

Article

Diversity of Curculionoidea in Humid Rain Forest Canopies of Borneo: A Taxonomic Blank Spot

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Abstract: From 1992 to 2009, 334 trees were sampled by insecticidal knockdown on Borneo, Malaysia. Here, we describe the taxonomic composition of the 9671 specimens and 1589 species Curculionoidea collected (with additional notes on Cerambycidae). We found a largely unknown fauna with an assumed proportion of over 80% of species new to science, including all 33 Apionidae and 26 Ceutorhynchinae species. Specialists could usually identify only a few specimens leaving the remaining beetles for further investigation. The samples contain numerous genera, two tribes (Egriini, Viticiini), one subfamily (Mesoptiliinae) and one family (Belidae) new to Borneo and several genera not recorded west of the Wallace line before. These data show how little is known about canopy diversity. The lack of taxonomic knowledge implies a respective lack of autecological knowledge and is alarming. Some taxa differed conspicuously between primary and disturbed forests. In contrast to common literature, our results let us conclude that current efforts to narrow down the extent of tropical diversity and its ecological importance must consider the enormous species diversity of the canopy.

Keywords: Borneo; tropical forest canopies; fogging; diversity; forest disturbance; weevil fauna; longhorned beetle (Cerambycidae); new species

1. Introduction

Despite all efforts, the global extent of biodiversity is still insufficiently known and controversial [1,2]. This lack is mostly due to poor knowledge of tropical rain forests where large areas and habitats like the canopy remain insufficiently researched. Although scientists have known for decades that arthropod richness is very high in the canopy of tropical trees [3,4], no comprehensive data or long-term studies have yet been published from the canopy of any near-equator rain forest worldwide. Considering the importance of biodiversity for ecosystem function and services [5] research in tropical rain forests—and from our perspective in the canopy—should be prioritized. Primary forests are ruthlessly exploited worldwide and pushed back to a few wildlife sanctuaries [6]. Evidence is growing that disturbed forests differ fundamentally from primary forests not only in respect to species diversity but also to system services on which humans depend [7]. Understanding the fundamental processes requires working in pristine forests where most species are usually new to science [8–10], which makes research even more difficult. Besides preliminary work on morphospecies sorting only the exact identification of this largely unknown diversity ensures advanced future ecological analyses. Moreover, the lack of taxonomic knowledge causes an almost general ignorance about the autecological requirements of species and makes predictions concerning the future of disturbed forests rather imprecise.

There is an urgent need for well processed data documenting the distribution of biodiversity within and between forest types. Our work narrows this lack of knowledge by analyzing the faunistic and taxonomic composition of arboreal beetles which have been collected from 334 trees in primary and disturbed forests of southeast Asia from 1992 to 2009. Here, we present data on the Curculionoidea, one of the most diverse and abundant group of beetles [11]. We provide insight into the faunistic-taxonomic composition of the arboreal weevil fauna and report some striking differences in taxa abundance between primary and disturbed forests.

2. Materials and Methods

2.1. Study Area

All fogging sites are located in Sabah, the northeastern part of East Malaysia, Borneo. Research was carried out in different primary and disturbed forests. Most data were gathered in primary “Mixed Dipterocarpaceae lowland forests” between 300 m and 900 m a.s.l. mainly in different substations of the Kinabalu National Park, Malaysia (06°02′54.18″ N, 116°41′56.34″ E) but also on Gaya Island (6°0′51.36″ N, 116°1′13.74″ E) and in the National Parks Crocker Range (5°24′43.68″ N, 116°5′24.84″ E) and Tawau (4°24′1.26″ N, 117°53′24.66″ E) as the most southern area. There were in total 171 trees. In addition, 43 trees were sampled at different altitudes ranging from 1000 m to 2500 m a.s.l. at Mt. Kinabalu and in the Crocker Range. Different types of disturbed forest were also sampled: 10- to 15-year-old pioneer vegetation on the two small islands Bakkungan Kecil (6°10′0.66″ N, 118°6′32.88″ E) and Selingaan (6°10′31.38″ N, 118°3′41.10″ E)—10 trees together. Three secondary forests of 5, 15 and 40 years after natural regrowth which were growing close to the Kinabalu Park (6°19′0.84″ N, 116°44′2.1997″ E) and another three isolated secondary forests of 10, 20 and 50 years after natural regrowth in a distance of at least 10 km to the Crocker Range primary forest (5°26′0.68″ N, 116°7′58.78″ E). Altogether, these were 80 trees. We also sampled 15 oil palms that were growing in direct neighborhood to the primary forest of Tawau and 15 fruit trees of different species in garden areas (6°17′36.84″ N, 116°43′5.76″ E) in the Kinabalu region. All disturbed forests were found in areas originally covered with lowland forest (between 5 m and 400 m a.s.l.). More details including a map have been published in [9].

2.2. Collecting and Sorting of Canopy Beetles, Genus and Species Identification

During 1992 and 2009, arthropods were collected by means of insecticidal knock-down (‘fogging’). Natural pyrethrum diluted in a highly purified white oil was used as insecticide because it degrades within hours in sunlight leaving no poisonous substances in the trees. Fogging was carried out in the early morning or late in the afternoon when there was little wind. All arthropods that dropped into the collecting sheets installed beneath a tree crown after two hours following fogging were transferred into vials filled with ethanol. More technical information has been published elsewhere [12]. Here, we focus on weevils following preferably the classification proposed by Alonso-Zarazaga and Lyal [13], with slight modifications; see Oberprieler [14]. We are aware that there are also several changes at the subfamily level in between, but did not follow these proposals for practical reasons. Beetles were sorted to morphotypes (morphospecies) and specimens were distinguished by optical means. Morphotypes were treated as real species when sorted by taxa specialists. A dissection of the genitalia was usually not carried out and left to specialists.

Besides specialist knowledge, current taxonomic papers and revisions were used for species determination. Furthermore, the SDEI museum collections in Eberswalde (now Müncheberg) and Dresden were helpful, especially for Conoderinae, Dryophthoridae and Entiminae.

2.3. Sampled Trees

Tree diversity is very high with more than 1000 species found in the Kinabalu area and more than 3000 species reported from Borneo [15]. The sampled tree species represent 23 plant

families in the primary forests. These were Annonaceae, Burseraceae, Clusiaceae, Cornaceae, Dipterocarpaceae, Elaeocarpaceae, Euphorbiaceae, Fagaceae, Lamiaceae, Lauraceae, Lecythidaceae, Malvaceae, Meliaceae, Moraceae, Myrtaceae, Olacaceae, Phyllanthaceae, Podocarpaceae, Polygalaceae, Putranjivaceae, Rhizophoraceae, Sapotaceae, and Urticaceae. Twenty-one families were sampled in the disturbed forests, namely Anacardiaceae, Annonaceae, Aquifoliaceae, Arecaceae, Clethraceae, Combretaceae, Ericaceae, Escalloniaceae, Euphorbiaceae, Fabaceae, Lamiaceae, Lauraceae, Malvaceae, Meliaceae, Myrtaceae, Phyllanthaceae, Podocarpaceae, Sapindaceae, Sapotaceae, Symplocaceae, and Theaceae, with nine families represented in both types. Most foggings were carried out on *Aporosa lagenocarpa* A. Shaw and *A. subcaudata* Merr. (Phyllanthaceae) which were frequently found in the understory of the studied primary forests. Common trees in the secondary forests were *Melanolepis* sp. (Euphorbiaceae-Acalyphoideae), *Melochia umbellata* (Houlst.) Stapf (Malvaceae-Byttnerioideae) and *Vitex pinnata* L. (Lamiaceae-Verbenioideae). These trees were not found in the primary forests.

