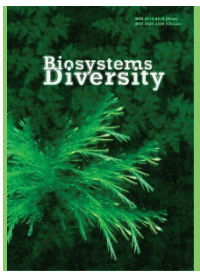

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Molecular revision of Rhagiini sensu lato (Coleoptera, Cerambycidae): Paraphyly, intricate evolution and novel taxonomy

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Due to classical taxonomy, the subfamily Lepturinae is divided into two large tribes Rhagiini s.l. and Lepturini s.l. However, this division is clearly artificial and does not correspond to the evolutionary relationships between the groups of genera with different morphologies that are part of these two tribes. However, there is a consensus among researchers supporting the monophyly of Lepturini s.l. while there is no such consensus for Rhagiini s.l. Over the past three decades, there have been several attempts to revise the tribe Rhagiini s.l. and divide it into smaller tribes. These attempts were somewhat successful based on larval and adult morphology. In general, eight tribes are distinguished within Rhagiini s.l. These include Teledapini, Xylosteini, Encyclopini, Oxymirini, Enoploderini, Rhamnusiini, Rhagiini and Sachalinobiini. However, the new system of Rhagiini s.l. is not always unambiguously accepted by different researchers, which causes discussions among experts. First of all, this is due to the fact that this system is only partially natural and far from fully reflects the phylogeny not only of Rhagiini s.l., but also of entire subfamily Lepturinae. In addition to the classical morphologic methods of studies, the use of the modern molecular phylogenetic methods opens up wide prospects for solving this puzzle. However, there have been very few such studies. Moreover, all of them were based on the use of only one gene. In this study, I used a general time-reversible (GTR) model of sequence evolution based on three mitochondrial (12S rRNA, 16S rRNA, COI) and two nuclear (18S rRNA, 28S rRNA) genes. My analysis yielded a well-resolved phylogenetic maximum likelihood tree, which clearly demonstrates the paraphyly of Rhagiini s.l. It consists of at least three clades representing different and distantly related evolutionary branches: 1) PaRh, 2) OSaXyR-SEP, 3) GAC. The extant Rhagiini s.l. are mostly heterogeneous relict groups with an intricate evolutionary and phylogeographic history. Most of these groups are represented by one or very few species, often isolated geographically on different continents. In particular, numerous cases of parallel and convergent evolution and homoplasy, a chimeric combination of plesiomorphic and apomorphic morphological characters, were found in all clades. Therefore, the evolutionary "tree" of Rhagiini s.l. is more like a "bush" with numerous relict branches. Finally, I proposed a new taxonomic model of Rhagiini s.l., which is the most consistent with their natural phylogeny, with new developments in nomenclature.

Keywords: longhorn beetles; Lepturinae; multigene analysis; phylogeny; homoplasy; systematics; new taxa; nomenclature.

Introduction

Rhagiini s.l. belongs to a relatively small subfamily Lepturinae of the longhorn beetles, which includes about 1,500 species from 210 genera worldwide (Monné & Monné in Wang, 2017). However, the taxonomical position of Rhagiini s.l. as well as the internal phylogeny (i.e., subdivision into tribes) of Lepturinae is still unresolved. Consensus on monophyly exists only for Lepturini (Švácha & Lawrence, 2014; Danilevsky, 2020; Semaniuk & Zamoroka, 2020; Zamoroka, 2022), while regarding Rhagiini s.l., researchers' opinions differ in a wide range: from monophyly (Zahajkevych, 1991; Vitali, 2018) to the complete polyphyly (Švácha & Lawrence, 2014; Danilevsky, 2020). Not only do different researchers recognize different numbers of tribes (Fig. 1), but this division is highly subjective and largely artificial. In particular Švácha & Lawrence (2014) recognize 6 tribes within Lepturini; Danilevsky (2014) and Dutrillaux & Dutrillaux (2018) recognize 8 tribes; Bouchard et al. (2011) and Monné & Monné (in Wang, 2017) recognize 9 tribes; Danilevsky (2020) recognizes 10 tribes. In addition, the list of tribes varies in different authors.

Kirby (1837) was the first who made an attempt to subdivide Lepturinae into tribes. He separated Rhagiidae from Lepturidae only for the sole genus *Rhagium* Fabricius, 1775. Similarly, Mulsant (1839) recognized Rhagiidae. However, he expanded the concept of Rhagiidae to two groups, including Vesperaires (*Vesperus* Dejean, 1821) and Rhagiaries (*Rhagium*). The remaining genera he placed within Lepturidae, i.e., Toxotaries (*Toxotus* Dejean, 1821 and *Pachyta* Dejean, 1821) and Lepturaires (*Leptura* Linnaeus, 1758, *Strangalia* Audinet-Serville, 1835, *Anoplodera* Mulsant, 1839, *Grammoptera* Dejean, 1835). Blanchard (1845) placed 5 groups within Lepturides, which included Desmocerites, Cometites, Stenoderites, Vesperites and Lepturites. Motschulsky (1849) recognized only two groups: *Leptures* and *Pachytes*. Later, Thomson (1861) divided Lepturitae into two groups: Pseudolepturitae and Lepturitae verae (Lepturitae, Stenocoritae, Desmoceritae). Leconte & Horn (1883) placed Lepturinae within Cerambycinae as the tribe Lepturini, which included *Rhagium*, Toxoti and Lepturae. They also separately recognized the tribes Desmocerini and Encyclopini. Reitter (1912) used very similar system. However, he divided Lepturini into four groups of genera ("Gattungsgruppen"): Xylosteina, Stenochorina, Lepturina and Necydaliina. Boppe (1921) subdivided Lepturinae into seven tribes: Philini, Vesperini, Desmocerini, Dorcasomini, Rhagii, Toxotini, Lepturini. In general, at the end of the XIX and at the beginning of the XX centuries, the internal system of Lepturinae still remained unstable.

In the XX century, several systems of Lepturinae were established, which dominated in the scientific papers on the different continents. However, a unified understanding of the internal system of Lepturinae was never formed. The North American scientists usually recognized three tribes within Lepturinae: Desmocerini, Lepturini and Necydalini (Linsley, 1940; Linsley & Chemsak, 1972; Turnbow & Thomas, 2002). All species of Rhagiini s.l. were included in the tribe Lepturini. In North Asia, scientists used system with four tribes Xylosteini, Stenocorini, Lepturini and Necydalini (Plavilschikov, 1936) or three tribes Xylosteini, Rhagiini, Lepturini (Cherepanov, 1988). In the European tradition Lepturinae are usually subdivided on two tribes: Rhagiini and Lepturini sometimes to-

gether with Vesperini and Necydalini (Villiers, 1974; Bily & Mehl, 1989; Zahajkevych, 1991; Vitaly, 2018). The same system was used in Japan (Ohbayashi et al., 1992). It is the special interest, Vives (2000) used the system proposed by Boppe (1921) and divided Rhagiini s.l. into two groups: Rhagiini (*Rhagium* + *Rhamnusium*) and Toxotini (the rest of Rhagiini).

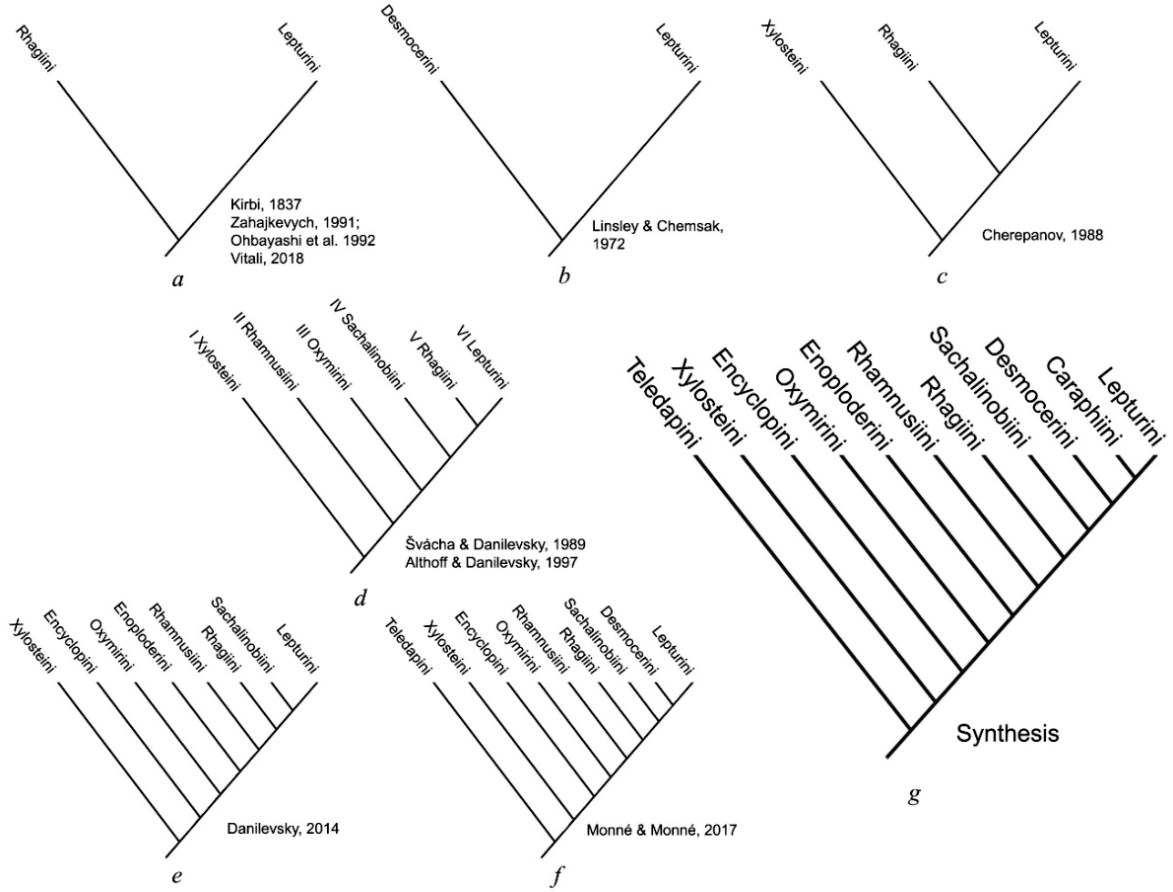

Fig. 1. Historical visions (*a–f*) and the current synthesis (*g*) of taxonomic composition of the subfamily Lepturinae

The attempts to create a comprehensive system for the Lepturinae subfamily, which would unite all species and be phylogenetic, began at the end of the XX century and continues to the present day. Švácha & Danilevsky (1989) proposed such system on the comparative characteristics of larval morphology. They distinguished six morphological groups of larvae that were candidates for separate tribes, although these taxa were not formalized and described at the time. All new groups were separated within the tribe Rhagiini s.l. These groups were formalized into tribes much later (Althoff & Danilevsky, 1997; Sama & Sudre, 2009; Löbl & Smetana, 2010; Danilevsky, 2014). Althoff & Danilevsky (1997) established three new tribes Oxymirini, Enoploderini and Rhamnusiini, separated them from Rhagiini s.l. Moreover, what is very important to emphasize, none of them was formally described, but only names were proposed. A formal description of the tribe Rhamnusiini was made later by Sama (Sama & Sudre, 2009). Another two tribes Oxymirini and Enoploderini were very sparingly described almost two decades later (Danilevsky, 2014). Moreover, Oxymirini was described exceptionally on the basis of larval morphology and there is still no description of the tribe by imago. Nevertheless, these names have already been used in scientific publications by other authors. In particular, Bousquet et al. (2009) indicated for Lepturinae eight tribes, including Desmocerini, Encyclopini, Lepturini, Oxymirini, Rhagiini, Rhamnusiini, Teledapini, Xylosteini. In the Catalogue of Palaearctic Coleoptera, Löbl & Smetana (2010) Lepturinae is subdivided into seven tribes: Encyclopini, Lepturini, Oxymirini, Rhagiini, Rhamnusiini, Sachalinobiini, Xylosteini. Later, Danilevsky (2014) proposed an eight tribes' system of Lepturinae, including Xylosteini, Encyclopini, Oxymirini, Enoploderini, Rhamnusiini, Rhagiini, Sachalinobiini, Lepturini. In a short while, Ohbayashi et al. (2016) described a new additional tribe Caraphiini for sole genus *Caraphia* Gahan, 1906. Monné & Monné (Wang, 2017) made an attempt to combine existed systems of Lepturinae into one with nine tribes. They added the North American tribe Desmocerini to Danilevsky's system (Danilevsky, 2014). However, they were not included in Enoploderini and Caraphiini. Finally, Danilevsky (2020) recognizes 10 tribes within Lepturinae in the Palaearctic, including Caraphiini, Encyclopini, Enoploderini, Lepturini, Oxymirini, Rhagiini, Rhamnusiini, Sachalinobiini, Teledapini, Xylosteini. Today, a total of 11 tribes are recognized within the Holarctic. These include Caraphiini, Desmocerini, Encyclopini, Enoploderini, Lepturini, Oxymirini, Rhagiini, Rhamnusiini, Sachalinobiini, Teledapini, Xylosteini.

