Journal of Vasyl Stefanyk Precarpathian National University
http://journals.pnu.edu.ua
Vol. 10 (2023), 63-75

UDC 57.065:592/599:595.768.11
doi: 10.15330/jpnubio.10.63-75

PHYLOGENY OF JUDOLIA MULSANT, 1863 (COLEOPTERA: CERAMBYCIDAE)

ANDREW M. ZAMOROKA

Abstract. *Judolia* Mulsant, 1863 is a small Holarctic genus, the range of which covers Europe, North and East Asia and North America. Within the range there are several centers of diversification, to which species characterized by significant morphological differences are confined. This indicates the relict nature of the genus as a whole and its complex phylogeographic and evolutionary history. Because of this, the taxonomy of the genus remains problematic and unresolved. In modern morpho-taxonomic publications, there are two radically opposite visions of *Judolia*: 1) genus is monophyletic and 2) genus is polyphyletic. While publications on molecular phylogeny always note the monophyletic nature of the genus *Judolia*. The aim of the current study is to finally resolve the taxonomic debate surrounding *Judolia* by combining advanced molecular phylogenetic and classical morphological methods. The key result of our study was the confirmation of the monophyletic view of *Judolia* by means of single- and multigene phylogenetic analysis. For single-gene analysis, 658 nucleotide fragments of the 1st subunit of the mitochondrial cytochrome c oxidase (COI) gene were used. A combination of consensus sequences of two mitochondrial (16s rRNA, COI) and one nuclear (28S rRNA) genes was used for multigene analysis. As a result, the most likelihood phylogenetic trees with a high degree of branch support were obtained. Topographically, the phylogenetic trees are divided into three large clades, which represent three morphologically distinct groups of the genus *Judolia*. The synthesis of molecular and morphological data allowed establishing the intrageneric structure of Judolia, dividing it into four subgenera: *Pachytodes* **nom. & stat. res.**, *Florijudolia* **subgen. nov.**, *Judolia*, *Sierrojudolia* **subgen. nov.** In addition, the genetic and morphological similarity of the genera *Oedecnema* and *Judolidia* became decisive for their assignment to the subgenus *Judolia*. In turn, the subgenus Judolia is divided into four infragenera: *Boreojudolia* **infragen. nov.**, *Oedecnema* **stat. nov.**, *Judolia*, *Judolidia* **stat. nov.** A new scheme of the intrageneric taxonomy of Judolia is also presented, as well as keys to its morphological identification.

Keywords: the longhorn beetles, molecular phylogeny, multigene analysis, evolution, cladistics, integrative taxonomy.

1. INTRODUCTION

The longhorn beetles (Cerambycidae) are the one of the most divers families of beetles, comprising near 33 thousand species worldwide (Slipinski & Escalona, 2013; Wang, 2017; Zamoroka et al., 2022). Morphological and ecological variability of the longhorn beetles exhibits the multidirectional evolutionary processes, starting from adaptive radiation and multiple mimicry, ending with numerous cases of homoplasy and convergence (Zamoroka, 2022 b). Such enormous diversity requires extraordinary approaches to solving problems related to their systematics. Modern biology offers a number of advanced molecular tools (Hebert et al., 2003; Pentinsaari et al., 2016) that, in combination with classic and computational morphological and anatomical studies, create a new and better opportunities for the implementation of integrative taxonomy in general, and for the longhorn beetles in particular (Zamoroka et al., 2022).

Judolia Mulsant, 1863 is a genus within tribe Lepturini in the subfamily Lepturinae (Zamoroka, 2022 a; Monné & Nearns, 2023). *Judolia* widespread within Holarctic, including Europe, North and

East Asia, North America (Nakane & Ohbayashi, 1957; Danylevsky, 2014; Vitali, 2018; Monné & Nearns, 2023). Despite the fact that *Judolia* is a small genus (18 species), within its range it forms separate, isolated centers of species diversity. This indicates a fairly significant evolutionary age and intricate history of the genus. Due to this, historically, different interpretations of the *Judolia* taxonomy have developed. Today, there are two diametrically opposed visions of the internal taxonomy of the genus *Judolia*: 1) monophyly (Özdikmen, 2011; Vitali, 2018) and 2) polyphyly (Sama, 2003; Löbl & Smetana, 2010; Danilevsky, 2014). This creates significant difficulties for faunistic works, since one or another researcher has to choose one of the existing systems of the genus, which at the same time contradict each other.

The few available molecular studies, mostly cursory on the genus *Judolia*, support its monophyly (Sýkorová, 2008; Semaniuk & Zamoroka, 2020; Zamoroka et al., 2022). In addition, particular studies show that genera such as *Oedecnema* Dejean, 1835 and *Judolidia* Plavilstshikov, 1936 should be considered as part of the genus *Judolia* (Semaniuk & Zamoroka, 2020; Zamoroka et al., 2022). Solving the question of the internal phylogeny of *Judolia* and establishing natural taxonomy is an important task of modern taxonomy of the longhorn beetles.

The current study presents the results of the most comprehensive phylogenetic analysis that confirms the monophyly of the genus *Judolia* with its congeners *Oedecnema* and *Judolidia*.

2. MATERIALS AND METHODS

To resolve the intrageneric phylogenetic relationships of *Judolia*, we used 102 partial gene sequences (Tab. 1), representing the mitochondrial genes 16S ribosomal RNA (16S rRNA) and cytochrome c oxidase subunit I (COI) and nuclear gene 28S ribosomal RNA (28S rRNA). Only COI sequences available for each individual were used for broad phylogenetic analysis. This made it possible to trace the distribution of specimens by species and confirm the correctness of the final identification. It also demonstrated the wide intraspecies variability of single nucleotide substitutions. To eliminate this factor, where possible, consensus sequences were generated and used together with 16S rRNA and 28S rRNA gene sequences to construct a hybrid tree (for details see Zamoroka et al., 2022).

Analysis was performed using Seaview 5.0, a multi-platform software for multiple sequence alignment, molecular phylogenetic analyses, and tree reconciliation (Gouy et al., 2021).

The Multiple alignments were generated using the MUSCLE (Multiple Sequence Comparison by Log-Expectation) algorithm built into Seaview 5.0. Alignments were revised and edited manually to correct regions containing missing data and to exclude unalignable positions.

