Phylogenetic Relationships of Chinese *Coptotermes* (Blattodea: Isoptera: Rhinotermitidae) Termites and a New Synonym Inferred from Morphological Data[1]

Yunling Ke, Shijun Zhang, and Zhiqiang Li[2]

Guangdong Key Laboratory of Animal Conservation and Resource Utilization, Guangdong Public Laboratory of Wild Animal Conservation and Utilization, Institute of Zoology, Guangdong Academy of Sciences, Guangzhou, 510260, No. 105, Xingang Xi Road, Haizhu District, Guangzhou, Guangdong province, P. R. China

J. Entomol. Sci. 57(1): 64–81 (January 2022)

Abstract *Coptotermes* (Blattodea: Isoptera: Rhinotermitidae) is an economically important genus. There are many problematic taxa within the genus because of small differences between different species and large variations within the same species with respect to morphology. *Coptotermes* species, especially those in China, are in need of careful monographic revisions. In this paper, type specimens of 14 *Coptotermes* species were reexamined. Their relationship was preliminarily studied with statistical methods. The phylogenetic relationships among the 21 species that are recorded in China were investigated based on soldier morphological characters. The cladistic analysis inferred that Chinese *Coptotermes* species are divided into two main clades and there were some species closely related to *C. formosanus* Shiraki and *C. gestroi* (Wasmann), respectively. Based on a comparison of measurement data of the closely related species *C. cochlearus* Xia and He and *C. gestroi* in the cladogram, we propose that *C. cochlearus* is a new synonym of *C. gestroi*. In the situation where it is difficult to obtain more molecular data of Chinese *Coptotermes* species, the present work serves as a basis for further revisionary work on *Coptotermes*.

Key Words *Coptotermes*, measurements, cladistics, synonymy, China

Termites (Isoptera) consist of 9 families, 282 genera, and 2,933 species (Krishna et al. 2013). The classification of termites from the mid-18th century to the 20th century relied mainly on measurements of morphological characters of soldiers and imagoes. The morphological characters have proved very useful in termite classification, especially in the division of the higher taxa. The imagoes emerge in or near the nests only at specific times and are often difficult to collect with other castes of the same colony, which results in the morphological characters of soldiers serving as the most important or even only evidence for taxonomic study in many termite taxa. However, the morphological characters of soldiers can be influenced by many factors, such as the age, developmental condition of colonies, and the environment, and consequently exhibit wide variation. The inherent difficulties in termite classification based on morphology caused misidentification and taxonomic

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

---

[1] Received 28 January 2021; accepted for publication 13 February 2021.

[2] Corresponding author (email: lizhiqiang61@163.com).

confusion among some species in *Coptotermes*, *Reticulitermes*, *Nasutitermes*, and other genera (Kirton and Brown 2003, Scheffrahn et al. 2005, Yeap et al. 2007).

In China, the number of new species described according to morphological characters from 1950 to 2000 was 450, which was more than 18 times the number recorded in 1949 and nearly 39% of the total number in the Oriental region to date (Huang et al. 2000, Krishna et al. 2013). The number and the rate of new species described increased rapidly in China, where geographical and climatic conditions are diverse and when termite taxonomic studies were flourishing. Regardless, the large number of species described from relatively high latitudes raised some skepticism and needs to be further studied (Eggleton 1999). Many of those described species may prove to be invalid (Krishna et al. 2013). Some of the invalid species names are likely due to giving different names to different castes or different colonies of the same species. To revise the synonyms, further study of early specimens, especially type specimens, sampling from the largest geographic range possible, and combining morphological method with biochemical and molecular methods are necessary.

Species in the genus *Coptotermes* (Blattodea: Isoptera: Rhinotermitidae) are morphologically similar, while the color and the shape of the same species varies greatly in different populations or even in different ages of the same population (Huang et al. 2000, Scheffrahn et al. 2015). Between 1984 and 1986, 21 of 44 Oriental *Coptotermes* species were described in China (Huang et al. 2000). There is no additional research for many of those described species except for the original description, and only a few revisionary works have been undertaken. The Chinese *Coptotermes* species are in need of careful monographic revisions (Vargo and Husseneder 2009). Morphological methods combined with molecular methods would undoubtedly make the revision more reliable and more efficient. However, type specimens are not in condition for the molecular analyses, and re-collecting new conspecific specimens from the type locality did not always yield the same species whose characters agreed with the original description. These factors negated the use of molecular methods in the revision of Chinese *Coptotermes* species. As carriers of scientific names, type specimens serve as the basis for comparison with other specimens in determining whether they are members of the same species or not. Thus, the conclusions based on studying type specimens should be reliable and convincing. Fortunately, nearly 70% of Chinese *Coptotermes* type species were found in several scientific institutions, allowing for a study with mainly type materials. The study reported herein focused on examination of phylogenetic relationships among *Coptotermes* species in China based on morphological data mainly from the type specimens remeasured, and then identifying synonymous relationships among the species according to phylogenetic analysis and original descriptions. The study should provide a baseline of data and references for the further revision of the genus *Coptotermes*, using multiple methods.

Materials and Methods

Materials examined. There are 21 species in the genus *Coptotermes* recorded in China (Huang et al. 2000; Li et al. 2011, 2012b). Type series for all of these

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

species, except for *C. formosanus* Shiraki and *C. gestroi* (Wasmann), are housed in Chinese mainland. Because more than half of the species (11 of 21) have no specimens or descriptions of imagoes, morphological data of only soldiers were used in the study.

There were 14 species with both original descriptions and type specimens. The species were restudied by examining as many type specimens as possible. Those examined were *C. chaoxianensis* Huang and Li (*n* = 17), *C. grandis* Li and Huang (*n* = 10), *C. hainanensis* Li and Tsai (*n* = 12), *C. longistriatus* Li and Huang (*n* = 4), *C. monosetosus* Tsai and Li (*n* = 9), and *C. varicapitatus* Tsai and Li (*n* = 14) deposited in the National Zoological Museum of China (NZMC); *C. bannaensis* Xia and He (*n* = 7), *C. changtaiensis* Xia and He (*n* = 16), *C. cochlearus* Xia and He (*n* = 4), *C. dimorphus* Xia and He (*n* = 15), *C. hekouensis* Xia and He (*n* = 7), *C. longignathus* Xia and He (*n* = 9), and *C. suzhouensis* Xia and He (*n* = 11) in the Chinese Academy of Sciences–Shanghai Entomological Museum (CAS-SEM); and *C. cyclocoryphus* Zhu, Li, and Ma (*n* = 18) in the Institute of Zoology, Guangdong Academy of Sciences (GIZ). Other abbreviations of scientific institutions are: Kemner Collection in the Museum of Zoology, Lund, Sweden (KMZS); Museo Civico di Storia Naturale di Genova (NHMG); National Museum of Natural History, Smithsonian Institution (NMNHS); Naturhistoriska Riksmuseet, Sektionen för Entomologi, Sweden (NHRS).