Thus, the number of described tribes in the subfamily Lepturinae has increased over the past few decades. And their absolute number is separated from the tribe Rhagiini s.l. Many researchers believe that the modern division into tribes does not correspond to phylogeny and evolution of Lepturinae and Rhagiini s.l. in particular (Švácha & Lawrence, 2014; Dutrillaux & Dutrillaux, 2018). Švácha & Lawrence (2014) indicate the non-monophyletic nature of Rhagiini s.l., based on the study of larval morphology. They consider Rhagiini s.l. to be a non-monophyletic, artificial group, based on previous results of a molecular phylogeny using the 16S rRNA gene (Sýkorová, 2008). At the same time, Dutrillaux & Dutrillaux (2018, 2019) consider Rhagiini s.l. to be a monophyletic tribe based on the study of Lepturinae karyotypes. Since classical research methods are almost exhausted, molecular phylogeny methods can be an alternative way to solve this puzzle.

In the current study I presented the results of the five-genes phylogenetic analysis of 88 species, including 59 species of Rhagiini s.l., 22 species of Lepturini and 7 species of the outgroup. I revealed the paraphyly of Rhagiini s.l. which consists of three successive sister clades. Moreover, I found numerous cases of parallel evolution in different evolutionary lineages with chimeric combinations of plesiomorphic and apomorphic features and homoplasy. My results generally match with ideas of Švácha & Lawrence (2014), especially in case of evolutionary unity of Oxymirini, Sachalinobiini, Xylosteini and Rhamnusiini. In addition, I revealed hidden

phylogenetic clades within Rhagiini s.l. and established new taxa, including Stenocorini, nom. res., Evodinini, trib. nov., Pidoniini trib. nov. and Cariliini, trib. nov. Finally, I presented novel taxonomy for Rhagiini s.l. in particular and for entire subfamily Lepturinae in general.

Materials and methods

In the current study, I used GenBank publicly available DNA partial sequences (Table 1) of 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). For avoiding the statistical noises caused by multiple point mutations, I produced consolidated sequences for genes sets (if available) of the separate specimens. The genes were assembled in the matrix in the following order: 12S rRNA – 16S rRNA – COI – 18S rRNA – 28S rRNA with the total length 4.276 kilobase (kb). Limitations of the current study are related to the lack of sequences of five genes for all represented species. In particular, for 19 species, the sequences of only one gene (mostly COI) were available. Multiple alignments were generated using the Muscle software in the environment of SeaView 4 (Gouy et al. 2010). 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 (Guindon & Gascuel, 2003). 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 (Anisimova & Gascuel, 2006; Guindon et al., 2010). 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 (Gascuel, 1997).

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

Species	Voucher number
Acmaeops marginatus (Fabricius, 1781)	KM286367.1
A. proteus (Kirby, 1837)	JF887631.1; JN310749.1; KM850928.1; KM847564.1; KM845520.1
A. septentrionis (C. G. Thomson, 1866)	KM443722.1; KJ964105.1; KJ962917.1; KJ962493.1; KJ963260.1; MF776951.1; MF776955.1
Akimerus schaefferi (Laicharting, 1784)	MW981937.1
Anastrangalia dubia sequensi (Reitter, 1898)	KY773687.1; KY683642.1; AF332923.1; MN609573.1; HM046524.1
Anisorus quercus (Götz, 1783)	KM286023.1; KU907817.1
Anoplodera rufipes (Schaller, 1783)	KU911920.1; KU908669.1; KU908153.1; KM286191.1
A. sexguttata (Fabricius, 1775)	KJ966542.1; KM439643.1; KM447872.1; KM450584.1; KU909582.1
Anthophylax cyaneus (Haldeman, 1848)	KR131097.1; KR124719.1
Brachysomida (Brachysomida) bivittata (Say, 1824), com. nov.	KM844018.1
Brachysomida (Pseudogaurotina) cressoni (Bland, 1864), comb. nov.	JF887521.1; KM845711.1; KM847052.1; KM850299.1; KM850553.1
Brachyta amurensis (Kraatz, 1879)	OL343466.1; OL343465.1; OL343464.1
B. bifasciata (Olivier, 1797)	KY683688.1
B. interrogationis (Linnaeus, 1758)	KX087246.1; KJ962314.1; KJ964769.1; KM441129.1; KU909866.1; KX087246.1
B. sachalinensis Matsumura, 1911	KY683706.1
Brachytodes clathratus (Fabricius, 1793), comb. nov.	JF889475.1; KM286084.1; KM448444.1; KU906227.1; KU917336.1
Carilia tuberculicollis (Blanchard, 1871)	KF737658.1; KF737721.1; KF737784.1; KF142070.1; KF142006.1; KF142135.1
Carilia virginea (Linnaeus, 1758)	HQ832599.1; HQ954589.1; KJ961983.1; KM445527.1; KM439292.1; KM445387.1; AF267401.1; AJ841532.1
Cerambyx cerdo (Linnaeus, 1758)	MK084977.1; MK088075.1; KM285966.1; MK084975.1; MK084976.1; MK084977.1
Cortodera femorata (Fabricius, 1787)	KJ966406.1; KU910483.1; KU914327.1; KU914836.1
Cortodera humerata (Fabricius, 1787)	KX087264.1; KX087264.1; KX087264.1; HQ954073.1; KM285870.1; KM286194.1; KU914520.1; KU919048.1
Desmocerus aureipennis Chevrolat, 1855	KM848393.1; KM847644.1; KM846518.1; KM849945.1; MW597108.1
Desmocerus californicus dimorphus Fisher, 1921	MN196288.1; MN196284.1; MN199329.1; MN267861.1; MN267862.1; MN267863.1; MN262461.1; MN262460.1; MN262462.1; MN262463.1; MN262464.1; MW597088.1
Dinoptera collaris (Linnaeus, 1758)	KM450437.1; KM449303.1; KM286140.1; KM446985.1; JF889454.1; AF267400.1
Dinoptera minuta (Gebler, 1832)	KU188499.1; KU188500.1; KU188501.1; KY683667.1
Enoploderes vitticollis (LeConte, 1862)	MW983274.1; AB811776.1
Evodinus borealis (Gyllenhal, 1827)	KY683607.1; KJ964387.1; KJ963179.1; KJ963441.1
Evodinus monticola (Randall, 1838)	JF888508.1; JF888509.1; KU875074.1; KM846576.1; MF632622.1
Fallacia elegans (Faldermann, 1837)	MW983555.1
Gaurotes cyanipennis (Say, 1824)	KU255631.1; JF890954.1; KT620089.1; KM845025.1; KR120722.1; KM843572.1
Gnathacmaeops pratensis (Laicharting, 1784)	JF887384.1; JF887388.1; KJ202737.1; KM844316.1; KM845546.1
Grammoptera abdominalis (Stephens, 1831)	HQ953607.1; KM286027.1; KU906755.1; KU909239.1; KU909274.1;JN619069.1
G. exigua (Newman, 1841)	MF632970.1
G. haematites (Newman, 1841)	KM844277.1
G. subargentata (Kirby, 1837)	HM411803.1; JF887637.1; JF887649.1; JF888014.1; JF888265.1
G. ustulata (Schaller, 1783)	KU917015.1; KU912907.1; KU907372.1; KM285829.1
Hemadius oenochrous Fairmaire, 1889	NC_025243.1; NC_025243.1; NC_025243.1; AB703463.1
Lamia textor (Linnaeus, 1758)	KJ961885.1; KM445206.1; MH613743.1; KJ965883.1; KJ966718.1
Lamiomimus gottschei Kolbe, 1886	KF737701.1; KF737764.1; KY683678.1; KF141953.1; KF142017.1; HM046546.1
Leptacmaeops militaris (LeConte, 1850)	KM842145.1; KM841473.1; KM850678.1; KM850702.1; MF638834.1
Leptalia macilenta (Mannerheim, 1853)	KU875353.1; KM850917.1
Leptorhabdium pictum (Haldeman, 1847)	MW984022.1
Leptura aethiops Poda, 1761	MN420475.1; AF332921.1; KM451953.1; KY683603.1; KY683629.1; HM046547.1
L. annularis Fabricius, 1801	KY796051.1; HM034792.1; KY683714.1; KY683632.1; KU914996.1; KM443478.1; KM451359.1; HM046542.1
L. quadrifasciata (Linnaeus, 1758)	KU919023.1; KU908893.1; KJ963368.1; KM446982.1; KM441356.1; JN619084.1
Metacmaeops vittatus (Swederus, 1787)	MN344159.1; MN343897.1
Monochamus sutor (Linnaeus, 1758)	AY258059.1; AB533603.1; AY260843.1; AY264403.1; EU556670.1; EU556676.1; EU556682.1; KC692745.1
Neanthophylax mirificus (Bland, 1865)	MW982963.1
Nivellia aspera (LeConte, 1873), comb. nov.	JF888494.1; JF888496.1; JF888497.1; KM848421.1; KM844783.1; MW597082.1
N. mutabilis (Newman, 1841), comb. nov.	HM411735.1; MG055943.1; KM849722.1; JF887365.1; JF887360.1
N. sanguinosa (Gyllenhal, 1827)	KJ966109.1; MH020294.1; MH020295.1