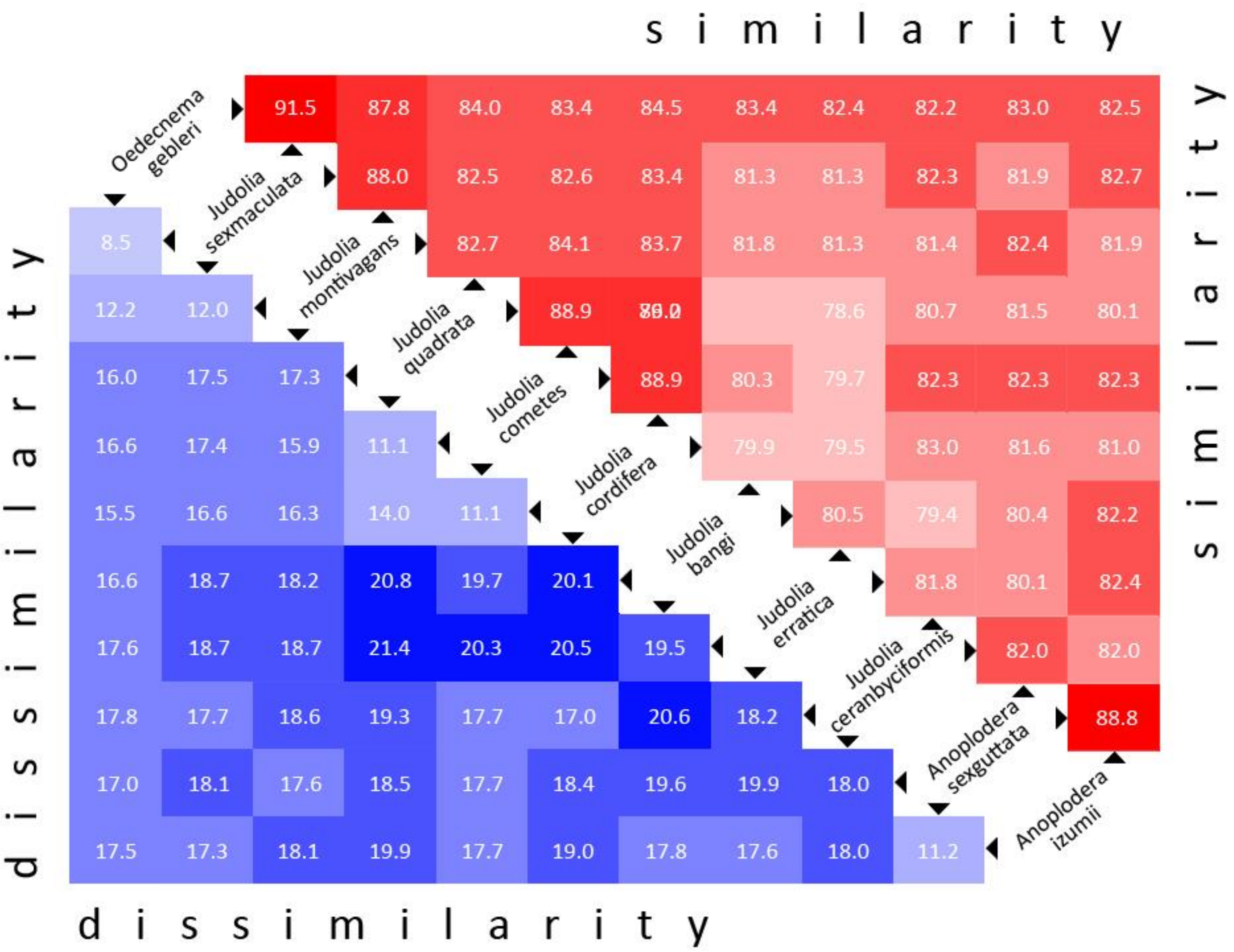
Phylogenetic trees were constructed using maximum-likelihood methods with PhyML algorithm (Guindon et al., 2010). Analyses were performed following a general time-reversible (GTR) model of sequence evolution with approximate likelihood-ratio test (aLRT) for branch support based on the Log Ratio between the likelihood value of the current tree and that of the best alternative (Anisimova & Gascuel, 2006; Guindon et al., 2010). The optimal tree's structure was estimated using the best combination of nearest-neighbor interchange (NNI) and Subtree Pruning Regrafting (SPR) algorithms. The neighbor-joining algorithm (BioNJ) optimizing trees topology for estimation of branch distances was used (Gascuel, 1997).

Table 1. The GenBank accession numbers of genes sequences used in the study

Species	Voucher number
Judolia cerambyciformis	HQ954555.1; MH115502.1; KU916580.1; KU916384.1; KU912066.1; KU909940.1; KU908754.1; KU908370.1; KU906517.1; KM286357.1; KM451327.1; KM451035.1; KM449455.1; KM448066.1; KM446449.1; KM445280.1; KM445175.1; KM441882.1; KM441504.1
Judolia cometes	LC733226.1; OP562678.1
Judolia cordifera	MN556948
Judolia erratica	KM445976.1
Judolia instabilis	MW597084.1
Judolia montivagans	MF635948.1; KM850814.1; KM849403.1; KM849195.1; KM848332.1; KM847151.1; KM847126.1; KM842964.1; KM842910.1; KM842500.1; KM842277.1; KM842171.1; KM845560.1; JF888507.1; JF888506.1; JF888505.1; JF888504.1; JF888503.1; JF888502.1; HQ961913.1; KR915309.1; KU875313.1; KU875312.1; KU875311.1; AY165712.1
Judolia quadrata	KM841928.1; KM845861.1; KU875314.1
Judolia sexmaculata	HM034788.1; KM445106.1; KM444180.1; KM443765.1; KJ963423.1; KJ963030.1; KJ967085.1; KJ965124.1; HQ559267.1; HM046539.1
Judolidia bangi	HM034785.1; MW983329.1; HM046536.1
Oedecnema gebleri	HM034778.1; MN905230.1; OL663430.1; OL663429.1; OL663428.1; KY683625.1; HM046530.1; MN851222.1
Anoplodera sexguttata	KU912642.1
Anoploderomorpha izumii	FJ559044.1
Anastrangalia dubia sequensi	HM034772.1; KY683642.1; AF332923.1; MN609573.1; HM046524.1
Cerambyx cerdo	HQ954095.1
Cerambyx scopolii	JF889538.1
Gibbocerambyx aurovirgatus	KF737736.1; KF737799.1; KF142115.1
Hemadius oenochrous	AB703463.1; AB703463.1
Leptura annularis	HM034792.1; HQ954574.1; KY683714.1; KY683632.1; KU914996.1; KM443478.1; KM451359.1; HM046542.1
Leptura aurosericans	KF737720.1; KF737783.1; KF142136.1
Leptura duodecemguttata	HQ832604.1; KY683662.1; HQ832607.1
Leptura quadrifasciata	KU919023.1

3. RESULTS

One gene phylogeny. Pairwise similarity/difference analysis of COI sequences (Fig. 1) revealed two groups of species with the most similar sequences. The first group constitute of three species including *Oe. gebleri*, *J. sexmaculata* and *J. montivagans* with 89,1% of average similarity level. The most similar sequences (91.5%) were observed between *Oe. gebleri* and *J. sexmaculata*. The species pair of *J. sexmaculata* and *J. montivagans* similar on 87,8% and pair *J. sexmaculata* and *J. montivagans* showed 88,0% of similarity.



