribosomal RNA (12S rRNA) and 16S ribosomal RNA (16S rRNA) and cytochrome c oxidase I (COI) and two nuclear genes: 18S ribosomal RNA (18S rRNA) and 28S ribosomal RNA (28S rRNA) generated from GenBank as a FASTA file. I also produced consolidated sequences for COI and 28S rRNA from the sets of separate specimens of the same species. This allowed to avoid the statistical noises caused by multiple point mutations which spread within the different populations of the certain species. The genes were assembled in the matrix as follows: 12S rRNA – 16S rRNA – COI – 18S rRNA – 28S rRNA with the total length 5.327 kilobase (kb). While the species set with complete 12S rRNA + 16S rRNA + COI + 18S rRNA + 28S rRNA sequences was limited, I filled the gaps of missing species with partial sequences of mentioned genes, which overlap at least 50% of their length (fig. 1).

Multiple alignments were generated using the Muscle software in the environment of SeaView 5 [24]. Alignments were provided with unlimited iterations and were edited manually to correct regions containing missing data and to exclude unalignable positions.

Phylogenetic trees were constructed using maximum-likelihood (ML) and Bayesian methods with PhyML [22]. Analyses were performed following a general time-reversible (GTR) model of sequence evolution. We performed an approximate likelihood-ratio test (aLRT) for branch support based on the Log Ratio between the likelihood value of the current tree and that of the best alternative [2, 23]. The values of branch support were considered: 1-0.90 – very strong, 0.70-0.89 – strong, 0.50-0.69 – moderate and less than 0.50 – weak support. The optimal tree's structure was estimated using the best combination of nearest-neighbour interchange (NNI) and Subtree Pruning Regrafting (SPR) algorithms. We also used the neighbour-joining algorithm (BioNJ) optimizing trees topology for estimation of branch distances [19].

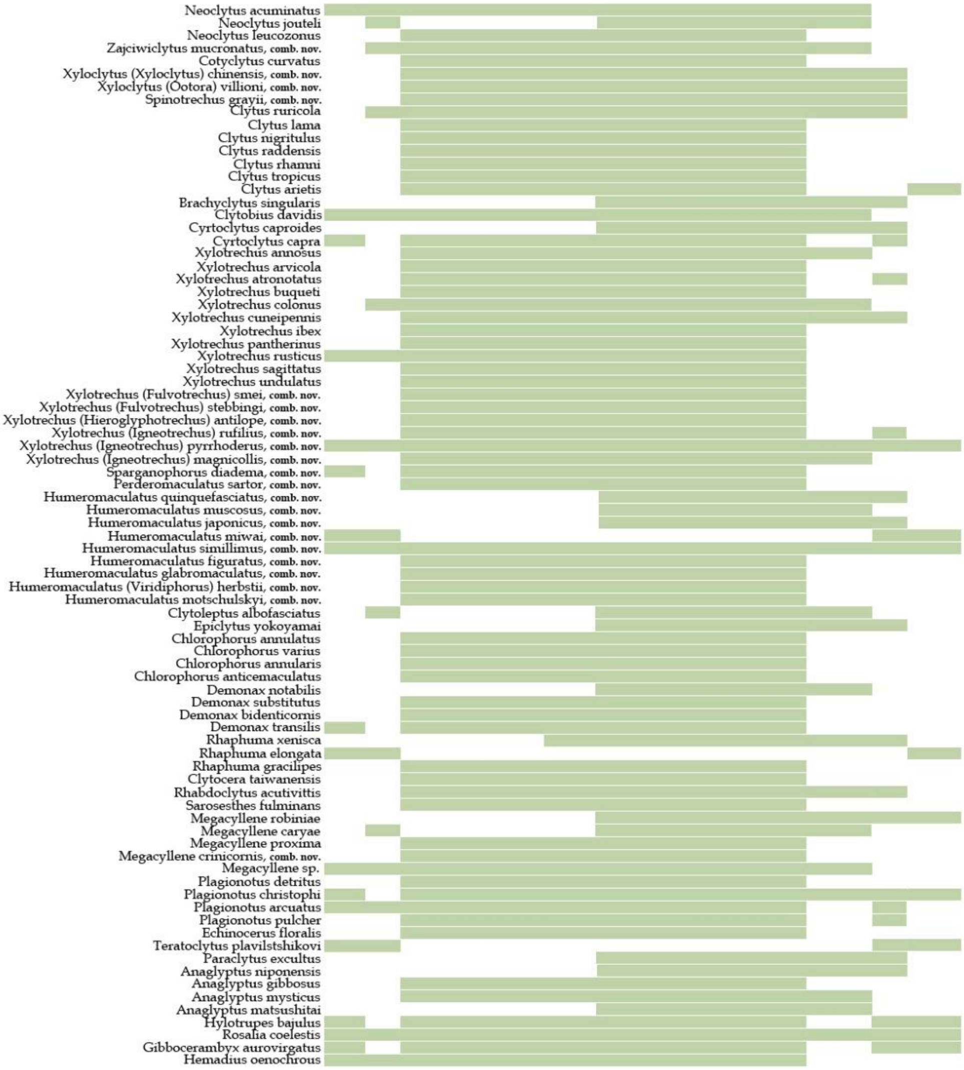

**Figure 1.** General scheme of overlapping of 12S rRNA, 16S rRNA, COI, 18S rRNA, 28S rRNA genes sequences fragments. *Hylotrupes bajulus*, *Rosalia coelestis*, *Gibbocerambyx aurovirgatus* and *Hemadius oenochrous* were used as outgroup.

## Results

Phylogenetic analysis resultantly showed that tribe Clytini s.l. is nonmonophyletic. On the obtained phylogenetic tree (fig. 1) three distinct clades are clearly allocated. The most basal of these is the tribe Anaglyptini. The crown part of the tree consists of two different clades, which are traditionally placed within Clytini s.l.