The specimens of *C. ochraceus* Ping and Xu (*n* = 14) were newly collected from its type locality, Xingyi of Guizhou Province. The specimens of *C. formosanus* (*n* = 25) were from 14 localities of seven provinces, and specimens of *C. gestroi* (*n* = 25) were from six localities of Yunnan Province.

Four species were studied with data from only original descriptions. They were *C. guangdongensis* Ping, *C. gulangyuensis* Li and Huang, *C. melanoistriatus* Gao et al., and *C. shanghaiensis* Xia and He. These type specimens could not be obtained but were included in the phylogenetic analysis. Because other studies on these four species are scarce, their character data were derived from original descriptions.

Morphological measurements. Measurements of morphometric features of soldiers were taken under a stereomicroscope based on Roonwal's (1969) standard. Those included nine important characters: head length to base of mandibles, head maximum width, left mandible length (upper base of condyle to tip), postmentum median length, postmentum maximum width, postmentum waist width, pronotum maximum length, pronotum maximum width, and hind tibia length. We also measured characters that are sometimes ignored in the literature, including labrum length, labrum maximum width, fontanelle pore width, fontanelle pore height, head maximum height, and head width at base of mandibles to supplement the cladistic analysis. The number of antennal segments was also enumerated and recorded.

Statistical analysis. The nine aforementioned important morphometric data collected from type specimens of 14 species and re-collected specimens of *C. ochraceus*, *C. formosanus*, and *C. gestroi* were analyzed using SPSS 17.0 statistical software. Character measurements were compared with one-way analysis of variance and, where merited by statistical significance, treatment means were separated by Tukey's HSD test at $P = 0.05$.

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

Phylogenetic analysis. Phylogenetic analysis was conducted with Phylogenetic Analysis Using Parsimony (PAUP*), version 4.0b10 (Swofford 2001) with maximum parsimony (MP) analysis (heuristic searches with random stepwise addition and tree bisection–reconnection branch swapping options) under ACCTRAN (accelerates the evolutionary transformation) optimization. Discrete characters were ordered and assigned a weight of 30 as Thiele (1993) suggested. The robustness of the strict consensus tree was examined after 1,000 bootstrap replicates using a general heuristic search.

All 21 *Coptotermes* species in China were analyzed in the study. *Reticulitermes flaviceps* (Oshima) and *R. leptomandibularis* Hsia and Fan (Blattodea: Isoptera: Rhinotermitidae), which are comparatively widespread in China, were selected as outgroup species because *Reticulitermes* is generally considered to be closely related to *Coptotermes* (Austin et al. 2004, Engel et al. 2009, Lo et al. 2004).

Thirty-six soldier morphological characters were selected for analysis, with 29 cephalic and 7 thoracic and abdominal characters.

1. Sides of head capsule in dorsal view: (0) nearly parallel; (1) distinctly convex, widest in middle or at back of head. The shape of soldier head is nearly rectangular in *Reticulitermes*, and oval in *Coptotermes*. According to Donovan et al. (2000), convex sides of head capsule were derived from straight ones.
2. Fontanelle: (0) small, not extended; (1) extended above surface of head capsule on distinct tube, apical with an open pore. In the Infraorder Isoptera, only species in Rhinotermitidae, Serritermitidae, and Termitidae have the fontanelle. It is punctiform in most species in these families. Extended tubular fontanelle is considered to be a synapomorphic character of the genus *Coptotermes*.
3. Shape of fontanelle pore: (0) nearly triangular; (1) nearly oval or circular. The shape of fontanelle pore can be divided roughly into a triangle and a circle. It varies from arched to oval and then to circular in some species, but is uniformly triangular in the remainder of Chinese *Coptotermes* species. Donovan et al. (2000) postulated that the more-or-less circular fontanelle pore was apomorphic.
4. Fontanelle pore in dorsal view: (0) invisible; (1) visible. The fontanelle opening can be perpendicular to the vertex, or forms an obtuse angle with the vertex. When they are vertical, the fontanelle opening is invisible. Otherwise, it is visible. The vertical orientation is considered to be plesiomorphic.
5. Number of setae around the rim of fontanelle: (0) two pairs; (1) one pair; (2) 0. The number of setae around the rim of fontanelle is usually fixed in *C. formosanus* and *C. gestroi*. It is thought to be a diagnostic character to distinguish the two species. Some Chinese *Coptotermes* species have two pairs of setae such as *C. formosanus*; others have one pair such as *C. gestroi*, while the outgroup species in *Reticulitermes* have no setae around the inconspicuous fontanelle.
6. Setae between fontanelle and antennal socket: (0) present; (1) absent. In the *Coptotermes* species with two pairs of setae around the rim of fontanelle, the seta can always be seen between fontanelle and antennal

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

socket. No seta appears between fontanelle and antennal socket in the remaining species. Characters 7, 8, and 18 are similar to Character 6.