	Oedecnema gebleri	Judolia sexmaculata	Judolia montivagans	Judolia quadrata	Judolia cometes	Judolia cordifera	Judolia bangi	Judolia erratica	Judolia ceranbyciformis	Anoplodera sexguttata	Anoplodera izumii
Oedecnema gebleri		91.5	87.8	84.0	83.4	84.5	83.4	82.4	82.2	83.0	82.5
Judolia sexmaculata	8.5		88.0	82.5	82.6	83.4	81.3	81.3	82.3	81.9	82.7
Judolia montivagans	12.2	12.0		82.7	84.1	83.7	81.8	81.3	81.4	82.4	81.9
Judolia quadrata	16.0	17.5	17.3		88.9	89.0		78.6	80.7	81.5	80.1
Judolia cometes	16.6	17.4	15.9	11.1		88.9	80.3	79.7	82.3	82.3	82.3
Judolia cordifera	15.5	16.6	16.3	14.0	11.1		79.9	79.5	83.0	81.6	81.0
Judolia bangi	16.6	18.7	18.2	20.8	19.7	20.1		80.5	79.4	80.4	82.2
Judolia erratica	17.6	18.7	18.7	21.4	20.3	20.5	19.5		81.8	80.1	82.4
Judolia ceranbyciformis	17.8	17.7	18.6	19.3	17.7	17.0	20.6	18.2		82.0	82.0
Anoplodera sexguttata	17.0	18.1	17.6	18.5	17.7	18.4	19.6	19.9	18.0		88.8
Anoplodera izumii	17.5	17.3	18.1	19.9	17.7	19.0	17.8	17.6	18.0	11.2	

Figure 1. Pairwise percentage variation in COI sequences within the studied species

The second group is represented by three other species including *J. quadrata*, *J. cometes* and *J. cordifera*, for which the average COI similarity level was 87.9%. *Judolia quadrata* and *J. cometes* were the most similar pairs – 89.0%, then *J. quadrata* and *J. cordifera* – 89.0%, and finally *J. cometes* and *J. cordifera* – 86%.

The two groups the most distinct from the other species are: 1) *J. bangi* and 2) *J. erratica* and *J. cerambyciformis*. The average level of sequence divergence of *J. bangi* is 19.53%, with the highest divergence observed in pairs with: *J. quadrata* – 20.8%, *J. cordifera* – 20.1% and *J. cerambyciformis* – 20.6%. In the second group, *J. erratica* shows the highest level of differences from the other species, especially of *J. quadrata* – 21.4%, *J. cometes* – 20.3% and *J. cordifera* – 20.5%.

The resultant analysis of the 71 sequence of 658-nucleotide fragments of the mitochondrial COI gene, the most likelihood phylogenetic tree (Fig. 2) of the relationship of the studied species was obtained. The key consequence from this was the proof of monophyly of the genus *Judolia*. The phylogenetic tree of Judolia consists of 4 clades with a high degree of monophyletic support SH=0.98. Topographically, the resulting phylogenetic tree is clearly divided into two basal and two crown clades.

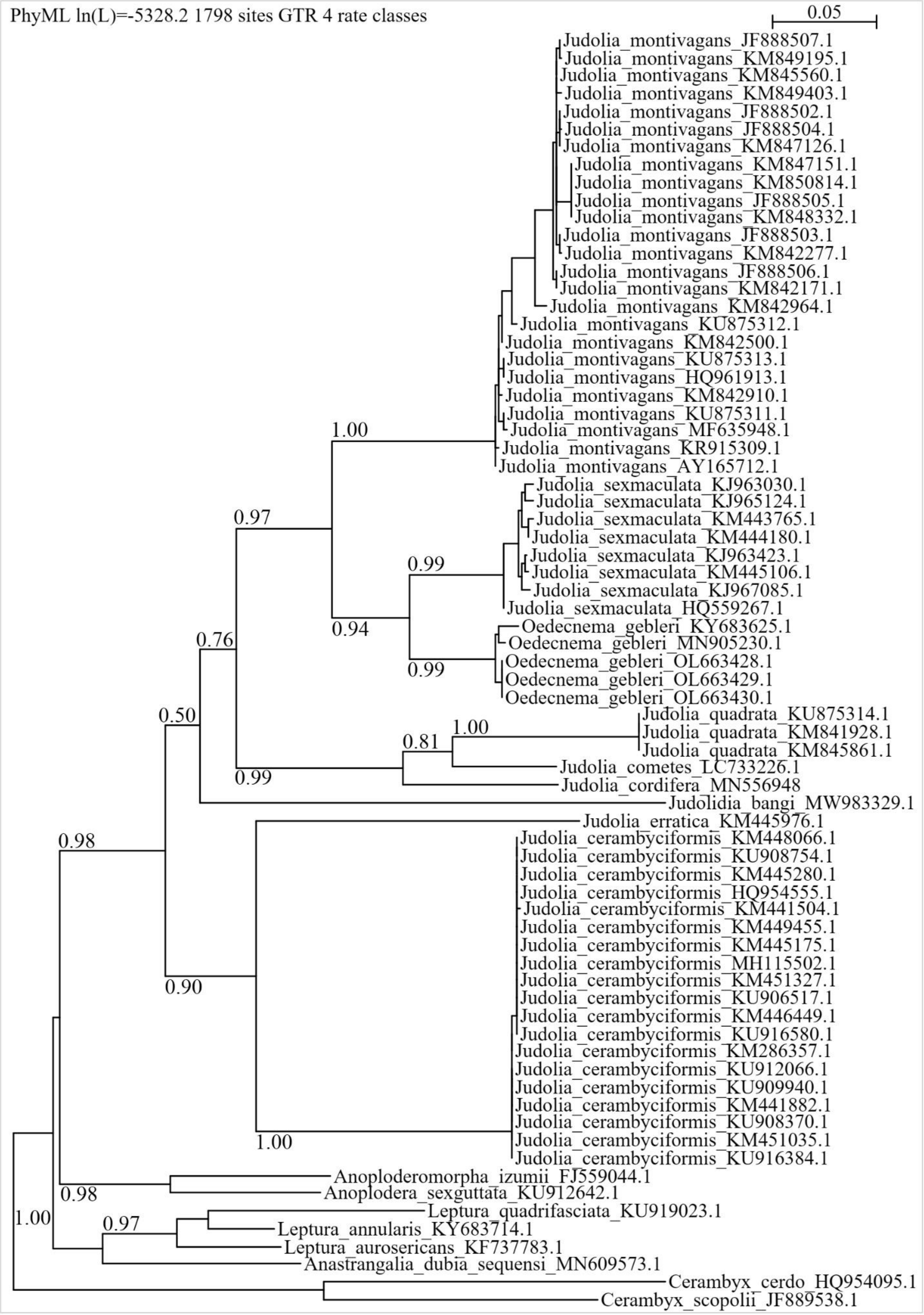


Figure 2. COI tree illustrating the phylogenetic hypothesis of relationships within genus Judolia; the branch support SH-like values are shown with the threshold rule SH>0.50

