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ORIGINAL ARTICLE



Resolving the intergeneric phylogeny of the large carrion beetles (Staphylinidae: Silphinae: Silphini)

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Abstract

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The worldwide distributed subfamily of rove beetles Silphinae contains two well-established tribes, based on both morphological and molecular data. The relationships within the tribe Nicrophorini have been mostly resolved; however, the tribe Silphini still lacks a robust phylogeny. Thus, here we resolved the phylogeny of the tribe based on 42 species of the 114 known species, using five molecular markers. Heterotemna tenuicornis Brullé clustered as sister to Silpha tristis Illiger, making the subgenus Silpha Linnaeus paraphyletic. Consequently, Heterotemna Wollaston is considered a junior subjective synonym of Silpha Linnaeus; requiring the following combinations: Silpha (Silpha) britoi (García & Pérez), comb. nov., Silpha (Silpha) figurata Brullé, comb. rest., and Silpha (Silpha) tenuicornis Brullé, comb. rest. Our estimate of the phylogeny agrees with current generic limits except it revealed that the genus Aclypea Reitter arose from within the genus Silpha, thus making the latter paraphyletic. Some ambiguity remains regarding the confidence of this finding; therefore, we refrain from synonymizing Aclypea until further study. Furthermore, it includes biogeographical information for each genus, which estimates the history of distributions of the Silphini across the Australian, Neotropical, and Oriental regions.

KEYWORDS

16S, 28S, COI, Coleoptera, molecular phylogeny, Pepck, Wingless

INTRODUCTION

Large carrion beetles (Coleoptera: Staphylinidae: Silphinae) are a small group of 189 extant species, with worldwide distribution (Ikeda et al., 2012; Newton, 2022; Sikes, 2008). Traditionally, morphologybased phylogenies of combined larval and adult characters placed the carrion beetles as a separate family (Silphidae), sister to rove beetles (Staphylinidae) (Beutel & Leschen, 2005; Grebennikov & Newton, 2009, 2012). However, as early as 1927, Hatch proposed the placement of carrion beetles as a subfamily of a broad concept of Staphylinidae; this was not accepted in subsequent contemporary papers (Hatch, 1928; Horion, 1951; Mroczkowski, 1955). More recently,

molecular phylogenies consistently recovered the family Silphidae as an internal lineage within Staphylinidae, as sister to Tachyporinae, Staphylininae + Scydmaeninae, or Scaphidiinae + Osoriinae (McKenna, Farrell, et al., 2015; McKenna, Wild, et al., 2015; Zhang et al., 2018). Taxonomically, this has been recently formalized by Cai et al. (2022), who downgraded the large carrion beetles to the subfamily Silphinae of a very broadly defined Staphylinidae, and placed it as sister to Osoriinae + Apateticinae + Scaphidiinae. However, the above-mentioned molecular phylogenetic studies suffer from limited taxon sampling. The only exception, with larger taxon sampling, is the analysis of Bocak et al. (2014), who analysed 87 species of large carrion beetles and 262 species of other Staphylinidae, and found Silphidae again as

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an internal lineage of Staphylinidae, with Tachyporinae (represented by five species) as the closest sister group. However, Bocak et al. (2014) did not formally discuss the internal classification of Staphylinidae. The sister group to the Silphinae within the Staphylinidae remains uncertain although some evidence points towards the Tachyporinae. Strong evidence supporting the hypothesis that large carrion beetles evolved from within Staphylinidae has been recently reviewed and summarized by Sikes et al. (2024).

The subfamily Silphinae (Coleoptera: Staphylinidae) currently consists of two tribes-Nicrophorini (burying beetles), which has a mostly resolved phylogeny (Sikes & Venables, 2013) and Silphini (large carrion beetles). The phylogeny estimated by Sikes and Venables (2013) is based on five molecular markers and includes 58 of 74 species. The tribes and genera/subgenera within the tribes are established predominantly based on pre-cladistic classification, using morphology (e. g., Hatch, 1927; Portevin, 1926) and only a handful of molecularbased phylogenies containing the subfamily Silphinae were published (e.g., Dobler & Müller, 2000; Ikeda et al., 2008; King et al., 2015; Luo & Meng, 2023). Based on these studies we now consider the tribe Silphini as a composite of 12 extant genera and subgenera that is sometimes divided into two subtribes-monophyletic Necrodina (with two genera-Necrodes Leach and Diamesus Hope) and paraphyletic Silphina (containing the remaining genera and subgenera) (e.g., Dobler & Müller, 2000; Ikeda et al., 2008; King et al., 2015; Peck, 2001b). These two subtribes are recently mostly not used in the literature, and Necrodini Portevin is considered a junior subjective synonym of Silphini Latreille (e.g., Newton, 2022). However, no rigorous taxonomic work has been done to test the validity of the genera and resolve the phylogenetic relationships among them.

