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# **Oriental Insects**

Publication details, including instructions for authors and subscription information: http://www.tandfonline.com/loi/toin20

The genus Schevodera Borchmann: Phylogeny and historical biogeography, with description of a new species (Coleoptera: Tenebrionidae: Lagriinae)

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To cite this article: Bin Chen & Xuhua Xia (2001): The genus Schevodera Borchmann: Phylogeny and historical biogeography, with description of a new species (Coleoptera: Tenebrionidae: Lagriinae), Oriental Insects, 35:1, 3-27

To link to this article: <u>http://dx.doi.org/10.1080/00305316.2001.10417279</u>

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## THE GENUS SCHEVODERA BORCHMANN: PHYLOGENY AND HISTORICAL BIOGEOGRAPHY, WITH DESCRIPTION OF A NEW SPECIES (COLEOPTERA: TENEBRIONIDAE: LAGRIINAE)\*

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ABSTRACT. Schevodera Borchmann belongs to the subfamily Lagriinae and its members are phytophagous. A new species, S. glabricollis is described from China. Redescriptions of the genus and two known species, S. gracilicornis and S. inflata with new records for China are given. A key to Chinese species is given. The phylogeny of the nine known species and one subspecies is çladistically analysed based on 21 morphological characters from adults. The confidence of the phylogram obtained from the cladistic analysis and its monophylies are examined with PTP and T-PTP tests. The ancestral distribution of the genus is also reconstructed based on the dispersal-vicariance analysis. The results suggest that the genus would be monophyletic. In the late Permian – late Triassic period around 255-220 million years ago, it is hypothesized to have originated from a Lagria-like ancestral species between western Yunnan, China and Burma in the Shan-Thai terrain. It dispersed from western Yunnan and northern Burma to Sumatra and Java, and then northward through Borneo to Palawan, Luzon and finally Mindanao. Based on phylogeny and historic biogeography, the genus is divided into three species groups: Yunnan, Indonesia and Philippines groups. The Yunnan group is the most primitive, consisting of S. inflata, S. glabricollis and S. gracilicornis, and is mainly distributed in Yunnan and Burma. The Indonesia group includes S. hirticollis and S. hirticollis salvazai, S. curticollis and S. dohrni, and occurs primarily in Indonesia but also reaches into Burma and the Philippines. The S. hirticollis salvazai has dispersed from Burma to Laos. The group originated from the ancestor of Yunnan group after Ecocene, i.e. no longer than 50 million years ago. The monophyletic Philippines group is composed of three endemic species: S. setosa, S. spoliata and S. insularis. It originated from the ancestor of the Indonesian group after the Miocene around 20 million years ago and dispersed from Palawan to Luzon and then Mindanao. The synapomorphies between these groups, interspecific phylogenetic relationships, time and place of origin and potential distribution of each species are also discussed in detail.

Key words: Coleoptera, Tenebrionidae, Lagriinae, *Schevodera*, phylogeny, historic biogeography, new species, new record, Oriental Region, China, southeastern Asia.

#### Introduction

The genus Schevodera, belonging to the subfamily Lagriinae, Tenebrionidae was erected by Borchmann (1937) for a group of seven species and one subspecies, which were earlier assigned to the genus Lagria Fabricius. The earliest species described belonging to this genus are Lagria gracilicornis Borchmann, 1910 and L. hirticollis Borchmann, 1910, followed by L. inflata Borchmann, 1925, L. insularis Borchmann, 1930, L. setosa Borchmann, 1930,

<sup>\*</sup> Supported by China National Natural Science Foundation (project no. 39970095).

L. spoliata Borchmann, 1930, L. curticollis Borchmann, 1934 and S. hirticollis salvazai Pic, 1934. Lagria gracilicornis and L. hirticollis were subsequently referred to by Borchmann (1915, 1930, respectively). In Borchmann's (1937) worldwide comprehensive monograph of the family Lagriidae, he also provided a key to these species. They are reportedly distributed among islands of the Philippines and Indonesia except that S. gracilicornis occurs in Burma (Carin) and S. hirticollis salvazai is known from Laos. Borchmann (1940) described an additional species, S. dohrni from Sumatra, Indonesia. However, the phylogenetic relationships and ancestral distribution of these species have not previously been examined.

The senior author's recent research on the lagriine beetles from China (Chen, 1995), revealed the occurrence there of the genus and its two species, S. gracilicornis (Borchmann) and S. inflata (Borchmann). A new species, S. glabricollis, was also identified. An examination of the morphological characters and distributional records yielded information about phylogenetic and historic biogeographical relationships among all the species of this genus.

In this contribution, the new species is described, and the genus and its two known species in China are redescribed. The phylogenetic and historic biogeographical relationships between the different species (including a subspecies), are discussed in detail using cladistic analysis, PTP and T-PTP tests, and dispersal and vicariance analysis.

#### Schevodera Borchmann, 1937

Schevodera Borchmann, 1937. Genera Ins., 204: 59.

Body very broad, usually clothed with dense and long hairs.

Head short, round, mouthparts short, terminal segment of maxillary palpus short securiform, neck moderately thick; eye slender with anterior margin strongly emarginate, Q interocular distance much wider than ocular transverse diameter,  $\sigma$  with distance slightly narrower; tempora roundly constricted backwards, about as long as ocular transverse diameter; antenna slender and long, its terminal segment about as long as 2-5 preceding segments together. Pronotum wider than head across eyes, mostly slightly transverse, subquadrate, usually uneven, finely and densely punctate, punctures fine and dense, densely clothed with long and erected hairs (except for S. glabricollis); anterior angles roundly prominent, maximum width a little before middle, either side at base moderately constricted. Scutellum wide, linquiform. Elytra at base much wider than pronotum at base, usually swollen convexly backwards, o relatively narrower; coarsely and densely punctate with fine rugae; epipleuron (Fig. 2) extremely wide with basal 2/5 especially wide and distal 3/5 gradually narrowing backwards, dorsal margin visible almost in entire length (with the exception of a bit at base) in dorsal view. Prosternal process very small and not raised, procoxae closed.

Type species: S. hirticollis (Borchmann, 1910) (Philippines, Indonesia, Laos), designated by Borchmann, 1937.

Distribution: China, Burma, Laos, Philippines, Indonesia.

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Schevodera Borchmann is related to Lagria Fabricius. It differs from the latter in usually having a much wider body, epipleuron (Fig. 2) extremely wide with upper margin visible almost the entire length in dorsal view, and pronotum densely clothed with long and erected hairs (except in *S. glabricollis*).

#### Key to the Chinese species of Schevodera

- -- Antenna yellow, Q with terminal antennal segment about as long as 3 preceding segments together; head and pronotum usually bluishblack; pronotum with punctures hardly visible........2. S. gracilicornis

1. Schevodera glabricollis, sp. nov. (Figs 1-3)

*Female:* Body very broad, convex; brownish black with antennae yellow and elytra bluish-black, elytra with blue shine; clothed with short, dense and decumbent pubescence, but pronotal pubescence even shorter. Length 10.2 mm, width 4.1 mm.