7. Subapical latero-setae of labrum: (0) present; (1) absent.
8. Setae on the median area of labrum: (0) present; (1) absent.
9. Surface of postmentum: (0) smooth; (1) wrinkled.
10. Postmentum with bulge at widest part in lateral view: (0) no; (1) yes.
11. Postmentum shape at anterior end in ventral view: (0) nearly flat; (1) slightly to distinctly concave, but not like a spoon; (2) distinctly concave, like a spoon. The postmentum is of a similar simple shape in most *Coptotermes* species; the wrinkled, bulgy, or other modified shapes as described in Characters 9, 10, and 11 are apomorphic.
12. Position of waist on postmentum: (0) almost in the middle of widest point to posterior end; (1) near posterior end. The waist of postmentum is usually distinct in *Coptotermes* species. Its position is in the posterior half of postmentum, either in the middle or near the posterior margin.
13. Shape of head in lateral view, without regard to frons: (0) distinctly convex; (1) nearly flat. In some *Coptotermes* species, the dorsal surface of the head capsule is distinctly convex, which was regarded as the plesiomorphic state in the analysis. The flat or slightly concave head capsule in other species and the outgroup is an apomorphic state.
14. Frons in lateral view: (0) lower or nearly in line with vertex; (1) higher than vertex. The frons is generally even with the surface of vertex or bent ventrally in *Coptotermes* species. In *Reticulitermes* species, the frons bulges more or less, making it higher than vertex. The bulged frons can be considered as a modified state.
15. Length of postmentum: (0) greater than 5× the width of waist; (1) less than 5× the width of waist. The shape of postmentum is relatively stable in distinguishing *Coptotermes* and *Reticulitermes* species. It is clearly shorter and wider in *Coptotermes* species, but longer and narrower in *Reticulitermes* species.
16. Width of postmentum waist: (0) less than 0.45× postmentum maximum width; (1) greater than 0.45× postmentum maximum width. In the *Coptotermes* species, the postmentum does not contract strongly at the waist. In the outgroup species, the postmentum narrows clearly at waist, which makes its waist distinct and narrower than 0.45× postmentum maximum width.
17. Width of head: (0) less than 0.75× length of head to lateral base of mandibles; (1) equal to or greater than 0.75× length of head to lateral base of mandibles. In the opinion of Donovan et al. (2000), the head capsule gradually shortens with the evolution of termites. At the same time, the shape of the postmentum can be affected by the length and the width of the head. When the head is wide and short, the postmentum generally shows similar shape. Thus, State 1 in Characters 15 and 16 is considered to be apomorphic.
18. Setae on the median area of pronotum: (0) present; (1) absent.
19. Anterior margin of pronotum in dorsal view: (0) distinctly concave in middle; (1) nearly straight in middle.

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

20. Posterior margin of pronotum in dorsal view: (0) distinctly concave in middle; (1) nearly straight in middle.
21. White middle longitudinal strip extending from posterior half of pronotum to abdominal end: (0) absent; (1) present. There is no obvious white middle longitudinal strip in most *Coptotermes* species. Whereas in the species *C. longistriatus* and *C. melanoistriatus*, a clear white middle longitudinal strip can be found extending from the posterior half of the pronotum to the abdominal end. It is the synapomorphy of the two species.

Characters 22 to 36 were continuous morphometric ones, as follows:

22. Length of head to lateral base of mandible.
23. Maximum width of head.
24. Length of left mandible (upper base of condyle to tip).
25. Median length of postmentum.
26. Maximum width of postmentum.
27. Waist width of postmentum.
28. Length of pronotum.
29. Width of pronotum.
30. Length of hind tibia.
31. Length of labrum.
32. Width of labrum.
33. Width of head at base of mandibles.
34. Maximum height of head.
35. Width of fontanelle pore.
36. Height of fontanelle pore.

Based on the comparison of five methods for coding continuous characters (Garcia-Cruz and Sosa 2006), the morphometric characters involved were coded according to the gap-weighting method proposed by Thiele (1993). In his method, the sample mean for each character of every species is first $\log_{10}$ transformed, then the value (X) is range-standardized using the following formula: $Xs = ((X - \text{min})/(\text{max} - \text{min})) \times 30$; where “min” and “max” are, respectively, the minimum and the maximum sample mean values of the character for all species, and 30 is the maximum number of ordered character states (0–30 for 31 states). Thus, the standardized values are scaled to the rounded integer to a range from 0 to 30. Integers were converted into ASCII symbols in order of their ASCII numbers from ASCII 48 (0) to ASCII 80 (P), but excluding ASCII 59 (;) and ASCII 63 (?), since they are used by PAUP* as special characters. The data matrix is given in Table 1.

Results

Statistical analysis. The 17 species whose specimens were available for examination were first divided into two groups according to the number of setae around the rim of the fontanelle when analyzing their measurement data. One group was composed of 11 species with two pairs of setae around the rim of the fontanelle. Their measurements of every character in different species overlapped at a different level. The measurements of eight of the nine characters were not

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

Table 1. Data matrix of characters (0, plesiomorphic state; 1–2, apomorphic state; ?, unknown or uncertain; —, inapplicable).

										1	1	1	1	1	1	1	1	1	1
Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
R. flaviceps	0	0	—	—	2	1	0	?	0	0	0	0	1	1	0	0	0	0	1
R. leptomandibularis	0	0	—	—	2	1	0	?	0	0	0	0	1	1	0	0	0	0	1
C. grandis	1	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1
C. suzhouensis	1	1	1	0	0	0	0	0	1	1	0	0	1	0	1	1	1	0	1
C. changtaiensis	1	1	0	1	0	0	0	0	1	0	0	1	0	0	1	1	1	0	1
C. hekouensis	1	1	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	0	0
C. hainanensis	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
C. formosanus	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
C. cyclocoryphus	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
C. varicapitatus	1	1	0	0	0	0	0	0	0	0	0	0	?	0	1	1	1	0	0
C. chaoxianensis	1	1	0	0	0	0	0	0	0	0	0	1	?	0	1	1	1	0	0
C. longistriatus	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1
C. ochraceus	1	1	0	1	0	0	0	0	1	0	0	1	1	0	1	1	1	0	1
C. guangdongensis	1	1	1	0	0	0	0	0	1	0	0	1	1	0	?	?	1	0	1
C. gulangyuensis	1	1	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0
C. melanoistriatus	1	1	1	?	0	0	0	0	1	0	0	0	1	0	?	?	1	0	1
C. shanghaiensis	1	1	0	0	0	0	0	0	1	1	0	1	1	0	?	?	1	0	0
C. bannaensis	1	1	1	0	1	1	1	1	0	0	0	0	1	0	1	1	1	1	0
C. cochlearus	1	1	1	0	1	1	1	1	0	0	2	1	1	0	1	1	1	1	0
C. dimorphus	1	1	1	1	1	1	1	1	0	0	0	0	1	0	1	1	1	1	0
C. gestroi	1	1	1	0	1	1	1	1	0	0	0	1	1	0	1	1	1	1	0
C. longignathus	1	1	1	0	1	1	1	1	0	0	1	1	1	0	1	1	1	1	0
C. monosetosus	1	1	1	1	1	1	1	1	0	0	0	0	?	0	1	1	1	1	0

significantly different among *C. formosanus*, *C. cyclocoryphus*, and *C. varicapitatus*, as well as among *C. hekouensis*, *C. hainanensis*, and *C. changtaiensis* (Table 2). For *C. formosanus* and *C. cyclocoryphus*, *C. hainanensis* and *C. changtaiensis*, *C. ochraceus*, *C. suzhouensis*, and *C. grandis*, no characters showed significant differences in measurement data. The other group was composed of the remaining six species with one pair of setae around the rim of the fontanelle. Their measurements also overlapped. *Coptotermes cochlearus* and *C. gestroi* showed no

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

Table 1. Extended.