Basal clades represent two groups of species: 1) *J. erratica* and *J. cerambyciformis* (SH=0.90) and 2) *J. bangi* (SH=0.50). The clade of *J. erratica* and *J. cerambyciformis* is the most ancient in evolutionary terms in the genus *Judolia*. It is probably a relict group represented by a very limited number of species. The revealed position of the *J. bangi* clade is weakly confirmed by the approximate likelihood ratio test (SH=0.50). This may indicate the inadequacy of using only one gene (COI) to establish real phylogenetic relationships for *J. bangi* among *Judolia*.

The crown group of our phylogenetic tree consists of two other sister clades: 1) *J. cordifera*, *J. cometes* and *J. quadrata* (SH=0.99) and 2) *J. montivagans*, *J. sexmaculata* and *Oe. gebleri* (SH=0.96). Both clades are evolutionarily progressive and represent species-rich groups within *Judolia*. It should be noted that in the *J. montivagans* + *J. sexmaculata* + *Oe. gebleri* clade, *Oe. gebleri* is the terminal taxon, which makes the clade paraphyletic in relation to the existing taxonomy.

Multigene phylogeny. The hybrid phylogenetic tree (Fig. 3), constructed by combining consensus sequences for three genes (16S rRNA+COI+28S rRNA), showed the monophyly of the genus *Judolia*. Three clades constituted the phylogenetic tree. These include the first clade *J. erratica* + *J. cerambyciformis* (SH=0.88), the second clade *J. cordifera* + *J. quadrata* + *J. cometes* + *J. instabilis* (SH=1.00) and the third clade *J. montivagans* + *Oe. gebleri* + *J. sexmaculata* + *J. bangi* (SH=0.93).

Like in the phylogenetic tree based on only COI gene, the basal clade of the hybrid phylogenetic tree is the first clade represented by the two species *J. erratica* and *J. cerambyciformis*. The crown part of the obtained phylogenetic tree consists of the second and the third clades.

The main difference between COI and three genes hybrid tree is the position of *J. bangi*. According to the results of the multigene analysis, *J. bangi* is part of the third clade, grouping with *J. sexmaculata* and *Oe. gebleri*. These three species, according to the consensus sequences of the three genes 16S rRNA+COI+28S rRNA, show significant similarity each other. In particular, the level of similarity for the pair *J. bangi* and *J. sexmaculata* was 91.8%; for *J. sexmaculata* and *Oe. gebleri* was 92.8%; *Oe. gebleri* and *J. bangi* was 88.7%. These are significantly higher similarity scores than for a single COI gene (Fig. 1). That is, the additional contribution of both mitochondrial and nuclear ribosomal 16S rRNA and 28S rRNA genes to the overall similarity statistics makes it possible to determine the phylogenetic position of *J. bangi* more clearly with greater confidence. In general, the terminal taxon of the third clade is *J. bangi*, not *Oe. gebleri* as shown in the COI tree. It should be emphasized that all three mentioned species are distributed in the Palearctic, while the fourth species of the third clade, *J. montivagans*, is distributed in the Nearctic and occupies basal most position. This demonstrates the complex phylogeographic history and intricate evolutionary patterns of the third clade.