Head short and round, slightly wider than long (43:40), a little narrower than pronotum (43:45); mouthparts short, labrum cordiform, clypeus transverse, both with anterior margins deeply emarginate, frontoclypeal groove very short, like a shallow pit; frons uneven, densely punctulate; vertex somewhat convex, tempora slightly longer than ocular transverse diameter, neck moderately constricted; eye small with anterior margin deeply emarginate, interocular distance about twice ocular transverse diameter; antenna (Fig. 3) slightly exceeding elytral humerus, segment 3 much longer than segment 4, segments 4-10 gradually shortening distad, last segment slightly longer than 2 preceding segments together, with apex acute.

Pronotum slightly longer than wide (48:45), campanulate; densely and obviously punctulate; front angles round, hind angles somewhat projecting, anterior and posterior margins distinct, median area depressed and clearly different from the rest of pronotum, central disc with a shallow longitudinal impression, either side at base with a shallow and large pit. Elytra 1.7 times as long as wide (220:130), 1.9 times wider than pronotum (130:45); densely and coarsely punctate, finely rugose; epipleura (Fig. 2) with basal 2/5 very wide and distal 3/5 gradually narrowing toward apex; a little acute at apex. Surface of abdomen much lower than that of metasternum in ventral view. Habitus: Fig. 1.

Male: Unknown.

Holotype: Q, P. R. CHINA: Yunnan: Cheli, 620m, 25.iv.1975, Coll. Zang Lingchao. Deposited in Insect Collection, Institute of Zoology, Academia Sinica, P. R. China.

*Remarks:* The new species is similar to *S. gracilicornis*, but differs from the latter in that antennae have segment 3 much longer than segment 4 and the female has the terminal antennal segment only slightly longer than 2 preceding segments together; pronotum with pubescence very short and punctures coarse and dense, possessing a shallow longitudinal impression on central disc; abdominal sterna much lower than metasternum in ventral view.

### 2. Schevodera gracilicornis (Borchmann) (Fig. 4)

Lagria gracilicornis Borchmann, 1910. Bull. Ent. Soc. Italy, p 204; Borchmann, 1915. Archiv für Naturg., p 83.

Schevodera gracilicornis: Borchmann, 1937. Genera Ins., 204: 60.

Body very broad, convex; bluish-black, slightly shining, antenna yellow, mouthparts blackish-brown; dorsal surface densely clothed with long and erected black hairs, ventral pubescence short, sparse and semi-erected. Length 8-10mm.

Head short and round, slightly longer than wide (47:42), narrower than pronotum (42:48); mouthparts short and small, labrum cordiform, clypeus transverse, both with anterior margins emarginate, frontoclypeal sulcus long, arcuate and deep; frons slightly convex with punctures fine and dense, vertex convex, tempora roundly constricted, slightly longer than ocular transverse diameter; eye slender and long, slightly convex, anterior margin emarginate, interocular distance about 0.5 times wider than ocular transverse diameter; antenna (Fig. 4) exceeding elytral humerus, densely clothed with short hairs, segments 3 and 4 subequal in length, segments 4-10 gradually thickening and shortening distad, terminal segment about as long as 4 ( $\sigma$ ) or 3 ( $\varphi$ ) preceding segments together.

Pronotum slightly wider than long (48:45), subquadrate, anterior and posterior angles distinct, maximum width a little before middle; slightly uneven, punctures hardly visible, with a transverse pit on disc just before posterior margin. Elytra 0.4 times longer than wide (207:146), 2 times wider than pronotum (146:48), very broad, swollen out convexly backwards; finely and densely punctate, transversely rugose; epipleuron with basal 2/5 extremely wide and distal 3/5 gradually narrowing; apex obtusely round.

Specimens examined: P. R. CHINA: Yunnan: Jinghong: Xiaomengyang, 850 m., 29, 28.viii.1958, Coll. Zhang Yiran.

Distribution: P. R. China: Yunnan; Burma: Carin.

Remarks: This species is somewhat similar to S. inflata, but can be distinguished from the latter in having yellow antennae; female with terminal antennal segment about as long as the 3 preceding segments together; pronotum with punctures hardly visible; and head and pronotum not paler in color.

#### Schevodera inflata (Borchmann) (Fig. 5) 3.

Lagria inflata Borchmann, 1925. Treubia, p 348. Schevodera inflata: Borchmann, 1937. Genera Ins., 204: 60.

Body very broad, convex; black with slight bluish shine, head and sometimes pronotum blackish-brown; dorsum with dense, long, slender and erect hairs, venter with hairs short and decumbent. Length 8-10 mm.

Head as long as wide (38:38), as wide as pronotum; mouthparts short and small, labrum small, clypeus transverse, frontoclypeal sulcus long and arcuate; frons densely and finely punctate, with a shallow pit on posterior disc; tempora roundly constricted, subequal to ocular transverse diameter in length, vertex slightly convex, neck moderately constricted; eye slender and long with anterior margin deeply emarginate, interocular distance about twice ocular transverse diameter; antenna exceeding elytral humerus, relatively thick, segment 3 slightly longer than segment 4, segments 3-10 gradually thickened and shortened, last segment about as long as three ( $\sigma$ ) or slightly longer than two (Q) preceding segments together.

Pronotum slightly longer than wide (40:38), punctures fine, but visible, either side at base constricted, distally slightly narrowed, base of disc with a shallow to deep and large pit on either side, some with an impression just before centre of posterior margin. Elytra 0.7 times longer than wide (190:110), 1.9 times wider than pronotum (110:38), swollen backwards, densely and coarsely punctate, with fine, transverse rugae; epipleuron with basal 2/5 extremely wide and distal 3/5 gradually narrowed distally. Tibiae of male with inner margin dentate, those of female with preapical part finer.

Specimens examined: P. R. CHINA: Yunnan: Menghai, 750m, 29, 5.vi.1958, Coll. Chunpe; Yunnan: Mengla, 29, China, 12.v.1959, Coll. Pu Fuji; Yunnan: Jinghong, 10, 19, 540m, 18.iii.1957, Coll. Liu Dahua; Yunnan: Xishuangbanna, 10, 16.vi.1964, Coll. Chen Yuhan.

Distribution: P. R. China: Yunnan; Indonesia: Java.

#### Materials and methods for phylogenetic analysis

Terminal taxa and data matrix

The terminal taxa are all nine known species and one subspecies of the genus Schevodera as ingroup, and two species of Lagria as outgroup (Table 2).

Originally, 25 characters were sieved out and coded for each taxon, but four of them were identified as invariant or uninformative (autapomorphic) characters for parsimony criterion using the "CSTATUS" option of PAUP\* and thus were excluded from the analysis. Among these 21 characters, five

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characters have two states, six characters have three states, and 10 characters have four states. All 21 informative characters and their states are listed in Table 1.

