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Article

Phenotypic variations among selected synanthropic beetles collected in urban areas of Mindanao, Philippines

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Abstract

Coleopterans present challenges in their classification due to their highly variable morphological traits. In the Philippines, beetle classification was limited to describing species based on a few character traits, which might result in taxonomic incongruencies. Hence, this research utilized Cladistic analysis to determine the morphological diversity of synanthropic beetles. This work included 48 synanthropic beetle taxa using 82 qualitative morphological characters. Tree searches found eight parsimonious trees with a length of 683 steps, a consistency index of 20, and a retention index of 46. These trees produced a strict consensus tree revealing three major clades with recurring traits, suggesting high homoplasy among Coleopterans. Furthermore, three polytomies were observed in the preferred tree, particularly species in Cerambycidae and Melolonthinae groups, indicating that these groups underwent various evolutionary mechanisms, such as parallel evolution, homoplasy, or convergent evolution. Analysis of the individual character traits revealed five uninformative morphological features and nine character traits that can be examined for character evolution. The results of Cladistic analysis are generally congruent with the molecular studies and enhance our understanding of the systematic relationships among synanthropic beetle species.

Keywords Cladistics; Coleopterans; evolution; systematic relationships.

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1 Introduction

Beetles exhibit considerable size variation and a wide array of morphological traits, leading to inconsistencies in their classification, especially when only a few characters are used for comparison within, between, and among species. The extensive morphological variability observed within and between beetle species

(Lawrence et al., 2011; McKenna et al., 2019) complicates species designation, as relying on minor variations in a limited number of traits across Coleopteran populations can result in taxonomic discrepancies. This is because individual beetles may exhibit differences in certain traits, with Operational Taxonomic Units (OTUs) aligning in some morphological characteristics but diverging in others (Gutierrez Jr. et al., 2011). Furthermore, some traits may evolve convergently due to environmental pressures, causing unrelated species to appear morphologically similar.

In Mindanao, Philippines, research efforts have primarily focused on the discovery and description of new beetle species, particularly in upland forest ecosystems. Additionally, some investigations have emphasized the taxonomy and description of newly discovered species, as well as their biodiversity and conservation. However, earlier studies on beetles have often relied on limited morphological traits and primarily compared individual specimens to a narrow range of species, without conducting comprehensive comparisons within, between, and among species.

The increasing discovery of new beetle species underscores the need to assess their morphological diversity, particularly among synanthropic beetle species. While several studies have explored the sensitivity and diversity of Coleopterans in anthropogenic environments (Barrat et al., 2015; Pompeo et al., 2017; Park & Lee, 2021; Magura & Lövei, 2021), the morphological diversity of synanthropic beetles remains underexplored. In Mindanao, Philippines, there is also a notable lack of comprehensive comparative morphological analyses of synanthropic beetles using Cladistics. To address this gap, the present study utilized multiple character traits and applied Cladistic analysis to compare the morphological diversity of these insects. Moreover, this investigation identified the homoplasious and autapomorphic characters of synanthrope beetles; determined the character evolution of traits; and depicted the phenetic relationship of beetles based on their strict consensus tree. This approach provides insights into their shared traits and evolutionary patterns.

2 Materials and Methods

2.1 Sampling sites

Beetles were collected from eight regions in Mindanao, Philippines, using opportunistic sampling techniques (Fig. 1). Collection methods included pitfall traps, insect netting, and manual collection. Samples were preserved in 70% ethanol and transported to the laboratory for anatomical dissection.

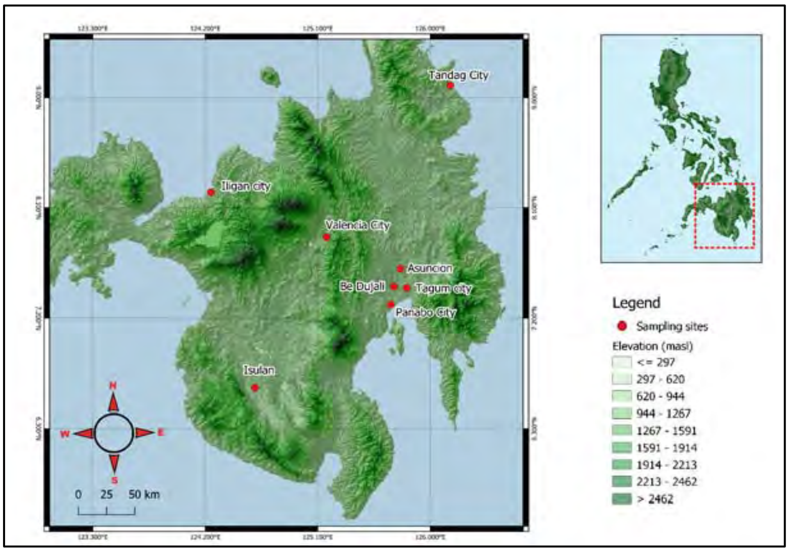

Fig. 1 Map of Mindanao, Philippines and the location of collection sites.

2.2 List of taxa

The outgroup selected for this study was *Polistes stigma* Fabricius, 1793 (Hymenoptera: Vespidae), a synanthropic tropical paper wasp, belonging to Hymenoptera, the sister taxon of all holometabolous insects, including Coleoptera (Ishiwata et al., 2011). A total of 48 OTUs from the families Anthribidae, Buprestidae, Cantharidae, Carabidae, Cerambycidae, Chrysomelidae, Cicindelidae, Curculionidae, Coccinellidae, Dytiscidae, Elateridae, Lampyridae, Lucanidae, Lycidae, Passalidae, Prionoceridae, Scarabaeidae, and Tenebrionidae were analyzed (Table 1). Additionally, two Lycidae specimens and one Scarabaeidae specimen, identified to the genus level, were included. Taxonomic classification followed references such as the *Handbook of Zoology, Volume 2: Coleoptera, Beetles* (Kristensen & Beutel, 2010), *The Book of Beetles* (Bouchard et al., 2014), and *Australian Beetles* (Lawrence & Slipinski, 2013). Diagnostic keys and distribution data were also used to confirm beetle identifications.

Table 1 Beetles used in this study.