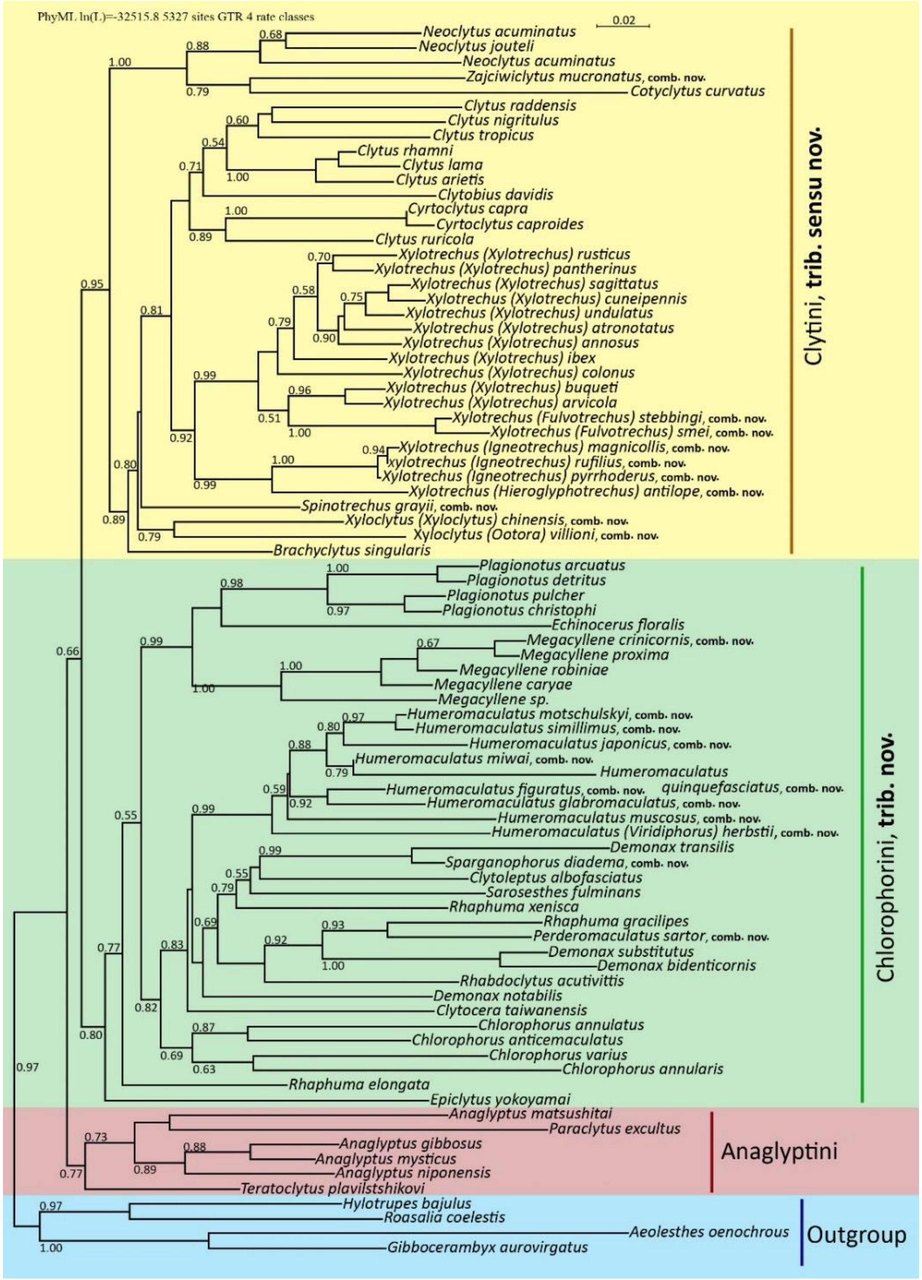

**Figure 2.** The polyphyly hypothesis of Clytini s.l. based on 12S rRNA, 16S rRNA, COI, 18S rRNA, 28S rRNA genes sequences phylogeny. The branch support SH-like values are shown with the threshold rule SH>0.50. *Hylotrupes bajulus*, *Rosalia coelestis*, *Gibbocerambyx aurovirgatus* and *Hemadius oenochrous* were used to root the tree.

The first clade includes the largest genera *Neoclytus* Thomson, 1860, *Clytus* and *Xylotrechus*, as well as their allies (e.g., *Brachyclytus* Kraatz, 1879, *Cyrtoclytus* Ganglbauer, 1881, *Cotyclytus* Martins & Galileo, 2011). The second clade unites such large genera as *Chlorophorus*, *Demonax*, *Rhaphuma*, *Plagionotus*, *Megacyllene* Casey, 1912 and their relatives (*Epiclytus* Gressitt, 1935, *Placosternus* Hopping, 1937, *Sarosesthes* Thomson, 1864, *Clytocera* Gahan, 1906, *Rhabdoclytus* Ganglbauer, 1889). Each of these clades has very high statistical support of the aLRT test. For the first clade SH=98, and for the second SH=99. This gives the reason to consider each of these clades as separate tribes: Clytini, **trib. sensu nov.** and Chlorophorini, **trib. nov**. Both tribes are related to Anaglyptini, forming a monophyletic superclade, which I consider in the rank of supertribe Chlorophoritae, **supertrib. nov.**

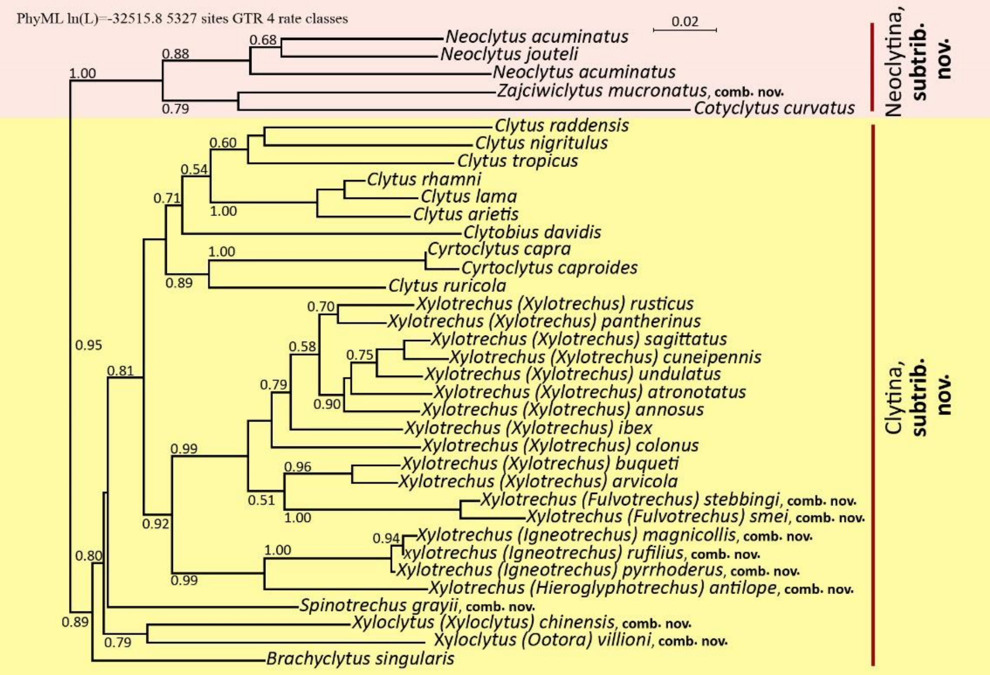

**Figure 3.** Phylogenetic subtree of Clytini, **trib. sensu nov.** based on 12S rRNA, 16S rRNA, COI, 18S rRNA, 28S rRNA genes sequences phylogeny. The branch support SH-like values are shown with the threshold rule SH>0.50.

Clytini, **trib. sensu nov.**

The clade consists of two subclades: 1) *Neoclytus* + *Cotyclytus*; 2) *Brachyclytus*, *Clytus* + *Cyrtoclytus* + *Clytobius* and *Xylotrechus*. Both subclades are well separated from each other with a high level of branches support (SH=1.00 and SH=0.89 respectively), which means that they should be considered as separate subtribes: Neoclytina, **subtrib. nov.** and Clytina, **subtrib. nov.** Genus *Neoclytus* Thomson, 1860 is polyphyletic. At least *Neoclytus mucronatus* (Fabricius, 1775) belongs to a separate genus and distantly related to *Cotyclytus curvatus* (Germar, 1821). *Clytus* also is polyphyletic. *Clytus ruricola* (Olivier, 1795) is related to *Cyrtoclytus* Ganglbauer, 1881. *Clytobius davidis* (Fairmaire, 1878) represents the separate clade related to *Clytus*. *Xylotrechus* is totally polyphyletic and represented by at least three distinct clades: 1) *Xylotrechus chinensis* Chevrolat, 1852 + *Xylotrechus villioni* Villard, 1892; 2) *Xylotrechus grayii* (White, 1855); 3) *Xylotrechus* s.str. All of them should be considered as independent genera. Although, it is likely that *Xylotrechus* s.str. (the third clade) also, nonmonophyletic. In this paper, I accepted statement that *Xylotrechus* s.str. is monophyletic in general.

Chlorophorini, **trib. nov**.

The clade consists of four subclades: 1) *Epiclytus yokoyamai* (Kano, 1933); 2) *Rhaphuma elongata* Gressitt, 1940; 3) (*Plagionotus* + *Echinocerus*) + (*Megacyllene* + *Placosternus*); 4) *Chlorophorus*, *Demonax*, *Clytoleptus*, *Sarosesthes*, *Rhaphuma*, *Clytocera*, *Rhabdoclytus*. First two subclades are basal and independent of the others. The last two subclades represent crown species rich part of phylogenetic tree. Both clades well separated with strong branches support (SH=0.99 and SH=0.82 respectively) and have crucial morphological differences. I propose recognize them as subtribes: Plagionotina, **subtrib. nov.** and Chlorophorina, **subtrib. nov.** *Echinocerus* is a separate genus independent of *Plagionotus* s.str. The genus *Placosternus*, **syn. nov.** is part of the genus *Megacyllene*. Genus *Chlorophorus* is completely polyphyletic and clearly divided on three distinct unrelated lineages: 1) *Chlorophorus* s.str. (*Chlorophorus annulatus* (Hope, 1831), *Chlorophorus varius* (O.F. Müller, 1766), *Chlorophorus signaticollis* (Laporte de Castelnau & Gory, 1841), *Chlorophorus anticemaculatus* Schwarzer, 1925); 2) *Chlorophorus sartor* (O.F. Müller, 1766); 3) *Chlorophorus diadema* Motschulsky, 1853; 4) the rest 9 studied species of *Chlorophorus*. *Chlorophorus sartor* is an ally of *Rhaphuma gracilipes* (Faldermann, 1835), nested within the same clade with *Demonax* (*Demonax substitutus* Gressitt, 1951 + *Demonax bidenticornis* Hayashi, 1974) and *Rhabdoclytus acutivittis* (Kraatz, 1879). *Chlorophorus diadema* belongs to the clade with *Demonax transilis*, *Clytoleptus albofasciatus* (Laporte & Gory, 1835), *Sarosesthes fulminans* (Fabricius, 1775) and *Rhaphuma xenisca* (Bates, 1884). Genus *Rhaphuma* is completely polyphyletic.