3. Results and Discussion

3.1. Suitability of Fogging for Collecting Canopy Weevils

From all 334 trees, we collected 9671 individual Curculionoidea in 1589 species. Due to the high number of species from the groups Curculionini, Ochyromerini and Rhynchitidae, as well as smaller groups like Ceutorhynchinae, Nanophyidae or Rhamphini, the data show that canopy fogging is well-suited to collect arboreal species that inhabit leaves, flowers and fruits of trees. This seems to hold also for several groups that are usually regarded as saproxylic, like Anthribidae, Conoderinae, Cossoninae, Cryptorhynchinae, Molytinae and Scolytinae which were also represented by more than 100 species each. Lower numbers than expected were found in Attelabidae with one species apart from genus *Euops* and Dryophthoridae (15 species in each family).

3.2. Faunistic-Taxonomic Classification of Canopy Beetles

The fogging results are presented in Table 1. It contains all relevant taxonomic weevil groups found in the samples, the number of species and specimens, the experts included in the analyses and the number of identified genera and species before 2013.

Table 1. Canopy weevils from the superfamily Curculionoidea in the samples from Malaysia (Borneo).

Taxa	Number of Morpho-Species	Number of Specimens	Identified (Genus/Species Level)	Identified by *
CURCULIONOIDEA				
Anthribidae	217	710	-	
Belidae	1	1	1/0	
Rhynchitidae	110	358	-	
Attelabidae	15	60	14/0	Riedel
Brentidae	32	65	22/9	Bartolozzi, Mantilleri
Apionidae	33	279	3/0	Wanat
Nanophyidae	44	162	-	
Dryophthoridae	15	29	10/0	
CURCULIONIDAE				
Baridinae	36	141	16/1	Prena
Ceutorhynchinae	26	203	13/0	Yoshitake, Colonnelli
Conoderinae	171	418	-	
Cossoninae	107	494	-	
Cryptorhynchinae	106	258	-	
Curculioninae-Acalyptini	32	521	8/0	Sprick
Curculioninae-Anoplini	6	12	6/0	
Curculioninae-Anthonomini	5	93	4/1	Sprick
Curculioninae-Curculionini	122	649	-	
Curculioninae-Demimaeini	3	3	3/0	
Curculioninae-Derelomini	1	50	1/1	
Curculioninae-Ochyromerini	133	1090	93/3	Sprick
Curculioninae-Rhamphini	52	178	42/3	Sprick
Curculioninae-Storeini	2	7	2/0	

Table 1. Cont.

Taxa	Number of Morpho-Species	Number of Specimens	Identified (Genus/Species Level)	Identified by *
CURCULIONIDAE				
Entiminae	38	658	-	
Hyperinae	1	1	1/1	
Mesoptiliinae	1	3	0/0	
Molytinae	139	455	-	
Scolytinae	111	2665	109/50	Beaver
Platypodinae	17 **	99	11/14	Beaver
doubtful assignments	ca 20–30			
CHRYSOELOIDEA				
Cerambycidae	219	621	199/37	Holzschuh, Weigel

*: if no specialist is mentioned there is only morphospecies sorting carried out by the authors without complete determination of the group; **: seventeen further morphotypes had been found in later samples.

3.3. Special Part

Belidae-Oxycoryninae

There is one specimen of the genus *Metrioxena* in the sense of Alonso-Zarazaga and Lyal [13]. According to Legalov [16], it is now placed in *Vladimirixena* (Figure 1). *Metrioxena* is distributed in Malaysia and Indonesia, and *Vladimirixena* in Indonesia. *Metrioxena* sensu lato was also detected in Baltic Amber indicating a minimum age of 35 million years. It is the first record on Borneo, also of the entire family, even though its occurrence was to be expected there.

Attelabidae

In our data, we found one *Allolabus* species and 14 of the genus *Euops*, mainly subgenus *Suniops* (Figure 1). Five morphospecies were identified to species level but all are in need of confirmation by the study of type specimens. Thus, at least 10 species are undescribed.

Apionidae

Our samples contain 33 species of which 21 are in the tribe Piezotrachelini, 11 in the tribe Ixapiini and 1 in the Rhadinocybini. None of the specimens could be identified to species and thus all of them may be new to science (Wanat, pers. comm.). Only three genera could be identified: *Microconapion*, *Ommatocybus* and *Piezaplemonus* with one species each (Figure 1). The last genus, described by Wanat [17], was hitherto known only from Thailand and the genus *Microconapion* from Japan, Taiwan and Vietnam. *Ommatocybus* was erected by Wanat [18] during his study on Australo-Pacific Apionidae. This means that all the genera were not previously recorded from Borneo and Malaysia, and this is also true for the tribe Rhadinocybini (see Alonso-Zarazaga and Lyal [13]). According to Wanat, the remaining 30 species represent four as yet undescribed genera. At least these data show that the Bornean Apionidae canopy fauna is completely unexplored.

Brentidae

There are 32 species and, apart from the circumtropical *Cylas formicarius* (Fabricius, 1798), eight of them were identified to the species level. A further species was described as new, *Microtrachelizus floreni* Mantilleri, 2012 [19], and 11 species were identified to a genus level of which three will be described later (*Cordus* sp., *Homophylus* sp., *Hypomiolispa* sp.) (Figure 2). The samples contained 10 species, mainly of the subfamily Cyphagoginae, which remained unidentified (without genus diagnosis). The genus *Cordus* was up to now only known from Australasia (Australia, New Guinea, Solomon Islands) and the species *Calodromus insignis* (Senna, 1895) only from Sumatra (Figure 3).

The checklist of Brentidae includes 204 species from Borneo including three mentioned species known only from “Indonesia” without further location [20]. From all species fogged, only nine (28%) could be determined to the species level, representing 4.4% of the known Bornean fauna of Brentidae. If the difficult genus *Cyphagogus* is excluded, the values change to 32% and 4.9%, respectively. The data demonstrate that, within a group for which all available data are summarized at the present time (see the world catalogue of Sforzi and Bartolozzi [20]), the tree crowns apparently harbor a rather little known Brentidae fauna on Borneo.



Figure 1. *Metrioxena* s.l., now. to *Vladimirixena* sp. (Belidae) (a); *Allolabus* sp. (b); *Euops* sp. (both Attelabidae) (c); *Ommatocybus* sp. (d); and a new species of the tribe Ixapiini (both Apionidae) (e).



Figure 2. *Achrionota* sp. (a) and *Homophylus* sp. (both Brentidae) (b).

