

A Preliminary Phylogenetic Study on the Systematics of *Lycocerus* Gorham (Coleoptera: Cantharidae)

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Abstract. The genus *Lycocerus* Gorham, 1889 is a highly speciose group of Asian soldier beetles. Okushima (2005) divided this genus into several species groups and presumed their potential phylogenetic relationship based on anatomical comparison, and a few more species groups were subsequently proposed by various authors. In this study, I reinvestigated the relationship within *Lycocerus* using phylogenetic analyses of morphological data and extended the taxa sampling to corroborate all currently known major lineages. The resulting topology only partially agrees with Okushima (2005), but supports the synonymy of *Athemus* Lewis, 1895, *Athemellus* Wittmer, 1972, *Mikadocantharis* Wittmer & Magis, 1978, *Andrathemus* Wittmer, 1978 and *Isathemus* Wittmer, 1995 with *Lycocerus*.

Key word: Soldier beetles, Cantharinae, systematics, morphological phylogenetics, Asia

Introduction

Cantharidae is a diverse elateroid beetle family with a brightly colored soft-body, originating from the Late Jurassic and maintaining the high rate of diversification since then (McKenna et al., 2019). *Lycocerus* Gorham, 1889 is a highly species-rich Asian genus of soldier beetles, with more than 300 species distributed in the Oriental and eastern Palaearctic regions (Kazantsev & Brancucci, 2007). Okushima (2005) revised the Japanese fauna and summarized nine major species groups with a couple of subgroups based on both external and genitalic characters. Subsequently, four species groups of *Lycocerus* were established, including the *L. michiakii* Group based on species from Laos (Okushima & Brancucci, 2008), the *L. hickeri* Group based on species from China and Vietnam (Yang et al., 2014), the *L. rhagonychiformis* Group based on the Taiwanese species (Hsiao & Okushima, 2016), and the *L. fainanus* Group based on species from China, Taiwan and Vietnam (Okushima & Hsiao, 2017).

Currently, most research on *Lycocerus* was predominantly focused on the alpha and beta taxonomy, with only few studies attempting to approach the issues of systematics. Okushima (2005) assumed the phylogeny of *Lycocerus* based on the comparative anatomy, and Hsiao et al. (2016) attempted to reconstruct the *Lycocerus* phylogeny using a cladistics analysis based on 29 adult traits and geographic distribution, covering all proposed species groups. Nonetheless, the main purpose of the phylogenetic analysis in Hsiao et al. (2016) aimed to clarify the systematic placement of some species related to the *L. hanatanii* Group and the relationship among most species groups was unresolved. In the present study, I reanalyze the relationship within *Lycocerus* to examine the phylogenetic hypothesis in Okushima (2005). Also, I include all genera and subgenera synonymized with *Lycocerus* by Okushima (2005) to test this taxonomic treatment.

Material and methods

Taxon sampling and character selection

The ingroup contained 15 species, representing all known species groups (Table 1). *Lycocerus pallidulus* (Wittmer) of *L. maculicollis* Group and *L. japonicus* (Kiesenwetter) of *L. lineatipennis* Group were also selected representing *Isathemus* Wittmer and *Mikadocantharis* Wittmer & Magis. Two species of *Themus* Motschulsky, namely *Th. (Th.) nobilis nobilis* (Gorham) and *Th. (Telephorops) sauteri* (Pic), were used as outgroups.

The data matrixes from Okushima (2005) and Hsiao et al. (2016) were used as a starting point for morphological character coding. After reconsideration of characters used in previous phylogenies of *Lycocerus*, 21 characters were kept, seven were amended, four were added and one was deleted to obtain a matrix pertinent to the taxa included in analyses. No geographic character was used. In total, 46 adult characters were coded for the phylogenetic analysis (Tables 2, 3). I assembled the matrix using MESQUITE v. 3.61 (Maddison & Maddison, 2019). Inapplicable data were scored as ‘-’ in the character matrix.

Table 1. Taxa included in the phylogenetic analysis.