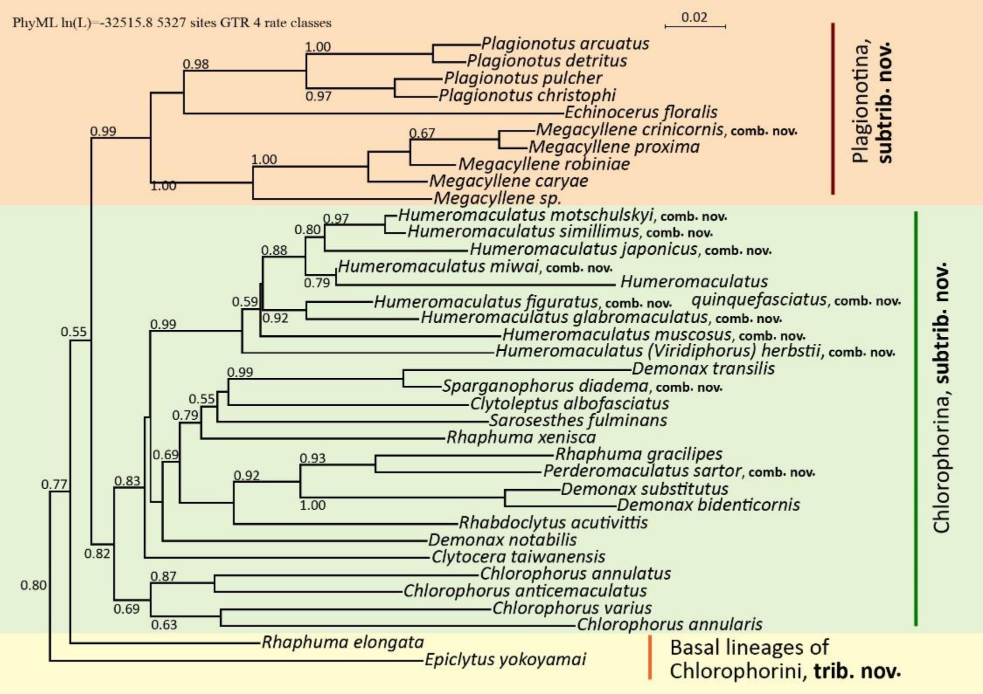

**Figure 4.** Phylogenetic subtree of Chlorophorini, **trib. nov.** based on 12S rRNA, 16S rRNA, COI, 18S rRNA, 28S rRNA genes sequences phylogeny. The branch support SH-like values are shown with the threshold rule SH>0.50.

## Discussion

The current study has clearly shown that Clytini s.l. is nonmonophyletic, which confirms the ideas of previous studies [25, 39]. Grebennikov and al. suggested polyphyly of Clytini s.l. due to placement of Obriini Mulsant, 1839 within them on the phylogenetic tree [25]. However, this model is not confirmed by the current study or the results of Lee & Lee [39]. I fully agree with the definition of Lee & Lee [39] that Clytini s.l. is paraphyletic when Anagliptini included in the analysis. However, my findings show deeper differences between clades than paraphilia, indicating the polyphyletic nature of Clytini s.l. According this, Clytini s.l. constitutes two well-separated clades, which are considered as separate tribes: Clytini, **trib. sensu nov.** and Chlorophorini, **trib. nov**. The results show that the molecular difference between Clytini, **trib. sensu nov.** and Chlorophorini, **trib. nov**. strongly corresponds to the morphological differences between them. In particular, Chlorophorini, **trib. nov.** easily distinguished from Clytini, **trib. sensu nov.** by following features: 1) narrow forehead with closely spaced antenna bases; 2) metepimera four times longer than wider. In contrast, Clytini, **trib. sensu nov.** has wide forehead, widely separated antenna and twice as long as wider metepimera [7, 17, 58].

All three tribes Anaglyptini, Clytini, **trib. sensu nov.** and Chlorophorini, **trib. nov.** are closely related and constitute large monophyletic superclade. I considered it as supertribe Chlorophoritae, **supertrib. nov.** This confirmed an idea of Leconte & Horn [37] who divided Clytini on three groups of genera: "Anaglypti" = Anaglyptini, "Cliti" = Clytini, **trib. sensu**

**nov.** and "Cyllenes" = Chlorophorini, **trib. nov.** on the basis of morphology. It also should be emphasized that Chlorophoritae, **supertrib. nov.** is the most progressive and evolutionary young clade within Cerambycinae [25, 39, 50, 72].

Several large groups of genera have been identified within Clytini, **trib. sensu nov.** and Chlorophorini, **trib. nov**. Lee & Lee showed that *Neoclytus mucronatus* (Fabricius, 1775) is the sister lineage to *Clytus* + *Perissus* + *Xylotrechus* clade [39]. In the current study, I confirm overall results of Lee & Lee [39]. I found that *Neoclytus* and *Zajciwiclytus*, **gen. nov.** and *Cotyclytus* comprise a common clade that is the sister to the rest Clytini, **trib. sensu nov**. I have concluded that both clades should be considered as separate subtribes Neoclytina, **subtrib. nov.** and Clytina, **subtrib. nov.** Lee & Lee also showed that *Plagionotus* is the sister clade to the clade *Chlorophorus* + *Demonax* + *Rhaphuma* [39]. Their results are confirmed in the current study. Furthermore, I showed that Palearctic *Plagionotus* and Nearctic *Megacyllene* constitute the monophyletic clade, that is sister to the clade *Chlorophorus* + *Demonax* + *Rhaphuma*. Thus, I considered both of them in the rank of subtirbes: Plagionotina, **subtrib. nov.** and Chlorophorina, **subtrib. nov.** respectively.

Internal phylogeny of Clytini, **trib. sensu nov.** and Chlorophorini, **trib. nov**. remains intricate and unclear in many ways. The current results make only a partial contribution to its understanding. While the phylogeny of *Neoclytus*, *Xylotrechus*, *Clytus*, *Plagionotus*, *Meacyllene* is more or less clear, then for *Chlorophorus*, *Demonax*, *Rhaphuma* it remains mostly unresolved.

***Neoclytus***. I found that genus *Neoclytus* is nonmonophyletic. At least North American *Neoclytus mucronatus* belongs to separate clade then rest studied species (*Neoclytus acuminatus* (Fabricius, 1775); *Neoclytus jouteli* Davis, 1904; *Neoclytus leucozonus* (Laporte de Castelnau & Gory, 1836). Furthermore, Ray and al. indicated several species groups of *Neoclytus* which differs by pheromones [59]. For instance, males of *Neoclytus mucronatus* and several other species produced (R)-3-hydroxyhexan-2-one only one component of pheromone. Contrary them, males of *Neoclytus acuminatus* produced (2S, 3S)-2,3-hexanediol as their dominant or sole pheromone component. Over more, according to my results *Neoclytus mucronatus* is nested in the common clade with South American *Cotyclytus curvatus* (Germar, 1821). However, both species are very distant relatives with significant morphological differences [43]. I considered to establish genus *Zajciwiclytus*, **gen. nov.** for *Neoclytus mucronatus* = *Zajciwiclytus mucronatus*, **comb. nov**.