All character data for this study were derived from the morphology of adults. Data attributes were coded directly from specimens, but some information was also incorporated from published descriptions. Missing or unknown state values are labeled with question marks (?), which were ignored in the phylogenetic analysis. Where two states of the same character occurred simultaneously for a single species we treated designated a polymorphism, labeled with "\*". The final character state matrix for both ingroup and outgroup species is provided in table 2.

#### Selection of outgroup

The only previous study on the phylogenetic relationships among genera of Lagriinae is Chen's (1995) preliminary cladistic analysis among 21 of 29 known genera of this subfamily in China, using 28 characters derived from the morphology of adults, including male genitalia. Results showed that *Lagria* Fabricius is the most primitive of the 21 genera and the monophyletic *Schevodera* was derived from the ancestor of *Lagria*. Therefore, two species of *Lagria*, *Lagria* (*Lagria*) ventralis Reitter and *Lagria* (*Ammocera*) chapaensis Pic were selected as outgroups of *Schevodera* in the present study.

#### Cladistic analysis

Cladistic analysis was conducted using version 4.0 (beta version) of PAUP\* (Swofford, 1998). Cladograms from this analysis were drawn by TreeView 1.31 (Page, 1996).

There are two approaches to search for optimal trees: exact algorithms and heuristic methods. For exact algorithms, it is doubtful whether exhaustive search for data sets of more than 11 taxa is practical, but the branchand-bound method can be applied to data sets of up to 25 taxa (Forey *et al.*, 1992). The size of our data fits the use of branch-and-bound method (use the command "BANDB" in PAUP\*) to compute minimum length cladograms. Of 16 multistate characters with more than two states, characters 2, 11-12, and 14-15 were treated as ordered because their intermediate states could be determined. However, we did not hypothesize direction of evolution between any two states in order to preclude arbitrariness. All other 11 multistate characters were treated as unordered to avoid *a priori* bias regarding character state evolution.

In general, the greater the number of states observed for a character, the greater will be that character's influence (Swofford, 1993). In order to make each character have the same influence in discriminating among alternative tree topologies, we used the SCALE option to request that weights were assigned such that the minimum possible length for each character is the same for all characters in the present study. However, the default "base weight' in PAUP\* is 1000 and it only uses intergers to store tree lengths and character weights, which means that in our data containing a mixture of two-, three-, and four-state characters, the scaled weights resulting from a base weight of 1000 are 1000, 500 and 333, respectively. Suppose two trees are being evalu-

ated and that exactly one character is homoplastic (i.e., requires extra steps) on each tree. Further suppose that the first tree requires three extra steps (homoplasies) in a four-state character and that the second requires two extra steps in a three-state character. Even though the two trees should be considered equally parsimonious, the first tree is deemed shorter, since  $3 \times 333 =$  999 is less than  $2 \times 500 = 1000$ . Therefore, in our case we used a base weight of 6 to solve the problems, thus making the scaled weights 6, 3, and 2.

The terms "tree" and "cladogram", and "most parsimonious" and "minimum-length" are used interchangeably in this paper. The cladograms were rooted between the outgroups and ingroup. Polarity decisions for character states (Table 1) were made *a posteriori* based on the cladograms (Fig. 6) produced from the analysis. Because *S. hirticollis* and *S. hirticollis salvazai* in character 6-11 each have two state values, we coded these characters as having multiple states, and used the MSTAXA command to specify these characters to be treated as polymorphisms. The MINFORFIT command was used to specify minimum-possible single-character lengths to be used for calculating CI, RI and RC indices. We also used STEPMATRIX = ALLSTATES to allow any possible character state to be assigned to an internal node, and INCLUDEANC = YES to include a hypothetical taxon possessing putative ancestral states for all character in the search so as to specify a tree root.

By default, branches with maximum branch length of zero were collapsed into polytomies for all trees, and only those trees that were unique after the collapsing was accomplished were kept. Characters were optimized on the trees in memory using "accelerated transformation" via the option OPT = ACCTRAN.

#### **Results of phylogenetic analysis**

Eight most parsimonious cladograms were found with tree length = 182, consistency index (CI) = 0.791 and retention index (RI) = 0.696. However, further comparison revealed that three of these trees had the lowest f-ratio (= (0.0201) and should be selected as optimal cladograms, whereas the other trees had higher f-ratios [0.0202 (two), 0.0337, 0.0758 and 0.3008, respectively]. The only difference among these three selected cladograms is the position of S. hirticollis and S. hirticollis salvazai. They either form a sister group, or either of them is a part of a large clade. The remaining parts of the topologies are identical. Because S. hirticollis salvazai is just thought of as a subspecies of S. hirticollis, the phylogeny with both of them gathered as a sister group, of the three cladograms with lowest f-ratio (0.0201), is regarded as optimal (Fig. 6). The branch length on each branch, all characters (except for character 4 and 19, above bars) and their states (below bars) on each branch are shown also on the phylogram. The black bars indicate synapomorphies, stipples show parallelism and white notes reversal. The minimum and maximum possible branch length values, and the character state changes, both supporting the labeled branches, are listed in the legends of the phylogram.

From the phylogram, we note the following results. First, Schevodera seems to be monophyletic and originated from the ancestor of Lagria. The monophyly is supported by seven synapomorphies (characters 1, 2, 9, 11, 12, 20 and 21) and the longest branch length, 25 steps. Second, S. inflata and S. glabricollis seem sister groups, and are the earliest separated species of the genus. They appear to be more closely related to S. gracilicornis than any other species. The second longest branch length, 18 steps and four synapomorphies (characters 6, 7, 8 and 13) in branch 4, suggests that S. glabricollis diverged far more, prior to speciation. Thus, S. inflata should be regarded as the most primitive species of the genus. Similar to S. glabricollis, S. gracilicollis also diverged significantly with 12 steps of branch length. Third, S. insularis and S. spoliata form a sister group with synapomorphic characters 5, 7 and 9, and a branch length of 13 steps (Fig. 6, branch 15). Both seem to represent the most derived species of the group and are closer to S. setosa than to any other species. In comparison with S. spoliata, S. insularis is more derived with a branch length of 10 steps and two synapomorphies (characters 11 and 15). Fourth, greater divergence in branches 5, 7 and 13 is also indicated, where the branch lengths are nine, nine, and six steps respectively, and the number of synapomorphies are four, two, and two, respectively.

Table 3 displays each character's hypothetical steps on the optimal phylogram, minimum and maximum possible steps in search for the most parsimonious cladograms, and the values CI and RI of the fit between the phylogram and a given character. CI = 1 when there is no homoplasy and decreases as homoplasy increases. The RI is high when state changes occur predominantly on internal nodes and low when changes are concentrated on branches leading to terminal taxa (Forey et al., 1992). Both the CI and RI of characters 2, 5-8, 11-15, and 20-21 are one, with the single exception of the RI of character 15. Thus, these characters completely fit the phylogram and all changes on the phylogram indicate synapomorphies, i.e. no parallelisms or reversals occur on the tree for these characters. These 12 characters are hypothesized to have played a more important role in the origin of the genus and its species. For characters 1, 3, 4, 9, and 17, the CI values range from 0.571 to 0.667, and the RI values from 0.25 to 0.80. They underwent more state changes than the minimum possible steps, but should certainly have contributed to the interspecific relationships. However, the RI values of characters 10, 16, 18 and 19 are all zero despite having the CI values of either 0.500 or 0.833. It casts a doubt as to whether these five characters contributed significantly to the phylogeny of the genus.