| | Genus/Subgenus | Species | Species group | Genus/Subgenus sensu Wittmer |
|-----------------|---|--|-------------------------------------|--|
| Outgroup | <i>Themus</i> (<i>Themus</i>) | <i>Th. (Th.) nobilis nobilis</i> (Gorham) | - | - |
| | <i>Themus</i> (<i>Telephorops</i>) | <i>Th. (Telephorops) sauteri</i> (Pic) | - | - |
| Ingroup | <i>Lycocerus</i> | <i>L. maculicollis</i> (Hope) | <i>L. maculicollis</i> Group | <i>Lycocerus</i> |
| | | <i>L. pallidulus</i> (Wittmer) | <i>L. maculicollis</i> Group | <i>Athemus</i> (<i>Isathemus</i>) |
| | | <i>L. japonicus</i> (Kiesenwetter) | <i>L. lineatipennis</i> Group | <i>Athemus</i> (<i>Mikadocanthis</i>) |
| | | <i>L. yamatensis</i> Okushima | <i>L. lineatipennis</i> Group | <i>Athemus</i> (<i>Andrathemus</i>) |
| | | <i>L. purpureus</i> Kazantsev | <i>L. purpureus</i> Group | <i>Athemus</i> (<i>Andrathemus</i>) |
| | | <i>L. vitellinus</i> (Kiesenwetter) | <i>L. vitellinus</i> Group | <i>Athemus</i> (<i>Andrathemus</i>) |
| | | <i>L. aegrotus</i> (Kiesenwetter) | <i>L. aegrotus</i> Group | <i>Athemus</i> (<i>Athemus</i>) |
| | | <i>L. masatakai</i> Okushima | <i>L. fainanus</i> Group | <i>Athemus</i> (<i>Athemus</i>) |
| | | <i>L. michiakii</i> Okushima & Brancucci | <i>L. michiakii</i> Group | <i>Athemus</i> (<i>Athemus</i>) |
| | | <i>L. suturellus suturellus</i> (Motschulsky) | <i>L. suturellus</i> Group | <i>Athemus</i> (<i>Athemus</i>) |
| | | <i>L. adusticollis</i> (Kiesenwetter) | <i>L. adusticollis</i> Group | <i>Athemus</i> (<i>Athemellus</i>) |
| | | <i>L. hanatanii</i> (Okushima) | <i>L. hanatanii</i> Group | <i>Athemus</i> (<i>Athemellus</i>) |
| | | <i>L. rhagonychiformis</i> (Wittmer) | <i>L.</i> <i>rhagonychiformi</i> | <i>Athemus</i> (<i>Athemellus</i>) |
| | | <i>L. sichuanus</i> Y. Yang & X. Yang | s Group <i>L. hickeri</i> Group | <i>Athemus</i> (<i>Athemellus</i>) |
| | | <i>L. watanabei</i> (Ishida & M. Satô) | <i>L. oedemeroides</i> Group | <i>Athemus</i> (<i>Athemellus</i>) |

Table 2. Character matrix used for the phylogenetic analysis of *Lycocerus*.

| Taxa \ Characters | 0000000001111111112222222223333333334444444 0123456789012345678901234567890123456789012345 |
|--|---|
| <i>Themus nobilis nobilis</i> | 201101000000-0110121100000000000000000-0-0-0 |
| <i>Themus sauteri</i> | 201101000000-011002100000000000000010200-0-0-0 |
| <i>Lycocerus maculicollis</i> | 2001101000010011111000000001010001100201010100 |
| <i>Lycocerus suturellus suturellus</i> | 2100011001111111110110000001010001100211010100 |
| <i>Lycocerus vitellinus</i> | 1100012001111111110111010001010001101201010100 |
| <i>Lycocerus purpureus</i> | 0011000001110111010111010001010001100201010111 |
| <i>Lycocerus adusticollis</i> | 1100011001111111110110000000000001100201110100 |
| <i>Lycocerus yamatensis</i> | 1100012001111111110111010001010001100201010100 |
| <i>Lycocerus watanabei</i> | 1100011001111101110110000001010001100211011100 |
| <i>Lycocerus aegrotus</i> | 2200001001111111110110000000000001100201011110 |
| <i>Lycocerus michiakii</i> | 1200011001111110113110000001010001100201110100 |
| <i>Lycocerus sichuanus</i> | 120001100111011110111010001010001100201010100 |
| <i>Lycocerus rhagonychiformis</i> | 01000011111110111011000000000001100111011100 |
| <i>Lycocerus hanatanii</i> | 01110021111110111011000000000001110111011100 |
| <i>Lycocerus masatakai</i> | 2200011001111111010110000001010001101201010100 |
| <i>Lycocerus pallidulus</i> | 1100001001111111110111111101111101100201010100 |
| <i>Lycocerus japonicus</i> | 1110012001111111110111111111111111100201010110 |

Table 3. List of characters and states used in the phylogenetic analysis.

| | | |
|----|--|---|
| 0 | Body size | 0. small (5-7mm) 1. medium (8-10mm) 2. large (> 10mm) |
| 1 | Body form judged on the ratio of the length to the width at the widest part of the conjoint elytra | 0. stout (about 2.2) 1. middle (2.5-3.0) 2. slender (mainly greater than 3.0) |
| 2 | Antennal length in males | 0. exceeding 1/2 elytral length 1. extending to 1/2 elytral length |
| 3 | Antennal length in females | 0. extending to 1/2 of elytral length 1. barely exceeding the humeri, but not extending to 1/2 elytral length |
| 4 | Antennae | 0. filiform 1. serrate |
| 5 | Grooves on antennal segments in male | 0. absent 1. present |
| 6 | Terminal maxillary palpomere | 0. stout; Hsiao et al., 2016: Fig. 1A 1. subtriangular; Hsiao et al., 2016: Fig. 1B 2. slender; Hsiao et al., 2016: Fig. 1C |
| 7 | Eyes | 0. large; Hsiao et al., 2016: Fig. 1D 1. small; Hsiao et al., 2016: Fig. 1E |
| 8 | Eyes | 0. prominent; Hsiao et al., 2016: Fig. 1D 1. not very prominent; Hsiao et al., 2016: Fig. 1E |
| 9 | Vertex | 0. flat 1. faintly hollowed |
| 10 | Vertex | 0. smooth 1. distinctly punctate |
| 11 | Pronotum | 0. disc-shaped, distinctly expanded; Hsiao et al., 2016: Fig. 1H 1. normal, trapezoid or subquadrate, not expanded as above |