The generic classification of Silphini has a complex history. Originally, most of the species were harboured in a few, mostly Linnean and Fabrician genera, defined very broadly (e.g., Gemminger & de Harold, 1868; Kraatz, 1876; Reitter, 1884; Heyden et al., 1883). At the beginning of the 20th century, the opposite tendency began to prevail, generally separating many species into separate genus groups, sometimes treated as subgenera (Ganglbauer, 1899; Hatch, 1928; Portevin, 1914, 1920a, 1920b, 1921). This splitting classification was followed by most European and Asian authors for many decades (e. g., Cho & Lee, 1992, 1995; Ciftci et al., 2018; Emetz, 1977; Guéorguiev & Růžička, 2002; Horion, 1951; Ikeda et al., 2008, 2009; Lafer, 1989; Lane et al., 2021; Mroczkowski, 1955; Nikolaev & Kozminykh, 2002; Nishikawa, 1986; Piloña et al., 2002; Růžička, 2002; Růžička & Schneider, 2004; Schawaller, 1979, 1982; Šustek, 1981). In parallel, Peck (2001a) changed the generic/subgeneric classification of Silphini, based on an unpublished classification proposed by R. B. Madge, generally lumping the classification, synonymizing several generic names and downgrading many genera to subgenera, but without any formal analysis or formal discussion. This was partly followed by some other authors, but again without any formal discussion(s) (Ikeda et al., 2013; Ikeda et al., 2012; Newton, 2022; Qubaiová et al., 2015; Růžička, 2015; Růžička et al., 2012, 2015; Růžička & Schneider, 2011; Sikes, 2008, 2016). Presently, the current classification of Silphini (as summarized e.g., by Newton, 2022) lacks any rigorous support and is in a need of broad formal revision.

Silphinae in general feed on organic matter and, therefore, play important roles in the ecosystem such as decomposers and predators (Sikes, 2008). Unlike the tribe Nicrophorini, which is associated almost exclusively with small carrion, the large carrion beetles (Silphini), are associated with large carrion as well, and therefore, they are an important bioindicator group for forensic entomology (e.g., Midgley et al., 2009). However, the feeding strategies within Silphini are much more diverse (Ikeda et al., 2008; Sikes, 2008). The early diverging genera within Silphini, Oxelytrum Gistel and Ptomaphila Kirby & Spence are indeed associated with large carrion, however, within the clade containing the genera Aclypea Reitter, Dendroxena Motschulsky and Silpha sensu lato (referred further in the text to as clade A) there are much more diverse feeding strategies, such as specialized predation of caterpillars (genus Dendroxena) or snails (genera/subgenera Ablattaria Reitter, Phosphuga Leach). Moreover, the species belonging to the genus Aclypea are/were considered agricultural pests due to their phytophagy, predominantly observed in the larval stage (Anderson & Peck. 1984: Sikes. 2016: Swift et al., 1979). Lately, the feeding strategies of some 'necrophagous' species were scrutinized in more detail as the 'one size fit all' categories seem sometimes arbitrary and the species were found to feed on multiple diets at different situations as well in different life stages (Jakubec et al., 2020). However, without a robust and detailed phylogeny of the subfamily it is difficult to generalize beyond single species.

The tribe Silphini is broadly distributed on all continents except Antarctica (Sikes, 2008, 2016). However, the biogeographical pattern is quite specific: two genera forming an early diverging lineage (*Oxelytrum* and *Ptomaphila*) (King et al., 2015) are restricted to Neotropical and Australian regions, respectively. The remaining Silphini are mostly distributed in nothern temperate areas, with only a few genera and species occurring in Ethiopian and Oriental regions, and a single species (*Diamesus osculans* (Vigors)) reaching Australia (Peck, 2001b; Růžička et al., 2023; Sikes, 2008). The highest diversity of Silphini is in the temperate zone, in eastern Asia (Růžička, 2015; Sikes, 2008). Sikes (2016) further suggested that Silphinae are presumably of northern temperate origin, with the two genera of Silphini (*Oxelytrum* and *Ptomaphila*) to be of Gondwanian origin. Recently, there have been documented introductions of several Palaearctic species to the Nearctic region (Ferreira, 2017; LaPlante, 1997).

Herein we provide a robust estimate of the phylogeny of the tribe Silphini using five molecular markers and the most comprehensive taxon sampling to date. We have included a broad and well-balanced sampling of taxa across all 12 genera and the entire distributional range of the Silphini. We also present a biogeographical analysis to address the long unresolved origin of the tribe.