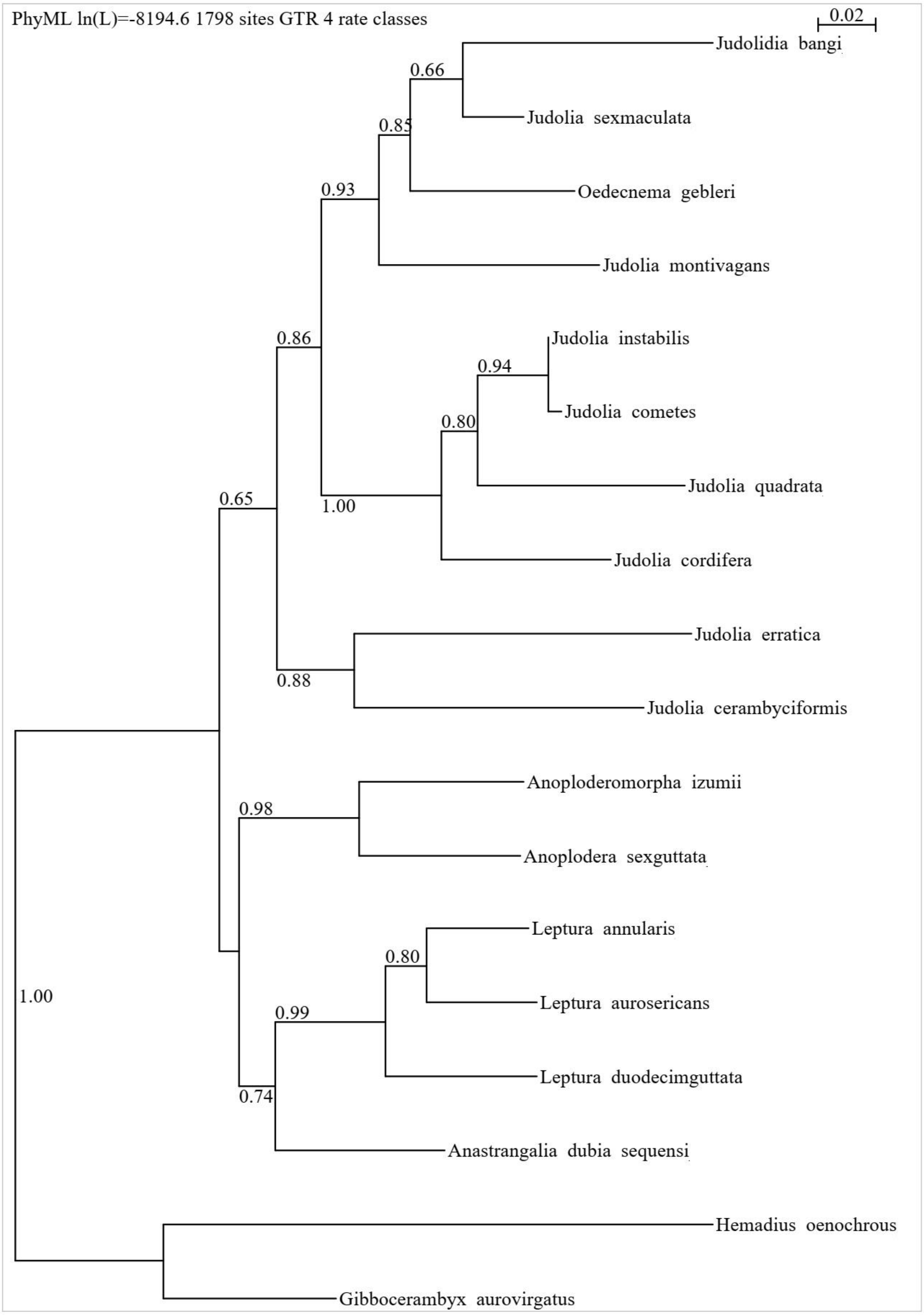


Figure 3. The hybrid three genes (16S rRNA+COI+28S rRNA) tree based on consensus sequences illustrating the phylogenetic hypothesis of relationships within genus Judolia; the branch support SH-like values are shown with the threshold rule SH>0.50

Taxonomical revision of *Judolia*. Based on the results of the phylogenetic analysis, as well as morphological data, we propose solution to the intrageneric taxonomy of *Judolia*. Thus, the genus *Judolia* consists of at least four subgenera, three of which established on the combination of molecular and morphological and one exceptionally on morphological data. Three species namely *Judolia impura* (LeConte, 1857), *Judolia japonica* (Tamanuki, 1943), *Judolia miyatakei* N. Ohbayashi & Bi, 2020 remain unclassified due to lack of study material. The proposed system is shown below (synonymy is omitted).

1. Genus ***Judolia*** Mulsant, 1863

1.1. Subgenus ***Pachytodes*** Pic, 1891 **nom. & stat. res.**

Subordinated taxa:

1.1.1. *Judolia* (*Pachytodes*) *cerambyciformis* (Schrank 1781)
1.1.2. *Judolia* (*Pachytodes*) *erraticus* (Dalman, 1817)

1.2. Subgenus ***Florijudolia*** **subgen. nov.**

Description / Diagnosis: Pronotum bell-shaped, laterally tuberculated (Fig. 4 c). Pronotal posterior margin with a clearly defined wide transverse furrow, interrupted in the middle.

Type species: *Judolia quadrata* (LeConte, 1873)

Etymology: From Latin *flos* and generic name *Judolia* – flower *Judolia*.

Subordinated taxa:

1.2.1. *Judolia* (*Florijudolia*) *cordifera* (Olivier, 1800) **comb. nov.**
1.2.2. *Judolia* (*Florijudolia*) *cometes* (Bates, 1884) **comb. nov.**
1.2.3. *Judolia* (*Florijudolia*) *instabilis* (Haldeman, 1847) **comb. nov.**
1.2.4. *Judolia* (*Florijudolia*) *quadrata* (LeConte, 1873) **comb. nov.**

Morphologically suggested species:

1.2.5. *Judolia* (*Florijudolia*) *gaurotoides* (Casey, 1893) **comb. nov.**
1.2.6. *Judolia* (*Florijudolia*) *bottcheri* (Pic, 1911) **comb. nov.**
1.2.7. *Judolia* (*Florijudolia*) *longipes* (Gebler, 1832) **comb. nov.**

1.3. Subgenus ***Judolia*** Mulsant, 1863

Subordinated taxa:

1.3.(1). Infragenus ***Boreojudolia*** **infragen. nov.**

Description / Diagnosis: Scutellum deeply sunken between the bases of the elytra.

Type species: *Judolia montivagans* (Couper, 1864)

Etymology: From Ancient Greek *Βορέᾱς* and generic name *Judolia* – northern *Judolia*.

1.3.(1).1. *Judolia* (*Judolia / Boreojudolia*) *montivagans* (Couper, 1864) **comb. nov.**

1.3.(2). Infragenus ***Oedecnema*** Dejean, 1835 **stat. nov.**

1.3.(2).1. *Judolia* (*Judolia / Oedecnema*) *gebleri* (Ganglbauer, 1887) **comb. nov.**

1.3.(3). Infragenus ***Judolia*** Mulsant, 1863

1.3.(3).1. *Judolia* (*Judolia / Judolia*) *sexmaculata* (Linnaeus, 1758) **comb. nov.**

Morphologically suggested species:

1.3.(3).2. *Judolia* (*Judolia / Judolia*) *dentatofasciata* (Mannerheim, 1852) **comb. nov.**

1.3.(4). Infragenus ***Judolidia*** Plavilstshikov, 1936 **stat. nov.**

1.3.(4).1. *Judolia* (*Judolia / Judolidia*) *bangi* (Pic, 1901) **comb. nov.**

Morphologically suggested species:

1.3.(4).2. *Judolia* (*Judolia* / *Judolidia*) *znojkoi* (Plavilstshikov, 1936) **comb. nov.**

1.4. Subgenus *Sierrojudolia* **subgen. nov.**

Description / Diagnosis: Pronotum subspherical with evenly rounded lateral side, without a distinct tubercle (Fig. 4 b). Pronotal posterior margin without transverse furrow. Males bear a pair of metasternal tooth-like structures – a secondary sexual feature.

Type species: *Judolia scapularis* (Van Dyke, 1920)

Etymology: From Spanish *Sierra* and generic name *Judolia* – mountain *Judolia*. The species of *Sierrojudolia* are widespread within the Sierra Nevada – mountains in the west of North America.

Morphologically suggested species:

1.4.1. *Judolia* (*Sierrojudolia*) *scapularis* (Van Dyke, 1920) **comb. nov.**
1.4.2. *Judolia* (*Sierrojudolia*) *sexspilota* (LeConte, 1859) **comb. nov.**
1.4.3. *Judolia* (*Sierrojudolia*) *swainei* (Hopping, 1922) **comb. nov.**

1.5. *Judolia* **incertae sedis**

1.5.1. *Judolia impura* (LeConte, 1857)
1.5.2. *Judolia japonica* (Tamanuki, 1943)
1.5.3. *Judolia miyatakei* N. Ohbayashi & Bi, 2020

Key to *Judolia* subgenera.