Species	Voucher number
Oxymirus cursor (Linnaeus, 1758)	MN473085.1
Pachyta bicuneata Motschulsky, 1860	KY765551.1; HM034794.1; DQ223727.1; GU003931.1; KF247291.1; HM062973.1; HM046544.1
P. lamed (Linnaeus, 1758)	KJ963034.1; KM843972.1; KU875735.1; KJ965887.1; KM449308.1
P. quadrimaculata (Linnaeus, 1758)	KM440118.1; KM441670.1; KM450998.1; KU906393.1; KU914386.1
Paragaurotes ussuriensis (Blessig, 1873)	KY683641.1; KY683650.1
Pidonia sp.	FJ559043.1
P. alticollis (Kraatz, 1879)	KY683696.1
P. debilis (Kraatz, 1879)	KY683611.1; KY683652.1; KY683697.1; MN609611.1; MN609613.1
P. gibbicollis (Blessig, 1873)	HM034777.1; HM062972.1; HM046529.1
P. lurida (Fabricius, 1793)	MN473083.1; HQ954590.1; KU906557.1; KU914297.1; KM286007.1; KM440086.1
P. puziloi (Solsky, 1873)	MN609542.1; MN609543.1; MN609544.1
P. ruficollis Pic, 1902	HQ551613.1; JF887640.1; KR484955.1; MG056918.1; MF640115.1
P. scripta (LeConte, 1869)	JF887394.1; JF887395.1; JF887397.1; JF887399.1; JF887401.1
P. similis (Kraatz, 1879)	HM034771.1; HM062968.1; HM046523.1
Prionus coriarius (Linnaeus, 1758)	JF889828.1; KJ964237.1; KM286000.1; KM441011.1; KU908107.1
P. laticollis (Drury, 1773)	KU255618.1; KU255661.1; MH110202.1; AF267413.1; KP419244.1; KP419600.1; MN851234.1
Proanthophylax attenuatus, (Haldeman, 1847) comb. nov.	GU013568.1; KR119228.1; KR121762.1; MG059322.1; KR485286.1
Rhagium bifasciatum Fabricius, 1775	KM285983.1; KM286225.1; KU909874.1; KU916896.1; KM442815.1
Rh. fortecostatum Jureček, 1933	MN473103.1
Rh. inquisitor (Linnaeus, 1758)	KU255625.1; HM433492.1; HQ954550.1; KJ962550.1; KM285814.1; KM440357.1; MF115593.1
Rh. mordax (Degeer, 1775)	JX412743.1; HQ948267.1; HQ954457.1; KJ962620.1; KM285811.1; KM441365.1; AY748118.1; MF776948.1; MF776952.1
Rh. sycophanta (Schrank, 1781)	KJ967423.1; KM286118.1; KM286146.1; KU907792.1; KU918187.1
Rhamnusium bicolor (Schrank, 1781)	KM285760.1; KM442342.1; KU911377.1; KU908853.1
Rutpela maculata (Poda, 1761)	OW386295.1; MH020343.1; KU914676.1; KU910296.1; KU907795.1; KM446337.1; KP419275.1; KP419628.1; MN851205.1
R. nigra (Linnaeus, 1758)	KX087348.1; MH020344.1; KU915828.1; KU908354.1; KM449359.1; KM442043.1; AJ841533.1
R. septempunctata (Fabricius, 1793)	KM452170.1
Sachalinobia koltzei (Heyden, 1887)	MN473113.1
S. rugipennis (Newman, 1844)	KR121923.1
Stenocorus amurensis (Kraatz, 1879)	HM034775.1; KY683613.1; KY683637.1; MN905256.1; KY683720.1; MN850963.1
S. meridianus (Linnaeus, 1758)	MN473082.1; JN619111.1
S. nubifer (LeConte, 1859)	JF887366.1; KM848464.1; KM842172.1; JF887367.1
S. obtusus (LeConte, 1873)	KM849035.1
Strangalia attenuata (Linnaeus, 1758)	HM034780.1; KM449502.1; MH020329.1; KM449936.1; MH020328.1; HM046532.1
S. bicolor (Swederus, 1787)	EU734906.1; EU839772.1; EU815289.1
S. luteicornis (Fabricius, 1775)	KU255638.1; KJ164383.1; KM850262.1; HM156709.1; HM156701.1
Toxotopsis cinnamopterus (Randall, 1838)	KU255609.1; HM433501.1; HM433502.1; HM433517.1; HM433514.1; HM433506.1
Xylosteus spinolae Frivaldszky, 1837	MN473086.1

Photographs of the body structures were taken by USB camera 3CMOS Series C-mount USB3.0 CMOS Camera 10 MP. Images were then aligned and stacked in the ToupTek ToupViev v.×64, 4.7.14643.20190511 software package and additionally, enhanced in Adobe Photoshop CS3 v. 10.0 for publishing purposes.

Results

The well-resolved phylogenetic maximum likelihood tree (Fig. 2) was yielded from multigene analysis of three mitochondrial (12S rRNA, 16S rNA and COI) and two nuclear (18S rRNA and 28S rRNA) genes. Almost all branches of the phylogenetic tree were strongly supported by the approximate likelihood-ratio test (aLRT). The resultant phylogenetic tree showed monophyly of subfamily Lepturinae. Tribe Lepturini (including Desmocerini) is monophyletic and occupies the crown position on the tree. On the contrary, tribe Rhagiini s.l. is paraphyletic and consists of three successive sister clades, namely PaRh-clade (*Pachyta* and *Rhagium*), OSaXyR-SEP-clade (*Oxymirus*, *Sachalinobia*, *Xylosteus*, *Rhamnusium*, *Stenocorus*, *Evodinus*, *Pidonia*) and GAC-clade (*Gaurotes* s.l., *Acmaeops* s.l., *Cortodera* s.l.). All these clades are well separated with high levels of branch support.

PaRh-clade (Fig. 3) consists of two genera *Rhagium* and *Pachyta* (SH = 0.71) and it is the most basal on the Lepturinae tree. This relatively small clade is clearly relict and probably it is the most ancient within Lepturinae. At the same time, it should be noted that the genus *Rhagium* is characterized by autapomorphic features. These include significant shortening of the forehead (several times wider than long, with deep transverse sulcus) and its almost vertical position. Very similar features I found in imago of *Encyclops caeruleus* (Say, 1826). However, it was not included to the study due to the lack of relevant gene sequences. Perhaps, *Encyclops caeruleus* also belongs to *Rhagium*-clade. A large vertical forehead is characteristic of the subfamily Lamiinae with which the Lepturinae shared a common ancestor. However, such characters in *Rhagium* and *Encyclops* are probably case of homoplasy. On the contrary, *Pachyta* lacks these features, being morphologically closer to the ancestral form.

OSaXyR-SEP-clade is a genera-rich branch (Figs. 2), which, splits into two clearly separated subclades: 1) subclade OSaXyR – *Oxymirus*, *Sachalinobia*, *Xylosteus*, *Rhamnusium* (Fig. 4); 2) subclade SEP – *Stenocorus*, *Evodinus*, *Pidonia* (Fig. 5).

Subclade OSaXyR (SH = 0.97) is the most basal including four groups of genera: 1) *Oxymirus* Mulsant, 1863, *Proanthophhylax* gen. nov., *Anthophylax* LeConte, 1850, *Neanthophylax* Linsley & Chemsak, 1972 (SH = 0.99); 2) *Sachalinobia* Jacobson, 1899 (SH = 1.00); 3) *Leptorhabdium* Kraatz, 1879, *Xylosteus* Frivaldsky, 1838 (SH = 0.87); 4) *Enoploderes* Faldermann, 1837, *Rhamnusium* Latreille in Cuvier, 1829, *Akimerus* Audinet-Serville, 1836 (SH = 0.85). Traditionally, all these groups are classified to separate tribes (Bouchard & al., 2011; Švácha & Lawrence, 2014; Monné & Monné in Wang, 2017; Danilevsky, 2020). According to the current results, all of them are grouped into one large cluster, well separated from the others. On the other hand, each of these groups is a clearly relict, being represented by a very few species with a very fragmented range within the Holarctic. In addition, I found that *Anthophylax* is paraphyletic. *Proanthophhylax attenuatus* (Haldeman, 1847) comb. nov. is not the part of *Anthophylax*, but it belongs to the sister branch. For this reason, I established separate genus *Proanthophhylax* gen. nov. (for the description see below).

Subclade SEP consists of three groups of genera: 1) *Stenocorus*-group; 2) *Evodinus*-group; 3) *Pidonia*-group. The *Stenocorus*-group (SH = 1.00) includes three closely related genera *Toxotopsis* Casey, 1913, *Anisorus* Mulsant, 1863 and *Stenocorus* Fabricius, 1775 (Fig. 5). This subclade is very compact and represents ancient relict genera with very few species.

The *Evodinus*-group (SH = 0.89) consists of two (Fig. 5) distantly related lineages: 1) *Metacmaeops* Linsley & Chemsak, 1972; 2) *Brachy-*

todes Planet, 1924, *Brachyta* Fairmaire in Jacquelin du Val, 1864 and *Evodinus* LeConte, 1850. This subclade contains a number of relict genera with sole or a few species geographically isolated within different part of the Holarctic. Metacmaeops is preglacial relict genus with the sole East Nearctic species *Metacmaeops vittata* (Swederus, 1781).

Brachytodes clathratus (Fabricius, 1793) is a Central European preglacial relict species. It is a separate genus, which represents a sister branch to *Evodinus* – *Brachyta* crown group. *Evodinus* is also a species-poor genus, including only 3 species, two of which was included into the current study. My finds clearly showed that *Evodinus* is monophyletic and *Evodinus borealis* does not belong to the separate genus *Evodinellus* Winkler, 1929. Finally, *Brachyta* is the most diverse genus in the subclade with almost three dozen species.

The Pidonia-group (SH = 0.83) consists of two branches: 1) *Fallacia* Mulsant & Rey, 1863 and *Leptalia* LeConte, 1873; 2) *Pidonia* Mulsant, 1863 (Fig. 5). Phylogenetic analysis shows that *Fallacia* and *Leptalia* are very well separated and represented by two different genera. Both genera are monotypic and both are preglacial relicts.

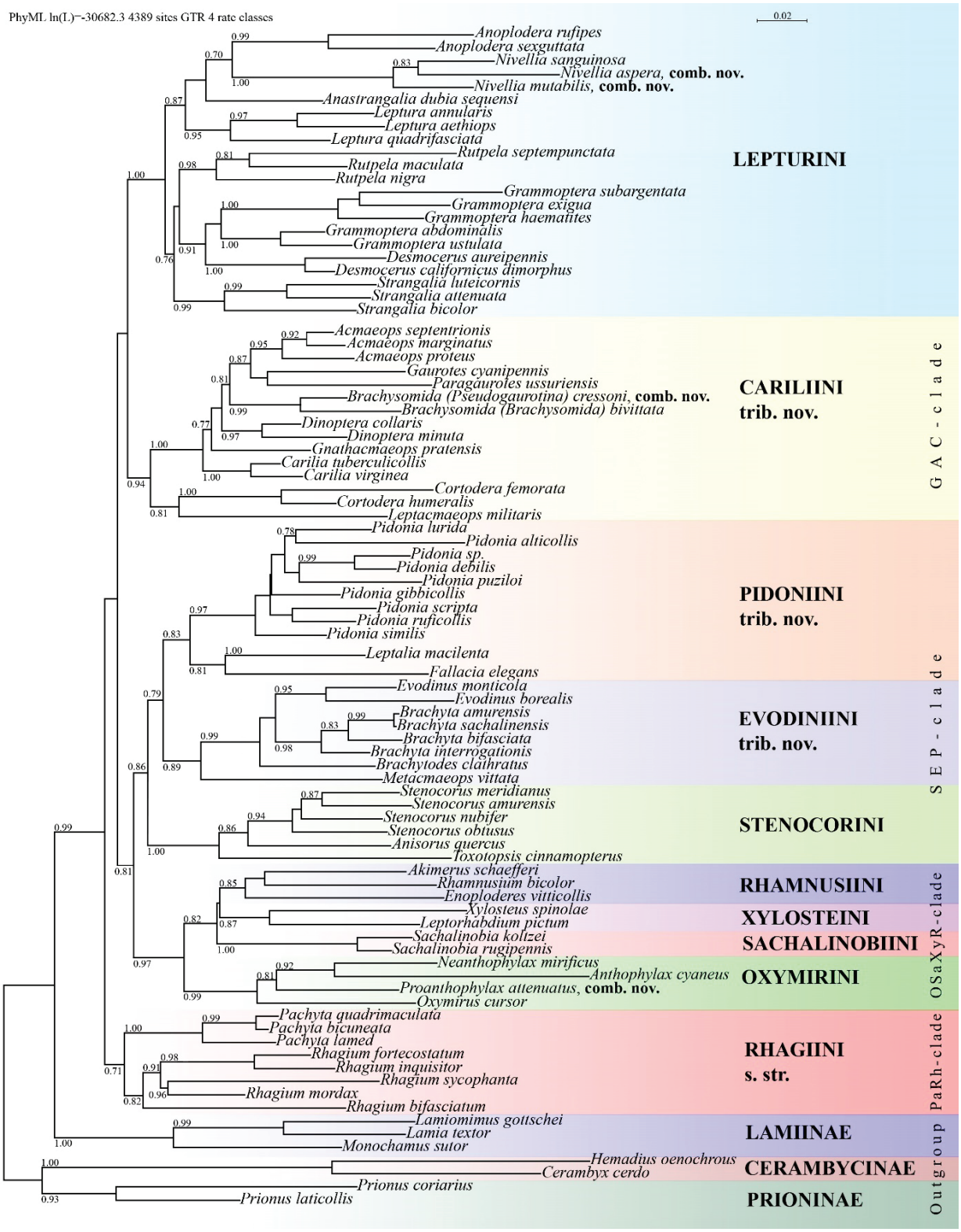

Fig. 2. The five genes (12 S rRNA+16 S rRNA+COI+18 S r RNA + 28 S rRNA) tree illustrating the phylogenetic hypothesis of relationships of Rhagiini s.l. within Lepturinae; the branch support SH-like values are shown with the threshold rule SH > 0.70