2	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**3**	**3**	**3**	**3**	**3**	**3**	**3**
0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**
1	0	P	8	J	I	K	<	>	=	0	N	I	?	?	—	—
1	0	N	:	P	P	F	0	H	@	8	N	P	?	A	—	—
1	0	I	P	L	C	N	M	M	P	H	M	G	N	P	=	8
1	0	I	P	G	D	P	P	M	N	P	P	J	A	N	I	J
1	0	H	N	E	C	F	L	H	L	L	N	I	8	L	C	J
1	0	D	K	G	:	D	H	M	J	?	H	C	>	C	G	N
0	0	C	K	C	:	>	I	F	H	F	A	8	A	E	F	@
1	0	>	>	<	:	:	B	=	@	@	C	<	8	C	C	B
1	0	=	I	>	9	:	D	>	=	D	>	>	0	>	I	=
1	0	8	D	9	6	8	E	A	B	B	D	>	:	A	<	=
1	0	7	:	6	5	0	A	5	8	=	C	8	8	<	B	6
1	1	D	K	A	9	>	F	F	F	F	F	A	I	J	E	9
1	0	H	P	C	B	K	L	P	N	O	>	I	P	P	N	B
0	0	A	N	J	B	D	H	I	L	E	?	?	D	E	?	?
1	0	7	D	9	3	0	D	3	=	=	?	?	:	?	?	?
1	1	C	I	C	=	>	H	A	D	H	F	8	?	?	?	?
1	0	3	0	9	0	8	E	0	0	8	0	0	?	0	0	0
1	0	D	K	>	E	K	P	M	P	K	I	N	:	G	P	P
1	0	>	D	9	@	>	L	F	H	B	D	>	3	A	D	=
1	0	>	D	>	@	D	O	I	N	F	M	L	5	E	L	H
1	0	=	D	9	>	D	L	C	H	E	D	I	:	9	<	0
1	0	:	:	G	<	8	I	8	:	7	>	9	0	9	>	4
1	0	0	8	0	4	3	F	3	6	4	C	4	8	6	B	7

significant differences in all measurements (Table 3). However, the largest species, *C. bannaensis*, differed significantly from the other five species in the measurements of three characteristics.

Cladistic analysis. The MP heuristic search resulted in 18 most parsimonious trees (length = 45 [1,349/30], consistency index = 0.640, retention index = 0.807, rescaled consistency index = 0.517). The strict consensus tree of 18 most parsimonious trees (Fig. 1) showed that the ingroup was divided into two

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

Table 2. Mean (± SE) measurements (mm) of morphological characters* of soldiers of 11 *Coptotermes* species possessing two pairs of setae around the rim of the fontanelle.**

Species	HL	HW
C. chaoxianensis	1.321 ± 0.020a	1.163 ± 0.017a
C. varicapitatus	1.414 ± 0.010ab	1.259 ± 0.022bc
C. cyclocoryphus	1.490 ± 0.013b	1.276 ± 0.014bcd
C. formosanus	1.508 ± 0.016bc	1.214 ± 0.010ab
C. hekouensis	1.619 ± 0.025de	1.329 ± 0.018cde
C. hainanensis	1.601 ± 0.018cd	1.352 ± 0.022de
C. changtaiensis	1.643 ± 0.027de	1.361 ± 0.015de
C. longistriatus	1.615 ± 0.009de	1.365 ± 0.017de
C. ochraceus	1.706 ± 0.010ef	1.3914 ± 0.013e
C. suzhouensis	1.694 ± 0.017def	1.351 ± 0.016cde
C. grandis	1.756 ± 0.023f	1.400 ± 0.033e
Statistics	df = 10, $F = 51.03$	df = 10, $F = 21.22$

* Morphological characters: HL, head length to base of mandibles; HW, head maximum width; LML, left mandible length (upper base of condyle to tip); POL, postmentum median length; POW, postmentum maximum width; PWW, postmentum waist width; PRL, pronotum maximum length; PRW, pronotum maximum width; HTL, hind tibia length.

** Means followed by the same letter in the same column are not significantly different by Tukey's HSD test ($P < 0.05$).

† *Coptotermes longistriatus* was excluded from the analysis on character PRL due to having only one measurement.

monophyletic clades. Clade 1 contained 15 species. Their phylogenetic relationships were not resolved completely, with three trichotomies in the cladogram. The apical monophyletic subclade consisted of *C. hainanensis*, *C. varicapitatus*, *C. formosanus*, *C. cyclocoryphus*, and *C. gulangyuensis*, in which *C. formosanus*, *C. cyclocoryphus*, and *C. gulangyuensis* formed an unresolved trichotomy. Clade 2 comprised the remaining six species. Their relationships were well resolved. *Coptotermes gestroi*, *C. cochlearus*, and *C. longignathus* formed a monophyletic subclade, with another monophyletic one formed by *C. dimorphus* and *C. monosetosus* as the sister. The basal species was *C. bannaensis*.

Discussion

Samples and characters. Because the descriptions of most new species of Chinese *Coptotermes* were published in the 1980s, it is difficult to re-collect fresh conspecific specimens from their type localities in which environmental conditions have changed. Specimens of only widely distributed species (e.g., *C. formosanus*

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

Table 2. Extended.