MATERIALS AND METHODS

Taxonomy and classification

The species and generic classification of carrion beetles used throughout this paper follows Newton (2022). Jan Růžička conducted morphological determination of the specimens used for newly generated sequences (Supporting Information S1, indicated by *), in total we generated 53 new sequences for this study. The phylogenetic relationships within the Silphinae were estimated based on all 12 genera of Silphini (Table 1). In total 49 species (Table 1 and Supporting Information S1) were used to produce the final phylogenetic tree (Figure 1) based on five genes (total length 2528 bp). The maximum likelihood (ML) and maximum parsimony (MP) trees were evaluated based on bootstrap values; the phylogenetic tree based on Bayesian inference (BI) was evaluated based on posterior probabilities. Two species belonging to the family Leiodidae and five species belonging to Nicrophorini (Table 1) were selected as an outgroup.

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DNA extraction and sequencing

Conducting a study that samples the taxa of interest across the entire area of distribution can be difficult, especially when it comes to appropriately stored specimens for molecular analyses. The majority of the specimens used in the present study were stored in 96% EtOH, however, several species were only available in dry collections. DNA was extracted using two commercial kits-Tissue & Blood DNA Mini Kit (Geneaid) and the NucleoSpin DNA Insect Mini kit (Macherey-Nagel), in dry specimens the period for lysis was extended to overnight and DNA was eluted to 50 µL of elution buffer (two consecutive elution steps consisting of 25 µL of elution buffer). Extracted DNA was used as a template for amplification of five genes-two mitochondrial (Cytochrome c oxidase subunit I COI, 16S rDNA) and three nuclear (28S rDNA, Wingless, Pepck) using previously published primers listed in Table 2. The DNA extraction followed the protocol of the manufacturer with the following modifications-the specimens were rinsed off in 70% EtOH and DNA/ RNA free water prior to lysis, the lysis period was extended to 12-16 h, the volume of elution buffer was decreased and the elution step was repeated twice. Furthermore, we designed two sets of shorter primers, targeting partial fragments of COI and Wingless (Table 2).

The polymerase chain reaction (PCR) amplification of target genes was carried out in 25 μ L reaction volume based on the provided protocol for PPP Master Mix (Top-Bio, s.r.o.) (12.5 μ L of 1 \times PPP Master Mix, 9.5 μ L PCR H₂O, 0.4 μ M of forward primer and 0.4 μ M reverse primer) under the cycling conditions listed in Table 3. The resulting products were visualized by gel electrophoresis (1% agarose gel, 100 V, 20 min). Purification of the PCR products was carried out using ExoSAP-ITTM (Applied BiosystemsTM), following the provided protocol. The purified PCR products were subsequently subjected to bidirectional sequencing using the same primers employed in the initial PCR reaction. Sanger sequencing was performed in BIOCEV (Vestec, Czech Republic). The newly generated DNA sequences were deposited in the GenBank database (Supporting Information S1).

Phylogenetic analyses

The electropherograms of newly obtained sequences were proofread and corrected for miss-called bases in Chromas v2.6.6. (Technelysium Pty Ltd). Additional sequences used in our study were obtained from previously published studies on carrion beetle phylogenies (e.g., Ikeda et al., 2008, 2009; King et al., 2015; Mahlerová et al., 2021) and from GenBank (http://www.ncbi.nlm.nih.gov) using BLAST (Altschul et al., 1990) for our aligned dataset as a template. Multiple sequence alignments were generated for each gene individually using MAFFT v7. implemented in online server https://mafft.cbrc.jp/alignment/ server/ (Katoh et al., 2019). Aligned sequences were further manually edited and trimmed to an equal length in BioEdit v7.0.5.3. (Hall, 1999). The GTR + F + I + G4 model was favoured over the other models for all the genes considered according to Bayesian information criterion using ModelFinder (Kalyaanamoorthy et al., 2017) implemented in IQ-TREE web server (Trifinopoulos et al., 2016). Sequences were consequently concatenated using MEGAX v10.1.8. (Kumar et al., 2018).

Concatenated sequences were analysed under the criterion of MP using PAUP v4.0a (Swofford, 2002). The MP analysis was conducted with heuristic search and 10,000 bootstrap replicates. The BI was estimated based on concatenated dataset using MrBayes v3.7a (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) implemented in the CIPRES Science Gateway (CIPRES) (Miller et al., 2010). The search was run for 10,000,000 generations, sampled every 1000 generations, substitution model for among-site rate variation used was invgamma (GTR + I + gamma), the average standard deviation of split frequencies reached 0.0013, the first 25% generated trees were discarded. The ML analysis was conducted using IQ-TREE web server (Nguyen et al., 2015; Trifinopoulos et al., 2016), based on GRT + F + I + G4 model, using Ultrafast bootstrap analysis (Hoang et al., 2018) and 1000 bootstrap replicates (Figure 1).