Curculionidae-Baridinae

Only one species could be identified without doubt to species level: *Anoplobaris sabahna*, described by Morimoto and Yoshihara [21], based on one specimen from Mt. Kinabalu. It has now been collected again in the same area, represented by four individuals. Two further species were identified provisionally. The following genera were determined: *Acythopeus* (1–2 species), *Anoplobaris*, *Athesapeuta*, *Centrinertus*, *Hollisiella* (1–2 species), *Lophobaris*, *Mononychobaris* (1–3 species) and *Nespilobaris* (3–4 species) and two further genera with doubt: *Aponychius* and *Omobaris*.

The genera *Centrinertus*, *Hollisiella*, *Lophobaris* and *Nespilobaris* are new to Malaysia and Borneo (Figure 3). The first was formerly known only from the Philippines, the second from China, the third from Taiwan to Java and the Philippines, so that its occurrence on Borneo could be expected. This is also true for *Nespilobaris*, which was known from Eastern Siberia, Japan, China, Australia and Africa [13,22]. The considerable number of Baridinae genera that had not been recorded from Borneo demonstrates the poor knowledge on the distribution of this group of weevils in Southeast Asia.

Curculionidae-Ceutorhynchinae

The morphospecies sorting revealed 24 species, but Enzo Colonnelli and Hiraku Yoshitake, who checked it in part, both separated one more species each, resulting in a total number of 26 Ceutorhynchinae species. The tribe Mecysmoderini is the main group, represented by 17 species, followed by Ceutorhynchini with five species, Hypohypurini with three and Egrini with one, a *Megahypurus* species (det. E. Colonnelli by photo). None of them could be identified to species level suggesting that all of them are new to science. Besides *Coelioderes* (one species) and *Watanabesaruzo* (two species), two genera just recently described by Yoshitake and Yamauchi [23] and Yoshitake and

Ito [24], there are two *Coeliosomus* and one *Cysmemoderes* species (aff. *C. gibbicollis* (Hustache, 1925), det. Yoshitake) and several species from further undescribed *Mecysmoderini* genera in the samples. The Ceutorhynchini are represented by *Hainokisaruzo* and the Hypohypurini by the single genus *Hypohypurus*. Unfortunately, Yoshitake, who was interested in receiving all Ceutorhynchinae weevils, has not described any to date.



Figure 3. Adult (a) and conspicuous hind tibiae (b) of *Calodromus insignis* (Brentidae), *Centrinertus* spec. (c); *Nespilobaris* sp. (both Baridinae) (d); *Watanabesazuro* sp. (Mecysmoderini) (e); and *Megahypurus* sp. from the tribe Egriini (both Ceutorhynchinae) (f).

The insufficient knowledge about this group in Malaysia and Indonesia is shown by the fact that *Watanabesaruzo* was found until now only in Bali (Indonesia), Yunnan (China) and Perak (Malaysia) [23, 25], *Coelioderes* in Eastern Siberia, Japan, Korea and China [24,26]) and *Hainokisaruzo* by several species in China, Taiwan, India and Japan [27,28]. The tribe Hypohypurini, erected by Colonnelli in 2004 [26], was recorded from China and Vietnam, North Australia, Madagascar and Central Africa, and the tribe Egriini was also not reported from Malaysia or Borneo before 2012 [29]. *Megahypurus* Korotyaev, 1989 was described from Vietnam (Figure 3). As previous collecting in Indonesia revealed a rather small number of Ceutorhynchinae (see, for example: [26]), fogging was very successful in collecting arboreal Ceutorhynchinae. In a current fogging study on Java, there were also a few Ceutorhynchinae of the genus *Watanabesaruzo* and other *Mecysmoderini* genera (A. Floren, own data).

Curculionidae-Curculioninae (Figures 4–7)

This group of weevils is represented by a great number of morphospecies in the samples. Due to the extensive work of mainly Japanese authors (see citations below), there is current information about the occurrence of some tribes in southeast Asia (especially Acalyptini, Anthonomini, Ochyromerini and Rhamphini). Here, we mainly present results for Acalyptini, Ochyromerini, Rhamphini and some species-poor tribes.

The following tribes could be identified (number of morphospecies in brackets): Acalyptini (31), Anoplini (6), Anthonomini (5), Curculionini (122), Demimaeini (3), Derelomini (1), Storeini (2), Rhamphini (52; see below), and Ochyromerini (previously Tychiini, subtribe Ochyromerina) (133). Morphotype differentiation in Acalyptini and in Ochyromerini is still a matter of some uncertainty because there is a rather large proportion of small yellowish weevils of great similarity (in Acalyptini, about two thirds of the total; Figures 4, 5 and 7). Hence, an analysis of the morphospecies numbers, including the dissection of the genitalia, could change the numbers. Usually, dissections were not made to avoid incidental destructions, as most species were present in only small numbers.