| | | |
|----|-------------------------------------|---|
| 12 | If pronotum not distinctly expanded | 0. trapezoid; Hsiao et al., 2016: Fig. 1F 1. subquadrate; Hsiao et al., 2016: Fig. 1G |
| 13 | Greatest width of pronotum in male | 0. wider than head 1. nearly as wide as head or narrower than head |
| 14 | Angular convexity on pronotum | 0. distinct; Hsiao et al., 2016: Fig. 1G 1. indistinct |
| 15 | Elytra | 0. Shortened, with abdomen largely exposed 1. entirely covered abdomen |
| 16 | Elytra | 0. with strong metallic lustre 1. lusterless or semi-lustrous |
| 17 | Elytra | 0. strongly depressed 1. normal |
| 18 | Elytra | 0. subparallel at the sides 1. apically expanded 2. moderately narrowed apically 3. strongly narrowed apically |
| 19 | Costae on elytra | 0. distinct 1. hardly recognizable |
| 20 | Legs | 0. stout; Hsiao et al., 2016: Fig. 1I 1. slender; Hsiao et al., 2016: Fig. 1J |
| 21 | Outer claws of forelegs in male | 0. simple 1. with tooth/lobe |
| 22 | Inner claws of forelegs in male | 0. simple 1. with tooth/lobe |
| 23 | Outer claws of mid legs in male | 0. simple 1. with tooth/lobe |
| 24 | Inner claws of mid legs in male | 0. simple 1. with tooth/lobe |
| 25 | Outer claws of hind legs in male | 0. simple 1. with tooth/lobe |
| 26 | Inner claws of hind legs in male | 0. simple 1. with tooth/lobe |
| 27 | Outer claws of forelegs in female | 0. simple 1. with tooth/lobe |
| 28 | Inner claws of forelegs in female | 0. simple 1. with tooth/lobe |
| 29 | Outer claws of mid legs in female | 0. simple 1. with tooth/lobe |
| 30 | Inner claws of mid legs in female | 0. simple 1. with tooth/lobe |
| 31 | Outer claws of hind legs in female | 0. simple 1. with tooth/lobe |
| 32 | Inner claws of hind legs in female | 0. simple 1. with tooth/lobe |

| | | |
|----|---|--|
| 33 | Dorsal plate of each paramere of aedeagus | 0. fused or nearly fused 1. separated |
| 34 | Laterophyses of aedeagus | 0. nearly fused 1. widely separated on both sides of median lobe |
| 35 | Laterophyses of aedeagus | 0. long, distinctly visible in lateral view 1. short, barely visible or invisible in lateral view |
| 36 | Median lobe of aedeagus | 0. simple 1. provided with a process dorsad |
| 37 | Apical part of median lobe of aedeagus | 0. widened apically 1. strongly narrowed apically 2. moderately narrowed apically |
| 38 | Apical part of vagina | 0. broad 1. extended apically as a thick duct |
| 39 | Diverticulum | 0. thick 1. thin |
| 40 | If diverticulum thin | 0. long 1. short |
| 41 | Spermathecal duct | 0. absent 1. present |
| 42 | If spermathecal duct present | 0. spermathecal duct short 1. spermathecal duct long |
| 43 | Spermatheca | 0. short, sac-shaped 1. long and thin, provided with spiral tube(s) |
| 44 | If spermatheca long and thin | 0. with a spiral tube 1. with two spiral tubes |
| 45 | Accessory gland | 0. simple (thin, filiform) 1. modified (abruptly expanded) |

Maximum Parsimony

Maximum parsimony (MP) analysis was carried out in TNT ver. 1.5 (Goloboff & Catalano, 2016), using the implicit enumeration search with all characters unordered and unweighted. The assembled data matrix was also analyzed under the implied weighting (Goloboff et al., 2017) using the same algorithm to resolve the previously unresolved relationship (i.e., polytomy). I investigated the sensitivity of clades to alternative character weighting schemes and the impact of strong to light downweighting of homoplastic characters on the inferred trees was examined by running implied weighting analyses under K values 3, 10 and 21 respectively. Character states were mapped on the most parsimonious tree using Winclada ver. 1.0 (Nixon, 2002), showing only unambiguous changes. Bootstrap (BS) support values were calculated with 2000 replicates in TNT ver. 1.5, with an ‘absolute frequencies’ option, to indicate the statistical support for each hypothesised clade (Felsenstein, 1985). Nodes with bootstrap values <50% were considered to be unsupported and not shown.

Bayesian inference

Bayesian inference (BI) was conducted using MrBayes 3.2.6 (Ronquist et al., 2012). The Mkv model was used with a gamma distribution. Two Markov chain Monte Carlo runs (MCMC) were executed with four chains for 5 million generations. The first 25% of trees were discarded as burn-in. Convergence was assessed by checking that all parameters had reached sufficient effective sample sizes (> 200) and by comparing results from two independent runs using Tracer v1.7.0 (Rambaut et al., 2018). Nodes with posterior probability (PP) > 0.95 were considered to be strongly supported, with PP = 0.90–0.94 moderately supported, with PP = 0.85–0.89 weakly supported, and PP < 0.85 unsupported according to Żyła et al. (2017). The 50% majority-rule consensus (MRC) tree was rooted with *Th. (Th.) nobilis nobilis* + *Th. (Te.) sauteri*. Additionally, I followed Zhou et al. (2019) to obtain the maximum clade credibility (MCC) tree from post burn-in trees (ESS > 200) by using Treeannotator (Bouckaert et al., 2014). The tree was displayed and edited in FigTree v1.4.3 (<https://github.com/rambaut/figtree/>).