Ancestral state reconstruction

To reconstruct the possible biogeographic history of the subfamily Silphinae we used a modification of dispersal-extinction-cladogenesis (DEC) (Ree & Smith, 2008) analysis DEC + J (Matzke, 2012, 2014). The DEC + J was determined to be the best-fitting model by the Akaike information criterion (Akaike, 1974) and performed using the R package BioGeoBEARS (Matzke, 2018). The maximum number of ancestral areas was set to six. The ancestral state reconstruction was performed on a phylogenetic tree obtained by BI. Species of each genus were grouped, and each genus/subgenus was coded as absent or present based on its true distribution in the seven classical zoogeographical regions (Cox & Moore, 2005; Wallace, 1876)-Western Palearctic region (A), Eastern Palearctic region (B), Nearctic region (C), Neotropical region (D), Afrotropical region (E), Oriental region (F), and Australian region (G). Presence or absence in the region was determined based on previously published studies (Peck, 2001b; Peck & Anderson, 1985; Peck & Kaulbars, 1987; Růžička, 2015; Růžička et al., 2012, 2015, 2023) (Figure 2).

RESULTS

Phylogenetic analyses

The phylogenetic trees obtained by ML and BI estimated an identical topology. The topology estimated by MP was largely the same and

TABLE 1 List of species used in this study.

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Species	Tribe	Subfamily	Family
Achinea onaca (Linnzeus 1758)	Silnhini	Silnhinae	Stanbylinidae
Active a undata (O. E. Müller, 1776)	Silphini	Silphinae	Staphylinidae
Dendroxena quadrimaculata (Scopoli 1772)	Silphini	Silphinae	Staphylinidae
Dendroxena sexcarinata Motschulsky, 1861	Silphini	Silphinae	Staphylinidae
Diamesus himaculatus Portevin 1914	Silphini	Silphinae	Staphylinidae
Diamesus osculans (Vigors 1825)	Silphini	Silphinae	Staphylinidae
Heterosilpha ramosa (Sav. 1823)	Silphini	Silphinae	Staphylinidae
Necrodes littoralis (Linnaeus, 1758)	Silphini	Silphinae	Staphylinidae
Necrodes nigricornis Harold, 1875	Silphini	Silphinae	Staphylinidae
Necrodes suringmensis (Eabricius 1775)	Silphini	Silphinae	Staphylinidae
Necrophila (Calosilpha) brunnicollis (Kraatz. 1877)	Silphini	Silphinae	Staphylinidae
Necrophila (Fusilpha) iakowlewi (A.P. Semenov, 1891)	Silphini	Silphinae	Staphylinidae
Necrophila (Eusipha) janonica (Motschulsky, 1861)	Silphini	Silphinae	Staphylinidae
Necrophila (Chrysosilpha) formosa (Laporte de Castelnau 1832)	Silphini	Silphinae	Staphylinidae
Necrophila (Chrysosilpha) viridis (Motschulsky, 1861)	Silphini	Silphinae	Staphylinidae
Necrophila (Necrophila) americana (Linnaeus 1758)	Silphini	Silphinae	Staphylinidae
Oiceontoma hypocrita (Portevin, 1903)	Silphini	Silphinae	Staphylinidae
Oiceontoma nakahavashii (Miwa 1937)	Silphini	Silphinae	Staphylinidae
Oiceontoma nigropunctatum (Lewis 1888)	Silphini	Silphinae	Stanhylinidae
Oiceontoma subrufum (Lewis 1888)	Silphini	Silphinae	Staphylinidae
Oiceoptoma thoracicum (Linnaeus 1758)	Silphini	Silphinae	Staphylinidae
Oxelvtrum cavennense (Sturm 1826)	Silphini	Silphinae	Staphylinidae
Oxelvtrum discicolle (Brullé 1840)	Silphini	Silphinae	Staphylinidae
Ptomanhila lacrymosa (Schreibers, 1802)	Silphini	Silphinae	Staphylinidae
Ptomaphila perlata Kraatz 1876	Silphini	Silphinae	Staphylinidae
Siloha (Ahlattaria) arenaria (Kraatz 1876)	Silphini	Silphinae	Staphylinidae
Silpha (Ablattaria) cribrata Mánétriés 1832	Silphini	Silphinae	Staphylinidae
Silpha (Ablattaria) laevigata Eshricius, 1775	Silphini	Silphinae	Staphylinidae
Silpha (Phosphura) atrata Linnaeus, 1758	Silphini	Silphinae	Staphylinidae
Silpha (Silpha) carinata Herbst 1783	Silphini	Silphinae	Staphylinidae
Silpha (Silpha) longicornis Portevin 1926	Silphini	Silphinae	Staphylinidae
Silpha (Silpha) obscura Linnaeus 1758	Silphini	Silphinae	Staphylinidae
Silpha (Silpha) olivieri Bedel 1887	Silphini	Silphinae	Staphylinidae
Silpha (Silpha) perforata Gebler. 1832	Silphini	Silphinae	Staphylinidae
Silpha (Silpha) puncticollis P. H. Lucas, 1846	Silphini	Silphinae	Staphylinidae
Siloha (Siloha) tristis Illiger. 1798	Silphini	Silphinae	Staphylinidae
Siloha (Siloha) tyrolensis Laicharting, 1781	Silphini	Silphinae	Staphylinidae
Silpha (Silpha) tenuicornis Brullé. 1836	Silphini	Silphinae	Staphylinidae
Thanatophilus mutilatus (Wiedemann, 1821)	Silphini	Silphinae	Staphylinidae
Thanatophilus rugosus (Linnaeus, 1758)	Silphini	Silphinae	Staphylinidae
Thanatophilus sinuatus (Fabricius, 1775)	Silphini	Silphinae	Staphylinidae
Thanatophilus truncatus (Sav. 1823)	Silphini	Silphinae	Staphylinidae
Outgroup			
Troglocharinus ferreri (Reitter, 1908)	Leptodirini	Cholevinae	Leiodidae
Troglocharinus senenti Escolà. 1966	Leptodirini	Cholevinae	Leiodidae
Nicrophorus (Nicrophorus) concolor (Kraatz. 1877)	Nicrophorini	Silphinae	Staphylinidae
Nicrophorus (Nicrophorus) japonicus Harold. 1877	Nicrophorini	Silphinae	Staphylinidae
Nicrophorus (Nicrophorus) maculifrons (Kraatz, 1877)	Nicrophorini	Silphinae	Staphylinidae
Nicrophorus (Nicrophorus) tomentosus (Weber, 1801)	Nicrophorini	Silphinae	Staphylinidae
Ptomascopus morio Kraatz, 1877	Nicrophorini	Silphinae	Staphylinidae