Species	
Acalolepta rusticatrix (Fabricius, 1801)	*Lema pectoralis* (Baly, 1867)
Aclees hirayamai (Kôno, 1933)	*Leucopholis furforosa* (Chevrolat, 1841)
Anomala flavipennis (Burmeister, 1844)	*Leucopholis pulverulenta* (Burmeister, 1855)
Anomala marginata (Fabricius, 1792)	*Macrolinus sulciperfectus* (Kuwert, 1891)
Anomala smaragdina (Eschscholtz, 1822)	*Metapocyrtus adspersus* (Schultze, 1925)
Apriona aphetor (Newman, 1842)	*Metriorrhynchus* sp. (sp1)
Batocera magica (Thomson, 1859)	*Metriorrhynchus* sp. (sp2)
Carlschoenherria sulcipennis (Laporte, 1840)	*Nupserha fricator* (Dalman, 1817)
Chalcosoma atlas (Linnaeus, 1758)	*Onitis phartopus* (Lansberge, 1875)
Cheilomenes sexmaculata (Fabricius, 1781)	*Onthophagus hielkemai* (Meindert, 2019)
Chrysochroa fulminans (Fabricius, 1787)	*Oryctes rhinoceros* (Linnaeus, 1758)
Cordylocera atricornis (Guérin-Méneville, 1838)	*Otiorhynchus pauxillus* (Rosenhauer, 1847)
Colophotia concolor (Olivier, 1886)	*Pentodon algerinus* (Fuessly, 1788)
Cryptalaus lacteus (Candeze, 1857)	*Platymetopus flavilabris* (Fabricus, 1798)
Cylindera discreta elaphroides (Doktouroff, 1882)	*Podontia quatuordecimpunctata* (Linnaeus, 1767)
Cylindera minuta (Olivier, 1790)	*Prionocerus coeruleipennis* (Perty, 1831)
Derosphaerus vicinus (Pic, 1923)	*Prosoplus bankii* (Fabricius, 1775)
Dorcus parvulus (Hope & Westwood, 1845)	*Protaetia fusca* (Herbst, 1790)
Epepeotes plorator (Newman, 1842)	*Pseudozaena orientalis* (Klug, 1831)
Eretes griseus (Fabricius, 1781)	*Pterolophia crassipes* (Weidemann, 1823)
Eucorynus crassicornis (Fabricius, 1802)	*Serica sp.*
Figulus sulcicollis (Hope, 1845)	*Sybra ochreovittipennis* (Breuning, 1964)
Holotrichia bipunctata (Brenske, 1892)	*Uloma culinaris* (Linnaeus, 1758)
Hoplocerambyx spinicornis (Newman, 1842)	*Zophobas morio* (Fabricius, 1776)

2.3 List of characters and states

The external morphology of the beetles' dorsal and ventral surfaces was carefully analyzed. Morphological traits, including size, color, and structural features, were characterized following the framework established by Lawrence et al. (2011). Traits applicable to male and female specimens were assigned numerical values, while inapplicable or unknown traits were marked with a '?' symbol. All characters were equally weighted and unordered to avoid assumptions about their evolutionary transformation (Torres et al., 2010). Additionally, the numerical coding of character states did not imply whether traits were plesiomorphic or apomorphic, as the study did not aim to infer species phylogeny. In this study, 82 characters were identified, of which 35 were binary and 47 were multistate. These characters and states were adapted from Lawrence et al. (2011) and were used to generate a character matrix for Cladistics (Table 2).

Table 2 List of characters and character states.

	Character	State
	Length	
0	Size	(0) Small (<5mm); (1) medium (<15mm); (2) large (>15mm)
	Head	
1	Dominant color of the head	(0) black to grayish black; (1) brown to reddish brown; (2) yellow to orange-yellow; (3) red to orange-red; (4) dark green to green-yellow; (5) blue
2	Dominant color of the pronotum	(0) black to grayish black; (1) brown to reddish brown; (2) yellow to orange-yellow; (3) red to orange-red; (4) dark green to green-yellow; (5) blue
3	Dominant color of the elytra	(0) black to grayish black; (1) brown to reddish brown; (2) yellow to orange-yellow; (3) red to orange-red; (4) dark green to green yellow; (5) blue
4	Head	(0) not concealed; (1) concealed
5	Clypeus	(0) not subdivided; (1) subdivided
6	Length of rostrum	(0) less than the width of the clypeus; (1) greater than the width of the clypeus
7	Labrum conspicuousness	(0) not concealed beneath the clypeus; (1) concealed beneath the clypeus
8	Labrum base	(0) same plane as apex; (1) lower plane than apex forming a deep groove between clypeus and labrum
9	Ocelli	(0) three; (1) two; (2) one; (3) none
10	Eye projection	(0) slightly protruding; (1) not protruding
11	Eyes	(0) undivided; (1) divided into lower and upper parts
12	Midcranial suture	(0) absent; (1) present
13	Interfacetal setae	(0) absent; (1) slender and short; (2) slender and long; (3) stout and at least long
14	Antenna cupule	(0) without cupule; (1) glabrous; (2) pubescent
15	Antenna socket location	(0) not located within a fossa; (1) situated within a fossa
16	Antennae setae	(0) more or less pubescent; (1) glabrous or with few hairs
17	Antennae pedicel	(0) not forming an angle with the scape; (1) creating a distinct angle with the scape
18	Antenna socket conspicuousness	(0) visible in either dorsal or frontal view; (1) concealed
19	Antenna scape size relative to pedicel	(0) shorter than pedicel; (1) longer than pedicel
20	Antenna scape shape	(0) parallel-sided; (1) distinctly bent; (2) ovoid
21	Number of antennomeres	(0) more than 12; (1) twelve; (2) eleven; (3) ten; (4) nine; (5) eight; (6) seven; (7) six; (8) four