(1) Pronotum subspherical, laterally evenly rounded, without a distinct tubercle (Fig. 4 a, b) ………………………………………… (2)

– Pronotum of a different shape ………………………………… (3)

(2) Pronotal posterior margin without transverse furrow (Fig. 4 b). Males bear metasternal teeth on the disc ………………………… 1. subgenus ***Sierrojudolia* subgen. nov.**

– Pronotal posterior margin with a deep transverse furrow (Fig. 4 a). Males have no metasternal teeth on the disc ………………………… 2. subgenus ***Pachytodes* nom. & stat. res.**

(3) Pronotum bell-shaped, laterally with well-defined tubercle (Fig. 4 c). Pronotal posterior margin with a deep transverse furrow, often interrupted in the middle ………………………………… 3. subgenus ***Florijudolia* subgen. nov.**

– Pronotum subconical, more or less elongated, with a vague lateral tubercle (Fig. 4 d, e). Pronotal posterior margin without or with indistinct very shallow transverse furrow ………………………………… 4. Subgenus ***Judolia***

Key to infragenera of subgenus *Judolia*

(1a) Pronotum very elongated (especially in males) (Fig. 4 e) ………………………… (2a)

– Pronotum slightly elongated (Fig. 4 d) ………………………… (3a)

(2a) Elytral apices deeply truncated. Genae as long as eye diameter. Males bear secondary sexual features: hypertrophied hind limbs and pair of metasternal longitudinal lameles. ………………………………… 4.1. infragenus ***Oedecnema* stat. nov.**

– Elytral apices rounded. Genae shorter than eye diameter. ………………………………… 4.2. infragenus ***Judolidia* stat. nov.**

(3a) Scutellum deeply sunken between the bases of the elytra ………………………………… 4.3. infragenus ***Boreojudolia* infragen. nov.**

– Scutellum and elytral bases surfaces on the same level ………………………………… 4.4. infragenus ***Judolia***

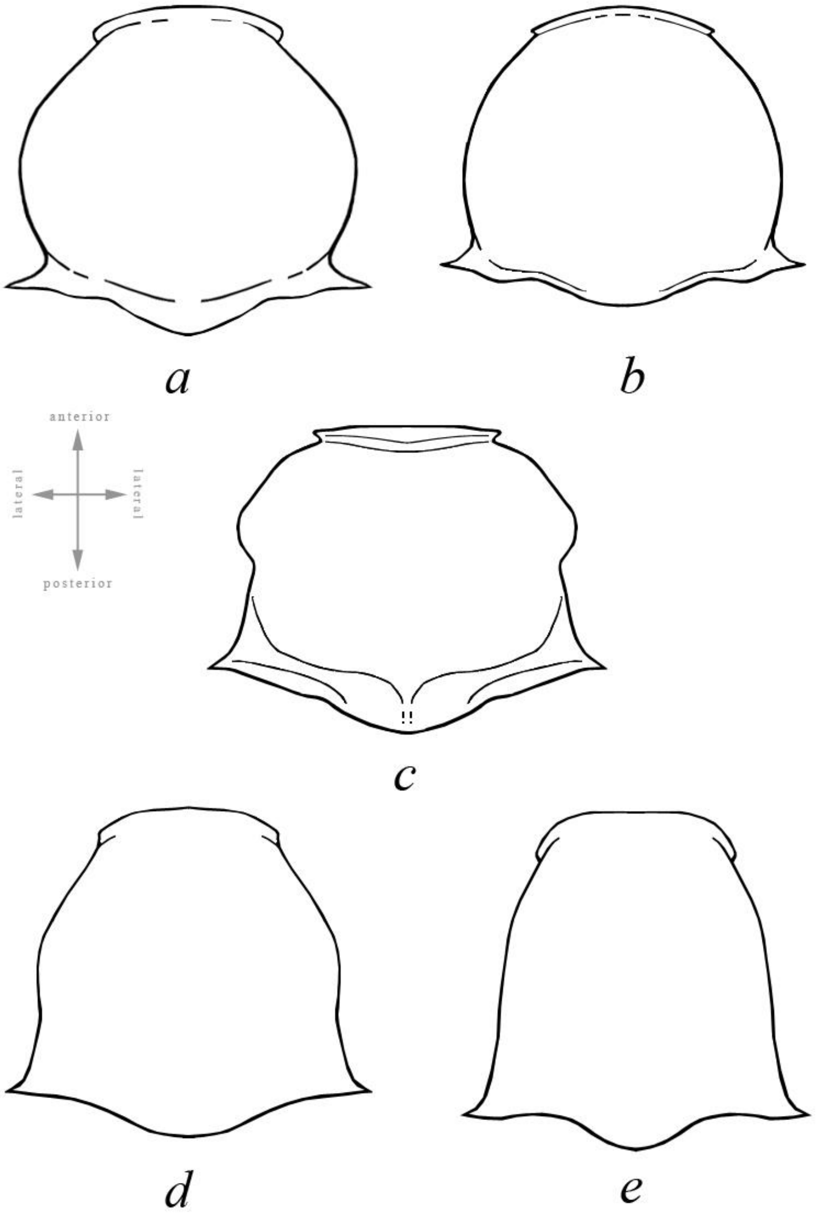


Figure 4. Pronotum shape variation in Judolia: (a) subspherical – Judolia (Pachytodes) erraticus; (b) subspherical – Judolia (Sierrojudolia) scapularis comb. nov.; (c) bell-shaped – Judolia (Florijudolia) instabilis comb. nov.; (d) subconical – Judolia (Judolia / Boreojudolia) montivagans comb. nov.; (e) subconical – Judolia (Judolia / Oedecnema) gebleri comb. nov.

4. DISCUSSION

Based on the obtained results, the genus *Judolia* should be considered unambiguously monophyletic. With the current study, it was confirmed Ozdikmen's (2011) assumption based on morphological data that *Judolia* and *Pachytodes* are congeneric. At the same time, our findings clearly confirmed the results of secondary phylogenetic studies by other authors regarding the monophyletic nature of *Judolia*. In particular, we confirmed the finds of Sýkorová (2008) on close relation of *Judolia* and *Pachytodes*. In addition, our results are fully consistent with the previous data of Semanuk & Zamoroka (2020) on the belonging of *Oedecnema* to *Judolia* and the data of Zamoroka et al. (2022) on the need for transfer *Judolidia* to *Judolia*.