***Xylotrechus.*** My current results showed that genus *Xylotrechus* s.l. is completely polyphyletic. It consists at least of three independent clades: 1) *Xylotrechus chinensis* + *Xylotrechus villioni*; 2) *Xylotrechus grayii*; 3) *Xylotrechus* s.str. Moreover, the third clade is deeply paraphyletic and represents two evolutionary lineages: 1) *Xylotrechus antilope* (Schönherr, 1817) + (*Xylotrechus pyrrhoderus* Bates, 1873 + *Xylotrechus magnicollis* (Fairmaire, 1888) + *Xylotrechus rufilius* Bates, 1884) and 2) *Xylotrechus* s.str. (for details see taxonomical summary below). The polyphyletic nature of *Xylotrechus* s.l. is also indicated by Lee and Lee [39] and Grebennikov and al. [25]. In contrast to molecular research, in modern taxonomic works *Xylotrechus* s.l. is considered monophyletic and is divided into 5 subgenera: 1) *Kostiniclytus* Danilevsky, 2009; 2) *Ootora* Niisato & Wakejima, 2008; 3) *Rusticoclytus* Vives, 1977; 4) *Xyloclytus* Reitter, 1913; 5) *Xylotrechus* s. str. [11, 12, 41, 61]. However, my results do not confirm this division. First, I found that *Xylotrechus chinensis* and *Xylotrechus villioni* form a common clade, which is separate from the others and is basal in Clytina, **subtrib. nov.** Therefore, I propose to consider this clade as an independent genus *Xyloclytus*, **gen. stat. nov.** with two subgenra: *Xyloclytus* and *Ootora*. Secondly, *Xylotrechus grayii* represents an independent clade, which I consider as a separate genus *Spinotrechus*, **gen. nov**. Third, all 17 remaining species included in the analysis form a large paraphyletic clade, which I consider to be genus *Xylotrechus* s.str. Within the clade there are two subclades. First of them represents a wide range of Palearctic, Oriental and Nearctic species with very diverse morphologies. Within the clade, a group of oriental species (*Xylotrechus smei* (Laporte de Castelnau & Gory, 1836) + *Xylotrechus stebbingi* Gahan, 1906) is clearly distinguished, which I propose to allocate to a separate subgenus of *Fulvotrechus*, **subgen. nov.** The grouping of *Xylotrechus arvicola* (Olivier, 1795) and *Xylotrechus buqueti* (Laporte de Castelnau & Gory, 1836) with high branch support (SH=0.96) remains unclear and will require further research in the future. The remaining species of subclades form a dense cluster, which I consider as a subgenus of *Xylotrechus* s. str. These include, among others, representatives of the current subgenus *Rusticoclytus*. My results show that *Rusticoclytus* is non-monophyletic: a close relationship is found between the European *Xylotrechus rusticus* (Linnaeus, 1758) and *Xylotrechus pantherinus* (Savenius, 1825), however, the North American *Xylotrechus annosus* (Say, 1826) is clearly of separate origin. I consider *Rusticoclytus* is synonymous of *Xylotrechus* s.str.

The second subclade is evolutionarily distant from the first subclade and is represented by two groups of species: 1) *Xylotrechus antilope* (Schönherr, 1817) and 2) *Xylotrechus pyrrhoderus* Bates, 1873 + *Xylotrechus rufilius* Bates, 1884 + *Xylotrechus magnicollis* (Fairmaire, 1888). I consider them as a separate subgenera *Hieroglyphotrechus*, **subgen. nov.** and *Igneotrechus*, **subgen. nov**. respectively.

Unfortunately, the determination of the taxonomic position of *Kostiniclytus* is impossible, as species of this subgenus remain unsequenced.

***Teratoclytus***. Lee & Lee (2020) found that Teratoclytus *plavilstshikovi* Zajciw, 1937 (*not Zaitzev* see comments in taxonomical summary) belongs to the tribe Anaglyptini. My results completely coincide with their conclusions. I consider it expedient to transfer the genus *Teratoclytus* to the tribe Anaglyptini

***Cyrtoclytus.*** According to Lee & Lee (2020), *Cyrtoclytus* is polyphyletic, but my results suggest otherwise. To finally clarify the internal phylogeny of *Cyrtoclytus*, a larger number of species should be studied.

***Clytus***. The current study demonstrate that the genus *Clytus* is nonmonophyletic. At least North American *Clytus ruricola* (Olivier, 1800) belongs to the common clade with *Cyrtoclytus*.

***Plagionotus***. The current study has also resolved a number of taxonomic disputes based on morphological classification. In particular, the data of molecular phylogeny indicate the separation of the genus *Echinocerus* from the genus *Plagionotus*. *Echinocerus* is a separate evolutionary branch. However, both *Echinocerus* and *Plagionotus* descended from the common ancestor. In fact, my results confirm the idea of Villiers [71] and the later conclusions of Kasatkin [31], obtained on the basis of studying the external morphological features and anatomical structure of the endophallus of *Plagionotus* s.l. Kasatkin proved the independence of the genus *Echinocerus* [31]. He introduced the substituting name *Paraplagionotus* Kasatkin, 2005, considering *Echinocerus* Mulsant, 1863 the younger homonym of *Echinocerus* White, 1846. Later, Alonso-Zarazaga proved the absence of the need to establish the substituting name for *Echinocerus* [1]. In the light of the current results, unlike some modern authors [52, 61], *Echinocerus* should be considered an independent genus, not a subgenus. However, it is impossible to determine the taxonomic position of *Neoplagionotus* Kasatkin, 2005, as species of this genus remain unsequenced. The internal phylogeny of the genus *Plagionotus* s.str. indicates the presence of at least two separate evolutionary branches: 1) West Palearctic *Plagionotus arcuatus* (Linnaeus, 1758) and *Plagionotus detritus* (Linnaeus, 1758); 2) Far Eastern *Plagionotus pulcher* Blessig, 1872 and *Plagionotus christophi* (Kraatz, 1879).

***Megacyllene***. The genus *Megacyllene* is monophyletic. Moreover, its terminal taxon is *Placosternus crinicornis* (Chevrolat, 1860). Hoping separated the genus *Placosternus* from the *Cyllene* Newman, 1840 on the basis of a number of morphological features, which include unspined antennae; face morphology; strongly tapered elytra with acutely spined apices [28]. Based on the results of the current molecular analysis, I consider *Placosternus* is synonymous of *Megacyllene*.

***Rhaphuma***. The phylogeny of the genus *Rhaphuma*, which has about 223 species, remains completely unclear. In the current study, suitable sequences were used for only three species, including *Rhaphuma xenisca*, *Rhaphuma gracilipes* and *Rhaphuma elongata*. As a result, I discovered complete polyphyly of the genus – each of the species, included in the analysis, is a separate evolutionary branch. It is currently not possible to establish intrageneric phylogenetic relations within *Rhaphuma*. Therefore, more detailed studies with sequencing of a significant number of species will be required in the future.

***Demonax***. The phylogeny of the genus *Demonax* remains unclear. Lee & Lee indicate polyphyly of *Demonax* [39]. The current results also indicate polyphyly of *Demonax* based on only four species that were included in the analysis. They divided in separate clades as follows: 1) *Demonax notabilis*; 2) *Demonax substitutus* + *Demonax bidenticornis*; 3) *Demonax transilis*. The genus needs a deep and comprehensive revision.

***Chlorophorus***. Lee & Lee found *Chlorophorus* polyphyly, despite the fact that only three species were included in their study [39]. They showed that *Chlorophorus diadema*, is a separate clade from the rest of *Chlorophorus*. My results, based on the analysis of sequences of 15 species, clearly demonstrate that the genus *Chlorophorus* is completely polyphyletic. Chlorophorus consists of at least four independent clades: 1) *Chlorophorus annularis* + *Chlorophorus varius* + *Chlorophorus anticemaculatus* + *Chlorophorus annulatus*; 2) *Chlorophorus sartor*; 3) *Chlorophorus diadema*; 4) *Chlorophorus herbstii* (Brahm, 1790) + *Chlorophorus muscosus* (Bates, 1873) + (*Chlorophorus glabromaculatus* (Goeze, 1777) + *Chlorophorus figuratus* (Scopoli, 1763)) + (*Chlorophorus quinquefasciatus* (Castelnau & Gory, 1841) + *Chlorophorus miwai* Gressitt, 1936 + *Chlorophorus japonicus* (Chevrolat, 1863) + *Chlorophorus simillimus* (Kraatz, 1879) + *Chlorophorus motschulskyi* (Ganglbauer, 1887)). These results are very different from the proposed by Özdikmen [53] division of *Chlorophorus* into 5 subgenera: 1) subenus *Chlorophorus* s. str. (*Chlorophorus annularis*); 2) subenus *Immaculatus* Özdikmen, 2011 (*Chlorophorus kanoi* Hayashi, 1963); 3) subenus *Humeromaculatus* Özdikmen, 2011 (*Chlorophorus sartor*) 4) subenus *Perderomaculatus* Özdikmen, 2011 (*Chlorophorus figuratus*), 5) subenus *Crassofasciatus* Özdikmen, 2011 (*Callidium trifasciatum* Fabricius, 1781). Molecular data do not confirm this division based on morphological features used by Özdikmen [53].