Based on the phylogeny and outgroups, the ancestral states and the direction of their evolution are assessed (Table 1). Those state changes occurring in at least two branches are taken as parallelisms and those state changes toward the ancestral state are considered reversals. For character 2, most species of the tribe Lagriini have normal body width which, therefore, is treated as plesiomorphic, while exaggerated body width which in *Schevodera* is regarded as a generic feature. The black or bluish-black elytral, mesothoracic, metathoracic and abdominal color are recognised as plesiomorphic on the phylogram, and the lighter color, the derived state (Table 1). Normally, the terminal antennal segment of male and female Lagria is as short as, or shorter than, the two preceding segments together. Thus a longer terminal segment is considered derived in characters 12 and 13. A ratio of about 2:1 for female interocular distance to ocular transverse diameter, like most species of Lagria, is plesiomorphic. A ratio of about 1:1 is considered the most derived state (character 14). The state of tempora, about as long as eye diameter, is plesiomorphic, and then it can evolve toward either the state of much shorter than ocular diameter or the state of much longer than ocular diameter (character 15). Pronotum with very long hairs is synapomorphic for the genus (i.e. generic feature). However, S. glabricollis lacks such long hairs while L. ventralis (outgroup) has independently evolved long hairs, which reduces the importance of character 16 in the cladistic analysis. The extremely wide epipleuron and visibility of epipleural upper margin in dorsal view near the humeri are peculiar to the genus, so their polarities go without saying in character 20-21.

#### Confidence tests of phylogenetic structure

Before further discussing the above results, the confidence of the cladistic structure of these data and the monophylies of this particular group should be examined. Several methods have been developed as statistical approaches to test the reliability of cladograms, e.g. bootstrapping (Felsenstein, 1985), data decisiveness (Goloboff, 1991), skewedness (Huelsenbeck, 1991) and permutation tail probability (PTP) (Archie, 1989; Faith & Cranston, 1991). In response to Carpenter's (1992) claim that randomization has no place in cladistics, Truemen (1993) briefly described, compared and commented on the above techniques and concluded that the methods other than PTP have little or no validity in testing the reliability of cladograms (Qin & Gullan, 1995). In the PTP test, each character's states are first reassigned randomly to taxa for producing a series of randomized data sets which represent random covariation among the characters. The PTP test then compares the length of the minimum-length trees produced from the actual data set, with the series of randomized data sets, using the parsimony criterion of cladistics in calculating the minimum-length trees. The proportion of all sets (actual and randomized) having lengths as short as or shorter than the length of minimumlength tree(s) from actual data yield the "cladistic permutation tail probability", or PTP (Faith & Cranston, 1991). When none of the randomized data sets produce a length as short as or shorter than the actual length, the PTP value is 0.01. When the PTP value is less than or equal to 0.05, the actual data are taken to have significant cladistic structure.

Faith (1991) extended the PTP test to evaluate the monophyly or nonmonophyly of a particular group and he named this method topologydependent cladistic permutation tail probability (T-PTP) test. The T-PTP test compares the difference in lengths of minimum-length trees produced from the actual data and the randomized data, respectively, under the constraints of monophyly and non-monophyly of a given group. The procedures for producing randomized data are the same as for the PTP test. The constraint of monophyly and non-monophyly has to precede any other procedure. If the

minimum tree length achieved for a topology constrained to include a monophyletic group is much shorter than that achievable for the best possible topology constrained to not include the monophyletic group, then the evidence for monophyly appears strong (Faith, 1991). The tree length difference is defined as the length of the shortest tree not compatible with constraint, minus the length of shortest tree compatible with constraint. The final proportion of the difference values (from both actual and randomized) equal to or larger than the original difference value from the actual data be referred to as the T-PTP to evaluate the monophyly of a given group. Similar to the PTP value, if the T-PTP value is less than or equal to 0.05, the actual data are regarded as producing significant evidence for the proposed monophyly of a given group.

In our present study, 99 randomized data sets were produced, and 100 data sets (including 99 randomized and the original) were analysed for both PTP and T-PTP tests, using PAUP\*. The branch-and-bound search was used to search for the shortest trees. The character states of all taxa including outgroups were randomized, because we think that inclusion of outgroups should be more representative for random covariation among characters, and thus the results should be more accurate. For the T-PTP test, the branches 1, 3, 5, 7, 13 and 15 of the phylogram (Fig. 6) were constrained as monophyletic, respectively.

The minimum-length trees (eight, one of them is illustrated in Fig. 6) from the original data set (Table 1) were each 182 steps long, whereas the minimum-length trees from 99 randomized data sets were 199-219 steps in length, i.e. 17-37 steps longer. The PTP (= 0.01) indicates further the obvious existence of phylogenetic structure of the given original data.

The results and conclusion of the T-PTP test are displayed in Table 4. The tree length differences for the original data between inclusion and exclusion of the constraints of monophylies, the tree length differences for 99 randomized data sets between with and without the constraints, and the T-PTP values as a whole provide the support for monophylies of branches 1, 5, 7, 13 and 15, and refute the monophyly of branch 2, which seems monophyletic in the phylogram (Fig. 6).

#### Historic biogeography

The known distributions of *Schevodera* species are demonstrated in Table 5 and Fig. 7, but historic distributions were previously unknown. In the present study, DIVA 1.1 (Ronquist, 1996) was employed to reconstruct the ancestral distribution of this lineage using the dispersal-vicariance analysis proposed by Ronquist (1997). The dispersal-vicariance analysis is based on vicariance and minimizes dispersal and extinction events. Unlike other methods in historic biogeography, it does not assume anything about the existence of general biogeographic patterns. Therefore, it is particularly useful in reconstructing the distribution history of a group of organisms in the absence of a general hypothesis of area relationships, and remains applicable even when area relationships are expected to be reticulate rather than hierarchic (Ron-

quist, 1997). Nordlander *et al.* (1996) has successfully studied the historic biogeography of the cynipoid wasp family Ibaliidae (Hymenoptera).

The historic biogeography of the *Schevodera* was analyzed in terms of three main distribution areas: Yunnan and its adjacent area, Indonesia, and the Philippines (Table 5, Figs 7-8). An exact search with DIVA 1.1 resulted in a single reconstruction of the distribution history, requiring five dispersal between areas. The optimal distributions at each ancestral node are illustrated in Fig. 8.