A key result of the current study is the elucidation of intrageneric relationships in *Judolia*. In particular, we proved that *Pachytodes* is the basal clade of the genus *Judolia*, while it is evolutionarily early and clearly separated from the rest of the phylogenetic tree. Therefore, it should be considered as a separate subgenus. It should be noted that Pic (1891) originally introduced the name *Pachytodes* to designate a separate subgenus within *Judolia*. However, *Pachytodes* was later introduced as an independent genus (Sama, 2003) and subsequently synonymized by Özdikmen (2011), suggesting that the name should no longer be used. Nevertheless, in the light of new evidence, we believe that the name *Pachytodes* should be used to designate a separate subgenus in the genus *Judolia*, in accordance with the original idea of Pic (1891).

The species group *J. cordifera*, *J. quadrata*, *J. instabilis* and *J. cometes* form one of the two crown clades of *Judolia* phylogenetic tree. This group has usually been considered part of the genus *Judolia* (Monné & Bezark, 2009), with the exception of *J. cometes*, which Danylevsky (2014) placed in the genus *Pachytodes*. However, our studies clearly demonstrate a close relationship between these species, which clearly form a monophyletic clade. This clade should be considered as an independent subgenus *Florijudolia* **subgen. nov.** as part of *Judolia*.

The terminal clade of the phylogenetic tree of the genus *Judolia* unites four species: *J. montivagans*, *Oe. gebleri*, *J. sexmaculata* and *J. bangi* with distinct morphology. *Judolia sexmaculata* was established as the type species for the genus *Judolia* (Mulsant, 1863). This means that the clade in which *J. sexmaculata* is nested, according to our system, represents the nominative subgenus *Judolia* in the genus *Judolia*. Previous studies as the terminal taxon of the clade placed *Oe. gebleri* (Semanuk & Zamoroka, 2020) or *J. bangi* (Zamoroka et al., 2022). However, none of them simultaneously included both species of *Oe. gebleri* and *J. bangi*. In the current study we solved the problem of interrelationships between *Oedecnema*, *Judolidia* and *Judolia*. Both species, *Oe. gebleri* and *J. bangi*, are closely related to *J. sexmaculata*, but far from each other and even more so from *J. montivagans*. Therefore, the clade consists of four successive sister branches of mentioned species. The basal of them is *J. montivagans*, the next successively branching from the clade *Oe. gebleri*, *J. sexmaculata* and *J. bangi* (Fig. 3). It should be noted that, *Oe. gebleri* is morphologically very different from other species. Based on its specific morphology, it was placed in an independent genus (Dejean 1835). Although some authors noted the morphological similarity of *Judolia* and *Oedecnema*, which indicates their relationship (Sama, 2003; Danylevsky, 2014). Danylevsky (2014) also points to an even greater morphological similarity between *Judolidia* and *Judolidia*. These seemingly minor observations by morphologists, supported by our phylogenetic analysis, indicate that *Oedecnema*, *Judolia* and *Judolidia* are congeneric. Considering the significant genetic relatedness of the species of this clade and the significant morphological difference between them, they should be considered as subordinate taxa (infragenera) in the subgenus *Judolia*.

5. CONCLUSION

In summary, based on the results of the molecular phylogenetic analysis, we proved the monophyletic nature of the genus *Judolia*. The phylogenetic tree of the genus *Judolia* consists of three clades that exhibit complex phylogeographic patterns and an intricate evolutionary history. Based on the synthesis of molecular and morphological data, it was possible to reveal the intrageneric taxonomic structure of *Judolia*. As a result, the genus *Judolia* is divided into four subgenera, two of which are described for the first time. The dilemma about the association of *Oedecnema* and *Judolidia* with *Judolia* was also resolved. Both of them nested as the rank of infragenera within the subgenus *Judolia*. Further prospects for the study of *Judolia* should be aimed at clarifying the phylogenetic position and taxonomy of *J. impura*, *J. japonica*, *J. miyatakei*, which could not be resolved in this study.

REFERENCES

[1] Anisimova, M., & Gascuel, O. (2006). Approximate likelihood ratio test for branches: A fast, accurate and powerful alternative. *Systematic Biology*, 55(4), 539–552.: https://doi.org/10.1080/10635150600755453

[2] Danilevsky, M. L. (2014). *Longicom beetles (Coleoptera, Cerambycoidea) of Russia and adjacent countries. Part 1*. HSC.

[3] Dejean, P. F. M. A. (1835). *Catalogue des Coléoptères de la Collection de M. le Comte Dejean*. 2ème edition, Méquignon-Marvis Père & Fils, Paris.

[4] Gascuel, O. (1997). BIONJ: an improved version of the NJ algorithm based on a simple model of sequence data. *Molecular Biology Evolution*, 14(7), 685–695. https://doi.org/10.1093/oxfordjournals.molbev.a025808

[5] Gouy, M., Tannier, E., Comte, N., & Parsons D. P. (2021). Seaview Version 5: A Multiplatform Software for Multiple Sequence Alignment, Molecular Phylogenetic Analyses, and Tree Reconciliation. *Methods in Molecular Biology*, 2231. 241–260. https://doi.org/10.1007/978-1-0716-1036-7_15

[6] Guindon, S., Dufayard, J. F., Lefort, V., Anisimova, M., Hordijk, W., & Gascuel, O. (2010). New Algorithms and Methods to Estimate Maximum-Likelihood Phylogenies: Assessing the Performance of PhyML 3.0. *Systematic Biology*, 59(3), 307–21. https://doi.org/10.1093/sysbio/syq010

[7] Hebert, P. D. N., Cywinska, A., Ball, S. L. & deWaard, J. R. (2003). Biological identifications through DNA barcodes. *Proceedings of the Royal Society B: Biological Sciences*, 270, 313–321. https://doi.org/10.1098/rspb.2002.2218

[8] Löbl, I., & Smetana, A. (Eds.) (2010). *Catalogue of Palaearctic Coleoptera, Vol. 6*. Stenstrup: Apollo Books.

[9] Monné, M. A., & Bezark, L.G. (2009). *Checklist of theCerambycidae of the Western Hemisphere*. http://www.cerambycoidea.com/titles/monnebezark2009.pdf

[10] Monné, M. L., & Monné, M. A. (2017). *General morphology, classification and biology of Cerambycidae*. In: Wang, Q. (Ed.). Cerambycidae of the world: Bi-ology and pest management. CRC Press, Boca Raton – London – New York.

[11] Monné, M. A., & Nearns, E. H. (2023). *Catalogue of the Cerambycidae (Coleoptera) of Canada and United States of America. Part II. Subfamilies Lepturinae and Necydalinae*. Available from: https://cerambycids.com/catalog

[12] Mulsant, E. (1863). In: *Histoire naturelle des coléoptères de France. Longicornes*. Ed. 2. Paris: Magnin, Blanchard et Cie, successeurs de Louis Janet.