LML	POL	POW
0.875 ± 0.011a	0.811 ± 0.026a	0.361 ± 0.006a
0.921 ± 0.008ab	0.866 ± 0.024ab	0.401 ± 0.005b
0.958 ± 0.003bc	0.899 ± 0.023abc	0.404 ± 0.006b
0.941 ± 0.012b	0.995 ± 0.010cde	0.417 ± 0.005bc
1.009 ± 0.015cd	0.930 ± 0.035abcd	0.441 ± 0.011cde
1.023 ± 0.007d	0.983 ± 0.018bcde	0.437 ± 0.008bcd
1.024 ± 0.008d	1.012 ± 0.029cdef	0.448 ± 0.006cdef
1.015 ± 0.015d	1.028 ± 0.036def	0.465 ± 0.018defg
1.037 ± 0.011de	1.064 ± 0.014ef	0.476 ± 0.005efg
1.041 ± 0.010de	1.074 ± 0.029ef	0.484 ± 0.009fg
1.091 ± 0.013e	1.128 ± 0.026f	0.489 ± 0.011g
df = 10, *F* = 35.37	df = 10, *F* = 16.66	df = 10, *F* = 31.45

and *C. gestroi*) can be obtained easily. Thus, the analysis based mainly on the type specimens and original descriptions should yield reliable results.

The data matrix for the phylogenetic analysis in the study was constructed by two types of data, discrete qualitative data and continuous quantitative data. Arguments both for and against the inclusion of continuous quantitative data emerged previously (Cranston and Humphries 1988, Thiele 1993, Wiens and Etheridge 2003). In our analysis, the topology of the strict consensus tree changed, with positions of many taxa unresolved when excluding the continuous quantitative data. It may be necessary to combine the data in an appropriate way to make the morphological phylogenetics more explicit and rigorous.

Relationships among Chinese *Coptotermes* species. According to the cladogram, the monophyly of the genus *Coptotermes* was strongly supported by a series of synapomorphies. Clade 1 was supported with bootstrap value of 71%. Within the clade, species with relatively larger body size were near the basal part, the subapical trichotomy contained eight species with smaller body size. Nevertheless, the resolution of relationships among these species was less than 50% bootstrap support. Compared with Clade 2, Clade 1 included more species whose sizes of body parts were similar or even overlapped. It was difficult to clarify their phylogenetic relationships solely with morphological data. The low bootstrap support for the topology of Clade 1 might also imply the existence of synonymy. From the taxonomic history of Chinese *Coptotermes* species, it was known that *C. formosanus*, the Formosan subterranean termite, had been given different names, including *C. communis* Xia and He, *C. eucalyptus* Ping, *C. guangzhouensis* Ping,

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

Table 2. Extended.

PWW	PRL	PRW	HTL
0.207 ± 0.003a	0.412 ± 0.008a	0.769 ± 0.011a	0.977 ± 0.016a
0.229 ± 0.003abc	0.490 ± 0.003bc	0.853 ± 0.007bc	1.061 ± 0.008ab
0.224 ± 0.002ab	0.478 ± 0.006b	0.820 ± 0.006ab	1.100 ± 0.005bcd
0.240 ± 0.003bc	0.481 ± 0.007bc	0.848 ± 0.011bc	1.092 ± 0.021bc
0.237 ± 0.007bc	0.533 ± 0.013de	0.917 ± 0.014cd	1.160 ± 0.017cde
0.268 ± 0.006de	0.534 ± 0.011de	0.972 ± 0.026de	1.176 ± 0.011cde
0.274 ± 0.006def	0.520 ± 0.010cd	0.946 ± 0.007d	1.223 ± 0.015ef
0.253 ± 0.005cd	0.520†	0.970 ± 0.026de	1.190 ± 0.017de
0.279 ± 0.004ef	0.599 ± 0.005e	0.987 ± 0.010de	1.296 ± 0.012f
0.297 ± 0.009f	0.576 ± 0.008e	0.967 ± 0.012de	1.293 ± 0.024f
0.291 ± 0.006ef	0.571 ± 0.010e	1.022 ± 0.028e	1.205 ± 0.022ef
df = 10, *F* = 36.32	df = 9, *F* = 40.62	df = 10, *F* = 36.26	df = 10, *F* = 34.05

C. heteromorphus Ping, *C. rectangularis* Ping and Xu, *C. xiaoliangensis* Ping, and *C. guizhouensis* He and Qiu, because of morphological differences in different colonies (Ping 1984, 1985; Ping et al. 1986; Xia and He 1986; Li et al. 2012b). According to the current cladogram, *C. hainanensis*, *C. varicapitatus*, *C. formosanus*, *C. cyclocoryphus*, and *C. gulangyuensis* formed a monophyletic subclade; their ranges of measurement data overlapped as well. Insufficient evidence precludes a definitive conclusion that the five species, or even more species, in Clade 1 are conspecific. Before these relationships are resolved, we suggest that *C. formosanus* and the other four species in the apical monophyletic subclade that were difficult to differentiate from *C. formosanus* morphologically be collectively referred to as the *C. formosanus* complex.

Clade 2 was a robust monophyletic group with a bootstrap value of 89%. This clade was supported by its less or scarce setae around the fontanelle (character state 5-1, 6-1), on the labrum (character state 7-1, 8-1), and on the pronotum (character state 18-1). It was incongruent with the result obtained for the 12S and 16S genes from East Asian and Australian *Coptotermes* (Yeap et al. 2009). In those phylogenetic trees, C. *dimorphus* and *C. cochlearus* fell within the subclade of *C. formosanus*. Because the samples of *C. dimorphus* and *C. cochlearus* used in those analyses were not type species, the result of their morphological identification should be tested after reexamining the type species. Within Clade 2, *C. gestroi* formed a 75% bootstrap support monophyletic subclade with a sister group of *C. cochlearus* and *C. longignathus*. *Coptotermes gestroi* is an invasive termite from Southeast Asia. The species had been reported invading Yunnan and Hainan