Maximum Likelihood

Maximum Likelihood (ML) phylogenetic reconstruction was performed using the web version of IQ-TREE (ver. 1.6.11, see <http://www.iqtree.org/>; Nguyen et al., 2015; Trifinopoulos et al., 2016). The prior substitution model was estimated by Model Finder (Kalyaanamoorthy et al., 2017) implemented in the same software for morphological data. Nodal support was estimated using an ultrafast bootstrap analysis with 1000 replicates and single branch test was obtained by SH-aLRT branch test with 1000 replicates, where BS values $\geq 80\%$ are clades supported (Guindon et al., 2010). The resulting phylogenetic tree was rooted with *Th. (Th.) nobilis nobilis* + *Th. (Te.) sauteri* and displayed in FigTree v1.4.3 as above.

Results

MP, BI and ML analyses of the entire matrix produced highly concordant topologies (Figs. 1–4). Implicit enumeration search under the equal weighting in the MP analysis of the taxa sampling with exclusion of *L. pallidulus* and *L. japonicus* resulted in 9 most parsimonious trees (tree length (L) = 87 steps, consistency index (CI) = 59, retention index = 63). The majority consensus tree (L = 87; CI = 59; RI = 63; Fig. 1), recovering monophyletic (99% BS) *Lycocerus* as synapomorphically supported by the not expanded pronotum (11:1), subparallel-sided elytra (18:1), simple outer claws of forelegs in female (27:1), simple outer claws of mid legs in female (29:1), separated dorsal plate of each paramere of aedeagus (33:1), widely separated laterophyses of aedeagus (34:1), thin diverticulum (39:1), spermathecal duct present (41:1) and long and thin spermatheca, with spiral tube(s) (43:1), but the relationship among crown groups was not resolved. The sister relationships between *L. pallidulus* (*L. maculicollis* Group: *L. pallidulus* Subgroup) and *L. japonicus* (*L. lineatipennis* Group: *L. japonicus* Subgroup), and between the *L. hanatanii* Group and the *L. rhagonychiformis* Group were supported, with 93% BS and 95% BS, respectively.

MP analysis of the same dataset under the implied weighting using various K values resulted in 9 most parsimonious trees when K=3 (strong downweighting impact of homoplastic characters) and 3 trees when K=10 and 21 (moderate to light downweighting impact). The respective majority consensus trees show highly consistent topologies, with minor differences in placement of few taxa, resolving the polytomy in previous analysis under the equal weighting (Fig. 2), which suggests the relationship *L. maculicollis* Group + (*L. aegrotus* Group + (*L. fainanus* Group + ((*L. suturellus* Group + (*L. oedemeroides* Group + (*L. rhagonychiformis* Group + *L. hanatanii* Group)))))) + ((*L. adusticollis* Group + *L. michiakii* Group) + ((*L. purpurascens* Group + *L. hickeri* Group) + ((*L. pallidulus* Subgroup + *L. japonicus* Subgroup) + (*L. vitellinus* Group + *L. lineatipennis* Group)))))) (L = 88; CI = 59; RI = 62) or *L. maculicollis* Group + (*L. purpurascens* Group + (*L. fainanus* Group + ((*L. suturellus* Group + (*L. oedemeroides* Group + (*L. aegrotus* Group + (*L. rhagonychiformis* Group + *L. hanatanii* Group)))))) + ((*L. adusticollis* Group + *L. michiakii* Group) + (*L. hickeri* Group + ((*L. pallidulus* Subgroup + *L. japonicus* Subgroup) + (*L. vitellinus* Group + *L. lineatipennis* Group)))))) (L = 87; CI = 59; RI = 63) within *Lycocerus*.

In the BI analysis, the majority-rule consensus tree strongly supports a monophyletic *Lycocerus* (PP = 1.00), and the clade containing all species groups except for the *L. maculicollis* Group and the clade including the *L. purpurascens* Group, *L. hickeri* Group, *L. pallidulus* Subgroup, *L. japonicus* Subgroup, *L. vitellinus* Group and *L. lineatipennis* Group are weakly supported, respectively. The affinities between the *L. rhagonychiformis* Group and *L. hanatanii* Group, and between *L. pallidulus* Subgroup and *L. japonicus* Subgroup are also strongly supported as MP analysis recovered. Nonetheless, the relationships among most of the species groups were not well resolved (Fig. 3A). The maximum clade credibility tree presents a well-resolved topology nearly consistent with the majority consensus tree produced by the MP analysis under the implied weighting using K = 3 (Fig. 3B).

The ML tree also recovered the strongly supported monophyletic *Lycocerus* (100% BS). The monophyly of the clade including all species groups except for *L. maculicollis* Group is supported (80% BS). ML tree also supported the following sister relationships: *L. rhagonychiformis* Group + *L. hanatanii* Group (100% BS), *L. vitellinus* Group + *L. lineatipennis* Group (86% BS) and (*L. pallidulus* Subgroup + *L. japonicus* Subgroup) (98% BS) (Fig. 4).