22	Antenna club	(0) not or slightly asymmetrical; (1) distinctly asymmetrical with serrate; (2) distinctly asymmetrical with lamellate or cupuliform segments
23	Number of apical antennomeres to form the antenna club	(0) five or more; (1) four; (2) three; (3) two; (4) one; (5) none
24	Antennomeres comprising antenna club	(0) loosely articulated; (1) tightly articulated, forming a compact club
25	Antenna scape length	(0) as long as the scape width; (1) 1 or 3 times long as the scape width; (2) more than three times as long as the scape width
	Pronotum	
26	Pronotal setae	(0) present; (1) absent
27	Pronotal surface	(0) flat; (1) bulged; (2) dent
28	Pronotum side	(0) spines present; (1) spines absent
29	Prothorax side	(0) not explanate; (1) laterally horizontally explanate
	Abdomen	
30	Scutellum	(0) exposed but elytra absent; (1) visible between elytra bases; (2) concealed by elytra bases
31	Tip of scutellum	(0) narrowly rounded or acute; (1) broadly rounded to angulate obtusely; (2) truncate; (3) emarginate
32	Anterior of scutellum	(0) not elevated; (1) distinctly elevated
33	Elytra	(0) concealing all abdominal tergites; (1) exposing at least one complete tergite; (2) exposing two or more complete tergites
34	Elytra dorsal surface	(0) without window punctures; (1) with window punctures
35	Elytra punctures	(0) irregularly aligned; (1) with more than five distinct puncture rows; (2) with more than five striae
36	Elytra striae	(0) present; (1) absent
37	Elytra apex	(0) conjointly rounded; (1) squarely or obliquely truncated; (2) independently rounded, separated by a distinct gap
38	Elytra apex (closed)	(0) unexposed sutural flange; (1) exposed sutural flange
39	Mesoventrite	(0) separated by complete sutures from mesanepisterna; (1) partly or entirely fused to mesanepisterna
40	Mesanepisternum	(0) distinctly separated at midline; (1) narrowly separated, or broadly joined at the midline
41	Paired procoxal rests on the anterior edge of mesoventrite	(0) absent; (1) horizontal or slightly inclined; (2) vertical or strongly inclined
42	Mesoventral cavity	(0) absent; (1) medium and shallow; (2) extensive and deep
43	Mesoventral process (Apex)	(0) divided; (1) undivided and narrowly rounded; (2) undivided and broadly rounded; (3) undivided and concave or biconcave
44	Mesanepisternum and mesepimeron	(0) separated by pleural suture; (1) fused
45	Mesocoxa	(0) not strongly projecting; (1) strongly projecting

46	Mesocoxal cavities	(0) circular to slightly transverse, and not or only slightly oblique; (1) strongly transverse and not or only slightly oblique; (2) strongly transverse and strongly oblique
47	Mesoventral and metaventral processes	(0) distinctly separated from one another or absent; (1) meeting at one point; (2) overlapping with mesoventrite ventrad of metaventrite; (3) overlapping with metaventrite ventrad of mesoventrite; (4) joined by monocondylic ball, and socket fitting; (5) joined by dicondylic ball and socket fitting; (6) solidly fused but separated by suture or line; (7) solidly fused with no separation
48	Metaventrite	(0) Without postcoxal lines or crural impressions; (1) with one pair of straight, slightly curved or sinuate postcoxal lines; (2) with two pairs of straight or curved postcoxal lines; (3) with one pair of recurved postcoxal lines usually delimiting crural impressions; (4) with single, curved postcoxal line
49	Metakatepisternal suture	(0) crossing midline and extending at least halfway across ventrite on each site; (1) crossing midline but extending less than half way across ventrite on each side; (2) absent or not crossing midline
50	Mesothoracic discrimen	(0) present; (1) absent
51	Metathoracic discrimen	(0) at least 0.8 times as long as metaventrite; (1) less than 0.8 times as short as metaventrite; (2) absent
52	Metacoxal plates	(0) concealing no ventrites; (1) concealing most of the first ventrite; (2) concealing most of the first three ventrites
53	Basal abdominal ventrite	(0) continuous across the base of the abdomen; (1) divided into two parts by metacoxae; (2) divided into three parts by metacoxae; (3) visible only between metacoxae
54	Basal abdominal ventrites connate	(0) none; (1) two; (2) three; (3) four; (4) five or more
	Appendages	
55	Profemoral antenna cleaner	(0) present; (1) absent
56	Protibial antenna cleaner	(0) present; (1) absent
57	Number of Protibial spurs	(0) two; (1) one; (2) none
58	Mesotibia	(0) not widened; (1) enormously widened
59	Outer edge of mesotibia	(0) without fixed lobes or teeth; (1) with fixed lobes or teeth
60	Spiniform setae on outer edge of mesotibia	(0) absent; (1) Moderately long and slender; (2) short and stout
61	Mesotibia spurs	(0) glabrous; (1) pubescent; (2) serrate or pectinate
62	Number of Mesotibial spurs	(0) two; (1) one; (2) none
63	Number of Metatibial spurs	(0) two; (1) one; (2) none
64	Tarsal formula	(0) 5-5-5; (1) 5-5-4; (2) 5-4-4; (3) 4-4-4; (4) 3-3-3; (5) 1-1-1
65	Mesotarsomeres	(0) not shorter than tarsomere 2; (1) shorter than tarsomere 2
66	Mesopretarsal claw	(0) simple; (1) toothed or bifid; (2) serrate or pectinate
	Wings	

67	Post-radial sclerite of the wing	(0) absent; (1) present
68	RA$_{3+4}$	(0) Complete and well scleroterized; (1) incomplete or very lightly scleroterized; (2) incomplete or basally absent
69	Basal edge of radial cell	(0) straight and perpendicular to the long axis; (1) moderately to strongly oblique; (2) distinctly curved or bowed
70	Posterobasal angle of radial cell	(0) right or obtuse; (1) acute
71	Anal lobe	(0) well developed; (1) highly reduced or absent
72	Anal embayment	(0) absent or gradual shallow; (1) abrupt, notch-like, or deep.
73	AP$_{3+4}$	(0) forked; (1) not forked; (2) absent
74	Hairs in wing margin	(0) absent; (1) lining posterior margin only; (2) lining or all of the wing margin; (3) restricted to basal portions of anterior and posterior wing margins; (4) restricted to anal lobe
75	Oblongum cell	(0) as long as broad or with a long axis parallel to the long axis of the wing; (1) with a long axis perpendicular to the long axis of the wing; (2) absent
76	Medial spur	(0) extending to or nearly to wing margin; (1) moderately long but ending well before margin; (2) a very short stub; (3) absent
77	Medial spur shape	(0) not curved posteriorly; (1) curved posteriorly
78	Number of free veins in the medial field	(0) five or rarely six; (1) four; (2) three; (3) two; (4) one; (5) none
79	CuA$_{1+2}$ or CuA$_1$	(0) joining MP$_{3+4}$; (1) joining MP$_4$; (2) not joining MP$_4$ or absent
80	CuA$_{3+4}$	(0) meeting AA$_3$ to close off wedge cell; (1) present
81	AA$_4$	(0) not joining anal fold posteriorly; (1) joining anal fold posteriorly