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

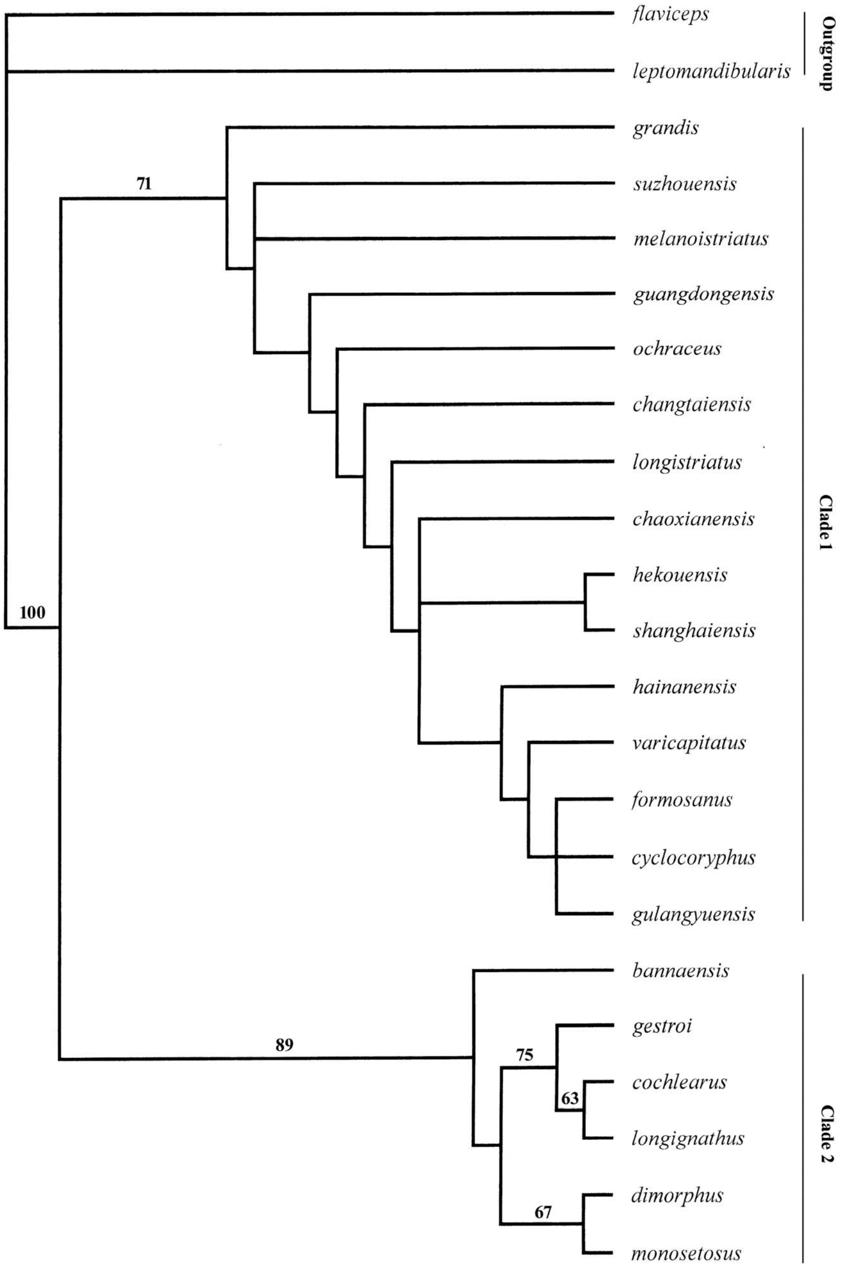

Fig. 1. The strict consensus tree of 18 most parsimonious trees. (Bootstrap values are shown above branches supported in at least 50% of 1,000 replicates in parsimony analysis.)

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

Table 3. Mean (± SE) measurements (mm) of morphological characters* of soldiers of six *Coptotermes* species possessing a pair of setae around the rim of the fontanelle.**

Species	HL	HW
C. monosetosus	1.267 ± 0.006a	1.169 ± 0.022ab
C. longignathus	1.429 ± 0.013b	1.144 ± 0.011a
C. gestroi	1.459 ± 0.014bc	1.223 ± 0.012ab
C. cochlearus	1.525 ± 0.020c	1.240 ± 0.022bc
C. dimorphus	1.490 ± 0.019bc	1.252 ± 0.021bc
C. bannaensis	1.627 ± 0.013d	1.316 ± 0.024c
Statistics	df = 5, $F = 32.48$	df = 5, $F = 7.85$

* Morphological characters: HL, head length to base of mandibles; HW, head maximum width; LML, left mandible length (upper base of condyle to tip); POL, postmentum median length; POW, postmentum maximum width; PWW, postmentum waist width; PRL, pronotum maximum length; PRW, pronotum maximum width; HTL, hind tibia length.

** Means followed by the same letter in the same column are not significantly different by Tukey's HSD test ($P < 0.05$).

Table 4. Comparison of soldier characteristics* of *C. cochlearus* and *C. gestroi*.

		Measurements (mm)		
Species	Sources	HL	HW	LML
C. gestroi	Tsai and Chen 2003	1.30–1.50	1.10–1.15	0.90–1.05
	Maiti 2006	1.50–1.53	1.20–1.25	0.90–0.98
	Yeap et al. 2007	1.12–1.44	0.95–1.50	0.78–0.90
	This study	1.28–1.54	1.06–1.32	0.82–1.04
C. cochlearus	Xia and He 1986 (original description)	1.50–1.58	1.20–1.30	0.90–0.96
	This study	1.49–1.58	1.20–1.30	0.90–0.96

* Soldier characteristics: HL, head length to base of mandibles; HW, head maximum width; LML, left mandible length (upper base of condyle to tip); POL, postmentum median length; POW, postmentum maximum width; PWW, postmentum waist width; PRL, pronotum maximum length; PRW, pronotum maximum width; HTL, hind tibia length; LL, labrum length; LW, labrum maximum width; FW, fontanelle pore width; FH, fontanelle pore height; HH, head maximum height; HBW, head width at base of mandibles; ASN, number of antennal segments.

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

Table 3. Extended.

LML	POL	POW
0.840 ± 0.016a	0.818 ± 0.018a	0.380 ± 0.004a
1.032 ± 0.007c	0.951 ± 0.010b	0.402 ± 0.007ab
0.913 ± 0.010b	0.975 ± 0.015b	0.420 ± 0.005bc
0.920 ± 0.020b	1.000 ± 0.022b	0.428 ± 0.006bc
0.964 ± 0.004b	0.992 ± 0.020b	0.437 ± 0.002cd
0.932 ± 0.025b	1.119 ± 0.027c	0.463 ± 0.005d
df = 5, *F* = 22.08	df = 5, *F* = 16.81	df = 5, *F* = 18.55

provinces of China where the remaining five species in Clade 2 are distributed (Li et al. 2011, 2012a). Their close phylogenetic relationships and same geographic distributions indicate that the species in Clade 2, especially *C. cochlearus*, *C. longignathus*, and *C. gestroi*, are likely the same species.

Synonymy. The Asian subterranean termite, *C. gestroi*, is exotic to China (Li et al. 2009). It can be distinguished from *C. formosanus* by different numbers of setae on the head and the pronotum. However, the similar morphological characteristics

Table 4. Extended.