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FIGURE 1 Phylogenetic tree of 42 ingroup and 7 outgroup species. Topology based on a phylogenetic tree generated by ML; node values BI posterior probability/ML bootstrap value/MP bootstrap value. Clade A is indicated in grey.

only differed in the topology of the clade A (Figure 1), which remained partially unresolved by MP (Supporting Information S3). The presented phylogenetic tree is based on the topology obtained by ML, it shows two well-distinguished groups within the subfamily Silphinae, which correspond to the established tribes—Silphini and Nicrophorini (100 BI/100 ML/100 MP).

Silphini (100/99/97) shows two basal clades—one containing the sister genera *Ptomaphila* Kirby & Spence and *Oxelytrum* Gistel (100/98/96), and the other containing sister genera—*Necrodes* Leach and *Diamesus* Hope (100/96/93). The monophyly of the genera *Thanatophilus* Leach (100/100/85), *Oiceoptoma* Leach (100/100/100) and *Dendroxena* Motschoulsky (100/100/94) are well supported. The genus *Necrophila* Kirby & Spence containing the subgenera *Calosilpha* Portevin (represented in our analysis by *Necrophila* (*Calosilpha*) *brunnicollis* (Kraatz)), *Chrysosilpha* Portevin (represented by *Necrophila*

(Chrysosilpha) formosa (Laporte de Castelnau) and Necrophila (Chrysosilpha) viridis (Portevin)), Eusilpha Semenov-Tian-Shanskij (represented by Necrophila (Eusilpha) jakowlewi (Semenov-Tian-Shanskij) and Necrophila (Eusilpha) japonica (Motschulsky)), and the monotypic Necrophila sensu stricto (represented by Necrophila (Necrophila) americana (Linnaeus)) was placed as the sister genus to the genus Heterosilpha Portevin (92/88/62) represented by Heterosilpha ramosa. Clade A, containing the genera Silpha Linnaeus (with three subgenera: Phosphuga Leach, Ablattaria Reitter and Silpha sensu stricto), Heterotemna Wollaston and Aclypea Reitter, is well supported (100/99/–) by two of the analyses (BI and ML). The subgenus Ablattaria, represented by three species, is placed as a sister group to the subgenus Phosphuga (99/92/–). The genus Aclypea represented by two species is placed into the genus Silpha (100/99/–) at the basal position within the subgenus Silpha (90/79/–). The placement of Heterotemna within the