2.4 Cladistics

A character matrix was created using WinClada software (Nixon, 1999) and imported into the TNT (Tree analysis using New Technology) program for cladistic analysis (Goloboff et al., 2008). Various algorithms were applied to generate reliable consensus trees, including the heuristic search with the '*xmult*' command, followed by ratchet ('*ratchet*'), tree-drifting ('*drift*'), sectorial searches ('*sectsch*'), tree-fusing ('*tfuse*'), and tree bisection reconnection ('*bbreak = fillonly*') algorithms in TNT (Goloboff et al., 2008). To identify the most reliable and informative characters, the Length (*L*), Consistency (*CI*), and Retention Indices (*RI*) were calculated for each character. Character mapping was performed with *CI* values of 50 and above, with a *CI* value of 100 indicating no homoplasy (Torres et al., 2010).

3 Results

3.1 Similarity of beetles

Tree searches based on 82 morphological characters yielded eight parsimonious trees with a length of 683 steps, a *CI* value of 20, and an *RI* of 46 (L = 683, CI = 20, RI = 46). These trees generated a strict consensus tree with two major separations. The first split is supported by homoplasious traits including a laterally explanate prothorax side (29:1), a prominently projecting mesocoxa (45:1), and basal abdominal ventrite divided by metacoxae (53:1). Conversely, the second split is defined by traits such as a single curved postcoxal line in the metaventrite (48:4) and the presence of a protibial antenna cleaner (56:1). The second separation further divides into two subgroups: one characterized by a concealed antenna socket (18:1) and the other by the absence of a mesothoracic discremen (50:1) and metatibial spurs (63:2), but possessing a post-radial sclerite in the hindwings (67:1). Additionally, three polytomies are observed—two within the Cerambycidae and one in the Melolonthinae group (Fig. 2).

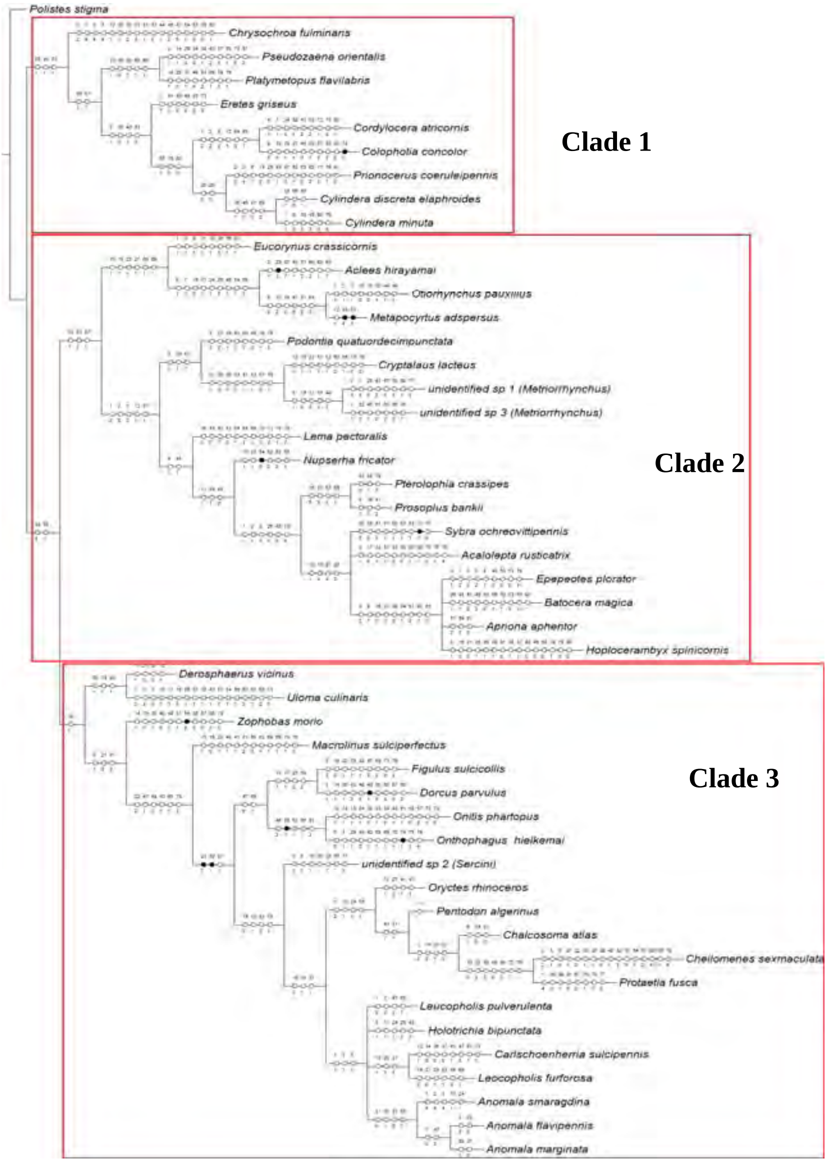

Fig. 2 Cladogram of Beetle species sampled. Open circles denote homoplasious characters, while closed circles are reversals.

The first clade showed that *C. fulminans* forms a monophyletic group with *P. orientalis, P. flavilabris, E. griseus, C. atricornis, C. concolor, P. coeruleipennis, C. discreta elaphroides*, and *C. minuta*. The clade is supported by three homoplasious characters: a laterally horizontally flattened prothorax (29:1), a strongly projecting mesocoxa (45:1), and a divided basal abdominal ventrite into two parts by metacoxae (53:1). Furthermore, *C. concolor* and *C. atricornis* form a clade, were the former has a unique trait of having hairs on its wing margin (74:2), distinguishing it from the latter.