Measurements (mm)				
POL	POW	PWW	PRL	PRW
0.90–1.00	0.35–0.40	—	0.40–0.45	0.80–0.85
1.00–1.08	0.40–0.45	0.25–0.28	0.48–0.50	0.90–0.95
0.67–1.15	0.33–0.43	0.18–0.26	0.27–0.48	0.64–1.06
0.78–1.10	0.34–0.44	0.22–0.31	0.42–0.53	0.78–0.97
0.94–1.00	0.43–0.44	0.25–0.28	0.48–0.50	0.88–0.94
0.94–1.04	0.41–0.44	0.25–0.29	0.48–0.53	0.88–0.94

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

Table 3. Extended.

PWW	PRL	PRW	HTL
0.238 ± 0.007a	0.420 ± 0.000a	0.790 ± 0.014a	0.9067 ± 0.019a
0.250 ± 0.000ab	0.457 ± 0.008b	0.807 ± 0.011a	0.9200 ± 0.009a
0.273 ± 0.005bc	0.490 ± 0.005bc	0.898 ± 0.009b	1.0852 ± 0.014bc
0.275 ± 0.009bc	0.505 ± 0.010c	0.910 ± 0.017b	1.0400 ± 0.022b
0.290 ± 0.006cd	0.551 ± 0.007d	0.980 ± 0.010c	1.1240 ± 0.008c
0.306 ± 0.007d	0.571 ± 0.009d	1.006 ± 0.017c	1.2133 ± 0.017d
df = 5, *F* = 13.70	df = 5, *F* = 44.98	df = 5, *F* = 44.89	df = 5, *F* = 47.18

of its soldiers with some other species caused synonyms, as happened in *C. formosanus*. In recent years, *C. havilandi* Holmgren and *C. vastator* Light, previously recognized as different species, have been synonymized as *C. gestroi* (Kirton and Brown 2003, Yeap et al. 2007). Chinese species *C. obliquus* Xia and He and *C. yaxianensis* Li were reduced to synonyms of *C. gestroi* as well (Li et al. 2011). The results of both statistical and phylogenetic analyses in our study indicate that Chinese indigenous species in Clade 2, especially *C. cochlearus*, is the

Table 4. Extended.

Measurements (mm)			
HTL	LL	LW	FW
—	0.30–0.35	0.20–0.30	—
—	0.33–0.35	0.30–0.34	—
—	0.26–0.40	0.23–0.34	—
0.89–1.14	0.32–0.43	0.30–0.35	0.14–0.16
0.98–1.04	0.36–0.41	0.29–0.31	0.14–0.16
0.98–1.08	0.36–0.41	0.29–0.31	0.14–0.18

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

potential synonym of *C. gestroi*. After comparison, most of the main measurements of the species were contained in the range of morphometric characters of *C. gestroi* (Table 4). *Coptotermes cochlearus* was known only from the soldier caste. In its original description, Xia and He (1986) thought that *C. cochlearus* was similar to *C. ceylonicus* Holmgren, a similar species to *C. gestroi*. Its diagnostic characters were as follows: the body size was larger, the number of antennal segments was 15, and the waist of the postmentum was at the posterior. Compared with the corresponding characteristics of *C. gestroi*, the position of its waist of the postmentum was congruent with that of *C. vastator* (junior synonym of *C. gestroi*); the number of antennal segments and the body size were congruent with those of *C. gestroi*, which were measured in both the literature and our collection. Therefore, the diagnostic characters of *C. cochlearus* were untenable. For reasons given above, *C. cochlearus* was believed to be a junior synonym of *C. gestroi*.

***Coptotermes gestroi* (Wasmann, 1896)**

Termes gestroi Wasmann, 1896, Ann. Mus. civ. stor. nat. Genova, 16: 628. Type: soldier [NHMG]. Type locality: Bhamò [Burma].

Coptotermes gestroi Holmgren, 1911, K. Svenska vetensk. Akad. Handl., 46: 73. Type: soldier [NHRS]. Type locality: Burma, Sumatra, Singapore, Borneo.

Coptotermes havilandi Holmgren, 1911, K. Svenska vetensk. Akad. Handl., 46: 74. Type: imago [NHRS]. Type locality: Thailand.

Coptotermes vastator Light, 1929, Philipp. J. Sci., 40: 422. Type: soldier [NMNHS]. Type locality: Luzon [Philippines].

Table 4. Extended.

Measurements (mm)			
FH	**HH**	**HBW**	**ASN**
—	0.80–0.90	—	14–15
—	0.80–0.85	0.75–0.78	14–15
—	—	0.46–0.75	—
0.10–0.14	0.76–1.00	0.64–0.80	14–15
0.11–0.12	0.89–0.91	—	15
0.11–0.14	0.89–0.91	0.67–0.67	15

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

Coptotermes javanicus Kemner, 1934, K. Svenska vetensk. Akad. Handl., 13: 59. Type: soldier [KMZS]. Type locality: Buitenzorg, Semarang [Indonesia].

Coptotermes menglunensis Tsai and Huang, 1985, Sinozoologia, 3: 104. Holotype: soldier [GIZ]. Type locality: Menglun town [Yunnan, China].

Coptotermesd obliquus Xia and He, 1986, Contrib. Shanghai inst. Entomol., 6: 172. Holotype: soldier [CAS-SEM]. Type locality: Shilu town, Changjiang county [Hainan, China].

Coptotermes yaxianensis Li, 1986, Entomotaxonomia, 8: 225. Holotype: soldier [GIZ]. Type locality: Yaxian [Hainan, China].

Coptotermes cochlearus Xia and He, 1986, Contrib. Shanghai inst. Entomol., 6: 169. Holotype: soldier [CAS-SEM]. Type locality: Jinghong [Yunnan, China]. **syn. nov.**

Acknowledgments

We are grateful to Weibing Zhu (Chinese Academy of Sciences–Shanghai Entomological Museum) and Kuiyan Zhang (National Zoological Museum of China) for providing type specimens used in this study. This work was supported by the National Natural Science Foundation of China (31172140), the Natural Science Foundation of Guangdong Province of China (2018B030311055), the GDAS Special Project of Science and Technology Development of China (2020GDASYL-20200301003, 2020GDASYL-20200102021).

References Cited

Austin, J.W., A.L. Szalanski and B.J. Cabrera. 2004. Phylogenetic analysis of the subterranean termite family Rhinotermitidae (Isoptera) by using the mitochondrial cytochrome oxidase II gene. Ann. Entomol. Soc. Am. 97: 548–555.