TABL	.E 2	Primers used	d in this study.
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Region	Primer name	Primer sequence (5'-3')	Forward/reverse	Source
COI mtDNA	C1-J-2183 (alias Jerry)	CAACATTTATTTTGATTTTTTGG	F	Simon et al. (1994)
	TL2-N-3014 (alias Pat)	TTCCAATGCACTAATCTGCCATATTA	R	Simon et al. (1994)
	COI_F1	GGTATAATTTATGCAATAATAG	F	Specific for this study
	COI_R1	AAATGAGCTACTACATAATAA	R	Specific for this study
16S rDNA	LR-J-12887	CCGGTCTGAACTCAGATCACGT	F	Simon et al. (1994)
	LR-N-13398	CGCCTGTTTAACAAAAACAT	R	Simon et al. (1994)
28S rDNA	Rd3.2a2	AGTACGTGAAACCGTTCAGGGG	F	lkeda et al. (<mark>2008</mark>)
	Rd5b	CCACAGCGCCAGTTCTGCTTAC	R	Whiting (2002)
Wingless nDNA	Wgnics	GTCATCGGBGACAACCTSAAGGACC	F	lkeda et al. (<mark>2008</mark>)
	Wgnica	AGGTCGCAGCCGTCAACGCCGAT	R	lkeda et al. (2008)
	Wgs	GAGTGTAAGTGTCATGGTATGTCTGG	F	lkeda et al. (<mark>2008</mark>)
	Wga	CGCAGCACCAGTGGAATGT	R	lkeda et al. (2008)
	WGL_F1	GTCATCGGTGATAACC	F	Specific for this study
	WGL_R2	GGGATTGTAGGGCT	R	Specific for this study
Pepck nDNA	Peps	GACGACATCGCYTGGATGCGYTT	F	lkeda et al. (2008)
	Рера	GCGGCDGTDGCYTCGCT	R	lkeda et al. (<mark>2008</mark>)
	Pepnics	GGAGATGATATYGCTTGGATG	F	lkeda et al. (<mark>2008</mark>)
	Pepnica	GCWGCAGCRGTAGCTTCACT	R	lkeda et al. (<mark>2008</mark>)

TABLE 3 Cycling conditions for individual primers used in this study.

Step	COI (both primer sets)	165	285	Wingless (all three primer sets)	Pepck
Initial denaturation	95°C; 3 min	95°C; 3 min	95°C; 3 min	95°C; 3 min	95°C; 3 min
Number of cycles:	35	35	35	35	35
Denaturation	95°C; 30 s	95°C; 30 s	95°C; 30 s	95°C; 30 s	95°C; 30 s
Annealing	50°C; 30 s	56°C; 30 s	49°C; 30 s	49°C; 30 s	53°C; 30 s
Extension	72°C; 45 s	72°C; 45 s	72°C; 45 s	72°C; 45 s	72°C; 45 s
Final extension	72°C; 10 min	72°C; 10 min	72°C; 10 min	72°C; 10 min	72°C; 10 min

subgenus *Silpha* is weakly supported (79/52/–); however, the proximity of *Heterotemna tenuicornis* (Brullé) to *S. tristis* is strongly supported by all three analyses (99/83/63) and the placement of *Heterotemna* within the genus *Silpha* is strongly supported by BI and ML (100/99/–).

According to DEC + J, the ancestral distribution area for the tribe Silphini is inferred to be across the areas Neotropical region (D), Oriental region (F) and Australian region (G) (DFG). The two sister genera *Oxelytrum* and *Ptomaphila*, are of Neotropical (D) and Australian (G) origin respectively (DG). The remaining genera of Silphini have the ancestral distribution in Oriental region (F). The genera *Necrodes*, *Diamesus*, *Thanatophilus* and *Necrophila* are inferred to be of Oriental region (F). The ancestral distribution of genera including *Necrophila*, *Silpha and Aclypea* is across Western Palearctic region (A) and Nearctic region (C). The genera *Silpha* and *Aclypea* are inferred to be across Western Palearctic region (A) (Figure 2).

DISCUSSION

A total of 47 species of the subfamily Silphinae was used to assess the intergeneric phylogenetic relationship within the tribe Silphini. The sampling across the subfamily covers all 12 established genera of Silphini and two out of three established genera of Nicrophorini.

Our estimate of the phylogeny shows two well-distinguished tribes; Silphini (former Silphinae) and Nicrophorini (former Nicrophorinae). The tribe Silphini has been historically divided into two tribes (e. g., Ikeda et al., 2008; Sikes, 2008) (currently subtribes): paraphyletic Silphina—containing all genera except *Necrodes* and *Diamesus*, that are considered Necrodina. The sister clade of the rest of the tribe Silphini consists of two sister genera *Ptomaphila* and *Oxelytrum*. Except for two recent phylogenetic studies (King et al., 2015; Mahlerová et al., 2021), these two genera were not included together in previous studies (Dobler & Müller, 2000; Ikeda et al., 2008; Sikes & Venables, 2013).



FIGURE 2 Ancestral area distribution of the tribe Silphini based on DEC + J model from BioGeoBears. Presence and absence of the genera are indicated in colour as follows—Western Palearctic region (A), Eastern Palearctic region (B), Nearctic region (C), Neotropical region (D), Afrotropical region (E), Oriental region (F), and Australian region (G). Most likely biogeographic areas are shown in the boxes at the nodes of the phylogenetic tree (derived from BI).