P. orientalis and *P. flavilabris* have formed a clade, indicating their similarity based on morphological characteristics and supporting the data that they belong to Carabidae. Five homoplasious character traits support this clade, which includes: elytra expose one tergite (33:1), presence of elytra striae (36:0), absence of mesothoracic discremen (50:1), mesotarsomere is shorter than tarsomere 2 (65:1), and a distinctly curved or bowed basal edge of the radial cell of the hindwing (69:2). The same is true for two tiger beetles, *C. discreta elaphroides* and *C. minuta*, which are morphologically similar and agree with the Cicindelidae group. Four homoplasious characters support the similarity between the two tiger beetles: unexposed sutural flanged in closed elytra (38:1), mesanepisternum is distinctly separated at the midline (40:0), presence of two protibial spurs (57:0), and a distinctly curved or bowed basal edge of the radial cell of the wing (69:2).

A. hirayamai is distinct from other species *O. pauxillus* and *M. adspersus* by having two antenommeres to form the antenna club (23:3). At the same time, *M. adspersus* is distinct from *A. hirayamai* and *O. pauxillus* by having two unique characters: having one antennomere that includes the antenna club (23:4), and basal abdominal ventrite is visible only between metacoxae (53:3). The monophyletic grouping of *A. hirayamai*, *O. pauxillus*, and *M. adspersus* support the Curculionidae family.

In addition, *N. fricator* is distinct from Cerambycidae clade by having four basal abdominal ventrite connate (54:3). Highly reduced anal lobe in wings (71:1) was noted to be autapomorphic for *S. ochreovittipennis*. The Cerambycidae beetles are reinforced by three homoplasious characteristics: eyes divided into up and down parts (11:1), exposed sutural flange when the elytra apex is closed (38:1), and short and stout spiniform setae on the outer edge of the mesotibia (60:2). In addition, polytomy in *E. plorator*, *B. magica*, *A. aphentor*, and *H. spinicornis* is united by nine (9) homoplasious characters forming a clade which is also a polytomy with *S. ochrevittipennis* and *A. rusticatrix*. The two polytomies in the Cerambycidae group are supported by a not protruding eye projection (10:1), shorter antenna scape than the pedicel (19:0), ten antennomeres (21:3), and antenna scape more than three times long as vast (25:2). Additionally, the Cerambycidae group forms a clade with *L. pectoralis* (Chrysomelidae) indicating their close resemblance. In the data presented, *L. pectoralis* and Cerambycidae species are united by two homoplasious characters: labrum is in the same plane as the apex (8:0) and a strongly projecting mesocoxa (45:1).

In clade 3, *Z. morio* is distantly similar to other Tenebrionid species *D. vicinus*, and *U. culinaris* by having three connate basal abdominal ventrite (54:2). Moreover, dung beetles *O. hielkemai* and *O. phartopus* (subfamily Scarabaeinae) are united by having an enormously widened mesothorax (5:1). However, *O. hielkemai* is distinct with *O. phartopus* by having a hair in the lining posterior margin of the wing (74:1).

D. parvulus and *F. sulcicollis* are closely similar and form a clade that supports their grouping with the Lucanidae family. *D. parvulus* has a metakatepisternal suture that crosses at the midline but extends less than halfway across ventrite on each side (49:1), making it distinct from *F. sulcicollis*. The subfamilies Scarabaeinae, Dynastinae (*O. rhinoceros*, *P. algerinus*, and *C. atlas*), and Melolonthinae, unidentified species (*Serica* sp.), *C. sexmaculata*, and *P. fusca* are united by two autapomorphic characters (three apical antennomeres to form an antenna club (23:2), and strongly transverse mesocoxal cavities (46:1)), and a homoplasious character, which is the AA_4 wing vein is joined to the anal fold posteriorly (81:1).

Polytomies are also evident in clade 3, particularly in Melolonthinae. *L. pulverulenta*, *H. bipunctata* form a polytomy with the clades of *C. sulcipennis* and *L. furforosa*, and the *Anomala* spp. The polytomy in this group is united by the brown to reddish brown coloration in their head, pronotum, and elytra (1:1; 2:1, 3:1).

3.2 Character map of traits

The Length (*L*), Consistency index (*CI*), and Retention index (*RI*) values per individual character revealed five uninformative traits. These include the anal lobe, ocelli, interfacetal setae, mesotibial spurs, and wing margin hairs. Moreover, nine (9) characters with *CI* values of 50 or above can be examined for character evolution. These characters include: antenna pedicel (17), number of apical antennomeres to form the antenna club (23), scutellum (30), mesoventrite (39), mesapinepisternum and mesepimeron (44), mesocoxal cavities (46), mesocoxal plates (52), mesotibia (58), and oblongum cell (75). An enormously wide mesotibia (58:1) obtained the highest CI value of 100, indicating that this trait shows no homoplasy (Table 3).

Table 3 Length, consistency, and retention indices of the beetle characters (NA = Uninformative characters).

Char	***L***	***CI***	***RI***	**Char**	***L***	***CI***	***RI***	**Char**	***L***	***CI***	***RI***
0	15	13	45	28	3	33	33	56	9	11	38
1	16	25	53	29	9	11	38	57	15	13	43
2	17	23	53	30	4	50	33	58	1	100	100
3	17	23	50	31	8	25	25	59	4	25	57
4	3	33	33	32	15	6	12	60	12	16	52
5	11	9	16	33	13	15	42	61	*NA*	*NA*	*NA*
6	3	33	50	34	5	20	20	62	15	13	40
7	8	13	65	35	8	12	65	63	11	18	50
8	8	12	30	36	8	12	46	64	9	33	70
9	*NA*	*NA*	*NA*	37	12	8	42	65	6	16	37
10	9	11	52	38	9	11	20	66	6	16	28
11	10	10	50	39	2	50	0	67	10	10	35
12	8	12	63	40	5	20	33	68	13	15	31
13	*NA*	*NA*	*NA*	41	12	16	9	69	11	18	30
14	12	16	37	42	5	40	40	70	9	11	0
15	7	14	14	43	25	12	21	71	*NA*	*NA*	*NA*
16	13	8	42	44	2	50	0	72	3	33	33
17	2	50	75	45	6	16	75	73	13	7	0
18	4	25	86	46	3	66	93	74	*NA*	*NA*	*NA*
19	3	33	75	47	15	26	52	75	2	50	
20	10	20	20	48	13	15	47	76	12	25	
21	13	30	64	49	8	25	50	77	6	16	
22	6	33	69	50	10	10	40	78	19	21	
23	7	57	72	51	13	15	21	79	8	25	
24	7	14	40	52	2	50	0	80	8	25	
25	10	20	38	53	11	27	46	81	15	13	
26	9	11	50	54	8	37	50				
27	8	25	66	55	4	25	0				