The first clade on my phylogenetic tree includes type species *Chlorophorus annularis*, thus I consider it as a genus *Chlorophorus* s. str. Based on the current results *Chlorophorus* s. str. is a basal clade in Chlorophorina, **subtrib. nov**. The second clade of *Chlorophorus sartor* is sister to *Rhaphuma gracilipes* and should be separated into genus

*Perderomaculatus*, **gen. stat. nov**. The third clade of *Chlorophorus diadema* is sister to *Demonax transilis*. I consider it as the separate genus *Sparganophorus* **gen. nov**. The fourth clade is the most diverse both in number of species and in morphology. I consider this clade in the rank of an independent genus *Humeromaculatus*, **gen. stat. nov**. with two subgenera: 1) *Humeromaculatus* s.str. and 2) *Viridiphorus*, **subgen. nov.** for *Chlorophorus herbstii*.

It should be noted that the phylogeny of *Chlorophorus* s.l. remains far from its final solution. In particular, the taxonomic position of two subgenera *Immaculatus* and *Crassofasciatus* proposed by Özdikmen [53] remains completely unknown in the light of the molecular phylogenetics. More sequences of species should be included in future studies to definitively elucidate the phylogeny of the *Chlorophorus* s.l.

## Taxonomical summary and new nomenclature acts

In this section the taxa are presented in phylogenetic order, due to phylogenetic tree (fig. 2).

### Supertribe Chlorophoritae, **supetrib. nov.**

**Type genus**: *Chlorophorus* Chevrolat, 1863: 290 [10]

**Description**: Body more or less elongated, narrow, subcylindrical. Clypeus shortened. Forehead shortened, almost steep, often with longitudinal keels or grooves. Antennae typically short, reaching the first third of the wings. Pronotum subspherical (transverse or oblong). Body covered with hair, typically with a contrasting pattern of hair bands. Legs typically elongated, often with thickened femora. Behavior and color of beetles usually mimic wasps and other Aculeata (Insecta: Hymenoptera).

**Diagnosis**: Pronotum subspherical; body elongated, subcylindrical, with a contrasting hair pattern.

**Definition**: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Chlorophorus annularis* (Fabricius, 1787), *Clytus arietis* (Linnaeus, 1758), *Anaglyptus mysticus* (Linnaeus, 1758), but not including *Cerambyx cerdo* Linnaeus, 1758, *Compsocerus barbicornis* Audinet-Serville, 1834, *Callidium violaceum* (Linnaeus, 1758).

### 1. Tirbe Anaglyptini Lacordaire, 1868: 404 [34]

Anaglyptides Lacordaire, 1868: 404 [34]
Anaglypti LeConte, 1873: 319 [34]

**Type genus**: *Anaglyptus* Mulsant, 1839: 91 [46]

**Definition**: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Anaglyptus mysticus* (Linnaeus, 1758), but not including *Clytus arietis* (Linnaeus, 1758), *Chlorophorus annularis* (Fabricius, 1787).

**Subordinated taxa**:

1. Genus *Teratoclytus* Zajciw [*not Zaitzev*], 1937: 213 [75] (type species *Teratoclytus plavilstshikovi* Zajciw [*not Zaitzev*], 1937: 213 [75])

– *Teratoclytus plavilstshikovi* Zajciw [*not Zaitzev*], 1937

**Coments:** The genus *Teratoclytus* and the species *Teratoclytus plavilstshikovi* were described by Dmytro Zajciw [75], a Ukrainian (and later Brazilian) entomologist who was associate professor at Kharkiv University. However, the description is attributed to the

Russian entomologist Philip Adamovich Zaitsev, due to the political motives of the Soviet totalitarian regime. Dmytro Zajciw managed to escape to Brazil from the mass repressions and executions of Ukrainian scientists on ethnic grounds that took place in the USSR. Until 1991 (the year of collapse of the USSR), his works were banned from distribution and confiscated from libraries by the Soviet totalitarian regime. Today, a copy of Dmitro Zajciw's original article on *Teratoclytus* is kept at the I.I. Schmalhausen Institute of Zoology NASU in Kyiv, Ukraine. Unfortunately, the original article, in addition to being written in Ukrainian, is physically inaccessible to experts in Cerambycidae outside of Ukraine. Therefore, there is still false information in the scientific literature about the authorship of the first description of *Teratoclytus*. I hope that with this work I will correct the unjust oblivion to which a famous entomologist was subjected during the Soviet occupation.

2. Genus *Anaglyptus* Mulsant, 1839: 91 [46] (type species *Leptura mystica* Linnaeus, 1758: 398 [40])

– *Anaglyptus niponensis* Bates, 1884
– *Anaglyptus mysticus* (Linnaeus, 1758)
– *Anaglyptus gibbosus* (Fabricius, 1787)
– *Anaglyptus matsushitai* Hayashi, 1955

3. Genus *Paraclytus* Bates, 1884: 234 [4] (type species *Paraclytus excultus* Bates, 1884: 234 [4])

– *Paraclytus excultus* Bates, 1884

### 2. Tribe Clytini Mulsant, 1839: 27 [46], **trib. sensu nov.**

Clytitae J. Thomson, 1860: 214 [67]
Clytides C. Thomson, 1866: 34 [66]
Clytinae Pascoe, 1869: 597 [56]
Plagithmysides Sharp, 1896: 238 [64]
Clytina Reitter, 1912: 46 [60]

**Type genus**: *Clytus* Laicharting, 1784: 88 [35]

**Description**: body elongated, subcylindrical. Head short, typically with longitudinal carinae or sulcus on the forehead. Forehead wide. Antennae short, widely spaced on the forehead, reaching the first third of the wings. Pronotum subspherical, oblong. Elytra elongated, apically truncated, with a hair pattern of spots and transverse stripes. Legs elongated. Femora gradually thickened posteriorly. Metepimera twice longer than wider, extend over hind angles of the 1st ventrite.

**Diagnosis**: Forehead wide; antennae widely spaced on the forehead; metepimera twice longer than wider.

**Definition**: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA +2 8S rRNA genes phylogeny. The least inclusive clade containing *Clytus arietis* (Linnaeus, 1758), but not including *Anaglyptus mysticus* (Linnaeus, 1758), and *Chlorophorus annularis* (Fabricius, 1787).

**Subordinated taxa**:

### 2.1. Subtribe Neoclytina, **subtrib. nov.**

**Type genus**: *Neoclytus* Thomson, 1860: 67 [67]

**Description**: Body elongated, subcylindrical, with a hair pattern of spots and transverse stripes. Head short, with a wide longitudinal sulcus on the forehead. Antennae short, gradually thickened posteriorly. Pronotum subspherical, oblong, enlarged, with short transverse keels or fields of coarse chitin grains. Elytra slightly attenuated posteriorly, apically truncated, acutely spined. Legs very elongated. Femora gradually thickened posteriorly, apically acutely spined.

**Diagnosis**: Pronotum with short transverse keels or fields of coarse chitin grains; femora thickened posteriorly, apically acutely spined.

**Definition**: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Neoclytus acuminatus* (Fabricius, 1775), but not including *Clytus arietis* (Linnaeus, 1758).

**Subordinated taxa**:

1. Genus *Neoclytus* Thomson, 1860: 67 [67] (type species *Callidium erythrocephalum* Fabricius, 1787: 156 [16] (= *Callidium acuminatum* Fabricius, 1775: 194 [15]);

– *Neoclytus leucozonus* (Laporte de Castelnau & Gory, 1836)

– *Neoclytus jouteli* Davis, 1904

– *Neoclytus acuminatus* (Fabricius, 1775)

2. Genus *Zajciwiclytus*, **gen. nov.** (type species *Callidium mucronatum* Fabricius, 1775: 193 [15]) – body elongated, subcylindrical, with a hair pattern of spots and transverse stripes. Pronotum subspherical, oblong, with a wide central longitudinal band of very coarse chitin grains. Elytra attenuated posteriorly, apically truncated, acutely spined on the outer edge of apex. Legs very elongated. Femora gradually thickened posteriorly, apically acutely spined. **Diagnosis**: Pronotum with a wide central longitudinal band of very coarse chitin grains; elytral apex acutely spined on the outer edge. **Etymology**: named in honor of Dmytro Zajciw an Ukrainian and Brazilian entomologist.