The subtribe Necrodina contains two species-poor genera– *Necrodes* (Nearctic and Palearctic regions, three species) and *Diamesus* (Australia, East Palearctic region and Oriental region, two species). The subtribe was established based on morphological characteristics; however, our data show that there is no need for further splitting the now-existing tribe Silphini, therefore we agree with synonymizing of the two subtribe names (Silphina and Necrodina), as was previously suggested in Newton (2022). Furthermore, we show that the relationship between the genera *Necrodes* and *Diamesus* should be further investigated. Our analysis did not support a clear separation of these two genera, which were clearly distinguished in Růžička et al. (2023), who investigated infraspecific variation within *Necrodes* and *Diamesus*. The weak branch support that makes *Necrodes* paraphyletic is possibly an artefact, and more data might show *Necrodes* to be monophyletic (especially if morphological data were combined with molecular data).

The genus *Thanatophilus* is represented by 4 out of 24 described species (Newton, 2022); for our analysis, we included species that are morphologically representative. The genus is monophyletic in agreement with all previously published molecular studies. The position of the genus fluctuates among published studies based on the molecular markers used: (1) the recovered topology was *Thanatophilus* + (*Necrodes* + clade A) in Dobler and Müller (2000) (MP; three mitochondrial markers: COI, COII and tRNA leucine). A similar topology (*Thanatophilus* + (*Diamesus* + *Necrodes*) + clade A) was also

recovered by Růžička et al. (2023) (ML, MP, BI; two mitochondrial [COI, 16S] and one nuclear [28S] markers). However, (2) an alternative topology (Necrodes + (Thanatophilus + clade A)) was recovered in Mahlerová et al. (2021) (BI, ML, MP; two mitochondrial [COI, 16S] markers). А verv similar topology, (Diamesus + Necrodes) + (Thanatophilus + clade A) was also recovered by Ikeda et al. (2008) (BI, MP; four markers: 16S, 28S, Wingless and Pepck) and Růžička et al. (2023) (ML, MP, BI; two mitochondrial [COI and 16S] markers). The same topology is also recovered here, using two mitochondrial and three nuclear markers. A formal molecular phylogenetic analysis of the genus Thanatophilus has not been done, but some morphologically distinct species within the genus should possibly be included in future analyses (e.g., T. coloradensis (Wickham), T. dentiger (Semenov), T. dispar (Herbst) and/or T. roborowskyi (Jakovlev)).

The genus *Oiceoptoma* is well distinguished as monophyletic across published molecular studies, and we sampled five species, exceeding the previously published studies (e.g., Dobler & Müller, 2000; Ikeda et al., 2008; King et al., 2015; Mahlerová et al., 2021; Růžička et al., 2023). The position of the genus in published analyses is stable, as a sister clade to *Necrophila* and the clade A.

The genus Necrophila contains five subgenera, in our analysis we included four out of the five—Chrysosilpha, Eusilpha, Necrophila, and Calosilpha; only the subgenus Deutosilpha is not included. The genus is

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supported as a monophyletic group across the published literature; however, further investigation of the internal phylogeny of this genus should be conducted, to fully test the monophyly of the individual subgenera. The genus *Heterosilpha* represented by *Heterosilpha ramosa* (Say) is placed as a sister genus, which is in agreement with the only study that included the genus *Heterosilpha* (Dobler & Müller, 2000).

In our study, the genus *Dendroxena* is represented by both of its species, confirming the previously established monophyly of the genus (Dobler & Müller, 2000; Ikeda et al., 2008; King et al., 2015; Mahlerová et al., 2021; Růžička et al., 2023). Clade A, containing three currently established subgenera of the genus *Silpha* (*Ablattaria, Phosphuga, Silpha* sensu stricto) also contains the genera *Aclypea* and *Heterotemna*.

The phylogenetic position of the genus Heterotemna has been previously studied and Mahlerová et al. (2021) placed it within Silpha sensu stricto as sister species of S. tristis, but did not propose a formal taxonomic change. Our new results agree with these conclusions, even with expanded dataset (two mitochondrial and three nuclear genes). Although only one species of the genus *Heterotemna* was included in the analyses, the studied species H. tenuicornis is the type species of the genus. Our results agree completely with the previous results and H. tenuicornis was again recovered as a sister species of S. tristis. The previous article discussed the relationship of H. tenuicornis with S. puncticollis, a taxon that had not been sampled in that study, but which could possibly be assumed as a closer relative of H. tenuicornis due to the geographical proximity of the species. They both co-occur in the Canary Islands (Spain), although S. puncticollis was probably introduced to these islands recently by human activities (Machado, 2014). This hypothesis is disproved in our study, which included S. puncticollis, as S. tristis remains the sister species of H. tenuicornis. The current classification of Heterotemna as a separate genus results in paraphyly of the genus Silpha and the subgenus Silpha. Consequently, Heterotemna Wollaston is considered a junior subjective synonym of Silpha Linnaeus, in which two of the three species were originally described. The following new and restored combinations are proposed: Silpha (Silpha) britoi (García & Pérez), comb. nov., Silpha (Silpha) figurata Brullé, comb. rest., and Silpha (Silpha) tenuicornis Brullé, comb. rest.