Character mapping of traits with *CI* values of 50 or above was examined on the strict consensus tree to determine character evolution (Fig. 3). There are five (5) characters that appear in the tree twice. These are 17:1, 39:1, 44:1, 52:1, and 58:1. The formation of a distinct angle with the scape (17:1) appears in two separate clades, Curculionidae (*A. hirayamai, O. pauxillus,* and *M. adspersus*) and Lucanidae clades (*F. sulcicollis* and *D. parvulus*) making them similar in terms of this character type. Likewise, *P. orientalis* and *O. pauxillus* are two unrelated species among other sampled Coleopterans that have a distinct mesoventrite that is fused to mesanepisterna (39:1). A fused mesanepisternum and mesepimeron is a character that appeared in two unrelated species, *C. fulminans* and *O. pauxillus* (44:1). At the same time, a mesocoxal plate that concealed the first ventrite is distinct between *C. concolor* and *C. lacteus* (52:1). Lastly, closely related species of *O. phartopus* and *O. hielkemai* are separated to other species of sampled beetles by having an enormously wide mesotibia (58:1).

Meanwhile, two apical antenommeres (23:3) and one apical antenommere (23:4) that forms the antenna club have evolved recently in the lineage leading to the speciation of *A. hirayamai* and *M. adspersus* respectively. A concealed scutellum by elytra bases (30:2) appeared in three groups: *C. fulminans*, Curculionidae clade, and *O. hielkemai*, making it distinct from other Coleopteran species. Most beetle species form a large cluster with circular mesocoxal cavities (46:0) followed by strongly transverse but not oblique mesocoxal cavities (46:1). Only the basal lineage *C. fulminans*, and the closely related *O. phartopus* and *O. hielkemai*, are distinct from these two large clusters (46:2). Likewise, the two Carabid species (*P. orientalis* and *P. flavilabris*) and *E. griseus* showed similarity in terms of the presence of an oblongum cell (75:1) with a long axis perpendicular to the wings, making these species distinct from the rest of the samples.

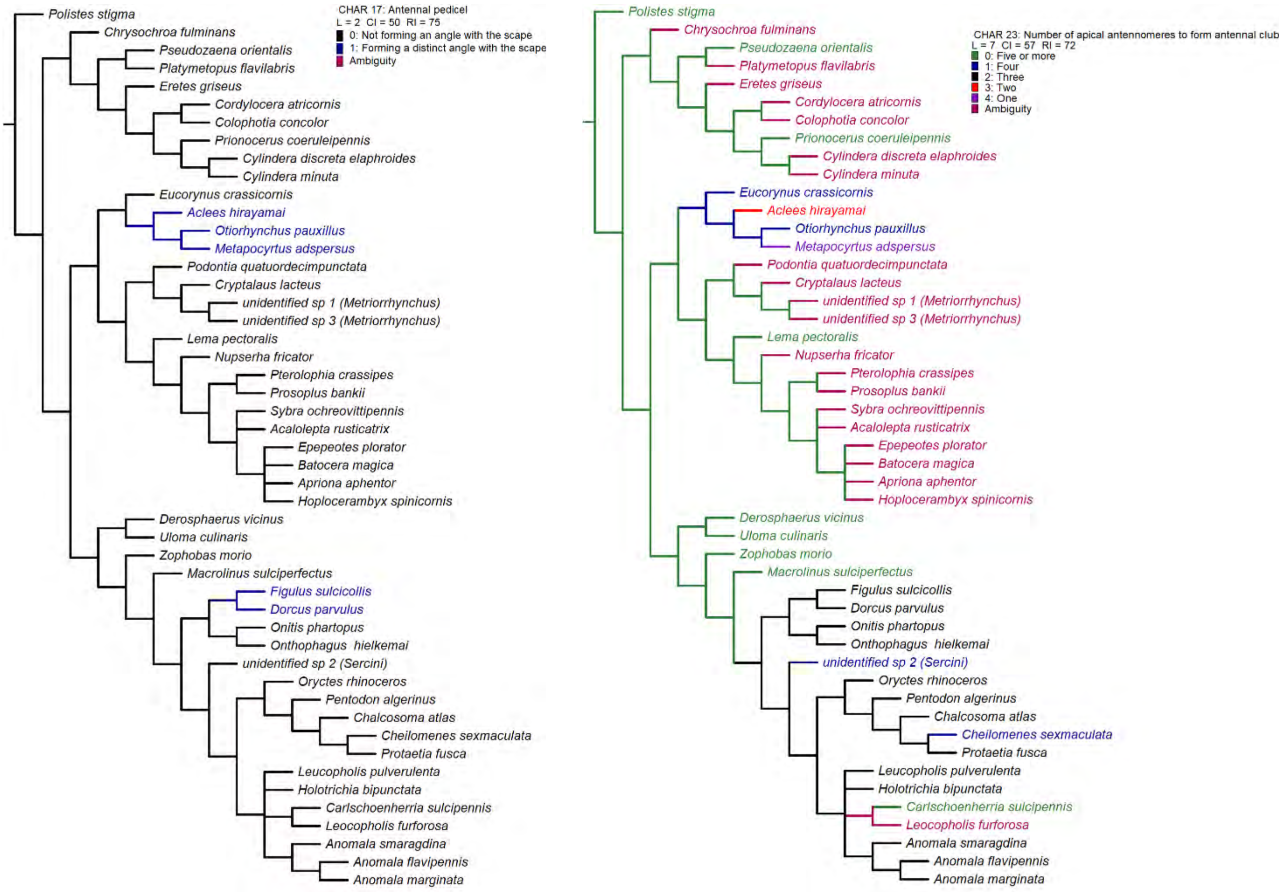

Fig. 3 Character mapping of traits with *CI* values of 50 and above (Characters 17 and 23).