The historic biogeography reconstruction (Fig. 8) suggests that Schevodera originated in Yunnan and its adjacent areas. Within the genus, two main dispersal events took place. One of them occurred between the most recent ancestor of S. gracilicornis and the common ancestor of the remaining part of the optimal reconstruction of ancestral distribution, and made the junior ancestor's distribution extend from Yunnan and its adjacent area to Indonesia prior to a vicariant event. Another occurred between the most recent ancestor of S. curticollis and that of S. dohrni, by which, accompanied with a vicariance event immediately before this, the distribution of the junior ancestor was extended from Indonesia to the Philippines. These two branches on which the two dispersal events took place, not only divide the species of the genus into three groups of different distribution, but also have been proved two monophylies at different levels (Fig. 6). Therefore, three natural species groups of biogeographical distribution were recognized and could be defined as: Yunnan group (including S. glabricollis, S. inflata and S. gracilicornis), Indonesia group (including S. dohrni, S. curticollis, S. hirticollis and S. hirticollis salvazai), and Philippines group (including S. insularis, S. spoliata, and S. setosa), which are mainly distributed in Yunnan and its adjacent areas, Indonesia and Philippines, respectively.

The Yunnan group is distributed in Yunnan and its adjacent areas except for S. inflata which also occurs in Indonesia. The group originated in this area from a Lagria-like ancestral species. A dispersal event from Yunnan to Indonesia took place during the formation of S. inflata. The known distribution of this species is only in Yunnan, China and Java, Indonesia (Table 5, Figs 7-8). The wide distribution disjunction of the species suggests probably unknown occurrences of this species in Thailand.

The distribution of the Indonesia group covers all of the three areas but mainly in Indonesia. Its ancestor originated from the ancestor of the Yunnan group, and then happened a vicariant event subdividing the ancestral distribution into two mutually exclusive areas, Yunnan and its adjacent area, and Indonesia. The species *S. hirticollis* is the most widely distributed species of the genus. The optimal biogeographic reconstruction indicates that a dispersal event resulted in its distributional extension from Burma to Indonesia, and then to the Philippines (Table 5, Figs 7-8). The distributional disjunction between Burma and Indonesia implies an unknown occurrence, too.

The Philippines group is restricted to the Philippines, suggesting that this group originated and diversified in this area (Table 5, Fig. 7-8). The an-

cestor of this group came from an ancestor which was shared with *S. dohrni* of Indonesia group. The ancestor possessed a distribution of both Indonesia and the Philippines, and allopatric speciation caused by a vicariant event led to subdivision of the ancestral distribution into two mutually exclusive sets of areas, Indonesia and the Philippines.

#### Discussion

The results of cladistic analysis, PTP and T-PTP tests in the present study (Fig. 6, Table 4) suggest that *Schevodera* would be a monophyletic group. The suggested monophyly is strongly supported by the following synapomorphies (Fig. 6, Table 1): 1. body not longer than 10.5 mm; 2. body extremely widened; 3. antennae yellow in color; 4.  $\sigma$  antennal terminal segment as long as three to four preceding segments together; 5.  $\mathfrak{P}$  antennal terminal segment slightly longer than two preceding segments together; 6. pronotum clothed with very long hairs; 7. epipleuron extremely widened; 8. epipleural upper margin visible near humeri in dorsal view.

In the late Permian, 255 million years ago, the Shan-Thai terrain had just begun its northward drift off north-western Australia (Burrett et al., 1991). In the late Triassic, around 220 million years ago, the terrain collided with the combined South China and Indochina terrain, which was still loitering in the middle of the Tethys ocean (van Oosterzee, 1997). The Shan-Thai terrain contained present western Yunnan of China, Burma, Thailand, Malaysia and Sumatra, which fits well the present distribution of the genus (Table 5, Fig 7). The genus does not cross the faunal barrier between Borneo and Sulawesi, the Wallace Line proposed by Wallace in 1859, separating the Indo-Malayan Region and Australo-Malayan Region. There are no reports regarding the distribution in regions west of Burma and Indochina (except for S. hirticollis salvazai, which has invaded to Laos). The senior author did not discover the genus in examining specimens of the family from Guangxi, Guangdong and Hainan provinces, China, either. From these facts, we can infer that the genus should have originated during the drift of the Shan-Thai terrain, i.e. in the late Permian-late Triassic period, around 225-220 million years ago.

From the optimal reconstruction of the ancestral distribution of the genus (Fig. 8), we can deduce that its place of origin was most probably in the area between western Yunnan, one end of the long and narrow Shan-Thai terrain, and Burma. These two regions were connected in the terrain, whereas Thailand was located between Burma and Malaysia, and Sumatra was at the another end of the terrain neighboring with Malaysia. The proposed historic distribution (Fig. 8) also shows that the genus dispersed from Yunnan and its adjacent area to Sumatra and Java and then north to the Philippines via Borneo. The distributional disjunction in Thailand suggests probably unknown occurrences of this genus. If we presumed Thailand as the place of origin, the genus would have had to disperse to Burma and Yunnan, and Sumatra, respectively, and Thailand should be species rich. Unfortunately, we have not seen any evidence for the hypothesis. The genus in distribution pattern should be much like the genera *Neogria* Borchmann, *Xenocera*  Borchmann, Aulonogria Borchmann and Lagriocera Fairmaire of the same tribe, Lagriini (Borchmann, 1937; Chen, 1995). It is also like many other groups of organisms such as pangolin, tapirs, rhinos, flying lemurs, hedgehogs, weasels, badgers, skunks, otters, barking deer and chevrotain (van Oosterzee, 1997). They range from Burma (some into India) and Yunnan (several northward to Sichuan) to Java and northward through Borneo to Palawan and the Philippines, and do not naturally cross the Wallace Line.

Chen (1995) suggested that the genus originated from a Lagria-like ancestral species. The phylogenetic analysis in the study supports the suggestion (Table 3, Fig. 6). Lagria, a genus with the widest distribution and the largest number of species in the subfamily Lagriinae, occurs over all continents in the world except for America (Borchmann, 1937; Chen, 1995). From the fact, we could deduce that this genus originated in Gondwanaland no later than the Ordovician period, around 500 million years ago, when North America and Europe had separated from the Gondwanaland (van Oosterzee, 1997). In the Ordovicián, the large parts, if not all, of Southeast Asia lay off the eastern tip of a continent-sized peninsula of Gondwanaland (Metcalfe, 1993). In the Devonian, central Asia, Siberia and Mongolia, Tibet, North China, South China, Indochina, and eastern Malaysia rifted from Gondwana and began their northerly journey across the Tethys Sea (Metcalfe, 1993). Therefore, the genera Cerogria Borchmann and Heterogria Fairmaire of the same subfamily Lagriinae, distributed both in Asia and Africa, should have originated no later than Devonian, around 400 million years ago. Before the origin of Schevodera there were only these three genera existing in the Shan-Thai terrain (Borchmann, 1937; Chen, 1995). Male Cerogria have the antenna with at least the 9th segment dentately expanded, and the frons possesses a basal, strongly swollen tubercle (connecting lateral expansion) (Borchmann, 1937; Chen, 1996). In Heterogria, the pronotum has well defined lateral margins and each elytron has punctures thick and clearly forming rows (Borchmann, 1937; Chen, 1995). All these synapomorphies exclude the possibility of Cerogria and Heterogria as the ancestor of Schevodera. Therefore, Schevodera is hypothesized to have originated from a Lagria-like ancestor, bur further phylogenetic research including above two genera is needed before making a final conclusion.