The two subgenera *Phosphuga* and *Ablattaria* are both specialized predators of gastropods (Colkesen & Sekeroglu, 1989; Heymons & Lengerken, 1932; Portevin, 1926); therefore, their proximity within the phylogenetic tree indicates a single origin of feeding on gastropods. Our results found the two subgenera as sister lineages, which is in agreement with the first molecular phylogeny of Silphinae based on mitochondrial markers COI, COII and tRNA leucine (Dobler & Müller, 2000). The only other molecular phylogeny containing both of the subgenera is a recently published phylogeny (Mahlerová et al., 2021), that includes only one species of *Ablattaria*, compared to our current sampling covering three out of four described species.

The genus *Aclypea* is also placed within the clade A, and within the genus *Silpha* sensu lato, which is in agreement with the handful of previously published phylogenies that contained this genus (Dobler & Müller, 2000; Mahlerová et al., 2021; Růžička et al., 2023). Our estimate of the phylogeny agrees with current generic limits except it revealed the genus *Aclypea* Reitter arose from within the genus *Silpha*, thus making the latter paraphyletic. Some ambiguity remains regarding the confidence of this finding, so we refrain from synonymizing *Aclypea* until further study. Clade A presented in this paper exhibits overall lower support for the genera; therefore, further analyses of the genera *Aclypea* and *Silpha* sensu lato are needed.

The food strategies of the carrion beetles are predominantly carnivorous—necrophagy or predatory throughout the phylogenetic tree; however, *Aclypea* is phytophagous (Anderson & Peck, 1984), and in some cases even causes economic crop damage (Savage, 1980; Šefrová, 2014). Based on its position in clade A, we can infer that phytophagy is a derived feature.

The ancestral trait reconstruction of Ikeda et al. (2008) suggested that the original feeding strategy of Silphini was necrophagy and also found that transition to predation occurred at least twice. King et al. (2015) further corroborated these results but emphasized the need for more ecological studies. Current knowledge of feeding strategies is often based on anecdotal observations of collectors (J. Růžička, unpublished) and in recent years also forensic case studies (e. g., Barreto et al., 2002; Barros de Souza et al., 2008; Eddie et al., 2016; Ivorra et al., 2023; Lira et al., 2020). Several other approaches were suggested, also by Ikeda et al. (2007), who studied feeding behaviour indirectly by interpreting isotope ratios, which are able to categorize individuals as predatory or necrophagous. This approach was criticized by Jakubec et al. (2020) who proposed behavioural-based methodology, which is able to show a degree of preference on a scale instead of the dichotomous categories. Despite these differences, all studies so far categorized the basal branches of Silphini as necrophagous (Thanatophilus, Oiceoptoma, Necrodes, Diamesus, Necrophila (Calosilpha)), including those at the base, Ptomaphila (Australian region) and Oxelytrum (Neotropical region). Currently, we see as the biggest issue being the scarcity of knowledge on the feeding strategies of larvae, as larvae are rather monophagous compared to their more polyphagous adults. However, they are often undescribed and, therefore, difficult to identify in the field, making even anecdotal observations difficult to gather.

The robust phylogeny of the genera together with the first biogeographical insight makes the valuable suggestion of an ancestor for the tribe Silphini that was most likely distributed across the Neotropical, Oriental and/or Australian regions. The distribution has been reviewed on the level of genera. Finer resolution could be possibly achieved using species ranges and broader taxon sampling.

AUTHOR CONTRIBUTIONS

Karolina Mahlerová: Methodology; writing – original draft; writing – review and editing; data curation; formal analysis; visualization; investigation; funding acquisition. Pavel Jakubec: Writing – review and editing; writing – original draft; investigation; funding acquisition. Karol Krak: Writing – review and editing; methodology; formal analysis. Jan Růžička: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; writing – review and editing; supervision; visualization; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

We provide the following data used in our study—S1: Full list of all species used for this study including the GenBank accession numbers; S2: Sequences used in this study including already published studies, S3: Topologies obtained by individual phylogenetic analyses.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1. Full list of all species used for this study including the GenBank accession numbers and the biogeographical distribution.

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Supporting Information S3. Topologies obtained by individual phylogenetic analyses.

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