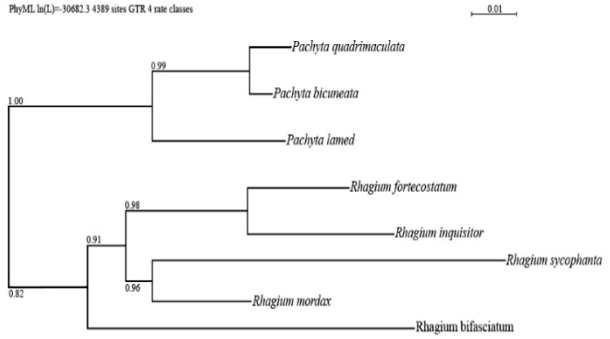

Fig. 3. The Subtree of the five genes (12 S rRNA+16 S rRNA+COI+ 18 S r RNA + 28 S rRNA) phylogenetic tree illustrating the composition of the PaRh-clade; the branch support SH-like values are shown with the threshold rule SH > 0.70

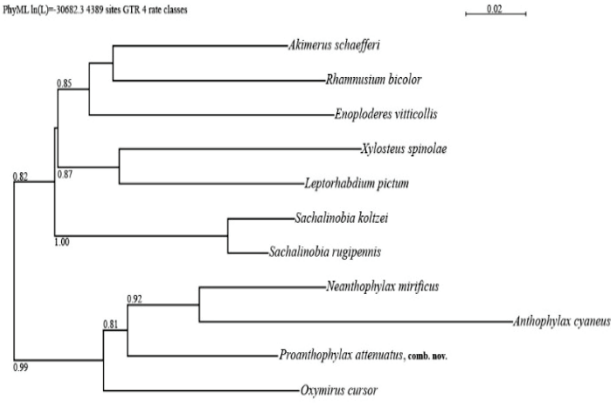

Fig. 4. The Subtree of the five genes (12 S rRNA+16 S rRNA+COI+ 18 S r RNA + 28 S rRNA) phylogenetic tree illustrating the composition of the OSaXyR-subclade; the branch support SH-like values are shown with the threshold rule SH > 0.70

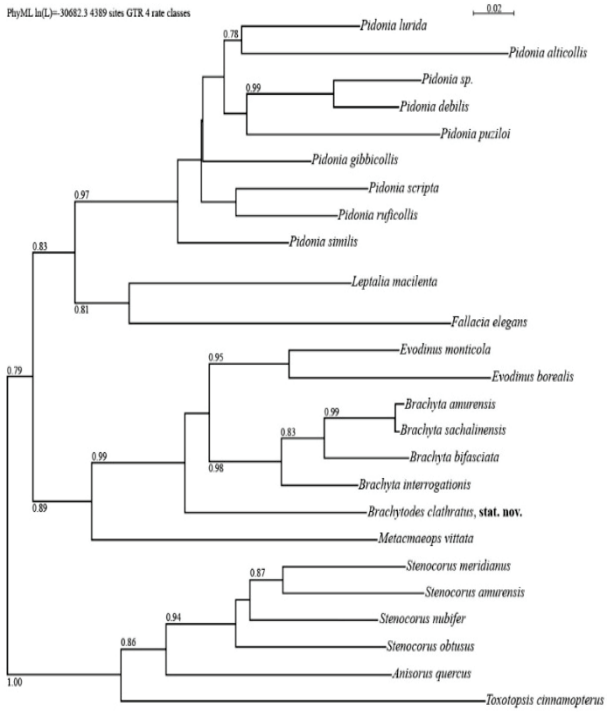

Fig. 5. The Subtree of the five genes (12 S rRNA+16 S rRNA+COI+ 18 S r RNA + 28 S rRNA) phylogenetic tree illustrating the composition of the SEP-subclade; the branch support SH-like values are shown with the threshold rule SH > 0.70

Genus *Fallacia* includes the sole Caucasian species *Fallacia elegans* (Faldermann, 1837) and *Leptalia* consists of the sole Holarctic species *Leptalia macilenta* (Mannerheim, 1853). The second branch represents lthe arge genus *Pidonia* (near 200 species). I was unable to elucidate the internal structure of the genus *Pidonia* due to the small number of available sequences. However, the phylogeny of this genus was proposed by Saito et al. (2003) based on a single ND5 gene.

GAC-clade (SH = 0.94) is the most diverse and species-rich (Fig. 6). It consists of two large branches: subclade of *Cortodera* Mulsant, 1863 and subclade of *Carilia* Mulsant, 1863. Subclade of *Cortodera* (SH = 0.81) comprises a large genus *Cortodera*, which however is clearly paraphyletic. Palearctic and Nearctic species of *Cortodera* are only distantly related. Thus, they should be recognized as separate genera.

Subclade of *Carilia* (SH = 1.00) represents a large group of genera, including *Carilia*, *Gnathacmaeops* Linsley & Chemsak, 1972, *Dinoptera* Mulsant, 1863, *Pseudogaurotina* Plavilshtshikov, 1958, *Brachysomida* Casey, 1913, *Paragaurotes* Plavilstshikov, 1921, *Gaurotes* LeConte, 1850, *Acmaeops* LeConte in Agassiz, 1850. This subclade is an amount of sister successive branches. The most basal genera within them are *Carilia*, *Gnathacmaeops* and *Dinoptera*. The next genera *Brachysomida*, *Pseudogaurotina*, *Paragaurotes*, *Gaurotes* and *Acmaeops* constitute the crown of the subclade. It should be noted that *Brachysomida* and *Pseudogaurotina* are closely related. Thus, both of them should be combined in one genus. In addition, phylogenetic analysis did not confirm Danilevsky's (2014) suggestion on erecting of *Euracmaeops* Danilevsky, 2014. *Acmaeops septentrionis* (C. G. Thomson, 1866), *Acmaeops marginatus* (Fabricius, 1781) and *Acmaeops proteus* (Kirby, 1837) to constitute a compact and monophyletic branch.

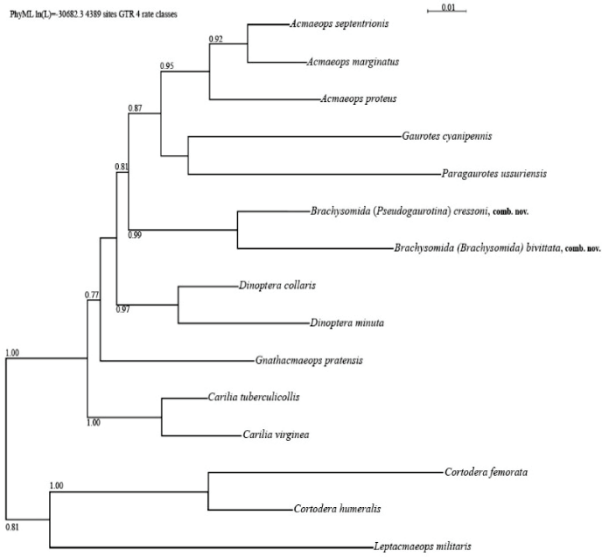

Fig. 6. The Subtree of the five genes (12 S rRNA+16 S rRNA+COI+ 18 S r RNA + 28 S rRNA) phylogenetic tree illustrating the composition of the GAC-clade; the branch support SH-like values are shown with the threshold rule SH > 0.70

Finally, the clade of Lepturini (SH = 1.00) represents the crown group of the Lepturinae subfamily. In the current study I do not consider the internal phylogeny of Lepturini. This was done early in the preliminary phylogenetic studies on Lepturini (Semaniuk & Zamoroka, 2020; Zamoroka et al., 2022). However, I will only make a few remarks here. First of all, I want to emphasize the position of *Desmocerus* Dejean, 1821 within Lepturini. The second, I confirm that the genus *Grammoptera* Dejean, 1835 belongs to the Lepturini. Moreover, *Grammoptera* is apparently a non-monophyletic genus consisting of two distant groups: Palearctic species from one side and Nearctic species from the other side. The third, Palearctic genus *Nivellia* Mulsant, 1863, in fact, belongs to Lepturinae and is closely related to Nearctic genus *Trachysida* Casey, 1913. Moreover, *Nivellia* and *Trachysida* syn. nov. are congeneric. Finally, the degree of relatedness between Desmocerini, Caraphiini and Lepturini, as well as their internal phylogeny, remains to be elucidated.

Discussion

Paraphyly of Ragiini s.l. The results of the current study clearly indicate the paraphyly of Rhagiini s.l. I found that Rhagiini s.l. consists of three different clades, which are characterized by numerous cases of parallel evolution with chimeric combinations of plesiomorphic and apomorphic features and homoplasy. The results are only partially consistent with current taxonomic visions of Rhagiini s.l. This confirms the idea that its tribal division is partly artificial and subjective without justification through appropriate criteria (Švácha & Lawrence, 2014). It should be noted that the non-monophyletic nature of the Rhagiini s.l. has been debated for a long time (Švácha & Danilevsky, 1989; Saito & Saito, 2003; Sykorova, 2008; Švácha & Lawrence, 2014; Dutrillaux & Dutrillaux, 2018, 2019). However, some researchers accept the classical division of Lepturinae into two or three tribes with monophyletic Ragiini (Zahajkevych 1991, Obayashi et al., 1992, Vitali, 2018). Other researchers subdivide Rhagiini s.l. into 5–8 tribes (Švácha & Danilevsky, 1989; Danilevsky, 2014, 2020; Švácha & Lawrence, 2014; Monné & Monné in Wang, 2017). To date, very few molecular studies of Lepturinae have been conducted (Saito & Saito, 2003; Sykorova, 2008; Semaniuk & Zamoroka, 2020; Zamoroka et al., 2022). These studies indicate that Rhagiini s.l. is non-monophyletic. However, to date, the data of molecular studies have not been taken into account in the systematics of Rhagiini s.l. The main criteria for systematics of Rhagiini s.l. still are the morphology of larvae and imago (Švácha & Danilevsky, 1989; Althoff & Danilevsky, 1997; Sama & Sudre, 2009; Švácha & Lawrence, 2014).