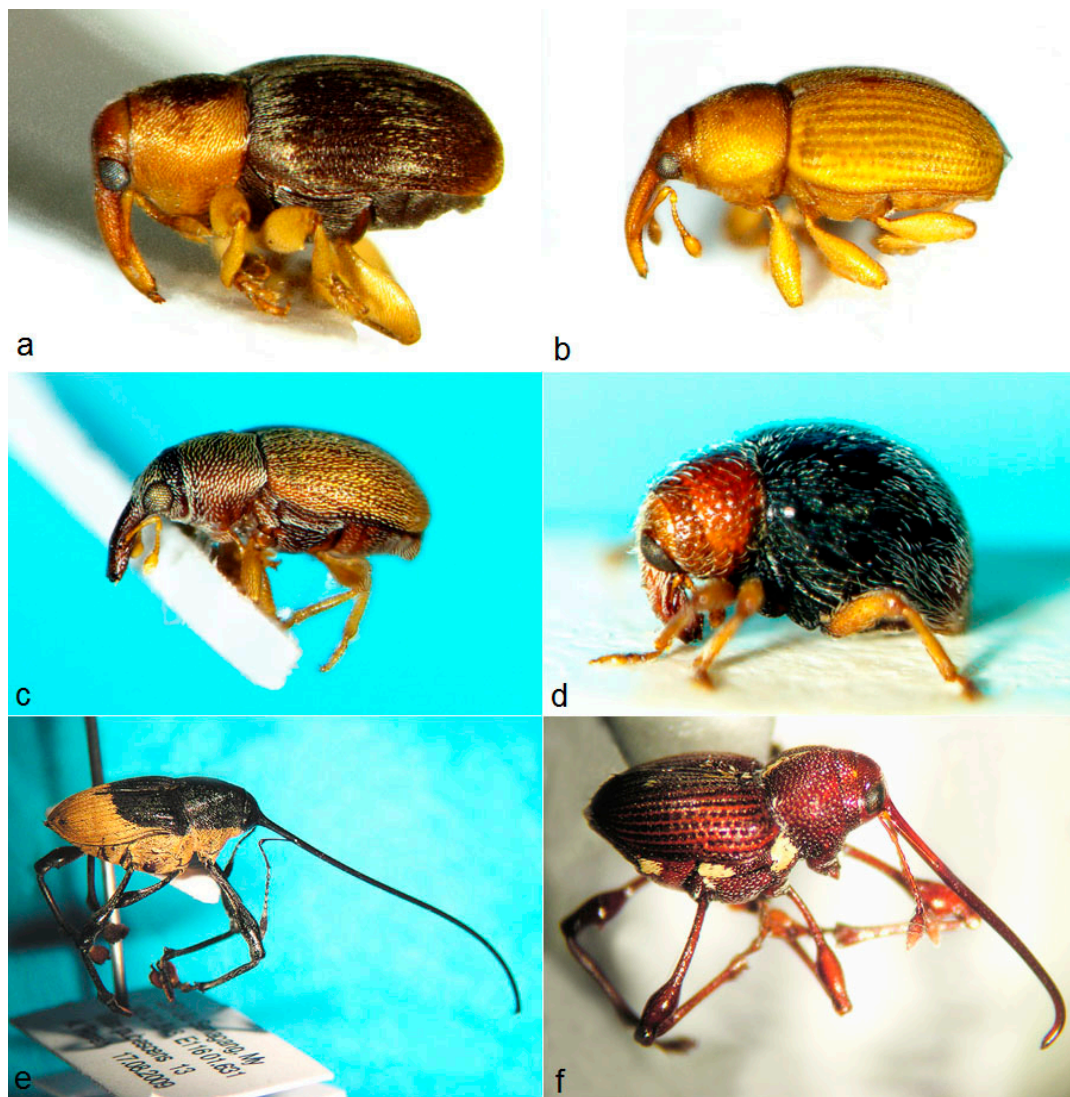


Figure 4. Curculioninae I. *Parimera* spec. (a) and two unknown small genera of Acalyptini (b,c); the latter cf. *Niseida* (c); a scymnine-like, red-and-black coloured *Demimaea* species with trifold hairs ventrally and at the base of the elytra (d) and two long-nosed Curculionini species (e,f); one of them (f) a *Pseudoculio* species.



Figure 5. Curculioninae II. Ochyromerini: *Opseoscapha* cf. *alternans* Faust, 1888 (a); *Katsurazo* sp. (b); *Viticis* spec. (c); *Lepidimerodes* sp. (d); *Endaeus* sp. (e); a small yellowish *Ochyromera* species (f); resembling *Endaeus* species, but with seven funicular segments, and one unidentified and possibly new genus with seven funicular segments (g). The last photo (h) shows a member of Anthonomini (*Usingerius parvidens*) resembling Ochyromerini.

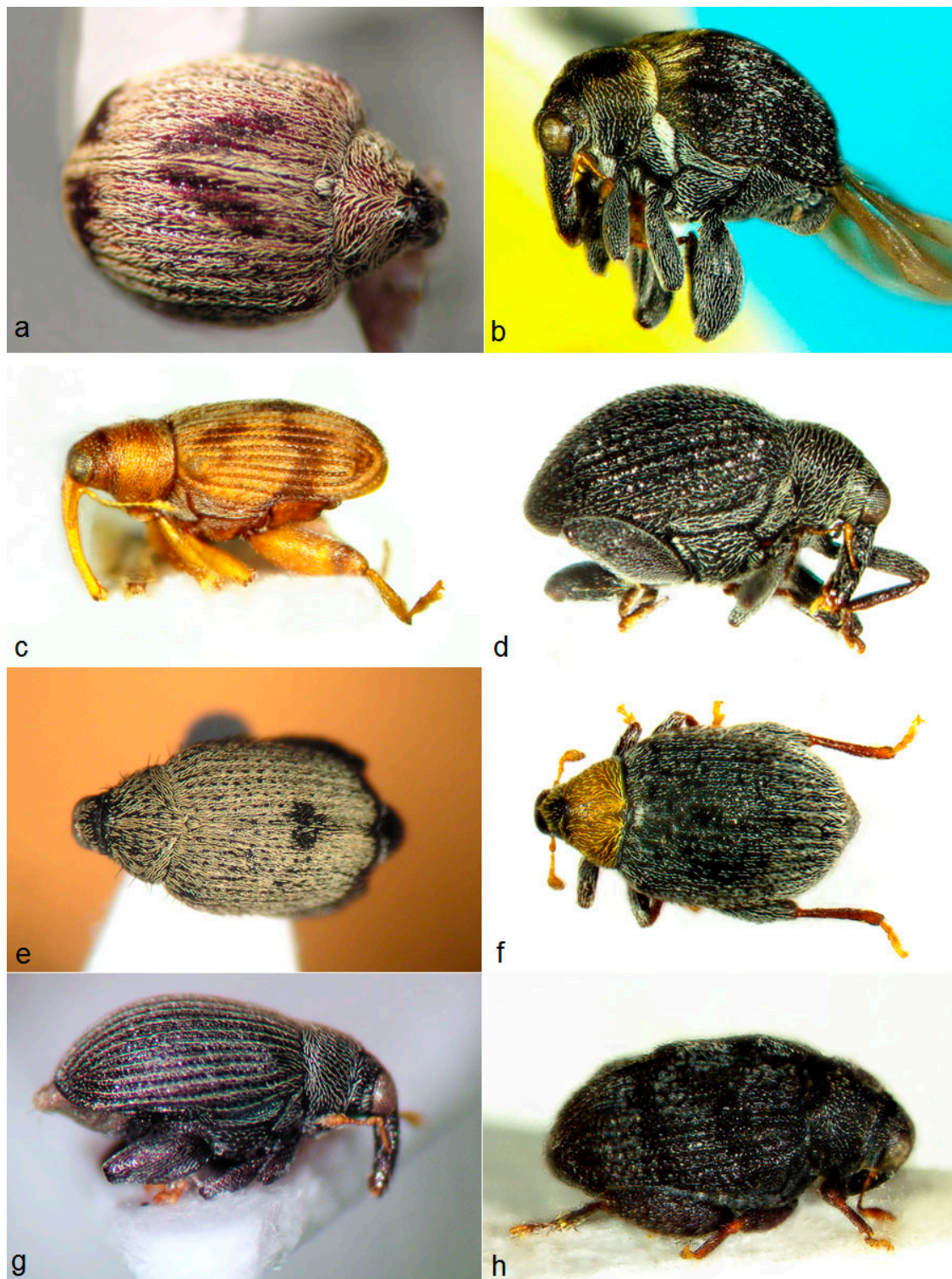


Figure 6. Curculioninae III. Rhamphini. *Sphaerorchestes* sp. (a); *Imachra siamensis* (b); *Indodinorrhopalus* sp. (c); *Morimotonomizo* sp. (d); *Orchestes* (*Orchestes*) sp. (e); *Orchestes* (*Nomizo*) sp. (f); and two unknown and probably new genera (g,h).