– *Zajciwiclytus mucronatus* (Fabricius, 1775), **comb. nov.**

3. Genus *Cotyclytus* Martins & Galileo, 2011: 127 [43] (type species *Clytus curvatus* Germar, 1821: 171 [20]);

– *Cotyclytus curvatus* (Germar, 1821)

### 2.2. Subtribe Clytina, **subtrib. nov.**

**Type genus**: *Clytus* Laicharting, 1784: 88 [35]

**Description**: Body elongated, subcylindrical, with a hair pattern of spots and transverse stripes. Head short, forehead wide, with longitudinal carinae or sulcus. Antennae short, gradually thickened posteriorly. Pronotum subspherical, slightly oblong, uniformly sculptured. Elytra parallel, apically truncated. Legs weak elongated. Femora gradually thickened posteriorly.

**Diagnosis**: Forehead with longitudinal keels or groove; pronotum subspherical and uniformly sculptured.

**Definition**: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Clytus arietis* (Linnaeus, 1758), but not including *Neoclytus acuminatus* (Fabricius, 1775).

**Subordinated taxa**:

1. Genus *Brachyclytus* Kraatz, 1879: 107 [33] (type species *Brachyclytus singularis* Kraatz, 1879: 107 [33]);

– *Brachyclytus singularis* Kraatz, 1879

2. Genus *Xyloclytus* Reitter, 1912: 46 [60], **gen. stat. nov.** (type species *Clytus chinensis* Chevrolat, 1852: 416 [8])

2.1. Subgenus *Xyloclytus* Reitter, 1912: 46 [60] (type species *Clytus chinensis* Chevrolat, 1852: 416 [8])

– *Xyloclytus* (*Xyloclytus*) *chinensis* (Chevrolat, 1852), **comb. nov.**

2.2. Subgenus *Ootora* Niisato & Wakejima, 2008: 442 [51] (type species *Clytus* (*Xylotrechus*) *villioni* Villard, 1892: [70])

– *Xyloclytus* (*Ootora*) *villioni* (Villard, 1892), **comb. nov.**

3. Genus *Spinotrechus*, **gen. nov.** (type species *Clytus grayii* White, 1855: 261 [73]) – Body elongated, subcylindrical, with a hair pattern of spots and transverse stripes. Head short, forehead wide, with three longitudinal carinae. Antennae short, gradually thickened posteriorly, 3-5th antennomeres with distinct spines. Pronotum subspherical, roughly sculptured. Elytra parallel, apically rounded, with acute spine on the outer edge of apex. **Diagnosis**: Frons with three longitudinal carinae; 3-5th antennomeres with distinct spines. **Etymology**: *spina* – thorn + *τρέχω* – to run.

– *Spinotrechus grayii* (White, 1855), **comb. nov.**

4. Genus *Cyrtoclytus* Ganglbauer, 1882: 736 [18] (type species *Callidium* (*Clytus*) *capra* Germar, 1823: 518 [21])

– *Cyrtoclytus capra* (Germar, 1823)
– *Cyrtoclytus caproides* (Bates, 1873)

5. Genus (group I) *Clytus* Laicharting, 1784: 88 [35] (type species *Cerambyx arietis* Linnaeus, 1758: 399 [40])

– *Clytus ruricola* (Olivier, 1800)

6. Genus *Clytobius* Gressitt, 1951: 261 [27] (type species *Clytus davidis* Fairmaire, 1878: 132 [13]);

– *Clytobius davidis* (Fairmaire, 1878)

7. Genus (group II) *Clytus* Laicharting, 1784: 88 [35] (type species *Cerambyx arietis* Linnaeus, 1758: 399 [40])

– *Clytus arietis* (Linnaeus, 1758)
– *Clytus lama* Mulsant, 1850
– *Clytus rhamni* Germar, 1817
– *Clytus tropicus* (Panzer, 1795)
– *Clytus raddensis* Pic, 1904
– *Clytus nigritulus* Kraatz, 1879

8. Genus *Xylotrechus* Chevrolat, 1860: 465 [9] (type species *Clytus* (*Xylotrechus*) *sartorii* Chevrolat, 1860: 492 [9]);

8.1. Subgenus *Xylotrechus* Chevrolat, 1860: 465 [9] (type species *Clytus* (*Xylotrechus*) *sartorii* Chevrolat, 1860: 492 [9]);

*Rusticoclytus* Vives, 1977, **syn. nov.**
– *Xylotrechus* (*Xylotrechus*) *colonus* (Fabricius, 1775)
– *Xylotrechus* (*Xylotrechus*) *ibex* (Gebler, 1825)
– *Xylotrechus* (*Xylotrechus*) *rusticus* (Linnaeus, 1758)
– *Xylotrechus* (*Xylotrechus*) *pantherinus* (Savenius, 1825)
– *Xylotrechus* (*Xylotrechus*) *annosus* (Say, 1827)
– *Xylotrechus* (*Xylotrechus*) *atronotatus* Pic, 1917
– *Xylotrechus* (*Xylotrechus*) *undulatus* (Say, 1824)
– *Xylotrechus* (*Xylotrechus*) *cuneipennis* (Kraatz, 1879)
– *Xylotrechus* (*Xylotrechus*) *sagittatus* (Germar, 1821)

– *Xylotrechus* (*Xylotrechus*) *arvicola* (Olivier, 1800)

– *Xylotrechus* (*Xylotrechus*) *buqueti* (Castelnau & Gory, 1841)

8.2. Subgenus *Fulvotrechus*, **subgen. nov.** (type species *Xylotrechus stebbingi* Gahan, 1906: 244 [17]) – Body elongated, subcylindrical, with a pale and non-contrasting hair pattern of transverse stripes. Integument brown. Head short, forehead wide, slightly attenuated anteriorly, with V-shaped longitudinal carina. Antennae short. Pronotum subspherical, enlarged, with rough sculptured central band of chitin grains and one or two round lateral spots. Elytra parallel, apically rounded, with acute spine on the outer edge of apex. **Diagnosis**: Integument fulvous; pronotum enlarged with rough sculptured central band of chitin grains and one or two round lateral spots. **Etymology**: *fulvus* – fulvous + *τρέχω* – to run.

– *Xylotrechus* (*Fulvotrechus*) *smei* (Castelnau & Gory, 1841), **comb. nov.**

– *Xylotrechus* (*Fulvotrechus*) *stebbingi* (Gahan, 1906), **comb. nov.**

8.3. Subgenus *Hieroglyphotrechus*, **subgen. nov.** (type species *Clytus antilope* Schönherr, 1817: 465 [62]) – Body elongated, subcylindrical, slightly widened, with contrasting hair pattern of transverse stripes. Head short, forehead wide with two poorly emerged longitudinal carinae. Antennae widely spaced on the forehead, short, reach first third of elytra. Pronotum subspherical, enlarged, with a rough sculpture of small transverse wrinkles. Elytra parallel, apically rounded, with acute spine on the outer edge of apex. **Diagnosis**: Pronotum roughly sculptured of small transverse wrinkles; forehead with two poorly emerged longitudinal carinae. **Etymology**: *hieroglyphicus* – hieroglyphic + *τρέχω* – to run; Drapiez described *Clytus antilope* as *Callidium hieroglyphicum* [14].

– *Xylotrechus* (*Hieroglyphotrechus*) *antilope* (Schönherr, 1817), **comb. nov.**

8.4. Subgenus *Igneotrechus*, **subgen. nov.** (type species *Xylotrechus pyrrhoderus* Bates, 1873: 200 [3]) – Body elongated, subcylindrical, slightly widened, with contrasting hair pattern of transverse stripes. Integument black except red (occasionally black) pronotum. Head short, forehead slightly narrowed with three poorly emerged longitudinal carinae: central longitudinal and two lateral form a V-shaped figure. Antennae widely spaced on the forehead, short, reach elytral humeri. Pronotum subspherical, enlarged, with a rough sculpture. Elytra parallel, apically rounded, with acute spine on the outer edge of apex. **Diagnosis**: Pronotum red; forehead with three poorly emerged longitudinal carinae. **Etymology**: *igneus* – fiery + *τρέχω* – to run.

– *Xylotrechus* (*Igneotrechus*) *pyrrhoderus* (Bates, 1873), **comb. nov.**

– *Xylotrechus* (*Igneotrechus*) *magnicollis* (Fairmaire, 1888), **comb. nov.**

– *Xylotrechus* (*Igneotrechus*) *rufilius* (Bates, 1884), **comb. nov.**

### 3. Tribe Chlorophorini, **trib. nov.**

Cyllenes Leconte & Horn, 1883: 302 [37], **syn. nov.**

**Type genus**: *Chlorophorus* Chevrolat, 1863: 290 [10]

**Description:** Body significantly elongated, subcylindrical, with a hair pattern of spots and transverse stripes. Head slightly elongated, clypeus well developed. Forehead narrowed with closely spaced antennae bases. Antennae elongated, reach at least the middle of elytra. Pronotum subspherical, transverse or oblong. Elytra elongate, parallel, apically truncated. Legs elongated. Femora gradually thickened posteriorly. Metepimera 4 times longer than wider, extend over hind angles of the 1st ventrite.