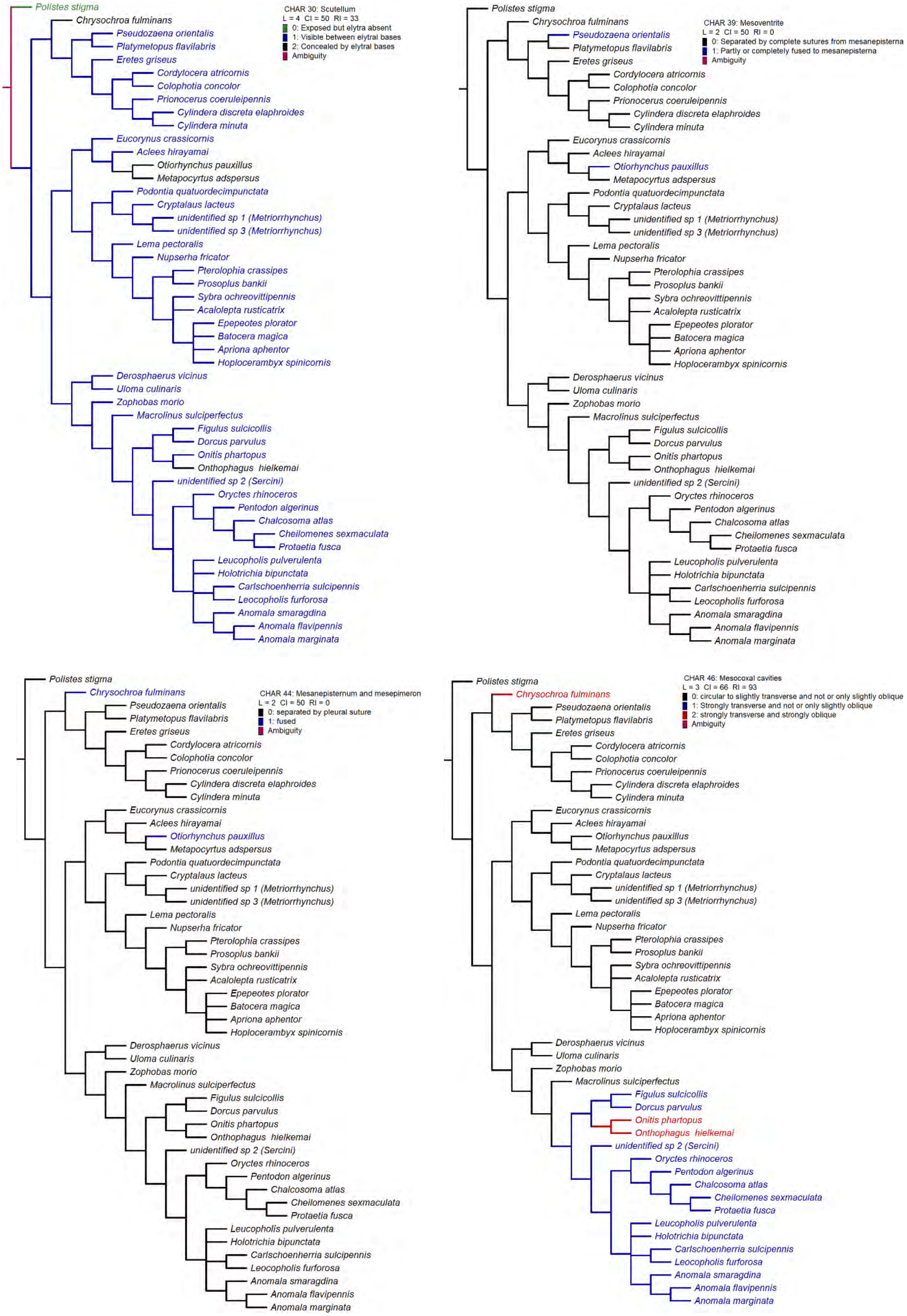

Fig. 3 cont. Character mapping of traits with *CI* values of 50 and above (Characters 30, 39, 44, 46).