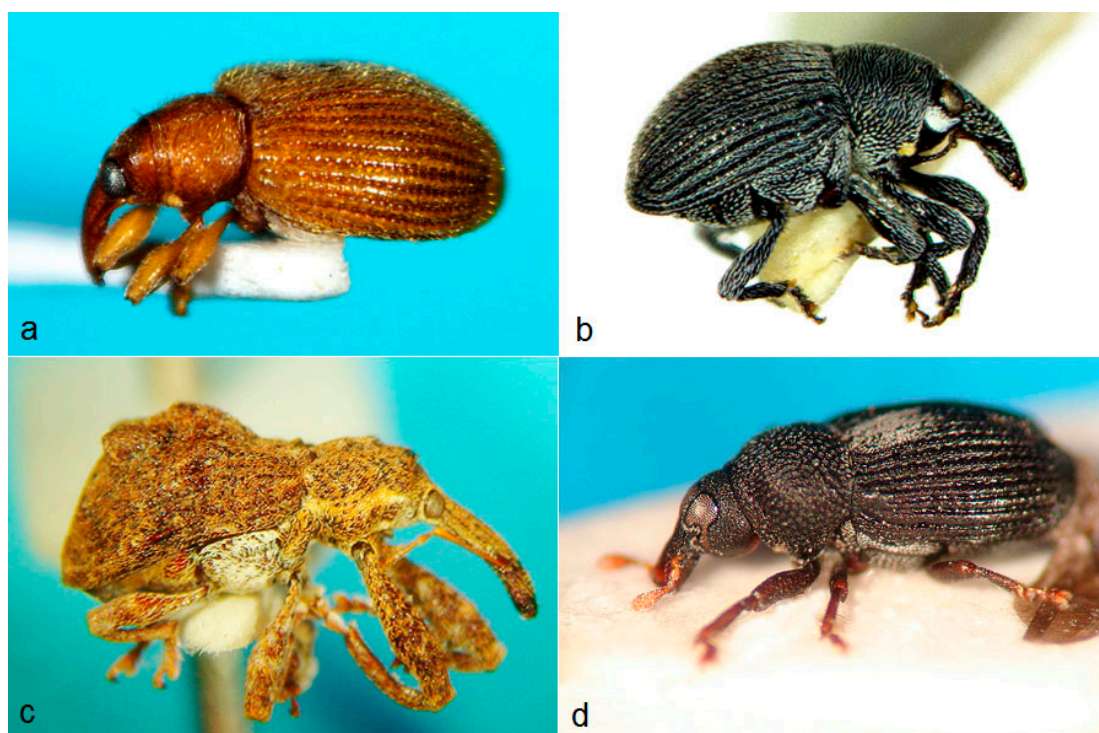


Figure 7. *Endaenidius* sp. (Ochyromerini) (a); *Sphinxis* sp. (Anoplini) (b); *Anthonomus* (*Tachypterellus*) (Anthonomini) sp. (c); the only recorded Laemosaccini species (Mesoptiliinae) with remarkable eye shape (d).

The following genera could be identified by the following works: [30–43] and museum collections: *Amorphoidea* (5 species) and *Parimera* (3) in Acalyptini, *Sphinxis* (6) in Anoplini (or Ochyromerini), *Anthonomus* (*Tachypterellus*) (3) and *Usingerius* (1) in Anthonomini, *Curculio* and *Pseudoculio* in Curculioninae, *Demimaea* in Demimaeini (3), *Elaeidobius* in Derelomini (1), *Imathia* in Storeini (2) as well as *Endaenidius* (35), *Endaeus* (17), *Eugryporrhynchus* (2), *Katsurazo* (3), *Lepidimerodes* (3), *Morimotozo* (2), *Ochyromera* (24), *Omphasus* (6) and *Opseoscapha* (1) in Ochyromerini. Two of the three *Katsurazo* species are clearly different from those described by Kojima (1997) from Sabah. *Elaeidobius kamerunicus* (Faust, 1898) from the tribe Derelomini is an introduced species inhabiting oil palms [41,44]. In Curculionini, the genera *Carponinus* and *Labaninus* were identified provisionally. Most species with a tumid base of the rostrum could not be assigned with certainty to *Indocurculio* due to insufficient illustration of the key of Pelsue and O'Brien [42]. The lack of well identified specimens which could be used for comparison is another serious obstacle.

In Acalyptini (Figure 4), there is a large proportion of species unidentified to genus. Most of them are very small, 1–2 mm long, and of a yellowish color. Apart from their small size, they resemble the Derelomini from palm flowers and may inhabit flowering trees. These species are not considered as members from the Acalyptini genus *Derelomorphus* because they have edentate femora. Two further species of a small size may represent the genus *Niseida* or a similar undescribed genus. *Niseida* is up to now restricted to Aru Island [41]. These results are of special interest because there are the only data for two Acalyptini genera (with one species each), *Amorphoidea* and *Eudela*, recorded from Borneo [41]. In the catalogue of Alonso-Zarazaga and Lyal [13], not a single genus of Acalyptini was listed for Borneo. This means that *Parimera* from our samples is another genus new to this island.

Three species of *Anthonomus* (*Tachypterellus*) have been recorded from Borneo [44]. In our samples, there are also three, but, without dissection of the genitalia, we cannot state if they are identical. With the availability of the paper of Kojima and Idris [43], the identification of *Usingerius parvidens* Zimmerman, 1946 was enabled, a genus that we regarded at first erroneously as Ochyromerini. The former Entiminae tribe Viticiini, represented by two small distinct species, with the genus

Viticis well characterized by the lack of tarsal claw segments [14], is now represented by two species. The genus is new to Borneo and at the same time the westernmost occurrence of this mainly Pacific genus (see [45]). These are the first records of the genus *Viticis* west of the Wallace line.

Despite current taxonomic work, the identification of Ochyromerini is difficult. Most of the many species are of small size (usually smaller than 3 or 4 mm, especially in *Endaeus*, *Endaenidius*, *Eugryporrhynchus*, *Lepidimerodes* and *Morimotozo*). Reliably identified species from other collections are lacking. The proportion of undescribed species is high. The identification of only three species is considered trustworthy: *Eugryporrhynchus malayanus* Kojima and Morimoto, 1995, *Morimotozo ovipennis* (Kojima and Morimoto, 1995) and *M. rotundicollis* (Kojima and Morimoto, 1995). However, a few species were also doubtfully assigned to this tribe: on first examination, three species looked like Cryptorhynchinae, but they have the abdominal segment sutures directed abruptly posteriad close to the margin. This is usually a good character to distinguish Ochyromerini from Anthonomini and Acalyptini. The number of weevils that could not be assigned with certainty to a higher taxon did not exceed 20 or 30 species and thus cannot really affect the data given in Table 1. (In some groups, for example, Anthribidae, Cryptorhynchinae, and in part Molytinae, an assignment to certain tribes proved to be impossible without extensive study and has been left to experts.)

Curculionidae-Curculioninae-Rhamphini (Figure 6)

This group was studied in detail by one of the authors (P.S.) based particularly on the papers on East Asian Rhamphini by Kojima [38], Morimoto [46], Kojima and Morimoto [47], and Morimoto and Miyakawa [48]. The morphospecies sorting revealed 52 species. These are far more than the total 35 described and three undescribed Rhamphini species from the entire area of southeast Asia from India to South China (Fujian included), Taiwan and Thailand to Indonesia and the Philippines [47,48].

Forty-two species were determined to genus level: 8 *Imachra*, 2 *Indodinorrhopalus*, 2 *Morimotonomizo*, 23 *Orchestes* (*Orchestes*), 4 *Orchestes* (*Nomizo*), 1 *Rhamphus* (*Trichorhamphus*) and 2 *Sphaerorchestes* species. In the remaining species, the genus could not be determined without doubt. These species should represent new genera or new subgenera of *Orchestes*. In *Orchestes* (s. str.), there were many rather small species that were also assigned here, due to the hollowed metatibiae, the outer margin of hind femora with denticles, and the raised setae on the elytra and pronotum. The genus *Indodinorrhopalus* has not been recorded from Borneo or Malaysia previously, *Morimotonomizo* not from Borneo and *Rhamphus* only by an undescribed species from East Malaysia [49]. All 52 species are rather small; there is not a single one measuring more than 3 mm. The remarkable southeast Asian Rhamphini genera *Dinorhopala* and *Ixalma* with body size usually >3.5 mm were not represented in the samples.