[13] Nakane, T., & Ohbayashi, K. (1957). Notes on the genera and species of Lepturinae (Coleoptera, Cerambycidae) with special reference to their male genitalia. *Scientific Reports of the Saikyo University*, Kyoto (Natural Science & Living Science A series) 2 (4), 47–52.

[14] Özdikmen, H. (2011). A propose for acception of a single genus as Judolia Mulsant, 1863 instead of the genera Judolia Mulsant, 1863 and Pachytodes Pic, 1891 (Coleoptera: Cerambycidae: Lepturinae: Lepturini). *Munis Entomology & Zoology*, 6 (2), 900–904.

[15] Pentinsaari, M., Salmela, H., Mutanen, M. et al. (2016). Molecular evolution of a widely-adopted taxonomic marker (COI) across the animal tree of life. *Scientific Reports*, 6, 35275. https://doi.org/10.1038/srep35275

[16] Pic, M. (1891). *Materiaux pour servir a l'etude Des longicornes*. Premier cahier. Lyon: L. Jacquet.

[17] Sama, G. (2003) *Atlas of the Cerambycidae of Europe and the Mediterranean Area. Volume 1: Northern, Western, Central and Eastern Europe. British Isles and Continental Europe from France (excl. Corsica) to Scandinavia and Urals*. Vít Kabourek, Zlín.

[18] Semaniuk, D. V., & Zamoroka, A. M. (2020). Preliminary phylogenetic analysis of Lepturini (Insecta: Coleoptera: Cerambycidae). Conference: XVI International scientific conference for students and PhD students "*Youth and Progress of Biology*". Lviv. 121.

[19] Slipinski, A., & Escalona, H. (2013). *Australian longhorn beetles (Coleoptera: Cerambycidae). Volume 1: Introduction and subfamily Lamiinae*. Csiro Publishing, Collingwood.

[20] Sýkorová, M. (2008). *Molecular phylogeny of the subfamilies Spondylidinae andLepturinae (Coleoptera: Cerambycidae) based on mitochondrial 16S rDNA*. South Bohemian University, Ceske Budejovice.

[21] Vitali, F. (2018). *Atlas of the Insects of the Grand-Duchy of Luxembourg: Coleoptera, Cerambycidae*. Ferrantia 79, Musée national d'histoire naturelle, Luxembourg.

[22] Wang, Q. (2017). *Cerambycidae of the world: Biology and pest management*. CRC Press, Boca Raton – London – New York.

[23] Zamoroka, A. M. (2022 a). The longhorn beetles (Coleoptera, Cerambycidae) of Ukraine: Results of two centuries of research. *Biosystem diversity*, 30(1), 46-74. https://doi.org/10.15421/012206

[24] Zamoroka, A. M. (2022 b). Molecular revision of Rhagiini sensu lato (Coleoptera, Cerambycidae): Paraphyly, intricate evolution and novel taxonomy. *Biosystem diversity*, 30(3), 295–309. https://doi.org/10.15421/012232

[25] Zamoroka, A. M., Trócoli, S., Shparyk, V. Yu., & Semaniuk, D. V. (2022). Polyphyly of the genus Stenurella (Coleoptera, Cerambycidae): Consensus of morphological and molecular data. Biosystem diversity, 30(2): 119-136. https://doi.org/10.15421/012212

Andrew M. Zamoroka, PhD, Associate Professor
Department of Biology and Ecology, Vasyl Stefanyk Precarpathian National University, Shevchenko str., 57, Ivano-Frankivsk, Ukraine, 76018
ORCID: https://orcid.org/0000-0001-5692-7997
Email: andrew.zamoroka@pnu.edu.ua

Received: November 7, 2023; **revised:** November 20, 2023; **accepted:** December 24, 2023; **published:** December 28, 2023.

Андрій М. Заморока. Філогенія роду квіткарка (Coleoptera: Cerambycidae: Judokia). *Журнал Прикарпатського університету імені Василя Стефаника*, 10 (2023), 63-75.

Judolia Mulsant, 1863 – невеликий голаркичний рід, ареал якого охоплює Європу, Північну і Східну Азію, Північну Америку. В межах ареалу існують декілька центрів диверсифікації, приурочені до яких види характеризуються значними морфологічними відмінностями. Це свідчить про реліктовість самого роду і його складні філогеографічну й еволюційну історії. У зв'язку з цим таксономія роду залишається проблематичною і нерозв'язаною. У сучасних морфо-таксономічних працях існує два кардинально протилежні бачення *Judolia*: монофілетичність і поліфіліфілетичність роду. У той час як працях з молекулярної філогенії завжди відмічається монофілетичність роду *Judolia*. Мета чинного дослідження полягає у остаточному вирішенні таксономічної дискусії довкола *Judolia*, поєднавши передові молекулярні філогенетичні та класичні морфологічні методи. Ключовим результатом наших досліджень стало підтвердження монофілетичного бачення *Judolia* шляхом одно- та мультигенного філогенетичного аналізів. Для одногенного аналізу було використано 658-ми нуклеотидові фрагменти I-ї субодиниці мітохондрієвого гену цитохром с оксидази (COI). Для мультигенного аналізу застосовувалась комбінація консенсусних секвенсів двох мітохондрієвих (16s rRNA, COI) та одного ядрового (28S rRNA) генів. В результаті було отримано філогенетичні максимально ймовірні дерева з високими ступенями підтримки гілок. Топографічно філогенетичні дерева розділені на три великі клади, які представляють три морфологічно відмінні групи роду *Judolia*. Синтез молекулярних і морфологічних даних дав нам можливість встановити внутрішньородову структуру *Judolia*, розподіливши її на чотири підроди: *Pachytodes* **nom. & stat. res.**, *Florijudolia* **subgen. nov.**, *Judolia*, *Sierrojudolia* **subgen. nov.** Окрім того, генетична і морфологічна подібності родів *Oedecnema* і *Judolidia* стали визначальними для поміщення їх у підрід *Judolia*. У свою чергу підрід *Judolia* розділено на чотири інфрароди: *Boreojudolia* **infragen. nov.**, *Oedecnema* **stat. nov.**, *Judolia*, *Judolidia* **stat. nov.** Також подано нову загальну схему внутрішньородової таксономії *Judolia* рівно як і ключі до її визначення.

Ключові слова: скрипунові жуки, молекулярна філогенія, мультигенний аналіз, еволюція, кладистика, інтегративна таксономія.