Based on phylogenetic relationships and two main historical dispersal events, Schevodera could be obviously divided into three groups (Fig. 6, 8): Yunnan group, Indonesia group and Philippines group. The Yunnan group has the common characters of body length 8.5-10.5 mm, black to darkish-blue in elytral color and tempora about as long as ocular diameter (Tables 1-2). The species are distributed mainly in Yunnan and its adjacent areas, it is the most primitive of these three groups (Table 5, Figs 6-8). Its origin should go back to late Permian-late Triassic during the drift of the Shan-Thai terrain. Schevodera inflata, without support of synapomorphy on the phylogram, should be the most primitive species of the genus and the dispersal to Java must have happened after Java's emerging, i.e. no more than 50 million years ago. The following synapomorphies suggest that after speciation S.

glabricollis experienced significant derivation: blackish-brown or brownishblack in the color of mesothorax, metathorax and abdomen, and antennal segment 3 much longer than segment 4 (Tables 1-2, Fig. 6). Schevodera gracilicornis has the following synapomorphies (Tables 1-3, Fig. 6): male antennal terminal segment as long as 4-5 preceding segments together; female antennal terminal segment about as long as 3 preceding segments together; antennal segment 3 and 4 subequal; and female interocular distance about 1.5 times that of ocular transverse diameter. Naturally, S. gracilicornis is the most derived species of the Yunnan group.

The Indonesia group is paraphyletic. It constitutes a monophyletic taxon with the Philippines group with the synapomorphies: head reddish-yellow or yellow in color, and female interocular distance equal to ocular transverse diameter (Fig. 6, Tables 1-3). The group is primarily distributed in Indonesia but covers Burma, Indonesia and the Philippines (Table 4, Figs 7-8). The common characters of this group's species are (Tables 1-2): black to darkishblue in elytral color; male antennal terminal segment as long as 4-5 preceding segments together; punctures of pronotum and elytron on disc coarse; elytral rugae on disc weak.

Schevodera hirticollis should be the most primitive species of the Indonesia group that originated from Burma, sharing a common ancestor with S. gracilicornis in Burma (Table 4, Figs 6-8). S. hirticollis salvazai diverged from the ancestral population of S. *hirticollis* in Burma and then migrated to the present place (Laos) after the late Triassic period. Pieters and Supriatna (1990) suggested that north and south Borneo collided in the Eocene (around 50 million years ago) and Burret et al. (1991) tentatively suggested that parts of Sumatra and southern Borneo collided with the remainder of Southeast Asia in the Ecocene. The island of Java was squeezed from the sea floor somewhat near the location of Timor today between Indo-Australia, Pacific and Eurasia Plates, and began shunting toward Southeast Asia around 50 million years ago (van Oosterzee, 1997). Thus, the dispersal of the group's members from the South China Peninsula to Indonesia should have been after the Eocene, i.e. no longer than 50 million years ago. Borneo, Sumatra and Java clearly lay on the same shallow bank or continental shelf. The faunas of these islands were as similar as distant areas could be expected to be, even without an intervening sea. The sea must have been a recent invader, flooding the lowlands and volcanic peaks that became these islands (van Oosterzee, 1997). Therefore, we can presume that S. hirticollis, S. curticollis and S. dohrni are distributed throughout Sumatra, Java and Borneo, three large islands of Indonesia.

The Philippines group is monophyletic, supported by the synapomorphy, metathorax and abdomen reddish-brown in color, and consists of three endemic species in the Philippine islands (Fig. 6, Tables 3-4). Palawan emerged as an island in the Miocene, around 20 million years ago, slowly drifting to its current position from Asia as part of the South China Sea off-rider of Asian Plate which split off 32 million years ago. At the same time, Luzon, now the largest island in the Philippines, began as a series of small, emergent volcanic islands more or less in the same position as it is today (van

Oosterzee, 1997). From these facts, we suggest that S. setosa, as the most primitive species of this group and occurring only in Palawan, originated after the Miocene and shared a common ancestor with S. dohrni in Borneo. The Palawan archipelago should be the bridge for dispersal to the Philippines. The species S. insularis and S. spoliata were derived from a common ancestor of S. setosa, and formed in Luzon island after the Miocene period, i.e. no further than 20 million years ago. Mindanao emerged from the sea in its entirety probably around five million years ago. This means that the populations in Mindanao of S. insularis and S. spoliata should have been present within past five million years, crossing a series of small islands between Mindanao and Luzon. These two species are the most recent and, of course, the most derived species of the genus. The genera Odontogria Borchmann, Lorona Borchmann, Bothrionota Borchmann and Phaedogria Borchmann of the tribe Lagriini are also endemic in the Philippines (Borchmann, 1937). Their speciation and dispersal model should be similar to the Philippines group.

#### Acknowledgments

We thank Prof. X. K. Yang, Insect Collection, Institute of Zoology, Academia Sinica, and Prof. L. Z. Hua, Institute of Entomology, Zhongshan University, China for their contribution of specimens. Special thanks are due to Prof. R. K. Butlin, School of Biology, The University of Leeds, UK and Dr. C. Burrett, Geology Department, University of Tasmania, Australia for reviewing early drafts of this paper. We are also grateful to Dr. Z. Q. Zhang, International Institute of Entomology, The Natural History Museum, London and Dr. O. Tadauchi, Faculty of Agriculture, Kyushu University, Fukuoka, Japan for helping us with literature.

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Fig. 1. Schevodera glabricollis, sp. nov. Fig. 2. Epipleuron of S. glabricollis, lateroventral view. Figs. 3-5. Antennae (Q): 3, S. glabricollis; 4, S. gracilicornis (Borchmann); 5, S. inflata (Borchmann).

Table 1. List of characters and character states used in the phylogenetic analysis of *Schevodera*. The numbers in square brackets are the coding of character states. The arrows indicate the polarity of the character states.