Only three species could be identified to species level: *Imachra bifasciata* Morimoto & Miyakawa, 1996, *I. ruficollis* Pascoe, 1874, and *I. siamensis* Morimoto & Miyakawa, 1996. *I. ruficollis* is widespread in the Oriental region, and its range is extended in one area just in the Palaearctic region (China: Fujian). *I. siamensis* was described from South Thailand, and *I. bifasciata* was re-discovered at the type locality (Kinabalu). Except for the three *Imachra* species and *Morimotonomizo* (with one species that could be identical with *M. sphinxoides* (Morimoto and Miyakawa, 1996) from West Malaysia), all remaining 48 Rhamphini species are very probably undescribed (see [47,48]).

Curculionidae-Mesoptiliinae (Figure 7)

Only one species (three specimens) in this subfamily has been collected. Apparently, it is a member of the tribe Laemosaccini, a tribe only known from Australia and New Zealand with the exception of the American genus *Laemosaccus*. This is the first record of a member of subfamily Mesoptiliinae on Borneo and west of the Wallace line.

Curculionidae-Scolytinae

These species were determined by Roger Beaver, e.g., [49]. He distinguished 111 species that makes this taxon together with Anthribidae, Rhynchitidae, Conoderinae, Cossoninae, Curculionini, Cryptorhynchinae, Molytinae and Ochyromerini (each over 100 species), one of the commonest in the

fogging data. From all 111 species, 50 could be identified to species level, the remainder at least to the genus level (two species with some doubt). The state of knowledge in this potentially economically relevant group is therefore much better than in all other weevils (except Platypodinae, see the next section). However, even in Scolytinae, 61 species could not be identified and are very probably new to science.

Curculionidae-Platypodinae

Species in this group were sorted and identified by Roger Beaver. However, he received only 50% of the species. From these, 17 species, 14 genera and 11 species could be identified. Six species are new to science.

Remaining Weevil Groups

There is only very scattered information about all the remaining weevil groups (see Table 1): Anthribidae, Nanophyidae, Rhynchitidae (11 Auletini, 36 Deporaini and 63 Rhynchitini species) and the Curculionidae subfamilies Entiminae, Conoderinae, Cossoninae, Cryptorhynchinae and Molytinae. In Figure 8, some long-legged weevils from the subfamilies Conoderinae and Molytinae, which may be typical for tree crowns, are shown. In Nanophyidae, one species could be identified with the key of Lyal and Curran [50] as *Damnux tenebriosa* Lyal, 2003, but all others remained unidentified.

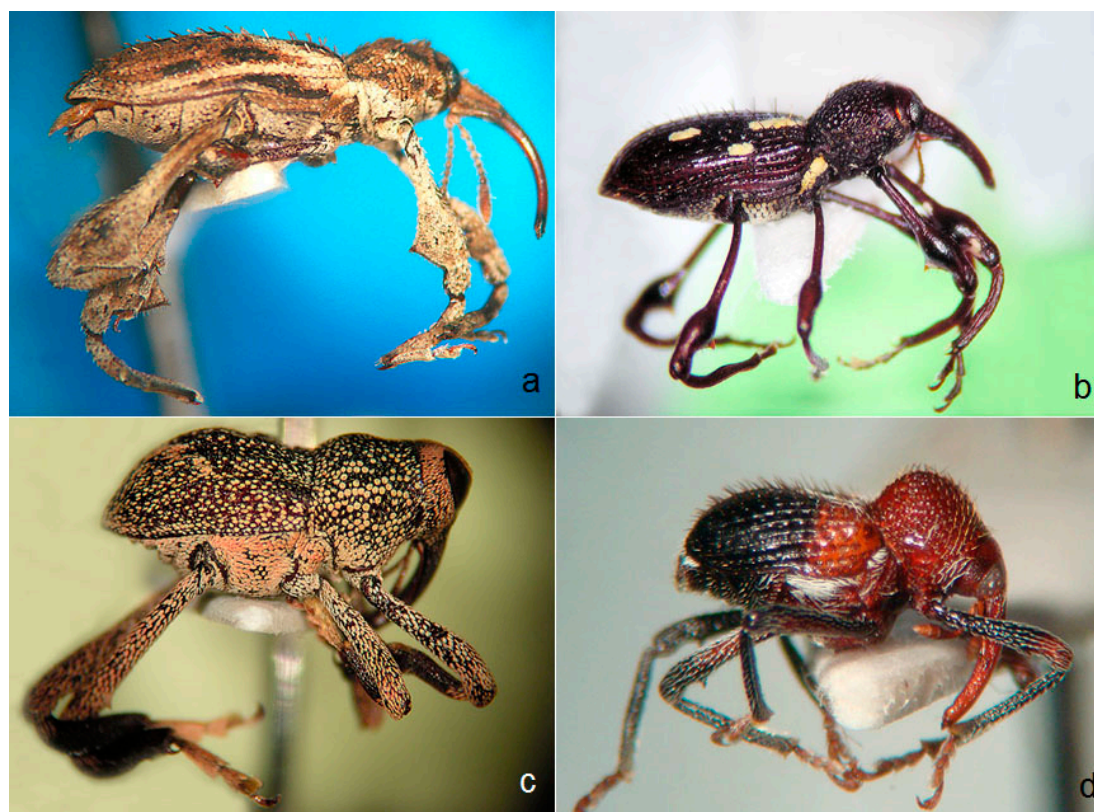


Figure 8. Long-legged weevils. Long legs may be an adaptation to life in the canopy and were mainly found in Curculionini (see Figure 4), Trachodini and Conoderinae, e.g., *Acicnemis* (a); *Pseuderodiscus* (b); *Odoacis* (c); and *Talimanus* (d). More than 60 Trachodini morphotypes were recognized.

The Dryophthoridae were represented by only four sizable specimens of the genera *Aplotes*, *Cryptoderma* and *Laogenia*, probably a species of Diocalandrini, and mainly by several Litosomini species of the genera *Sitophilus* (six species) and *Myocalandra* or a closely related genus (four species). In Entiminae, there are single *Dermatodes* (Dermatodini) and *Eugnathus* (Sitonini) species, some Ottistirini and many Cyphicerini, but there is also a rather large number of species of unidentified tribes (perhaps in part Myllocerini). *Apocyrtdius chlorophanus* Heller, 1908, is the only member of

Pachyrhynchini on Borneo, and it is represented by 47 specimens in samples from the Mesilau region of Kinabalu in the montane forest.

In Conoderinae (Figure 8), the bulk of the 171 morphospecies probably belong to Othippiini and a rather significant number to the usually black-and-white-coloured Menemachini, the remaining to Coryssomerini, Mecopini (s.l.), Campyloscelini and unidentified tribes. We are aware that the taxonomy of the higher tribes is rather uncertain especially in this subfamily [51]. A few genera could be identified with little doubt by the keys of Hustache [52], the Intkey CD [53], and museum collections: *Phaenomerus*, *Talimanus*, *Telephae* and *Tomicoproctus*—and with some doubt: *Agametis*, *Metialma*, *Odoacis*, and *Osphilia*, but none of the probably largest tribe Othippiini, which has mainly small species. According to Alonso-Zarazaga and Lyal [13], the well-characterized genus *Tomicoproctus*, represented by one species, was not recorded from Borneo previously, only east of the Wallace line and in Africa.