It is of special interest that two groups of genera are distinguished within Rhagiini s.l., which differ in karyotypes (Dutrillaux & Dutrillaux, 2018, 2019). The first group includes GAC-clade with the set of chromosomes 2n = 22 = 20 + XX/XY. The second group consists of PaRh-clade and OSaXyR-SEP-clade with karyotype 2n = 20 = 18 + XX/XY. My results clearly indicate that GAC-clade is monophyletic and occupies a special position different from Lepturini and the rest of Ragiini s.l. I propose to consider this clade as separate tribe Cariliini, trib. nov. Dutrillaux & Dutrillaux (2019) also placed Grammoptera within Rhagiini s.l. on the basis of its special karyotype formula 2n = 24 = 22 + XX/XY. My multigene phylogenetic analysis showed that *Grammoptera* is related to *Desmocerus* and both are related to the rest of Lepturini (Fig. 2). The karyotype formula of *Desmocerus* is 2n = 24 = 20 + XXXX/XXY0 and in Lepturini it is 2n = 20 = 18 + XX/X0 (Dutrillaux & Dutrillaux, 2018, 2019). Dutrillaux & Dutrillaux (2019) hypothesized that additional sex chromosomes of *Desmocerus* originated *de novo*. Thus, the basic set of chromosomes of *Desmocerus* (without the neo-sex chromosomes) is very similar to Lepturini, which lost Y chromosome. The karyotype origin of *Grammoptera* remains unclear. Nevertheless, karyotypes of *Grammoptera* and *Desmocerus* are unique within the entire Lepturinae. In the combination with the molecular data presented here it indicates that such karyotypes have originated independently from their common ancestor. Its origin is not connected with Cariliina, trib. nov. as is hypothesized by Dutrillaux & Dutrillaux (2019). From these data it is clear that loss and duplication of chromosomes occurred several times and independently within the entire subfamily Lepturinae.

According the current multigene phylogenetic analysis, the most basal group of Rhagiini s.l. is *Rhagium*-clade, which includes *Rhagium* and *Pachyta*. Besides the antiquity of *Rhagium*, it should be considered a highly specialized relict genus, which is characterized by both conserved plesiomorphic (sharp lateral pronotal thorn; anal cell on the wings of imago) and apomorphic features (shortened and almost vertical forehead in imago; reduction of caudal spine on 9th abdominal sternite in larva; two internal mandibular keels in larva). Švácha & Danilevsky (1988) emphasized the importance of the presence of the caudal ugomphs in larvae, defining them as plesiomorphic features. Their reduction is suggested as an apomorphic feature. In fact, caudal ugomphs are reduced in the most genera of Rhagiini s.l. except for several groups, discussed below.

Švácha & Lawrence (2014) suggested that Xylosteini (*Xylosteus*, *Leptorhabdium*, *Centrodera*), Rhamnusiini (*Rhamnusium*, *Enoploderes*), Oxymirini (*Oxymirus*, *Anthophylax*, *Neanthophylax*) and Sachalinobiini (*Sachalinobia*) are basal and the most ancient within Rhagiini s.l. Their suggestion based on the presence of the plesiomorphic feature: three inner mandibular larval keels. The remaining Rhagiini s.l. have only two keels on the inner side of the larval mandibles. My results almost completely confirm their idea, except the fact that all four mentioned tribes constitute a distinct evolutionary lineage within Lepturinae. Moreover, on the current phylogenetic tree (Fig. 2) Oxymirini, Sachalinobiini, Xylosteini and Rhamnusiini are grouped in one large cluster, well separated from the rest of Rhagiini s.l. I propose to establish a supertribe Archaecarinatitae, supertrib. nov. (for description see below) for Oxymirini, Sachalinobiini, Xylosteini and Rhamnusiini. Molecular data confirmed the monophyly of the tribe Oxymirini, which was established only on the base of larval morphology. Up till now, its description at the imaginal stage has been absent. Below, I provide this description. Danilevsky (2014) suggested Sachalinobiini as a sister tribe to Lepturini, based on the absence of anal cell on the wings. However, my phylogenetic data clearly showed that Sachalinobiini is a part of Archaecarinatitae, supertrib. nov. and confirmed the same idea propounded by Švácha & Lawrence (2014). In addition, molecular data showed that Enoploderini and Rhamnusiini are the closest relatives. Thus, I consider that they should be synonymized: Enoploderini, syn. nov. = Rhamnusiini. Surprisingly, Akimerus is a terminal branch within Rhamnusiini together with *Rhamnusium* and *Enoploderes*. This fact should be carefully studied in future due to the limitation of the current study (see methods). Archaecarinatitae, supertrib. nov. is sister to SEP subclade.

SEP-subclade is clearly paraphyletic with three distinct groups of genera *Stenocorus*, *Evodinus* and *Pidonia*. These genera possess a distinct morphology and evolutionary history that allow me to recognize them as separate tribes: Stenocorini, nom. res. & sensu nov., Evodinini, trib. nov., Pidoniini trib. nov. respectively. *Stenocorus* are usually suggested as basal within Rhagiini s.l. (Švácha & Danilevsky, 1988). Species from the subclade of *Evodinus* typically were considered as sister to *Pachyta* and Cariliini, trib. nov., due to morphological similarity (Švácha & Danilevsky, 1988; Althoff & Danilevsky, 1997; Sama, 2002; Danilevsky, 2014, 2020). The results of my study of multigene phylogeny demonstrate that such similarity is likely the result of convergent evolution. The situation is very similar with the taxonomical position of *Pidonia* and *Fallacia*, which were considered to be relatives of *Cortodera* (Švácha & Danilevsky, 1988; Danilevsky, 2014). However, my phylogenetic analysis shows that they belong to different evolutionary lineages and their general morphological similarity is also likely to be the result of convergent evolution. Moreover, I found that *Leptalia*, *Fallacia* and *Pidonia* are very closely related. According to Švácha & Danilevsky (1988) *Fallacia* and *Leptalia* are congeneric. However, molecular data shows that they are very well separated and represented two different genera. Moreover, *Leptalia* usually is placed within Encyclopini (Bousquet et al., 2017). However, my results indicate the fallacy of such a placement. I propose to exclude *Leptalia* from Encyclopini.

Evolutionary model of Rhagiini s.l. Švácha & Lawrence (2014) noted that the current system of Lepturinae in unstable and its subdivision into tribes is at least artificial. In my opinion, this is true because of the wide acceptance of the misconception of the linearity of the evolutionary process – gradual loss of plesiomorphic and acquisition of apomorphic features. At the same time, researchers almost completely exclude or try to avoid cases of homoplasy. My multigene phylogenetic analysis showed that evolutionally Rhagiini s.l. does not resemble a "tree" but rather a "bush" with numerous shoots that branch off from a common root (Fig. 7). It is important to emphasize that the recent Ragiini s.l. is a number of relict groups which have survived to the present day from past geological epochs. Many of the recent genera of Rhagiini s.l. are represented by sole or a very few species (e.g., *Metacmaeops*, *Evodinus*, *Fallacia*, *Leptalia*, *Sachalinobia*, *Oxymyrus*, *Rhamnusium*, *Enoploderes* etc.). At the same time, the relict groups are present in all clades of Rhagiini s.l. On the other hand, the relict groups are often represented by highly specialized forms which have completely or partly lost plesiomorphic features (e.g., *Rhagium*, *Sachalinobia*, *Stenocorus*, *Pachyta* etc.). Thus, building a system based only on morphological features leads to inaccurate conclusions, since the evolutionary parallelisms and convergence are not so obvious. In this regard, the use of molecular methods makes it possible to detect cases of convergent and parallel evolution and homoplasy.

It is widely accepted that entire round eyes, antennae nested between eyes, sharpened lateral pronotal tubercules, closed anal cell on the wings

are plesiomorphic features for the imago of Rhagiini s.l. Such larval features as developed ugomphs, three inner mandibular keels and seven abdominal ambulatory ampullae are also plesiomorphic (Švácha & Danilevsky, 1988; Zahajkevych, 1991; Danilevsky, 2014; Švácha & Lawrence, 2014). The general evolutionary trend is directed towards loss of ancestral plesiomorphic features and acquisition of new apomorphic features. However, this process within Rhagiini s.l. was far from linear, and chimeric combinations of plesiomorphic and apomorphic features are spread among its different evolutionary lineages. The loss of plesiomorphic features occurred multiple times and independently. Instead, the appearance of apomorphic features very often has the character of homoplasy. For instance, the loss of the sharpened lateral pronotal tubercles occurred several times. This feature is completely absent in Cariliini, trib. nov., Pidoniini, trib. nov., Evodiniini, trib. nov., Stenocorini. It is also absent in Pachyta but present in Rhagium, both belong to Ragiini s.str. The sharpened lateral pronotal tubercles also absent in some Archaecarinatitae, supertrib. nov. (e.g., Sachalinobiini and Rhamnusiini), but present in Oxymirini and Xylosteini. The loss of the closed anal cell on the wings occurred independently in Sachalinobiini and Lepturini, while it is present in the rest Rhagiini s.l. Developed larval ugomorphs are conserved in Oxymirini and Stenocorini but totally reduced or modified into caudal spine in other tribes. Modification of larval mandibles and loss of one of the three inner keels also occurred repeatedly. In particular, this feature is preserved only in Archaecarinatitae, while in the rest of Lepturinae one keel is lost. The appearance of the above-mentioned homoplasies is the result of parallel and convergent evolution, which included the development of apomorphic features due to preadaptations and living in similar environments.

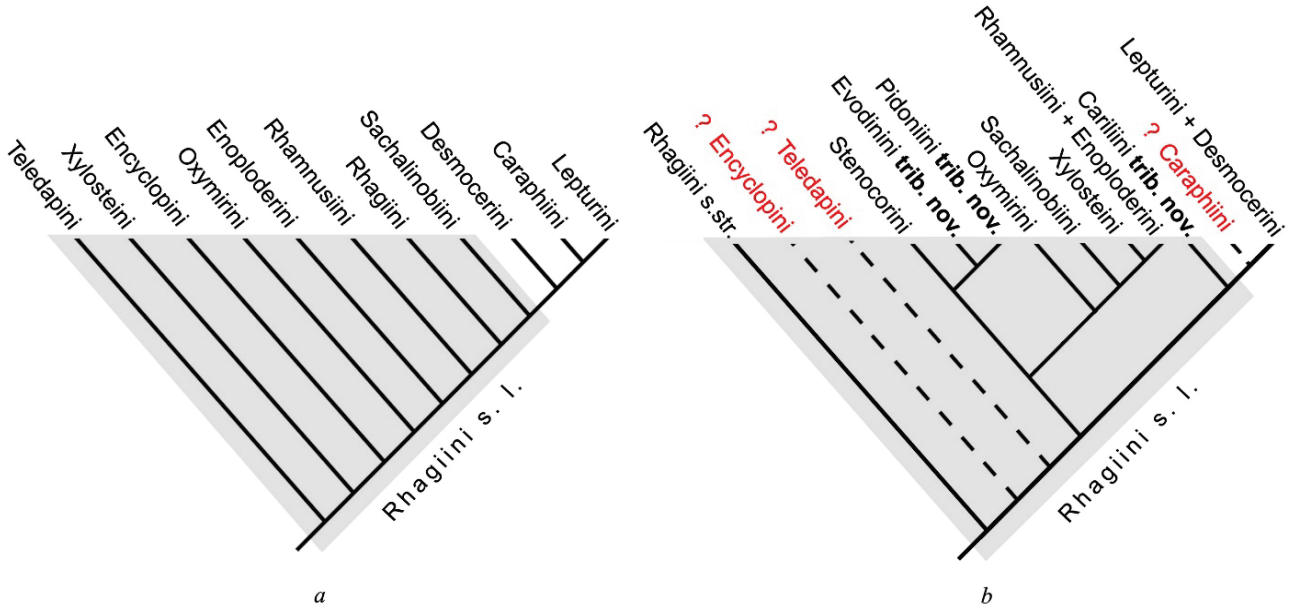

Fig. 7. Comparison of two models of Lepturinae taxonomic subdivision: *a* – synthetic model, *b* – phylogenetic model

Systematics. Since Rhagiini s.l. is parphyletic I propose its phylogenetic system including nine tribes. These include tribes 1) Rhagiini, sensu novo; 2) Oxymirini; 3) Sachalinobiini; 4) Xylosteini; 5) Rhamnusiini; 6) Stenocorini, nom. res. & sensu nov.; 7) Evodiniini, trib. nov.; 8) Pidoniini, trib. nov.; 9) Cariliini, trib. nov. Tribes Oxymirini, Sachalinobiini, Xylosteini and Rhamnusiini united in supertribe Archaecarinatitae, supertrib. nov. Tribes Encyclopini and Teledapini were not evaluated and their phylogenetic position remain unknown (Fig. 7). Neither of these tribes is included in the system proposed below.