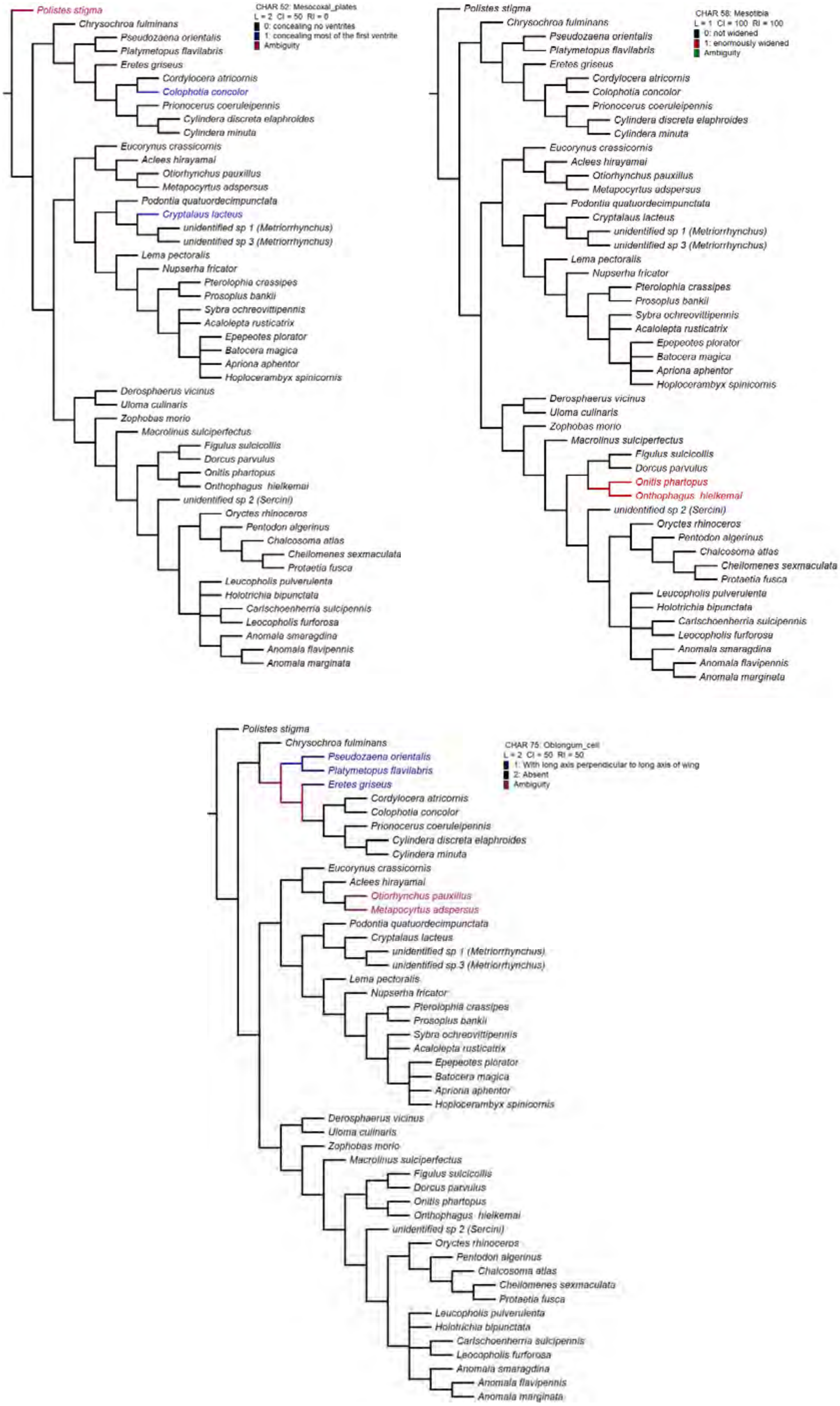

Fig. 3 cont. Character mapping of traits with *CI* values of 50 and above (Characters 52, 58, 75).

4 Discussion

The tree topology based on morphological characters confirmed some molecular phylogenetic studies conducted on beetle groups. The present data suggest that the similarity between Carabid beetles *P. orientalis* and *P. flavilabris*, is distantly related to the two morphologically similar tiger beetles, *C. discreta elaphroides* and *C. minuta*. The relationship concurs with the strict consensus and NJ trees in the current study. However, most contemporary taxonomists agree that tiger beetles (Cicindelidae) should be considered a subfamily of ground beetles (Carabidae) (Choate, 2008). On the contrary, studies on higher-level taxonomy of tiger beetles based on many genetic loci demonstrated that Cicindelidae beetles are unaffectedly distinct from Carabidae (Duran and Gough, 2020). On the other hand, the shared similarity between *C. concolor* (Lampyridae) and *C. atricornis* (Cantharidae) is consistent with previous data that they belong to a large group of beetles (Coleoptera: Elateroidea). Elateroid beetles are heterogenous groups composed of 'true elateroids' (Elateridae, Eucnemidae, and Throscidae) and soft-bodied 'cantharoids' (Cantharidae, Lycidae, and Lampyridae) (Kusy et al. 2018).

The grouping of *A. hirayamai, O. pauxillus,* and *M. adspersus* in a clade aligns with the family Curculionidae, which is the most prominent weevil family and is supported as a monophyletic group (Lawrence et al., 2011). Furthermore, the current findings suggest that *E. crassicornis* (Anthribidae) forms a monophyletic clade with the three Curculionidae species, implying a close similarity within this group. This clade is consistent with the morphological and molecular analyses conducted, where Anthribidae and Curculionidae are closely related and share a common ancestor within the superfamily Curculionoidea (Marvaldi et al., 2002).

Based on the character matrix used in the present research, the tree length value (L) suggests the taxa sampled may have undergone rapid diversification, which resulted in many evolutionary changes in a relatively short period. The impressive diversification of Coleopterans can be accredited to their rapid adaptive radiation, which involves significant changes in ecological characteristics and morphology that allow the beetles to thrive in distinct environmental niches (Marvaldi et al., 2002; McKenna et al., 2019). In addition, the diversification of beetles may result from the different adaptations of beetles in their anthropogenic environment. Magura and Lövei (2021) implied that urbanization induces various changes in morphological characters in beetles, particularly ground beetles (Carabidae). Moreover, their diversification may also be attributed to phenotypic plasticity, the ability of a single genotype to display diverse phenotypes in various environments, which are common among insects (Whitman and Agrawal, 2009). The capacity of phenotypic plasticity to respond promptly to environmental changes makes it a critical factor in diversification. This is because the various genetic components of the developmental pathways that underlie the environmentally-induced phenotypes can respond to selection (Pfennig et al. 2010).

However, the low *CI* values per character might be due to character trait recurrences. As such, the repetitions in the character traits are due to their interaction with the external environment and genetic drift (Torres et al., 2010; Washburn et al., 2016). Moreover, the qualitative morphological data may contain a high degree of homoplasy, where similar characters have evolved independently in the different lineages leading to convergent or parallel evolution, and cannot be explained by descent from a common ancestor (Torres et al., 2010; Washburn et al., 2016). Therefore, the evolutionary processes in the present data, which give rise to similar phenotypes, is that identical selective forces may drive a trait's development in multiple lineages (Washburn et al., 2016).

The cladistic analysis provided insights into the systematic relationships of Coleopteran species found in anthropogenic environments. The results suggest that Coleopterans inhabiting the area experienced similar environmental pressures that triggered the evolution of similar traits. The resulting tree and character mapping revealed distinct clades, subgroups, and polytomies, indicating evolutionary patterns among beetle species. However, the present study on the similarities of Coleopterans still requires further examination, particularly on adding internal morphological traits. These attributes will help illuminate our fundamental comprehension of the different evolutionary processes that contribute to the distinctiveness of Coleopteran species. A novel approach in taxonomy and systematics must be explored, such as integrating ecological data, molecular data from nuclear and mitochondrial DNA, and multiple morphological characters to ensure comprehensive results that are valuable for determining the relationship between these species.

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