In Molytinae, there was a great number of Trachodini (63 species), including two *Pseuderodiscus* species, previously placed in Curculioninae-Erodiscini, followed by Ithyporini (37), Hylobiini (16), Mecysolobini (14), Lithinini (about eight species, one of them identified as *Seleuca* by C. Lyal by photo) and Trigonocolini (1), but, among Ithyporini, there may also be other tribes with small species, one of them, for example, looking like *Seticotasteromimus* (tribe Pissodini), a genus recently erected by Germann [54]. In “Ithyporini sensu lato”, the differentiation from Cryptorhynchinae was not clear in several cases. Some species from these groups and from Ochyromerini, with more or less doubtful assignments, are depicted in Figures 9 and 10. The genus *Phaeopholus* (Figure 9a) is the only representative of Hyperinae; prior to this study, it has only been recorded from China and Japan and is thus another genus new to Borneo.

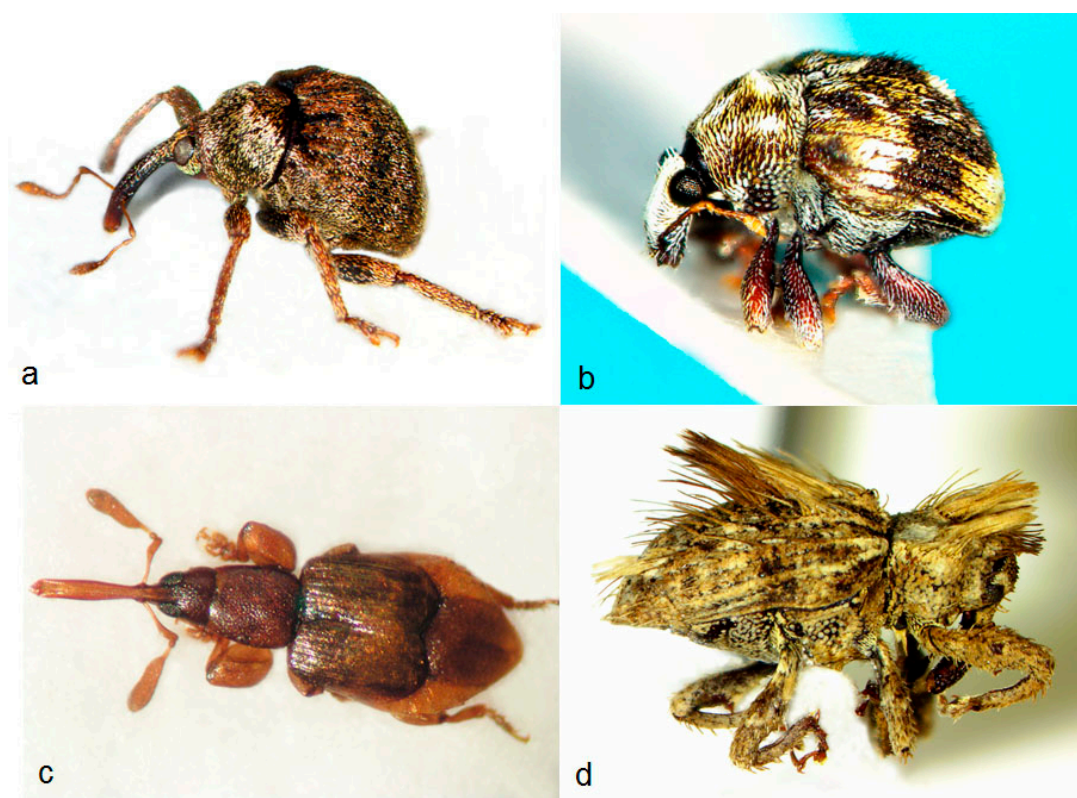


Figure 9. Weevils with doubtful assignments I. The first species (a) represents the Hyperini genus *Phaeopholus* (confirmed by Jiří Skuhrovec). The second species (b) probably belongs to Microstylini, a tribe of rather uncertain placement (Curculioninae or Molytinae). The third species (c) has a very extraordinary habitus: small, flat, shortened elytra, very thick profemora, and a very long antennal club. There is also sexual dimorphism. The long-nosed female is shown. The assignment is unknown, perhaps Acalyptini (M.A. Alonso-Zarazaga, pers. comm.). The next species (d) is probably a Sophrorhinini species.