1. Tribe Rhagiini Kirby, 1837, sensu novo

Type genus: *Rhagium* Fabricius, 1775

Description: Eyes round, weakly emarginated (Fig. 8 a–c). Antennae bases close to each other, widely separated from edge of eyes . Pronotum (Fig. 9 a–c) subcylindrical with large sharpened or smoothed lateral tubercle. Prosternum (Fig. 10 a–c) short with deep transverse sulcus. Prosternal process wide, long, raised high above disc and completely separated procoxa. Mesosternal (Fig. 11 a–c) process very wide with V-shaped emargination.

Diagnosis: Presents a clear lateral pronotal tubercle; prosternal process wide, long, raised high above disc; mesosternal process wide with V-shaped emargination.

Definition: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA+ 28S rRNA genes phylogeny. The least inclusive clade containing *Rhagium*, but not including *Oxymirus*, *Sachalinobia*, *Xylosteus*, *Rhamnusium*, *Stenocorus*, *Pidonia*, *Evodinus*, *Carilia*, *Leptura*.

Subordinated taxa:

Genus *Rhagium* Fabricius, 1775 (type species *Cerambyx inquisitor* Linnaeus, 1758);

Genus *Pachyta* Dejean, 1821 (type species *Leptura 4-maculata* Linneus, 1758);

Supertribe Archaecarinatitae, supertrib. nov.

Type genus: *Oxymirus* Mulsant, 1862

Description: Morphologically heterogenic group. Body typically elongated. Head (Fig. 8 d–e) elongated with well-developed and protruding tempora and square forehead. Eyes convex, well emarginated. Antennae widely separated on forehead. Pronotum (Fig. 9 d–e) subcylindrical with large sharpened or smoothed lateral tubercle. Prosternum short (Fig. 10 d–e). Prosternal process thin, completely separated procoxa. Larval mandibles with three inner keels.

Diagnosis: Pronotum subcylindrical with large sharpened or smoothed lateral tubercle; three inner mandibular keels in larvae.

Definition: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Oxymirus*, *Sachalinobia*, *Xylosteus*, *Rhamnusium*, but not including *Rhagium*, *Stenocorus*, *Pidonia*, *Evodinus*, *Carilia*, *Leptura*.

Etymology: Ancient Greek "ἀρχαῖος" – "ancient" and Latin "carina" – "keel". The name referred to three inner mandibular keels an archaic feature in larvae of the subordinated taxa. This feature is unique to Archaecarinatitae, supertrib. nov. within Lepturinae.

Subordinated taxa:

Tribe Oxymirini Danilevsky, 2014, nec. Althoff & Danilevsky, 1997

Tribe Sachalinobiini Danilevsky, 2010

Tribe Xylosteini Reitter, 1912

Tribe Rhamnusiini Sama, 2009, nec. Althoff & Danilevsky, 1997

2. Tribe Oxymirini Danilevsky, 2014, nec. Althoff & Danilevsky, 1997

Švácha (Švácha & Danilevsky, 1988) provided description of the "Tribe III" without the name. Althoff & Danilevsky, (1997) provided the name Oxymirini without description (nomen nudum according ICZN, Art. 13.1.1). The formal description of Oxymirini, consisting of four words "Larvae with well-developed ugomphs" (in Russian) provided by

Danilevsky in 2014. Thus, it should be considered that the year of description of Oxymirini is 2014. Since the Oxymirini have been described only by larval morphology, I provide a description of the tribe by imago for the first time.

Type genus: *Oxymirus* Mulsant, 1862

Description: Head (Fig. 8 d) elongated with smoothed tempora. Eyes with deep emargination. Antennae widely separated on the forehead and touch (or almost touch) frontal margin of eyes. Forehead large, square. Pronotum (Fig. 9 d) subcylindrical with big sharpened lateral tubercle. Prosternal process thin, completely separated procoxa.

Diagnosis: Antennae touch (or almost touch) frontal margin of eyes.

Definition: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Oxymirus*, but not including *Sachalinobia*, *Xylosteus*, *Rhamnusium*.

Subordinated taxa:

Genus *Oxymirus* Mulsant, 1862 (type species *Cerambyx cursor* Linnaeus, 1758);

Genus *Proanthophylax*, gen. nov. (type species *Pachyta attenuata* Haldeman, 1847) – body elongated, covered with dense and recumbent hair. Integument brown except black head and pronotum; femora dark red. Elytra brown, with multiple patches of dense hair, without metallic shade and shine. Pronotum subconical with big sharpened lateral tubercle and two longitudinal tubercles on the disc. Differential diagnosis: elytra not metallic, reddish-brown, covered by dense tufts of white hairs. Etymology: Latin "pro" – "before" + "Anthophylax" – the genus name. This refers to phylogenetic position of *Proanthophylax attenuatus*, comb. nov. within Oxymirini. Monotypic genus, includes *Proanthophylax attenuatus* Haldeman, 1847, comb. nov.

Genus *Anthophylax* LeConte, 1850 (type species *Anthophylax viridis* LeConte, 1850);

Genus *Neanthophylax* Linsley & Chemsak, 1972: 78 (type species *Anthophylax tenebrosus* (LeConte, 1873).

Suggested taxa:

Genus *Neoxymirus* Miroshnikov, 2013: 455 (type species *Toxotus mirabilis* Motschulsky, 1838);

3. Tribe Sachalinobiini Danilevsky, 2010

Type genus: *Sachalinobia* Jacobson, 1899

Definition: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Sachalinobia*, but not including *Oxymirus*, *Xylosteus*, *Rhamnusium*.

Subordinated taxa:

Genus *Sachalinobia* Jacobson, 1899 (type species *Pachyta rugipennis* Newman, 1844);

4. Tribe Xylosteini Reitter, 1912

Type genus: *Xylosteus* Frivaldszky, 1837

Definition: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Xylosteus*, but not including *Oxymirus*, *Sachalinobia*, *Rhamnusium*.

Subordinated taxa:

Genus *Xylosteus* Frivaldszky, 1837 (type species *Xylosteus spinolae* Frivaldszky, 1838);

Genus *Leptorhabdium* Kraatz, 1879 (type species *Xylosteus gracilis* Kraatz, 1873 = *Xylosteus illyricus* Kraatz, 1871);

5. Tribe Rhamnusiini Sama, 2009, nec. Danilevsky in Althoff & Danilevsky, 1997: 9

= Enoploderini Danilevsky, 2014: 72, nec. Althoff & Danilevsky, 1997: 9, syn. nov. Althoff & Danilevsky, (1997) proposed the name Enoploderini without description, which contradicts ICZN, Art. 13.1.1. (Nomen nudum). Later, however he provided short description in Russian (Danylevsky, 2014). Thus, 2014 should be considered as year of the description. Since Enoploderus and *Rhamnusium* are phylogenetically very close and constitute one clade, I considered Enoploderini as synonym of Rhamnusiini.

Definition: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Rhamnusium*, but not including *Oxymirus*, *Sachalinobia*, *Xylosteus*.

Subordinated taxa:

Genus *Enoploderes* Faldermann, 1837 (type species *Enoploderes sanguineus* Faldermann, 1837)

Genus *Rhamnusium* Latreille in Cuvier, 1829 (type species *Cerambyx bicolor* Schrank, 1781);

Genus *Akimerus* Audinet-Serville, 1835 (type species *Leptura schaefferi* Laicharting, 1784)

6. Tribe Stenocorini Thomson, 1861, nom. res. & sensu nov.

Type genus: *Stenocorus* Geoffroy, 1762

Description: Body elongated. Head (Fig. 8 f–d) with smoothed tempora. Eyes round, convex, weakly emarginated. Antennae narrowly separated on the forehead, situated far from front margin of eyes. Forehead trapezoidal (narrowed between antennae). Pronotum (Fig. 9 f) subcylindrical, slightly elongated, with medium-sized smoothed lateral tubercle. Prosternum (Fig. 10 f) short, with deep transverse sulcus. Prosternal process narrow, slightly expanded apically, raised high above disc and completely separated procoxa. Metatibia apically deep emarginated with spur on its bottom.

Diagnosis: Pronotum slightly elongated; lateral pronotal tubercle smoothed; metatibia apically deep emarginated.

Definition: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Stenocorus*, but not including *Rhagium*, *Oxymirus*, *Sachalinobia*, *Xylosteus*, *Rhamnusium*, *Pidonia*, *Evodinus*, *Carilia*, *Leptura*.

Subordinated taxa:

Genus *Toxotopsis* Casey, 1913 (type species *Leptura cinnamoptera* Randall, 1838)

Genus *Anisorus* Mulsant, 1863 (type species *Cerambyx quercus* Goeze, 1783)

Genus *Stenocorus* Geoffroy, 1762 (type species *Leptura meridiana* Linneus, 1758)

Suggested genera:

Genus *Japanocorus* Danilevsky 2012 (type species *Toxotus coeruleipennis* Bates, 1873)

Genus *Paktoxotus* Holzschuh, 1974 (type species *Paktoxotus pallidus* Holzschuh, 1974)

7. Tribe Evodiniini, trib. nov.

Type genus: *Evodinus* Mulsant, 1863

Description: Body slightly widened. Tempora small, smoothed. Eyes round, convex, emarginated. Genae as long as eye diameter, or slightly short. Forehead (Fig. 8 g–h) transverse, rectangular. Antennae widely separated on the forehead, narrowly separated from front margin of eyes (do not touch eyes). Pronotum (Fig. 9 g–h) subconical with smoothed and wide lateral tubercle. Elytra elongated, apically flattened. Prosternum (Fig. 10 g–h) very slightly elongated. Prosternal process short, only partly separated procoxa. Mesosternal (Fig. 11 g–h) process very short, wide, apically slightly emarginated. Mesocoxa (Fig. 11 g–h) with deep groove on internal side.

Diagnosis: Tempora smoothed; Antennae narrowly separated from front margin of eyes; mesocoxa with deep groove on internal side.

Definition: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Evodinus*, but not including *Rhagium*, *Oxymirus*, *Sachalinobia*, *Xylosteus*, *Rhamnusium*, *Stenocorus*, *Pidonia*, *Carilia*, *Leptura*.

Subordinated taxa:

Genus *Metacmaeops* Linsley & Chemsak, 1972 (type species *Leptura vittata* Swederus, 1787);

Genus *Brachytodes* Planet, 1924, stat. nov. (type species *Rhagium clathratum* Fabricius, 1793);

Genus *Brachyta* Fairmaire, 1868 (type species *Leptura interrogationis* Linnaeus, 1758);

Genus *Evodinus* LeConte, 1850 (type species *Leptura monticola* Randall, 1838).