**Diagnosis**: Forehead narrowed with closely spaced antennae bases; clypeus well developed; metepimera 4 times longer than wider.

**Definition**: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Chlorophorus annularis* (Fabricius, 1787), but not including *Anaglyptus mysticus* (Linnaeus, 1758), and *Clytus arietis* (Linnaeus, 1758).

**Subordinated taxa**:

### 3.1. Subtribe Plagionotina, **subtrib. nov.**

**Type genus**: *Plagionotus* Mulsant, 1842: 71 [47]

**Description**: Body subcylindrical, weakly elongated, slightly dorsoventrally flattened, with a hair pattern of spots and transverse stripes. Head short. Forehead narrowed with closely spaced antennae bases. Antennae elongated, reach at least the middle of elytra. Antennomeres often with solid posterior spine. Pronotum subspherical, transverse. Prosternal process very wide. Elytra elongate, parallel, with longitude sutural carinae (North American genera) or without it (Eurasian genera), apically truncated. Legs elongated. Femora gradually thickened posteriorly, often apically acutely spined.

**Diagnosis**: Body slightly dorsoventrally flattened; pronotum transverse; prosternal process very wide.

**Definition**: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Plagionotus detritus* (Linnaeus, 1758), but not including *Chlorophorus annularis* (Fabricius, 1787).

**Subordinated taxa**:

1. Genus *Plagionotus* Mulsant, 1839: 71 [46] (type species *Leptura detrita* Linnaeus, 1758: 399 [40])

– *Plagionotus detritus* (Linnaeus, 1758)
– *Plagionotus arcuatus* (Linnaeus, 1758)
– *Plagionotus christophi* (Kraatz, 1879)
– *Plagionotus pulcher* (Blessig, 1872)

2. Genus *Echinocerus* Mulsant, 1862: 143 [48] (type species *Leptura floralis* Pallas, 1773: 724 [54])

– *Echinocerus floralis* (Pallas, 1773)

3. Genus *Megacyllene* Casey, 1912: 348 [6] (type species *Cyllene spinifera* Newman, 1840: 8 [49]);

*Placosternus* Hopping, 1937: 447 [29], **syn. nov.**

– *Megacyllene caryae* (Gahan, 1908)
– *Megacyllene robiniae* (Forster, 1771)
– *Megacyllene proxima* (Castelnau & Gory, 1841)
– *Megacyllene crinicornis* (Chevrolat, 1860), **comb. nov.**

### 3.2. Subtribe **Chlorophorina, subtrib. nov.**

**Type genus**: *Chlorophorus* Chevrolat, 1863: 290 [10]

**Description**: Body significantly elongated, subcylindrical, with a hair pattern of spots and transverse stripes. Head slightly elongated, clypeus well developed. Forehead narrowed with closely spaced antennae bases. Antennae elongated, reach the second third of elytra or longer. Antennomeres often with a large posterior spike or long process. Pronotum subspherical, oblong. Prosternal process narrow. Elytra elongate, parallel, apically truncated or rounded. Legs very elongated. Femora gradually thickened posteriorly.

**Diagnosis**: Head slightly elongated; clypeus well developed; prosternal process narrow.

**Definition**: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Chlorophorus annularis* (Fabricius, 1787), but not including *Plagionotus detritus* (Linnaeus, 1758).

**Subordinated taxa**:

1. *Epiclytus* Gressitt, 1935: 173 [26] (*Clytus yokoyamai* Kano, 1933: 275 [30])

– *Epiclytus yokoyamai* (Kano, 1933)

2. Genus (group I) *Rhaphuma* Pascoe, 1858: 240 [55], (type species *Clytus quadricolor* Castelnau & Gory, 1841: 104 [36])

– *Rhaphuma elongata* Gressitt, 1940

3. Genus *Chlorophorus* Chevrolat, 1863: 290 [10], **sensu nov.** (type species *Callidium annulare* Fabricius, 1787: 156 [16]) – Body slightly elongated, subcylindrical, with a hair pattern of spots and transverse stripes. Head slightly elongated, clypeus well developed. Forehead trapezoidal, widened anteriorly, with longitude medial line. Antennal bases closely spaced. Antennae elongated, reach the second third of elytra. Typical antennal formula 1>3>5=4: 1st antennomere longer than 3rd; 3rd antennomere longer than 5th; 5th antennomere equal 4th. Pronotum subspherical, slightly oblong, convex. Prosternal process narrow, approximately 2 times wider than the edging of the procoxal cavities. Legs elongated. Outer side of middle (and often hind) femur with a very narrow longitudinal keel. First metatarsomere significantly longer then 2-5th together. **Diagnosis:** Forehead trapezoidal, widened anteriorly; antennal formula 1>3>5=4; prosternal process 2 times wider than the edging of the procoxal cavities; outer side of middle femur with a very narrow longitudinal keel.

– *Chlorophorus annularis* (Fabricius, 1787)

– *Chlorophorus varius* (Müller, 1766)

– *Chlorophorus anticemaculatus* Schwarzer, 1925

– *Chlorophorus annulatus* (Hope, 1831)

4. Genus *Clytocera* Gahan, 1906: 279 (type species *Clytocera chionospila* Gahan, 1906: 280)

– *Clytocera taiwanensis* Hayashi, 1974

5. Genus *Humeromaculatus* Özdikmen, 2011: 537 [53], **gen. stat. nov.** (type species *Cerambyx figuratus* Scopoli, 1763: 55 [63]) – Body elongated, subcylindrical, with a hair pattern of spots and transverse stripes. Head elongated; clypeus well developed. Forehead trapezoidal, widened anteriorly. Antennal bases closely spaced. Antennae elongated, reach the second third of elytra. Typical antennal formula 1=3=5>4: 1st antennomere equal 3rd and 5th; 5th antennomere longer than 4th. Pronotum subspherical, oblong, convex. Prosternal process narrow, as wide (or narrower) as edging of the procoxal cavities. Legs elongated. First metatarsomere significantly longer then 2-5th together. **Diagnosis:** Forehead trapezoidal, widened anteriorly; antennal formula 1=3=5>4; pronotum oblong; prosternal process narrow, as wide as edging of the procoxal cavities.

5.1. Subgenus *Viridiphorus*, **subgen. nov.** (type species *Callidium herbstii* Brahm, 1790: 148 [5]) – Body notably elongated, subcylindrical, with contrasting hair pattern of spots. Head elongated; clypeus well developed. Forehead trapezoidal, widened anteriorly, laterally edged with thin ribs. Antennal bases closely spaced. Antennae elongated, reach the second third of elytra. Typical antennal formula 1<3>5=4: 3rd antennomere longer than 1st and 5th; 5th antennomere equal 4th. Pronotum subspherical, notably oblong, convex. Prosternal process narrow, as wide (or narrower) as edging of the procoxal cavities. Legs elongated.

First metatarsomere significantly longer then 2-5th together. **Diagnosis:** Forehead laterally edged with thin ribs; antennal formula 1<3>5=4; pronotum notably oblong; Etymology: *viridis* – green + *φέρω* – to carry.

– *Humeromaculatus* (*Viridiphorus*) *herbstii* Brahm, 1790, **comb. nov.**

5.2. Subgenus *Humeromaculatus* Özdikmen, 2011: 537 [52] (type species *Cerambyx figuratus* Scopoli, 1763 [63])

– *Humeromaculatus* (*Humeromaculatus*) *muscosus* Bates, 1873, **comb. nov.**

– *Humeromaculatus* (*Humeromaculatus*) *figuratus* Scopoli, 1763, **comb. nov.**

– *Humeromaculatus* (*Humeromaculatus*) *glabromaculatus* (Goeze, 1777), **comb. nov.**

– *Humeromaculatus* (*Humeromaculatus*) *quinquefasciatus* (Castelnau & Gory, 1841), **comb. nov.**

– *Humeromaculatus* (*Humeromaculatus*) *miwai* Gressitt, 1936, **comb. nov.**

– *Humeromaculatus* (*Humeromaculatus*) *japonicus* (Chevrolat, 1863), **comb. nov.**

– *Humeromaculatus* (*Humeromaculatus*) *simillimus* (Kraatz, 1879), **comb. nov.**

– *Humeromaculatus* (*Humeromaculatus*) *motschulskyi* (Ganglbauer, 1887), **comb. nov.**

**Coments**:

1) Deviation from the typical antennal formula is present in: *Humeromaculatus* (*Humeromaculatus*) *muscosus*, **comb. nov. –** 1>3>5=4; *Humeromaculatus* (*Humeromaculatus*) *quinquefasciatus*, **comb. nov. –** 1>3=5>4; *Humeromaculatus* (*Humeromaculatus*) *japonicus*, **comb. nov.** – 1≥3≥5=4.