- 1 Body size: Longer than 13 mm [0]; Not longer than 10.5 mm [1]; Not longer than 8.5 mm [2]. Polarity: 0→1→2, 0→2 (parallelism).
- 2 Body width: Normal [0]; Wide [1]; Extremely widened [2]. Polarity:  $1 \rightarrow 2$ ,  $1 \rightarrow 0$ .
- 3 Head color: Black or bluish black [0]; Blackish brown or brownish black [1]; Reddish brown [2]; Reddish yellow or yellow [3]. Polarity: 0→3→2, 0→1, 3→1 (parallelism).
- 4 Prothorax color: Black or bluish black [0]; Blackish brown or brownish black [1]; Reddish brown [2]; Reddish yellow or yellow [3]. Polarity: 0→3→2, 0→1, 3→1 (parallelism).
- 5 Elytron color: Black to darkish blue [0]; Reddish brown or yellowish brown [1].
  Polarity: 0→1.
- 6 Mesothorax color: Black or bluish black [0]; Blackish brown or brownish black [1]; Reddish brown [2]; Yellow [3]. Polarity: 0→3→2, 0→1.
- 7 Metathorax color: Black or bluish black [0]; Blackish brown or brownish black [1]; Reddish brown [2]; Red [3]. Polarity:  $0 \rightarrow 2$ ,  $0 \rightarrow 1$ ,  $0 \rightarrow 3$ .
- 8 Abdomen color: Black or bluish black [0]; Blackish brown or brownish black [1]; Reddish brown [2]; Red [3]. Polarity: 0→2, 0→1, 0→3.
- 9 Antenna color: Black [0]; Blackish brown [1]; Reddish brown [2]; Yellow [3]. Polarity: 0→3→2, 3→1, 3→0 (reversal), 0→2.
- 10 Leg color: Black or bluish black [0]; Blackish brown or brownish black [1]; Yellowish brown [2]; Yellow [3]. Polarity: 0→2→3, 0→1, 2→0 (reversal).
- 11 Length of  $\sigma$  antennal terminal segment: Shorter than 3 preceding segments together [0]; Shorter than 4 preceding segments together [1]; Shorter than 5 preceding segments together [2]; At least as long as 5 preceding segments together [3].  $0 \rightarrow 1 \rightarrow 2 \rightarrow 3$ .
- 12 Length of ♀ antennal terminal segment: Not longer than 2 preceding segments together [0]; Slightly longer than 2 preceding segments together [1]; About as long as 3 preceding segments together [2]. 0→1→2.
- 13 Antennal segment 3: Much shorter than segment 4 [0]; About as long as segment 4 [1]; Slightly longer than segment 4 [2]; Much longer than segment 4 [3]. Polarity: 2→1, 2→0, 2→3.
- 14 Ratio of ♀ interocular distance to eye transverse diameter: About 3 [0]; About 2 [1]; About 1.5 [2]; About 1 [3]. Polarity: 1→2→3, 1→0.
- 15 Tempora: Much longer than eye diameter [0]; About as long as eye diameter [1]; Much shorter than eye diameter [2]. Polarity: 1→2, 1→0.
- 16 Pronotal hairs: Short [0]; Very long [1]. Polarity:  $0 \rightarrow 1$ ,  $1 \rightarrow 0$  (reversal).
- 17 Pronotal punctures on disc: Coarse [0]; Fine [1]; Hardly visible [2]. Polarity: 1→0 (parallelism), 1→2.
- 18 Elytral punctures on disc: Coarse [0]; Fine [1]. Polarity:  $0 \rightarrow 1$  (parallelism).
- 19 Elytral rugae on disc: Weak [0]; Normal [1]; Strong [2]. Polarity: 0→2, 0→1 (parallelism).
- 20 Epipleuron width: Normal [0]; Extremely widened [1]. Polarity:  $0 \rightarrow 1$ .
- 21 Epipleural upper margin in dorsal view: Not visible nearby humeri [0]; Visible nearby humeri [1]. Polarity: 0→1.

**Table 2.** Character state matrix for ten *Schevodera* species (including one subspecies) and two outgroups (\*) used in the phylogenetic analysis. The numbers indicate the state of each character from character 1-21. The question marks (?) indicate missing or unknown data. The mark "\*" implies "both state 0 and 1" as polymorphism.

	Characters				
Taxa	00000	00001	11111	11112	2
	12345	67890	12345	67890	1
Schevodera inflata	12100	00000	11211	11101	1
Schevodera gracilicornis	12000	.00030	$2\ 2\ 1\ 2\ 1$	12111	1
Schevodera glabricollis	12110	11131	?1311	01001	1
Schevodera hirticollis	?2330	* * * * *	2??3?	11001	1
S. hirticollis salvazai	?2110	* * * * *	2??3?	11001	1
Schevodera curticollis	?2330	30033	2????	11001	1
Schevodera dohrni	?2220	30032	2????	11001	1
Schevodera insularis	$2\ 2\ 2\ 2\ 1$	$2\ 2\ 2\ 2\ 0$	$3\ 2\ 1\ 3\ 2$	10011	1
Schevodera setosa	$2\ 2\ 2\ 2\ 0$	$2\ 0\ ?\ 0\ ?$	$2\ 2\ 1\ 3\ 1$	11021	1
Schevodera spoliata	$2\ 2\ 2\ 2\ 1$	$2\ 2\ 2\ 2\ 2\ 2$	22?31	10001	1
Lagria (Ammocera) chapaensis*	20030	00000	00011	01000	0
Lagria (Lagria) ventralis*	01000	03300	00200	10010	0

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Table 3. Character fitting in search for the most parsimonious cladograms. CI = m/s, where m is the minimum possible steps and s is the actual steps in the character obtained on the tree. The RI can be thought of as the proportion of similarities on a tree interpreted as synapomorphic (Farris, 1989).

Number of charac- ters	Number of states	Minimum possible steps	Actual steps on the phylogram	Maxmum possible steps	CI	RI
1	2	2	3	4	0.667	0.50
2	2	2	2	3	1.000	1.00
3	<b>3</b> , ·	3	4	8 .	0.750	0.80
4	3	3	5	8	0.600	0.60
5	1	1	1	2	1.000	1.00
6	3	5	5	8	1.000	1.00
7	3	5	5	6	1.000	1.00
8	3	5	5	6	1.000	1.00
9	3	4	7	8	0.571	0.25
10	3	5	6	6	0.833	0.00
11	3	3	3	6	1.000	1.00
12	2	2	2	6	1.000	1.00
13	3	3	3	4	1.000	1.00
14	3	3	3	10	1.000	1.00
15	2	2	2	2	1.000	1.00
16	1	1	2	2	0.500	0.00
17	2	2	3	4	1.667	0.50
18	1	1	2	2	0.500	0.00
19	2	2	4	4	0.500	0.00
20	1	1	1	2	1.000	1.00
21	1	1	1	2	1.000	1.00

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Fig. 6. The optimal phylogram of interspecific relationships in Schevodera, obtained with the brand-and-bound algorithm using PAUP\* (Length=182, CI=0.791, RI=0.696, f-ratio=0.0201). Numbers above bars correspond to characters (all but character 4 and 19) as described in the text; numbers below bars correspond to states. Black bars represent synapomorphies, stippled bars parallelisms, and white bars reversals.