Discussion

Okushima (2005) proposed the potential phylogenetic relationship of the main species groups based on 18 adult characteristics, suggesting the relationship (*L. oedemeroides* Group + (*L. aegrotus* Group + *L. hanatanii* Group)) + ((*L. adusticollis* Group + *L. lineatipennis* Group) + (*L. purpurascens* Group + (*L. vitellinus* Group + (*L. maculicollis* Group + *L. suturellus* Group))))). The present study increases the taxa sampling from 9 species groups to 13 species groups (including 4 currently established groups) and 2 additional subgroups, representing main lineages of this taxonomically diverse genus, and the analyses using various methods (i.e. MP, BI and ML) resulted in generally consistent topologies (Figs. 1–4). My results provide a new perspective to the *Lycocerus* phylogeny in contrast to most of the clades suggested in Okushima (2005). Nevertheless, the close affinity among *L. aegrotus* Group, *L. hanatanii* Group and *L. oedemeroides* Group presumed by Okushima (2005) is recovered in my results.

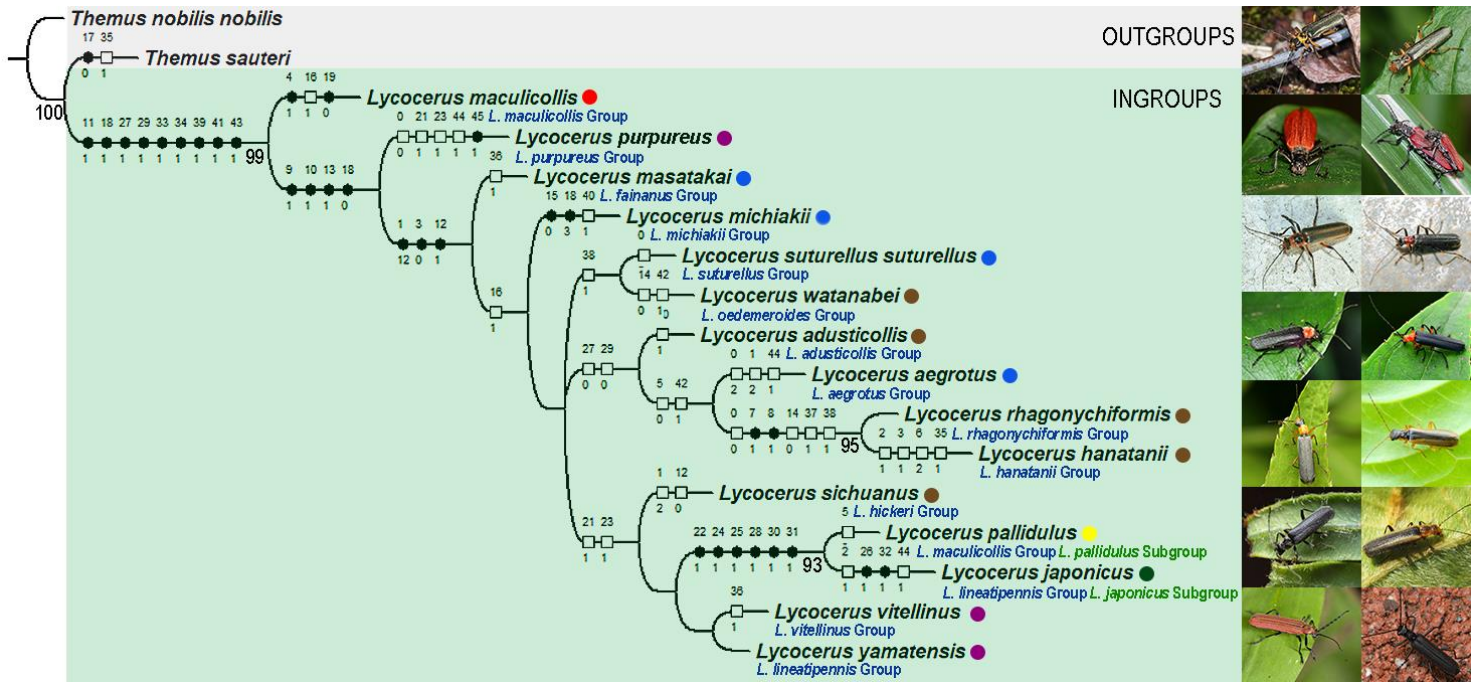


Figure 1. The majority consensus tree of 9 most parsimonious trees of diverse *Lycocerus* Gorham obtained by implicit enumeration search under equal weighting (L = 87; CI = 59; RI = 63). Black circles indicate synapomorphies; white rectangles indicate parallelisms or reversals; character numbers are given above circles, and character states are labelled below circles. Bootstrap values (BS > 49%) are shown near each of the corresponding nodes. Circles after species names indicate the genus/subgenus based on Wittmer’s classification, showing the non-monophyly: red circle: *Lycocerus*; blue circles: *Athemus* (*Athemus*); brown circles: *Athemus* (*Athemellus*); purple circles: *Athemus* (*Andrathemus*); yellow circles: *Athemus* (*Isathemus*); dark green circles: *Athemus* (*Mikadocantharis*).