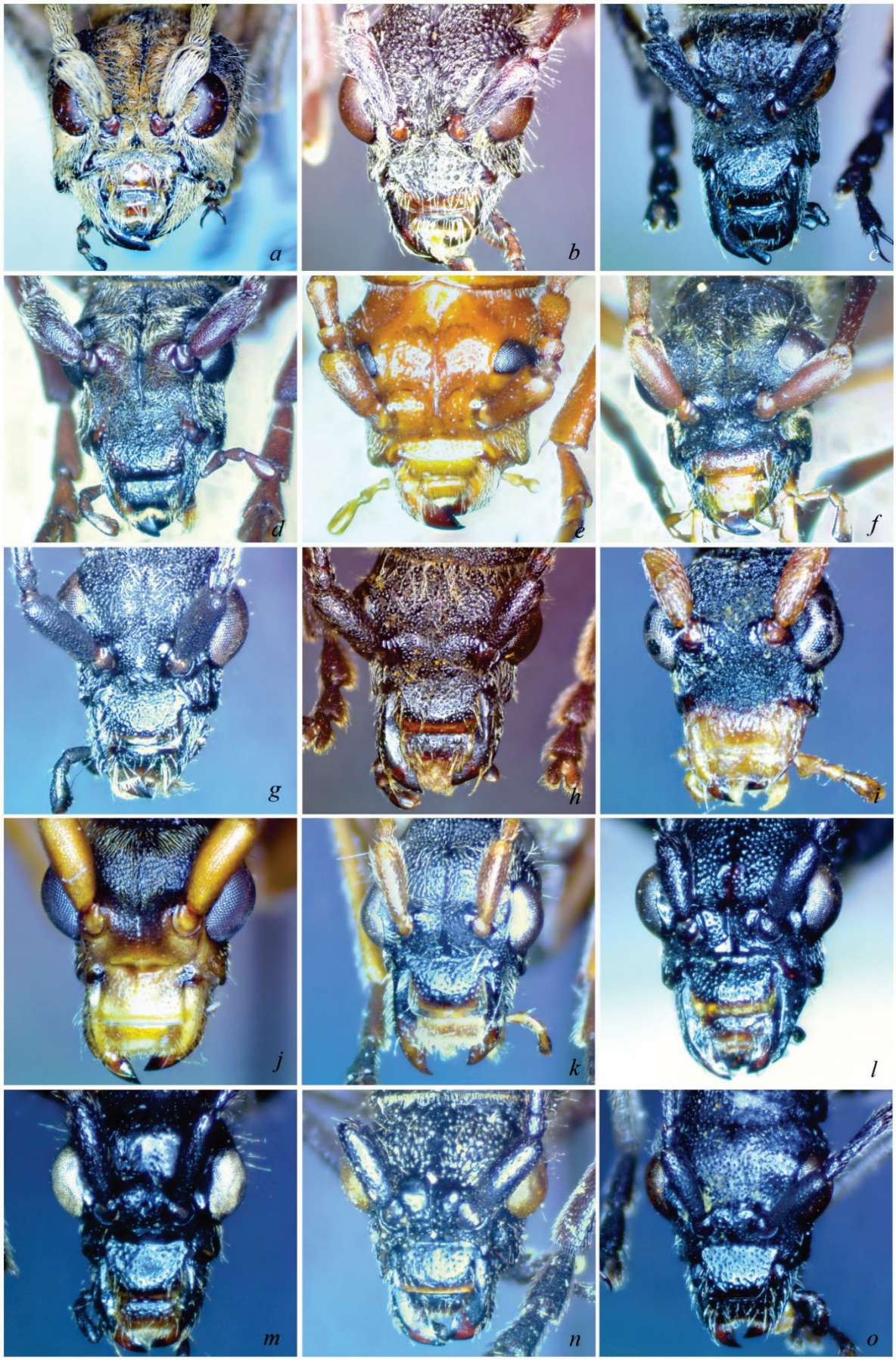

Fig. 8. Details of the head morphology of the selected taxa: *Rhagium sycophanta* (*a*), *Rhagium bifasciatum* (*b*), *Pachyta quadrimaculata* (*c*), *Oxymirus cursor* (*d*), *Rhamnusium bicolor* (*e*), *Stenocorus meridianus* (*f*), *Brachytodes clathratus*, comb nov. (*q*), *Brachyta interrogationis* (*h*), *Fallacia elegans* (*i*), *Pidonia lurida* (*j*), *Cortodera femorata* (*k*), *Carilia virginea* (*l*), *Dinoptera collaris* (*m*), *Brachysomida* (*Pseudogaurotina*) *excellens*, comb. nov. (*n*), *Acmaeops septemtrionis* (*o*)

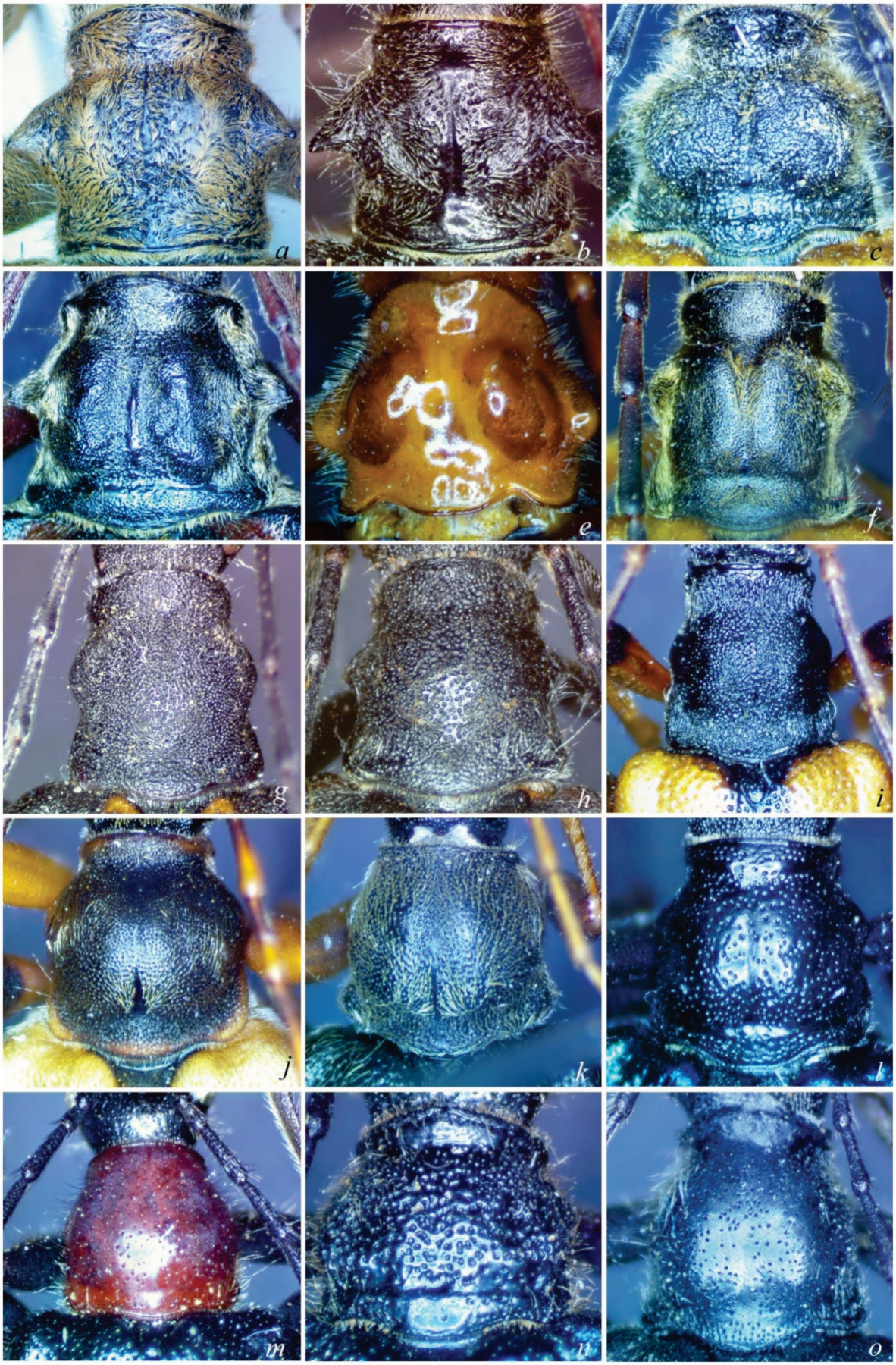

Fig. 9. Details of pronotum morphology of the selected taxa: *Rhagium sycophanta* (*a*), *Rhagium bifasciatum* (*b*), *Pachyta quadrimaculata* (*c*), *Oxymirus cursor* (*d*), *Rhamnusium bicolor* (*e*), *Stenocorus meridianus* (*f*), *Brachytodes clathratus*, comb nov. (*q*), *Brachyta interrogationis* (*h*), *Fallacia elegans* (*i*), *Pidonia lurida* (*j*), *Cortodera femorata* (*k*), *Carilia virginea* (*l*), *Dinoptera collaris* (*m*), *Brachysomida* (*Pseudogaurotina*) *excellens*, comb. nov. (*n*), *Acmaeops septemtrionis* (*o*)

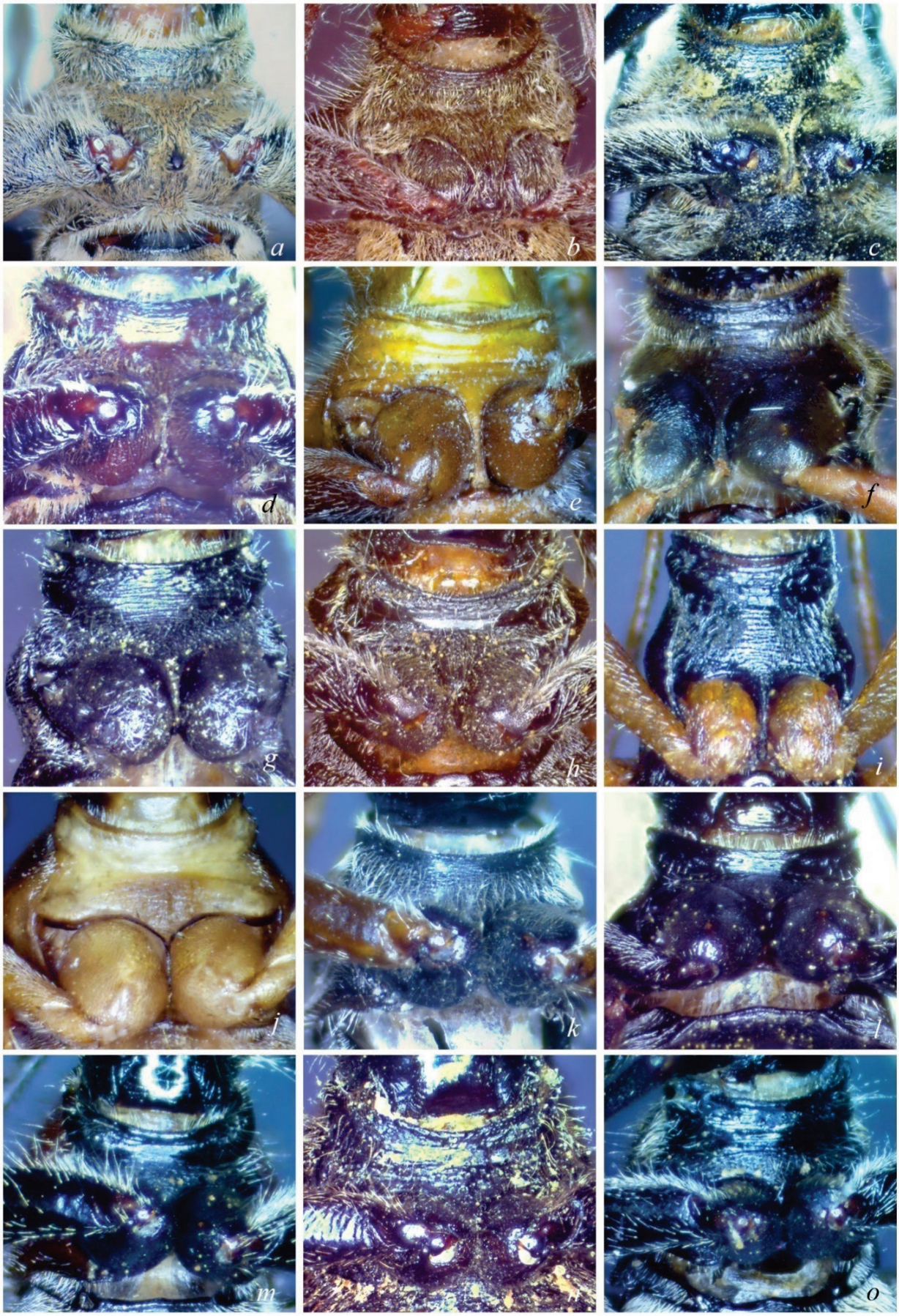

Fig. 10. Details of prosternum morphology of the selected taxa: *Rhagium sycophanta* (*a*), *Rhagium bifasciatum* (*b*), *Pachyta quadrimaculata* (*c*), *Oxymirus cursor* (*d*), *Rhamnusium bicolor* (*e*), *Stenocorus meridianus* (*f*), *Brachytodes clathratus*, comb nov. (*q*), *Brachyta interrogationis* (*h*), *Fallacia elegans* (*i*), *Pidonia lurida* (*j*), *Cortodera femorata* (*k*), *Carilia virginea* (*l*), *Dinoptera collaris* (*m*), *Brachysomida* (*Pseudogaurotina*) *excellens*, comb. nov. (*n*), *Acmaeops septemtrionis* (*o*)