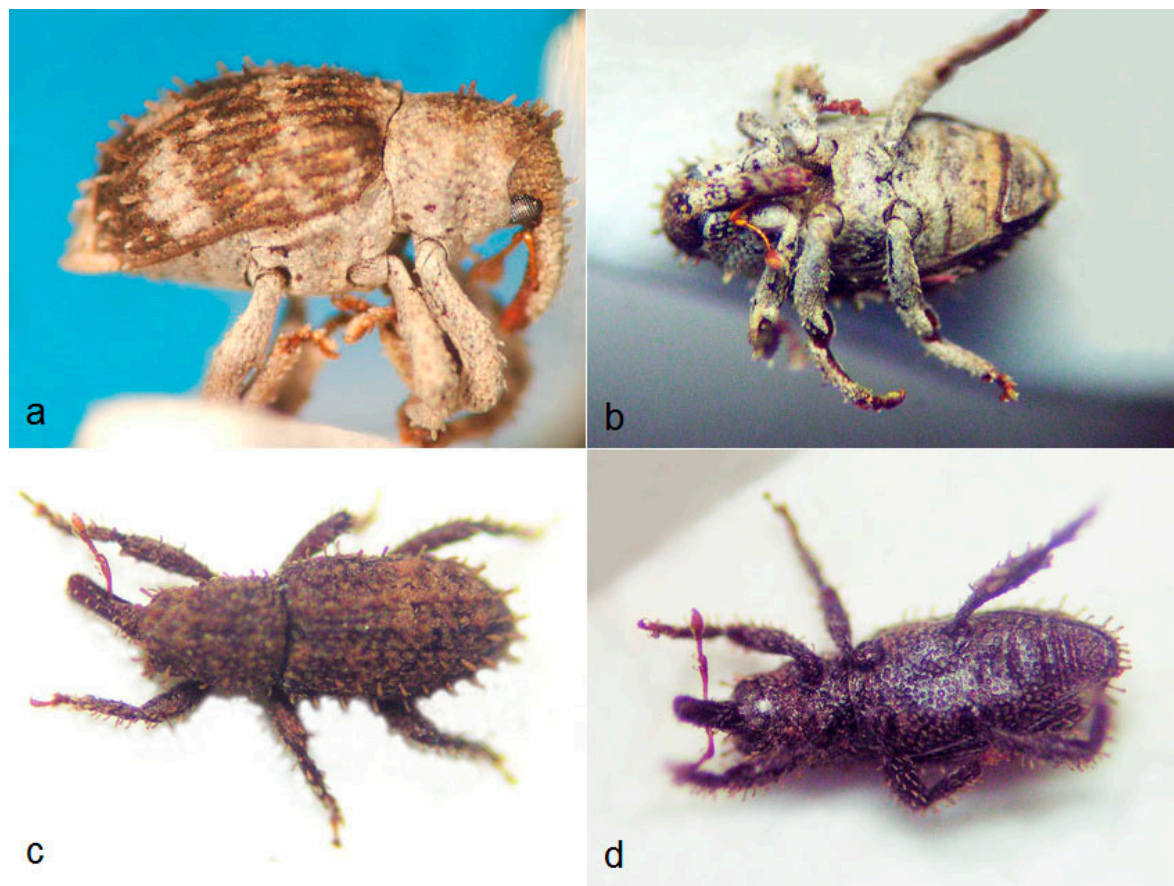


Figure 10. Weevils with doubtful assignments II. The weevil on the first photos (a,b) is provisionally regarded as Ithyporini. Species with a similar habitus look like inhabitants of the soil, but they were found in rather large numbers in the tree crowns; usually, they have a rostral furrow. In the last small species, such a furrow is absent, and this species is regarded provisionally as *Seticotasteromimus* (Pissodini) or a closely related genus (c,d).

Cerambycidae

For reasons of comparison, the highly diverse longhorned beetles, many of great economic importance and of special interest for collectors, were also included in this work. Like in the other beetle taxa, there are many undescribed species, underlining how little is still known about the canopy fauna of Bornean primary forests. In addition, 219 species were distinguished by Carolus Holzschuh. Nine species could not be identified to genus level and another 11 with doubt, 37 species were identified to species level and another 19 with doubt. Thirteen species from this dataset were described by Holzschuh as new [55–57]; and work is still in progress. A current checklist of Bornean Cerambycidae contains 1270 species [58], but the total number is estimated to exceed more than 2000 species [55]. The most species-rich tribes in the samples were Apomecynini with 61 and Pteropliini with 31 species, both in subfamily Lamiinae, with genera like *Pterolophia*, *Ropica* and *Sybra*. Only 37 (16.9%) of the 219 recorded species could be identified up to 2012, representing only 2.9% of the Bornean fauna and revealing the conspicuous gaps of knowledge even in a ‘collectors’ group’.

3.4. Brief Summary

The analysis of the canopy weevils provides a first impression on the distribution of higher weevil taxa in Bornean rain forests. Except Brentidae and a few other groups with long narrow body form, there is a very large number of rather small species not exceeding 4 mm. The data suggest that the

proportion of species new to science is very high. Several taxa like Apionidae and Ceutorhynchinae contain what appear to be exclusively new species and others mainly new species, such as Baridinae, Brentidae and Rhamphini (Curculioninae). We also verified the existence of at least 15 genera, one subfamily and one family formerly not known from Borneo. Furthermore, a high proportion of non-identifiable specimens was confirmed even for larger groups of general interest like the bark and ambrosia beetles (Scolytinae) or the longhorned beetles (Cerambycidae). Information on several other taxa confirm a similar poor state of taxonomic knowledge; this refers to Alticinae (Chrysomelidae, processed by the late M. Döberl), Anthicidae (D. Telnov), Pselaphinae (Staphylinidae, V. Brachat), Scirtidae (B. Klausnitzer) and Tenebrionidae (Alleculinae and Lagriinae excluded; R. Grimm, H. J. Bremer), which were sorted and determined by several specialists. Taking all this into consideration, we cautiously estimate that the proportion of Curculionoidea, as one of the most species-rich taxa in beetles that are new to science, considerably exceeds 80%. Comparable results were found by other authors, too: Oberprieler et al. [11] reported similar proportions of undescribed species for litter-inhabiting species in Central America. In a case study on New Guinea, Basset et al. [59] found a ratio of 4.6:1 of undescribed to described species for arboreal weevils in poorly studied groups, such as Rhynchitidae, Entiminae, Molytinae and Curculioninae s.l. Lees et al. [10] found a ratio of 5.7:1 in Gracillariidae moths from the Neotropics demonstrating that similar faunistic and taxonomic limitations are also found in other taxa.

We also observed conspicuous changes in the species frequency distribution between primary and disturbed forests for several groups of arboreal weevils. These are especially noticeable for those groups which had increased in individual and/or species numbers in the disturbed forests despite a much lower number of foggings than in the primary forests (214 versus 120 samples, Table 2). The total number of collected beetles in both primary and disturbed forests was almost identical (4783 versus 4888), but species numbers were much higher in the primary forests (1287 vs. 473 species).

Table 2. Weevil groups showing the most conspicuous differences in individual and species numbers between primary and disturbed forests.

	Number of Species		Number of Individuals	
	Primary	Disturbed	Primary	Disturbed
Acalyptini	24	15	80	441
Ochyromerini	106	39	497	593
Baridinae	26	13	50	91
Scolytinae	53	68	251	2383

Similarity in numbers was largely caused by Scolytinae which were very abundant and—as the only group—collected with more species in the disturbed forests than in the primary forests. Ochyromerini occurred in large numbers especially in the disturbed forests whereas species richness was much higher in the primary forest. Acalyptini and Baridinae were also found in higher numbers, but lower species richness in the trees of the disturbed forests. It is also noteworthy that not a single individual of Ceutorhynchinae (203 specimens in 26 species) or Attelabidae (60 specimens in 15 species) was collected in the disturbed forests. To what extent these differences can be linked to anthropogenic forest disturbance as suggested for canopy spiders [60] is currently being analysed. The mentioned changes in the rank-abundance distribution were often based on a few species that occurred in large numbers. In Scolytinae, for example, one species of ambrosia beetles of the genus *Scolytogenes* was collected in more than 1500 individuals from *Vitex pinnata* (Lamiaceae-Verbenioideae). This might indicate an unknown relationship between this weevil and its host tree. In Acalyptini and Ochyromerini, with the many small light yellowish species, the high abundance in the disturbed forests may be partially attributed to flowering and fruit trees. Several Ochyromerini species and many specimens were collected from *Melochia umbellata* and from *V. pinnata*. The most abundant species of Acalyptini (341 individuals) was mainly collected from *Terminalia catappa* L., *Premna corymbosa* Rottl.

and Willd. and *Mallotus* spec. These few examples are representative for the limited knowledge on the diversity and biological interactions of beetles in the humid tropical forests.

4. Conclusions

In our opinion, the high diversity and the current poor taxonomic state of knowledge of tropical arthropods provide an inadequate basis to assess the extent of this diversity, its distribution or even its functional importance. There are very few studies dealing with the biology of arboreal weevils from southeast Asia and which provide data about their ecology like those of Lyal and Curran [50,61]. Scattered biological information was published in current taxonomic studies about SE-Asian, Japanese, New Zealand, Australian and Pacific weevils, but the overlap with the Bornean fauna is rather low. In light of the quickly disappearing primary forests of Borneo, this hints towards a massive loss of biodiversity and biological information. This also indicates that ecological analyses are still far behind those of Central European countries, e.g., Floren and Schmidl [62]. Given the importance of tropical rain forests and their ongoing destruction, it is incomprehensible why biodiversity and taxonomic research is not much more intensified.

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