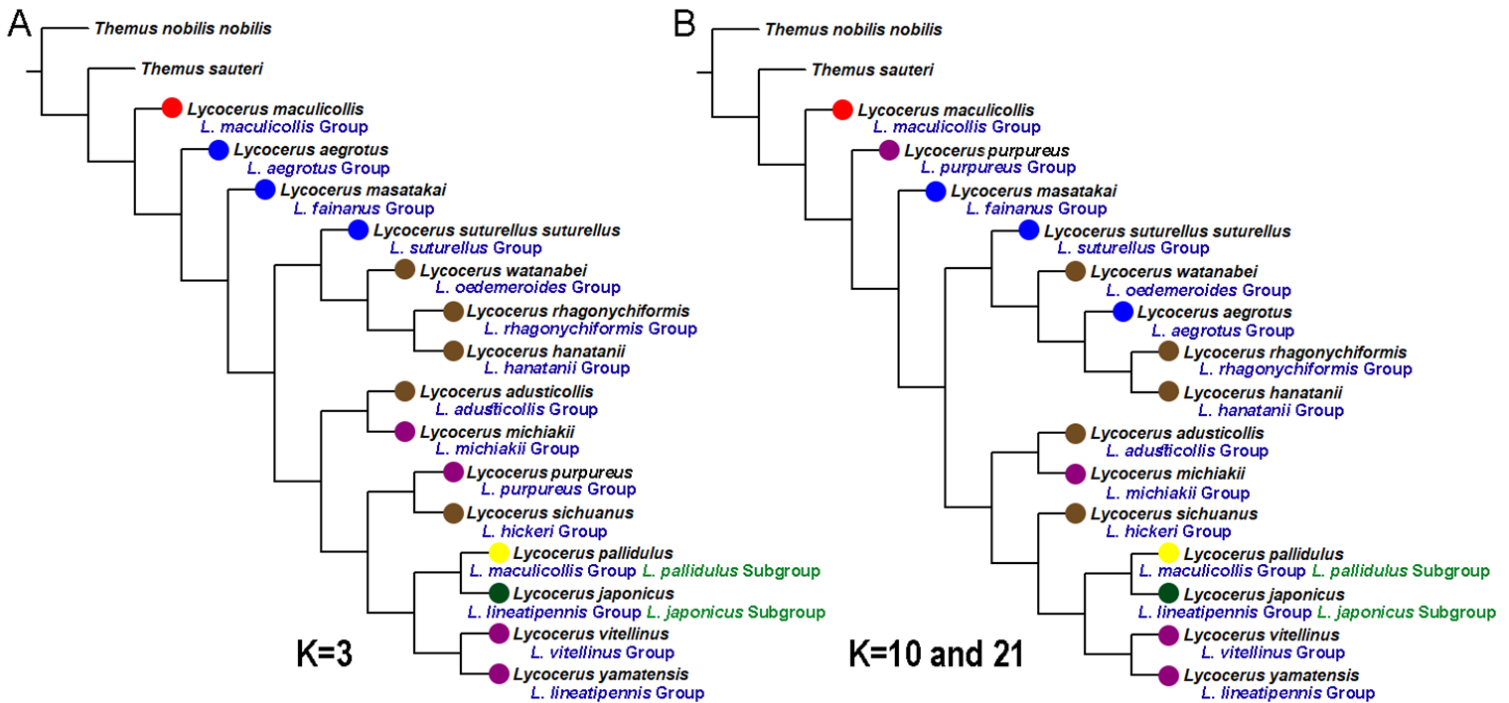


Figure 2. Phylogenies inferred from Maximum Parsimony under implied weighting. A - the majority consensus tree of 9 most parsimonious trees when K = 3 (L = 88; CI = 59; RI = 62); B - the majority consensus tree of 3 most parsimonious trees when K = 10 and 21 (L = 87; CI = 59; RI = 63). Circles after species names indicate the genus/subgenus based on Wittmer’s classification, showing the non-monophyly: red circle: *Lycocerus*; blue circles: *Athemus* (*Athemus*); brown circles: *Athemus* (*Athemellus*); purple circles: *Athemus* (*Andrathemus*); yellow circles: *Athemus* (*Isathemus*); dark green circles: *Athemus* (*Mikadocantharis*).