2) Genus *Humeromaculatus* is obviously paraphyletic, and in further studies its internal phylogeny will need to be reconsidered, using more sequences from more species.

6. Genus (group I) *Demonax* Thomson, 1861: 226 [68] (type species *Demonax nigrofasciatus* Thomson, 1861: 227 [68])

– *Demonax notabilis* (Pascoe, 1862)

7. Genus (group II) *Rhaphuma* Pascoe, 1858: 240 [55] (type species *Clytus quadricolor* Castelnau & Gory, 1841: 104 [36])

– *Rhaphuma xenisca* (Bates, 1884)

8. Genus *Sarosesthes* Thomson, 1864: 185 [69] (type species *Clytus fulminans* Fabricius, 1775: 192 [15])

– *Sarosesthes fulminans* (Fabricius, 1775)

9. Genus *Clytoleptus* Casey, 1912: 350 [6] (type species *Clytus albofasciatus* Castelnau & Gory, 1835: 96 [36])

– *Clytoleptus albofasciatus* (Castelnau & Gory, 1841)

10. Genus *Sparganophorus* **gen. nov**. (type species *Clytus diadema* Motschulsky, 1854: 48 [44]) – Body weakly elongated, subcylindrical, widened, with contrasting hair pattern of spots and transverse bands. Head elongated; clypeus well developed. Forehead trapezoidal, widened anteriorly, with median longitudinal carina. Antennal bases closely spaced. Antennae elongated, reach the middle of elytra. Typical antennal formula 1=3>5=4: 1st antennomere equal to 3rd; 3rd antennomere longer than 5th; 5th antennomere equal 4th. Pronotum subspherical, wide, convex. Prosternal process narrow, twice wider than edging of the procoxal cavities. Legs weakly elongated. First metatarsomere short, as long as 2-5th together. **Diagnosis**: Forehead with median longitudinal carina; antennal formula 1=3>5=4;

prosternal process twice wider than edging of the procoxal cavities; 1st metatarsomere as long as 2-5th together. **Ethymology**: *σπάργανα* – swaddling clothes + *φέρω* – to carry.

– *Sparganophorus diadema* (Motschulsky, 1854), **comb. nov.**

11. Genus (group II) *Demonax* Thomson, 1861: 226 [68] (type species *Demonax nigrofasciatus* Thomson, 1861: 227 [68])

– *Demonax transilis* Bates, 1884

12. Genus *Rhabdoclytus* Ganglbauer, 1887 [42] (type species *Clytus acutivittis* Kraatz, 1879: 111 [33])

– *Rhabdoclytus acutivittis* (Kraatz, 1879)

13. Genus (group III) *Demonax* Thomson, 1861: 226 [68] (type species *Demonax nigrofasciatus* Thomson, 1861: 227 [68])

– *Demonax substitutus* Gressitt, 1951

– *Demonax bidenticornis* Hayashi, 1974

14. Genus *Perderomaculatus* Özdikmen, 2011: 537 [53], **gen. stat. nov**. (type species *Cerambyx sartor* Müller, 1766, 188 [45]) – Body elongated, subcylindrical, with contrasting hair pattern of transverse bands. Head shortened; clypeus very reduced. Forehead square. Antennal bases widely spaced. Typical antennal formula 3>5>4>1: 3rd antennomere longer than 5th; 5th antennomere longer than 4th; 4th antennomere longer than 1st. The second antennomere twice long as wide. Pronotum subspherical, slightly oblong, convex. Prosternal process narrow, as wide as edging of the procoxal cavities. Legs elongated. First metatarsomere longer than 2-5th together. **Diagnosis:** Clypeus reduced; forehead square; antennal bases widely spaced; antennal formula 3>5>4>1; second antennomere twice long as wide.

– *Perderomaculatus sartor* (Müller, 1766), **comb. nov.**

15. Genus (group III) *Rhaphuma* Pascoe, 1858: 240 [55] (type species *Clytus quadricolor* Castelnau & Gory, 1841: 104 [36])

– *Rhaphuma gracilipes* (Faldermann, 1835)

## Conclusions

In summary, phylogeny based on 12S rRNA 16S rRNA COI 18S rRNA 28S rRNA genes revealed nonmonophyly of Clytini s.l., which consists two large clades: Clytini, **trib. sensu nov.** and Chlorophorini, **trib. nov**. Both tribes are related to Anaglyptini, forming a monophyletic supertribe Chlorophoritae, **supertrib. nov.** Internal phylogeny of Clytini, **trib. sensu nov.** and Chlorophorini, **trib. nov**. remains intricate and unclear in many ways. The current results make only a partial contribution to its understanding. While the phylogeny of *Neoclytus*, *Xylotrechus*, *Clytus*, *Plagionotus*, *Meacyllene* is more or less clear, then for *Chlorophorus*, *Demonax*, *Rhaphuma* it remains mostly unresolved.

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**Чи є осівцеві монофілетичними? Докази філоґенетичного аналізу за п'ятьма ґенами**

*Триба осівцеві (Coleoptera: Cerambycidae: Clytini) є однією із найбільших у родині жуків-скрипунів, налічуючи понад 1500 видів. Прогнозується, що розмаїття групи може перевищити 2000 видів. Надзвичайне розмаїття осівцевих ускладнює внутрішню систему триби, що потребує ревізії, як у світлі новітніх досліджень, так і передових методів їх провадження. До теперішнього часу осівцеві вважалися монофілетичними, при тому поєднуючи декілька груп родів із відмінними морфологічними характеристиками. А використання лише морфологічних ознак не дозволяло у цілковитій мірі розробити систему і філогенію осівцевих. Відомості молекулярної філогенетики, накопичені за останнє десятиліття, загалом, поставили під сумнів монофілетичність триби. У чинному дослідженні, вдалося здійснити вичерпний філогенетичний аналіз триби осівцевих на основі трьох мітохондрієвих (12S rRNA 16S rRNA COI) і двох ядрових (18S rRNA 28S rRNA) генів. Результати з високою достовірністю продемонстрували поліфілетичність осівцевих. Зокрема виявлено, що триба складена із двох* *філогенетично і морфологічно відмінних еволюційних груп родів, що дало змогу здійснити таксономічну ревізію осівцевих. В результаті, виокремлено дві триби: Clytini,* ***trib. sensu nov.*** *та Chlorophorini,* ***trib. nov.****, які окрім молекулярних, також добре диференційовані за морфологічними ознаками. Обидві триби, разом із Anaglyptini, утворюють велику монофілетичну кладу, яку виокремлено у нову надтрибу Chlorophoritae,* ***supertrib. nov.*** *В межах Clytini,* ***trib. sensu nov.*** *ідентифіковано дві великі групи родів, які відрізняються як морфологічно, так і молекулярно і встановлені в ранзі підтриб: Neoclytina,* ***subtrib. nov.*** *і Clytina,* ***subtrib. nov.*** *А у Chlorophorini,* ***trib. nov.*** *– Plagionotina,* ***subtrib. nov.*** *і Chlorophorina,* ***subtrib. nov.*** *Внутрішня філогенія підтриб все ще залишається заплутаною і не до кінця зрозумілою. Чинне дослідження вносить лише часткове її розуміння і окреслює перспективи подальшого пошуку розв'язання проблеми. Попри те, за уже отриманими результатами запропоновано низку нових номенклатурних актів, які включають описи 1-ї нової надтриби, 1-ї нової триби, 4-х нових підтриб, 3-х нових родів, 4-х нових підродів, 3-х нових статусів, 22-х нових комбінацій, 2-х нових синонімів, а також переописано 1 трибу та 3 роди.*

***Ключові слова****: Cerambycidae, філогенія, нові таксони.*

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