Cranston, P.S. and C.J. Humphries. 1988. Cladistics and computers: A chironomid conundrum. Cladistics 4: 72–92.

Donovan, S.E., D.T. Jones, W.A. Sands and P. Eggleton. 2000. Morphological phylogenetics of termites (Isoptera). Biol. J. Linn. Soc. 70: 467–513.

Eggleton, P. 1999. Termite species description rates and the state of termite taxonomy. Insectes Soc. 46: 1–5.

Engel, M.S., D.A. Grimaldi and K. Krishna. 2009. Termites (Isoptera): Their phylogeny, classification, and rise to ecological dominance. Am. Mus. Novitates 3650: 1–27.

Garcia-Cruz, J. and V. Sosa. 2006. Coding quantitative characters data for phylogenetic analysis: A comparison of five methods. Syst. Bot. 31: 302–309.

Huang, F.S., S.M. Zhu, Z.M. Ping, X.S. He, G.X. Li and D.R. Gao. 2000. Fauna Sinica, Insecta: Isoptera. Science Press, Beijing.

Kirton, G. and V.K. Brown. 2003. The taxonomic status of pest species of *Coptotermes* in Southeast Asia: Resolving the paradox in the pest status of the termites, *Coptotermes gestroi*, *C. havilandi* and *C. travians* (Isoptera: Rhinotermitidae). Sociobiology 42: 43–63.

Krishna, K., D.A. Grimaldi, V. Krishna and M.S. Engel. 2013. Termite evolution: Diversity, distributions, phylogeny, fossil record, Pp. 147–182. In Krishna, K., D.A. Grimaldi, V. Krishna, and M.S. Engel (eds.), Treatise on the Isoptera of the World. Vol. 1. American Museum of Natural History-Scientific Publications, New York.

Li, H.F., W. Ye, N.Y. Su and N. Kanzaki. 2009. Phylogeography of *Coptotermes gestroi* and *Coptotermes formosanus* (Isoptera: Rhinotermitidae) in Taiwan. Ann. Entomol. Soc. Am. 102: 684–693.

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access

Li, Z.Q., B.R. Liu, Q.J. Li, W.L. Xiao and J.H. Zhong. 2011. Two new synonyms of *Coptotermes gestroi* (Wasmann) (Isoptera: Rhinotermitidae) in China. Sociobiology 58: 449–456.

Li, Z.Q., B.R. Liu, W.H. Zeng and J.H. Zhong. 2012a. Genetic variation in *Coptotermes gestroi* (Isoptera: Rhinotermitidae) populations from Hainan, Taiwan, and Philippines. J. Agric. Urban Entomol. 28: 57–65.

Li, Z.Q., J.H. Zhong and W.L. Xiao. 2012b. A new synonymy of *Coptotermes formosanus* (Isoptera: Rhinotermitidae). Sociobiology 59: 1223–1227.

Lo, N., O. Kitade, T. Miura, R. Constantino and T. Matsumoto. 2004. Molecular phylogeny of the Rhinotermitidae. Insectes Soc. 51: 365–371.

Maiti, P.K. 2006. A taxonomic monograph on the world species of termites of the family Rhinotermitidae (Isoptera: Insecta). Zool. Surv. India 20: 32–88.

Ping, Z.M. 1984. Two new species of the genus *Coptotermes* (Isoptera: Rhinotermitidae). Trop. Subtrop. For. Ecosyst. 2: 184–189.

Ping, Z.M. 1985. Eight new species of the genus *Coptotermes* and *Reticulitermes* from Guangdong province, China (Isoptera: Rhinotermitidae). Entomotaxonomia 7: 317–326.

Ping, Z.M., Y.L. Xu, C.G. Xu and C. Gong. 1986. Trunk-dwellers termites and five new species from Guizhou province, China. Sci. Silvae Sin. 22: 153–160.

Roonwal, M.L. 1969. Measurement of termites (Isoptera) for taxonomic purposes. J. Zool. Soc. India 21: 9–66.

Scheffrahn, R.H., T.F. Carrijo, J. Křeček, N.Y. Su, A.L. Szalanski, J.W. Austin, J.A. Chase and J.R. Mangold. 2015. A single endemic and three exotic species of the termite genus *Coptotermes* (Isoptera, Rhinotermitidae) in the New World. Arthropod Syst. Phylogeny 73: 333–348.

Scheffrahn, R.H., J. Krecek, A.L. Szalanski, J.W. Austin and Y. Roisin. 2005. Synonymy of two arboreal termites (Isoptera: Termitidae: Nasutitermitinae): *Nasutitermes corniger* from the neotropics and *N. polygynus* from New Guinea. Fla. Entomol. 88: 28–33.

Swofford, D.L. 2001. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4.0b10. Sinauer Associates, Sunderland, MA.

Thiele, K. 1993. The holy grail of the perfect character: The cladistic treatment of morphometric data. Cladistics 9: 275–304.

Tsai, C.C. and C.S. Chen. 2003. First record of *Coptotermes gestroi* (Isoptera: Rhinotermitidae) from Taiwan. Formos. Entomol. 23: 157–161.

Vargo, E.L. and C. Husseneder. 2009. Biology of subterranean termites insights from molecular studies of *Reticulitermes* and *Coptotermes*. Annu. Rev. Entomol. 54: 379–403.

Wiens, J.J. and R.E. Etheridge. 2003. Phylogenetic relationships of hoplocercid lizards: Coding and combining meristic, morphometric, and polymorphic data using step matrices. Herpetologica 59: 375–398.

Xia, K.L. and X.S. He. 1986. Study on the genus *Coptotermes* from China (Isoptera: Rhinotermitidae). Contrib. Shanghai Inst. Entomol. 6: 157–182.

Yeap, B.K., A.S. Othman and C.Y. Lee. 2009. Molecular systematics of *Coptotermes* (Isoptera: Rhinotermitidae) from East Asia and Australia. Ann. Entomol. Soc. Am. 102: 1077–1090.

Yeap, B.K., A.S. Othman, V.S. Lee and C.Y. Lee. 2007. Genetic relationship between *Coptotermes gestroi* and *Coptotermes vastator* (Isoptera: Rhinotermitidae). J. Econ. Entomol. 100: 467–474.

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-02 via free access