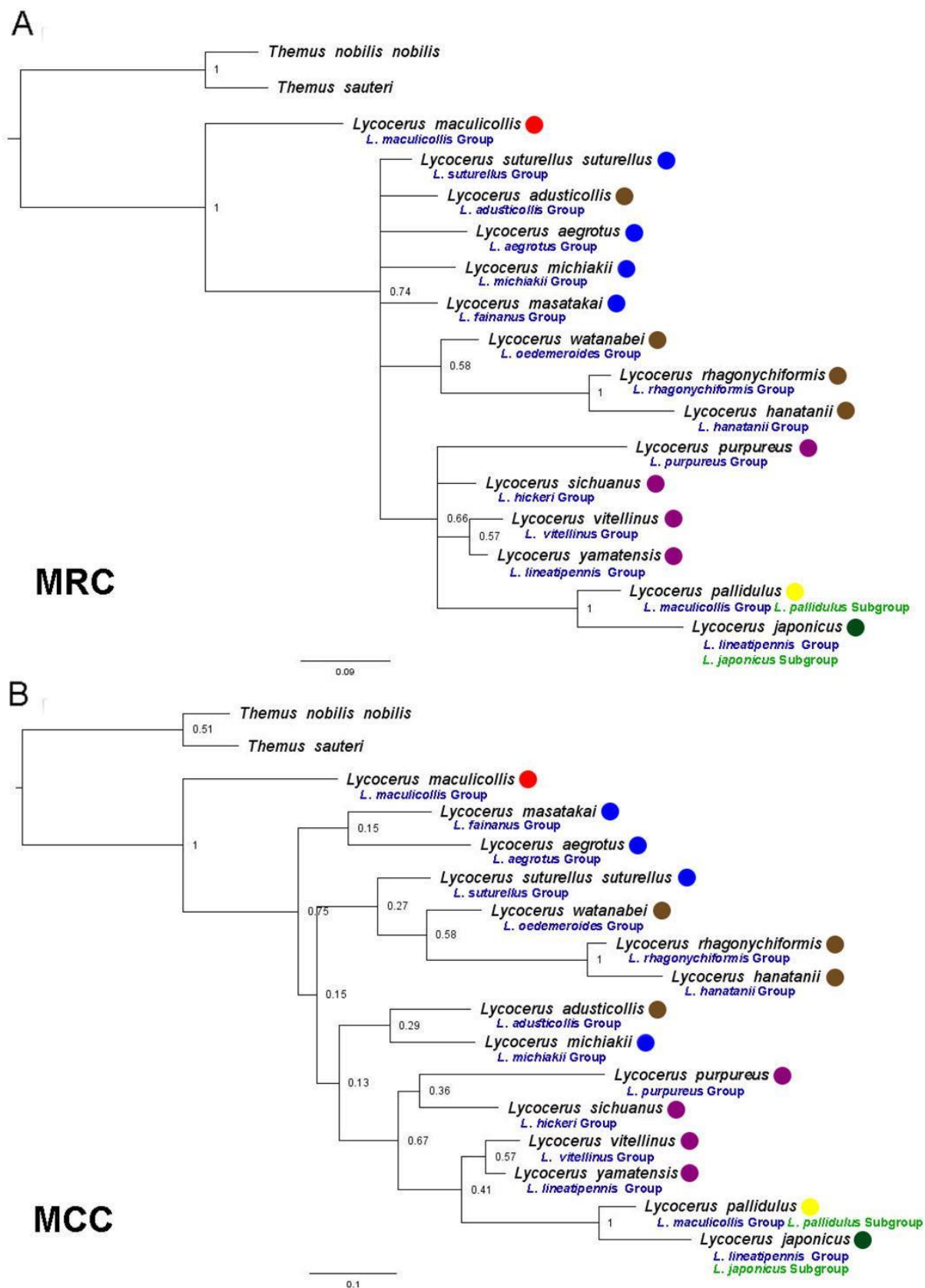


Figure 3. Phylogenies inferred from Bayesian inference. A – the 50% majority-rule consensus tree; B – the maximum clade credibility tree. Circles after species names indicate the genus/subgenus based on Wittmer’s classification, showing the non-monophyly: red circle: *Lycocerus*; blue circles: *Athemus* (*Athemus*); brown circles: *Athemus* (*Athemellus*); purple circles: *Athemus* (*Andrathemus*); yellow circles: *Athemus* (*Isathemus*); dark green circles: *Athemus* (*Mikadocantharis*).