The branches are labeled and the character state changes on these branches are as follows: branch 1:  $1(0\rightarrow 1)$ ,  $2(1\rightarrow 2)$ ,  $9(0\rightarrow 3)$ ,  $11(0\rightarrow 1)$ ,  $12(0\rightarrow 1)$ ,  $20(0\rightarrow 1)$ ,  $21(0\rightarrow 1)$ ; branch 2:  $3(0\rightarrow 1)$ ; branch 3:  $9(3\rightarrow 0)$ ,  $18(0\rightarrow 1)$ ; branch 4:  $4(0\rightarrow 1)$ ,  $6(0\rightarrow 1)$ ,  $7(0\rightarrow 1)$ ,  $8(0\rightarrow 1)$ ,  $10(0\rightarrow 1)$ ,  $13(2\rightarrow 3)$ ,  $16(1\rightarrow 0)$ ; branch 5:  $11(1\rightarrow 2)$ ,  $12(1\rightarrow 2)$ ,  $13(2\rightarrow 1)$ ,  $14(1\rightarrow 2)$ ; branch 6:  $17(1\rightarrow 2)$ ,  $18(0\rightarrow 1)$ ,  $19(0\rightarrow 1)$ ; branch 7:  $1(1\rightarrow 2)$ ,  $3(0\rightarrow 3)$ ,  $4(0\rightarrow 3)$ ,  $14(2\rightarrow 3)$ ; branch 8:  $9(3\rightarrow 0)$ ; branch 9:  $3(3\rightarrow 1)$ ,  $4(3\rightarrow 1)$ ; branch 10:  $6(0\rightarrow 3)$ ,  $10(0\rightarrow 2)$ ; branch 11:  $10(2\rightarrow 3)$ ; branch 12:  $3(3\rightarrow 2)$ ,  $4(3\rightarrow 2)$ ; branch 13:  $6(3\rightarrow 2)$ ,  $8(0\rightarrow 2)$ ,  $9(3\rightarrow 0)$ ; branch 14:  $19(0\rightarrow 2)$ ; branch 15:  $5(0\rightarrow 1)$ ,  $7(0\rightarrow 2)$ ,  $9(0\rightarrow 2)$ ,  $17(1\rightarrow 0)$ ; branch 16:  $10(2\rightarrow 0)$ ,  $11(2\rightarrow 3)$ ,  $15(1\rightarrow 2)$ ,  $19(0\rightarrow 1)$ ; branch 17:  $7(0\rightarrow 3)$ ,  $8(0\rightarrow 3)$ ,  $14(1\rightarrow 0)$ ,  $15(1\rightarrow 0)$ ,  $17(1\rightarrow 0)$ ,  $19(0\rightarrow 1)$ ; branch 18:  $1(0\rightarrow 2)$ ,  $2(1\rightarrow 0)$ ,  $4(0\rightarrow 3)$ ,  $13(2\rightarrow 0)$ ,  $16(1\rightarrow 0)$ .

The present branch length, minimum possible length and maximum possible length (the latter two are in brackets) on each branch are as follows: branch 1: 25(20, 25); branch 2: 2(2, 5); branch 3: 8(6, 8); branch 4: 18(18, 20); branch 5: 9(9, 11); branch 6: 12(12, 17); branch 7: 9(6, 9); branch 8: 2(0, 2); branch 9: 4(4, 4); branch 10: 4(2, 9); branch 11: 2(0, 4); branch 12: 4(4, 9); branch 13: 6(2, 9); branch 14: 3(3, 5); branch 15: 13(11, 14); branch 16: 10(9, 11).

Table 4. The results and conclusion of the T-PTP test used for testing the assumed monophylies located at branch 1, 2, 5, 7, 13 and 15 of Fig. 6. The branch-and-bound search was used for searching the shortest trees. 99 randomized data sets and the original data set were analyzed for each monophyly test. The character states of all taxa were randomized. The length of minimum-length trees from the original data set with any constraint listed in the table or combination of constraints is 182 steps, same with that in PTP test and in Fig. 6.

Shortest-tree length for original data with non- monophyly	Tree length difference for original data	Tree length differences for random data	T-PTP value	Support the mono- phyly
. 196	14	-20 - 3	0.01	yes
182	0	-20 - 4	0.11	no
182	0	-30 - 0	0.02	yes
182	0	-361	0.01	yes
184	2	-27 - 0	0.01	yes
193	11	-18 - 3	0.01	yes
]	Shortest-tree length for original data with non- monophyly 196 182 182 182 182 182 184 193	Shortest-tree length for original data with non- monophylyTree length difference for original data1961418201820182018211	Shortest-tree length for original data with non- monophylyTree length difference for original dataTree length differences for random data19614-20 - 31820-20 - 41820-30 - 01820-3611842-27 - 019311-18 - 3	Shortest-tree length for original data with non- monophylyTree length difference for original dataTree length differences for random dataT-PTP value19614-20 - 30.011820-20 - 40.111820-30 - 00.021820-36 - 10.011842-27 - 00.0119311-18 - 30.01

**Table 5.** Known distribution of species in the genus *Schevodera* and two outgroup species (\*) in the genus *Lagria*. The codings of distributional areas are in brackets. Y - Yunnan and its adjacent areas; I - Indonesia; P - Philippines.

Species	Distribution
Schevodera inflata	China: Yunnan (Menghai, Mengla, Jinghong, Xishuangbanna); Indonesia: Java. (YI)
Schevodera gracilicornis	China: Yunnan (Jinghong, Xiaomengyang); Burma: Carin (Ghecu, Cheba). (Y)
Schevodera glabricollis	China: Yunnan (Cheli).(Y)
Schevodera hirticollis	Burma: Pegu; Indonesia: Borneo; Philippines: Palawan. (YIP)
S. hirticollis salvazai	Laos. (Y)
Schevodera curticollis	Indonesia: Java. (I)
Schevodera dohrni	Indonesia: Sumatra. (I)
Schevodera insularis	Philippines: Mindanao, Basilan, Luzon. (P)
Schevodera setosa	Philippines: Palawan (Binaluan). (P)
Schevodera spoliata	Philippines: Luzon (Baguio, Benguet), Mindanao, Basilan. (P)
Lagria (Ammocera) chapaensis*	China: Yunnan; North Burma; North Vietnam. (Y)
Lagria (Lagria) ventralis*	China: Yunnan, Guizhou, Chongqing, South- ern China provinces; India; Nepal; Burma; Thailand; Vietnam; Laos, Kampuchea. (Y)



Fig. 7. Distribution of the species of Schevodera and representatives of Lagria: **0** S. inflata (Borchmann, 1925), **9** S. gracilicornis (Borchmann, 1909), **8** S. glabricollis, sp. nov., **0** S. hirticollis (Borchmann, 1909), **9** S. hirticollis salvazai (Pic, 1934), **6** S. curticollis (Borchmann, 1934), **6** S. dohrni Borchmann, 1940), **9** S. insularis (Borchmann, 1930), **9** S. setosa (Borchmann, 1930), **9** S. spoliata (Borchmann, 1930), **9** Lagria (Ammocera) chapaensis Pic, 1931, **■** Lagria (Lagria) ventralis Reitter, 1880.



Fig. 8. The optimal reconstruction of the ancestral distributions of the Schevodera obtained by dispersal-vicariance analysis, showing the biogeographical history of the genus. At each node, the optimal distribution prior to variance is given. Five dispersal events required by the optimal reconstruction are indicated on the branches. Note that in dispersal-vicariance analysis, the cost of dispersal is one per area added to an ancestral distribution, thus the cost of the assumption that S. hirticollis dispersed from Burma (the region Yunnan and its adjacent areas) to the other two regions, Indonesia and Philippines (+IP) is two dispersals. Implied between-area vicariance events are indicated by hyphens in the ancestral distribution.