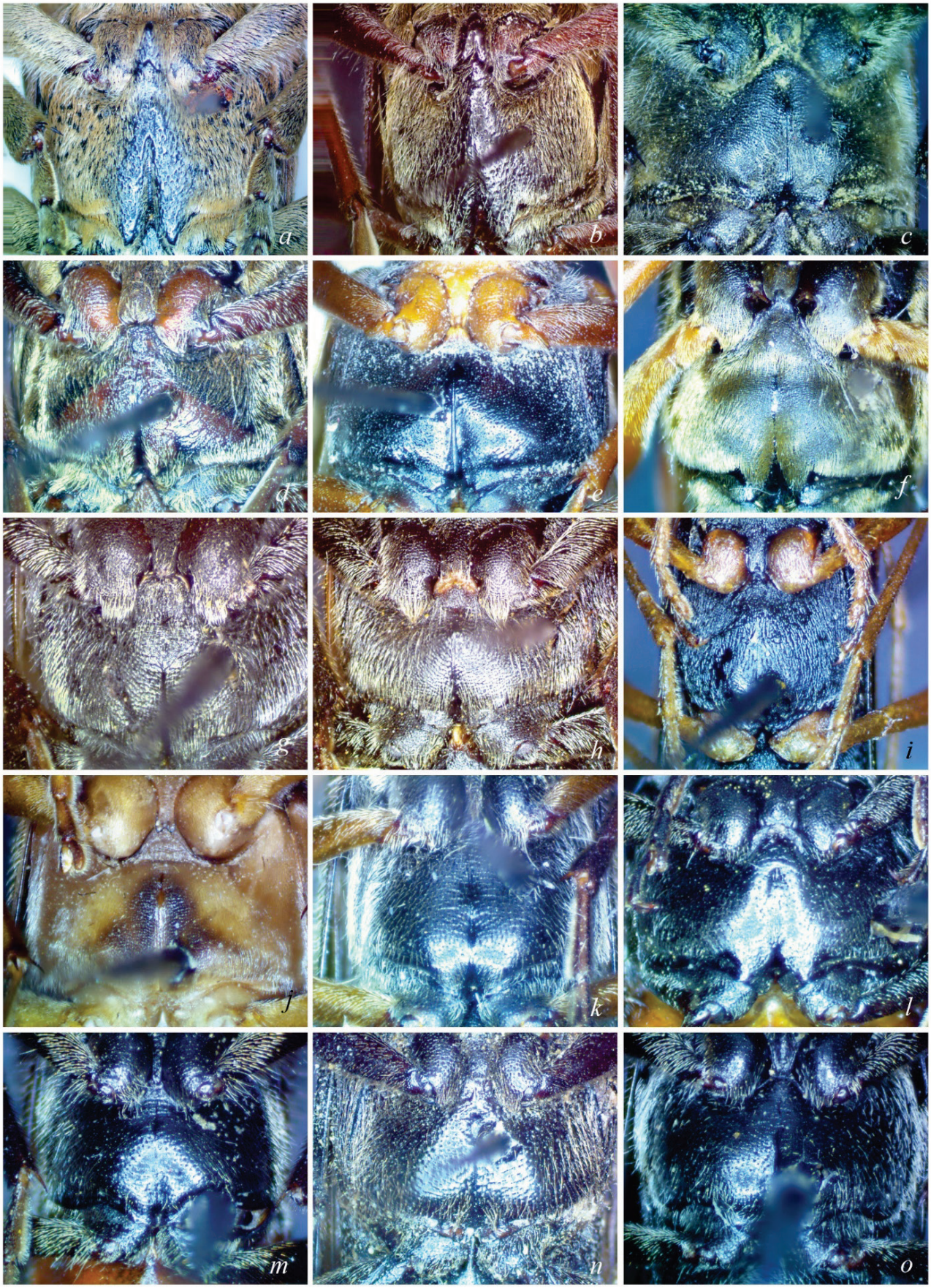

Fig. 11. Details of metasternum morphology of the selected taxa: *Rhagium sycophanta* (*a*), *Rhagium bifasciatum* (*b*), *Pachyta quadrimaculata* (*c*), *Oxymirus cursor* (*d*), *Rhamnusium bicolor* (*e*), *Stenocorus meridianus* (*f*), *Brachytodes clathratus*, comb nov. (*q*), *Brachyta interrogationis* (*h*), *Fallacia elegans* (*i*), *Pidonia lurida* (*j*), *Cortodera femorata* (*k*), *Carilia virginea* (*l*), *Dinoptera collaris* (*m*), *Brachysomida* (*Pseudogaurotina*) *excellens*, comb. nov. (*n*), *Acmaeops septemtrionis* (*o*)

8. Tribe Pidoniini, trib. nov.

Type genus: *Pidonia* Mulsant, 1863

Description: Body elongated. Tempora large, protruding, as large as eye diameter. Eyes pear-shaped, emarginated. Antennae (Fig. 8 i–j) widely separated on the forehead, narrowly separated from front margin of eyes (do not touch eyes). Forehead large, square. Genae very short, as long as 1/2 of eye diameter. Pronotum (Fig. 9 i–j) subconical with very small smoothed lateral tubercle. Prosternum (Fig. 11 i–j) clearly elongated. Prosternal process extremely narrow, filmy, completely separated procoxa. Metasternum (Fig. 11 i–j) with deep basal pit or short transverse groove.

Diagnosis: Tempora large; prosternum elongated; prosternal process filmy, separated procoxa. Metasternum with deep basal excavation.

Definition: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Pidonia*, but not including *Rhagium*, *Oxymirus*, *Sachalinobia*, *Xylosteus*, *Rhamnusium*, *Stenocorus*, *Evodinus*, *Carilia*, *Leptura*.

Subordinated taxa:

Genus *Pidonia* Mulsant, 1863 (type species *Leptura lurida* Fabricius, 1793);

Genus *Fallacia* Mulsant & Rey, 1863 (type species *Fallacia longicollis* Mulsant & Rey, 1863 = *Grammoptera elegans* Faldermann 1837);

Genus *Leptalia* LeConte, 1873 (*Anoplodera macilenta* Mannerheim, 1853).

9. Tribe Cariliini, trib. nov.

Type genus: *Carilia* Mulsant, 1863

Description: Body slightly widened. Head (Fig. 8 k–o) elongated. Tempora smoothened or slightly protruding. Eyes round, entire or with very small emargination. Antennae narrowly separated on the forehead, situated far from front margin of eyes. Forehead trapezoidal (narrowed between antennae). Pronotum (Fig. 9 k–o) subspherical. Prosternum (Fig. 10 k–o) short with transverse sulcus. Prosternal process short, only partly separated procoxa. Karyotype: 2n = 20 + XX/XY.

Diagnosis: Antennae narrowly separated, situated far from front margin of eyes; forehead trapezoidal; pronotum subspherical; karyotype: 2n = 20 + XX/XY.

Definition: Monophyletic clade based on 12S RNA + 16S rRNA + COI + 18S rRNA + 28S rRNA genes phylogeny. The least inclusive clade containing *Carilia*, but not including *Rhagium*, *Oxymirus*, *Sachalinobia*, *Xylosteus*, *Rhamnusium*, *Stenocorus*, *Evodinus*, *Pidonia*, *Leptura*.

Subordinated taxa:

Genus *Cortodera* Mulsant, 1863 (partim – excluding Nearctic species) (type species *Grammoptera spinosula* Mulsant, 1863 = *Leptura humeralis* Schaller, 1783);

Genus *Leptacmaeops* Casey, 1913, nom. res. (type species *Leptura longicornis* Kirby, 1837); Genus *Cortodera* Mulsant, 1863 is paraphyletic, consists of Palearctic (*Cortodera* s. str.) and Nearctic (*Leptacmaeops*) lineages, which I considered separate genera. *Leptacmaeops* distinguished by clearly protuberant pronotum with basal furrow.

Genus *Carilia* Mulsant, 1863 (type species *Leptura virginea* Linnaeus, 1758);

Genus *Gnathacmaeops* Linsley & Chemsak, 1972 (type species *Leptura pratensis* Laicharting, 1784);

Genus *Dinoptera* Mulsant, 1863 (type species *Leptura collaris* Linnaeus, 1758);

Genus *Brachysomida* Casey, 1913 (type species *Acmaeops tumida* LeConte, 1857 = *Acmaeops californica* LeConte, 1850). According to the current multigene phylogeny, *Brachysomida* and *Pseudogaurotina* are closely related. Thus, I considered them as subgenera in the genus *Brachysomida*.

subgenus *Brachysomida* Casey, 1913 (type species *Acmaeops tumida* LeConte, 1857 = *Acmaeops californica* LeConte, 1850);

subgenus *Pseudogaurotina* Plavilshtshikov, 1958, stat. nov. (type species *Gaurotes splendens* Jakovlev, 1893).

Genus *Gaurotes* LeConte, 1850 (type species *Rhagium cyanipennis* Say, 1824);

Genus *Paragaurotes* Plavilstshikov, 1921 (type species *Gaurotes ussuriensis* Blessig, 1872);

Genus *Acmaeops* LeConte in Agassiz, 1850 (type species *Leptura proteus* Kirby,1837) = *Euracmaeops* Danilevsky, 2014, syn. nov. Phylogenetic analysis did not confirm Danilevsky's suggestion to erect *Euracmaeops*. *Acmaeops septentrionis* (C. G. Thomson, 1866), *Acmaeops marginatus* (Fabricius, 1781), *Acmaeops proteus* (Kirby, 1837) to constitute a compact and monophyletic branch.

Conclusions

The ultimate goal of the current study was revealing and establishing the natural phylogenetic system of Rhagiini s.l. With the help of multigene phylogenetic analysis, it was possible to test two competing morphological hypotheses on monophyly and paraphyly of Rhagiini. The results of the current study clearly indicate the paraphyletic nature of Rhagiini s.l. However, contrary to the hypothesis of paraphyly by morphology, I found numerous cases of parallel and convergent evolution and homoplasy in Rhagiini s.l. Therefore, the evolutionary "tree" of Rhagiini s.l. is more like a "bush" with numerous relict branches. As a result, I have proposed a new taxonomic model of Rhagiini s.l., which is most consistent with their natural phylogeny. Further phylogenetic studies of Rhagiini s.l. should be aimed at revealing the taxonomic position of the tribes Teledapini, Encyclopini and Caraphiini, which were not included in this study.

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