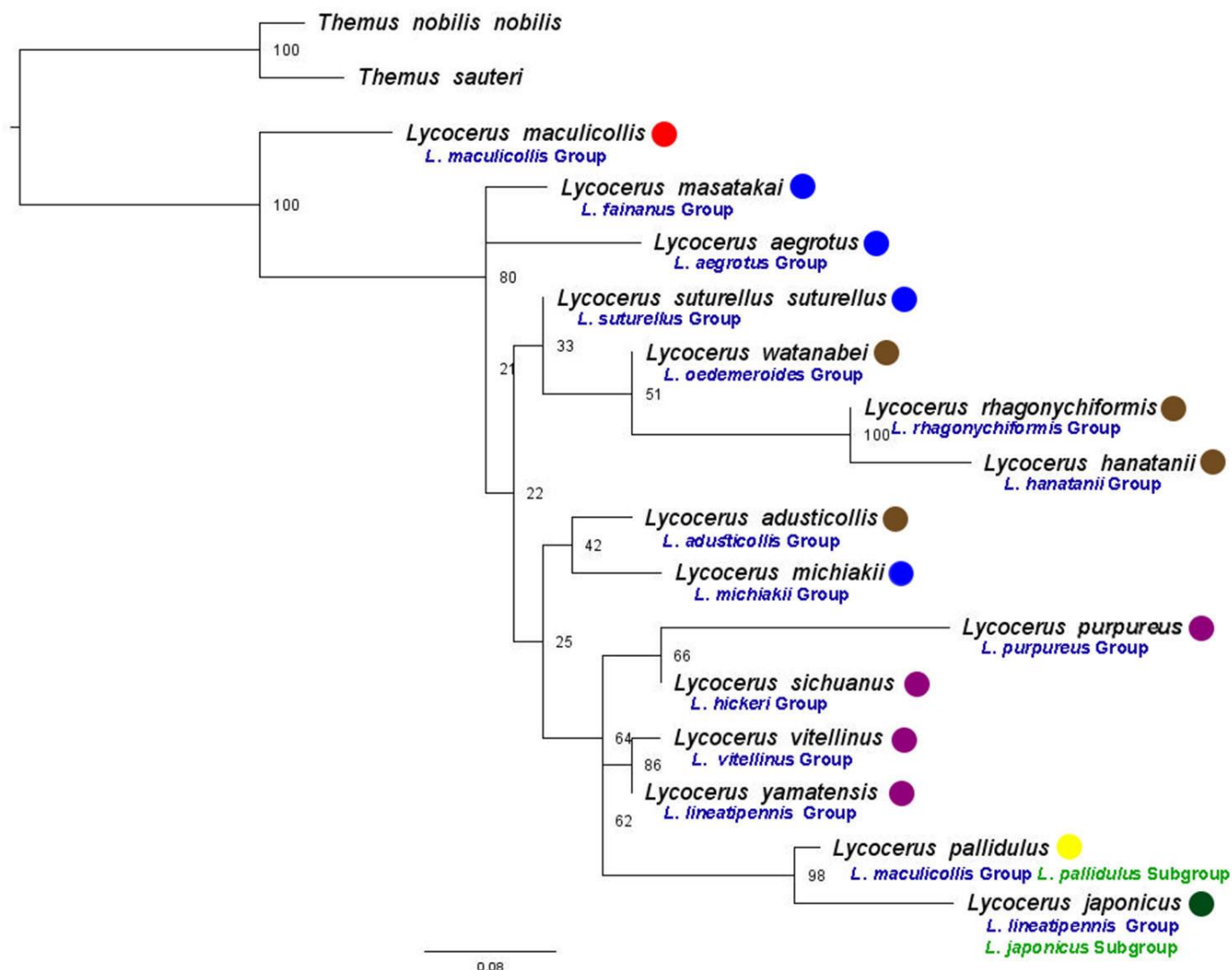


Figure 4. Maximum Likelihood phylogenetic tree of *Lycocerus* based on 46 morphological characters. Circles after species names indicate the genus/subgenus based on Wittmer's classification, showing the non-monophyly: red circle: *Lycocerus*; blue circles: *Athemus* (*Athemus*); brown circles: *Athemus* (*Athemellus*); purple circles: *Athemus* (*Andrathemus*); yellow circles: *Athemus* (*Isathemus*); dark green circles: *Athemus* (*Mikadocantharis*).

The type species of *Lycocerus* and *Athemus* can be easily distinguished from each other by characteristics of the antennae, vertex of the head, pronotum, male genitalia and the eighth abdominal sternite of females (Kasantsev, 1999), and it is thus seemingly reasonable to separate them into different genera. However, Okushima (2005) noted that these plausible diagnostic characteristics fail to apply for all *Lycocerus* and *Athemus* species and argued that a broadly defined genus, inclusive of these characteristics should be proposed, and thus two genera were synonymized. In the present phylogenies, despite the clear separation between *Lycocerus* and *Athemus* by several characters, the extremely low BS support values in MP and PP in BI, and weakly supported BS in ML still suggest that it is premature to separate the two genera without providing another objective evidence for this nomenclatural act.

Athemus Lewis, the junior synonym of *Lycocerus*, was one of the largest genera of Asian cantharids. It was divided into several subgenera (i.e. *Athemus*, *Andrathemus* Wittmer, *Athemellus* Wittmer, *Isathemus* Wittmer and *Mikadocantharis* Wittmer & Magis) based on differences only in the shape of the claws. With the consideration of all external characteristics and genitalic structures, Okushima (2005) indicated that the division based on the morphology of claws was artificial and should be synonymized. My analyses using morphological characters under various algorithms also reveal this unnatural subgeneric classification, with apparent non-monophyletic *Athemus*, *Andrathemus* and *Athemellus* (Figs 1–4), and thus support Okushima (2005)'s treatment.

Okushima & Hsiao (2017) upgraded *L. fainanus* Subgroup (*L. vitellinus* Group) to an independent species group based on its unique characteristics, namely large sized body, metallic elytra, and median lobe with a conspicuous process, which is supported by the present results as well. Additionally, these results indicate the distinct systematic position of the *L. pallidulus* Subgroup in the *L. maculicollis* Group and *L. japonicus* Subgroup in the *L. lineatipennis* Group, suggesting future investigation on the systematics

of other *Lycocerus* subgroups is required. The study herein provides a new insight into the phylogenetic relationship of a highly speciose genus of Asian Cantharidae.

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異菊虎屬系統分類學初探（鞘翅目：菊虎科）

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摘要: 異菊虎屬 (*Lycocerus* Gorham, 1889) 是多樣性極高的亞洲產菊虎類群。Okushima (2005) 將本屬劃分成數個種群並基於形態解剖比較推測異菊虎屬內的親緣關係，此後又有數位學者提出數個異菊虎種群。在本研究中，我們基於形態數據，透過系統發育分析重新探討異菊虎的屬內關係，並將取樣範圍延伸到目前已知主要的菊虎支系。分析結果與 Okushima (2005) 提出推測的樹型僅部分一致但支持其提出的異麗菊虎 (*Athemus* Lewis, 1895)、細身異麗菊虎 (*Athemellus* Wittmer, 1972)、米卡菊虎 (*Mikadocanthis* Wittmer & Magis, 1978)、安卓麗菊虎 (*Andrathemus* Wittmer, 1978) 和伊斯麗菊虎 (*Isathemus* Wittmer, 1995) 為異菊虎的同物異名處理。

關鍵詞: 菊虎、菊虎亞科、系統學、形態系統發育學、亞洲