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ABUNDANCE AND DIVERSITY OF LAND-SNAILS (MOLLUSCA: GASTROPODA) ON LIMESTONE HILLS IN BORNEO

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ABSTRACT. – Limestone hills in Malaysia have traditionally been considered to harbour particularly rich land-snail faunas, in terms of both total number of species and relative abundance of individuals. We quantified this by measuring land-snail abundance and diversity in standard plots on limestone hills and adjacent non-limestone substrates in two localities in Sabah, Malaysian Borneo. Abundance was positively correlated with both pH and calcium carbonate availability and hence higher (two- to 10-fold) on limestone compared to non-limestone. Data on the ratios of living and dead snails show that this is not an artifact of reduced rates of shell dissolution on limestone soils. After correction for abundance, however, diversities on limestone are not much higher than on non-limestone substrate. Only two or three species per study site are classified as obligate calcicoles. Nevertheless, it is clear that limestone hills are important reservoirs for the regional malacofauna.

KEY WORDS. – Calcium carbonate, Soil pH, Endemism, Malaysia, Sabah, Karst.

INTRODUCTION

Limestone in the humid tropics is subject to severe weathering because of high rainfall, humidity, and biological productivity (Crowther, 1987a). Often, this results in spectacular morphologies: blocks of limestone with steep cliffs and riddled with caves and sinkholes (Crowther, 1986). In Malaysia, numerous more or less isolated karst outcrops of this type are widely scattered over the landscape. In Peninsular Malaysia, about 500 such hills have been recorded (Price, 2001), while the East-Malaysian states of Sarawak and Sabah (which straddle the north-western one-third of the island of Borneo) hold at least 230 and 70, respectively (Lim & Kiew, 1997; Schilthuizen & Vermeulen, unpublished data; Wilford, 1964). Many of these hills are single, isolated limestone deposits that may ultimately be derived from detached chunks of ancient reef. Although other hills are geologically interconnected, forming the exposed parts of continuous underground limestone deposits, they, too, are usually separated by overlying, non-calcareous alluvial substrates.

Since the late 19th century, Malaysian limestone hills have attracted the interest of snail collectors. De Morgan (1885) wrote [in Tweedie's (1961) translation], 'these formations are very favourable to the development of molluscs, for I found everywhere where the limestone outcropped a great quantity of shells.' And Tenison-Woods (1888), said that the limestone hills on the Malay Peninsula 'are all distinguished by an abundance of genera and species of land shells.' These observations have given rise to the notion that Malaysian limestone hills, although occupying only 0.3% of the country's land surface (Gobbett, 1965; Price, 2001), play a major role in supporting its snail abundance and diversity (Tweedie, 1961). More explicitly, Vermeulen & Whitten (1999) estimated that a patch of limestone habitat will support two to five times more species than a similar patch of non-limestone habitat, and that the number of shells found there is 10-1000 times as high.

It is well-established that land-snails have high calcium requirements for the production of both their eggs and their shells; hence, calcium-poor substrates generally support fewer individuals and species of land snails when compared to calcium-rich ones (Graveland et al., 1994). Nevertheless, there are several reasons why the claims of high land-snail abundance and diversity on Malaysian limestone hills require verification and quantification. First, malacological activities in Malaysia have been almost exclusively restricted to limestone, and knowledge of the malacofauna of other substrates is limited to a few well-visited sites, such as Mount Kinabalu (Laidlaw, 1937; Tillier & Bouchet, 1988). Second, several snail taxa, most notably Diplommatinidae (see Tweedie, 1961), are considered to live only on limestone, with correspondingly high rates of allopatric speciation. The degree of obligate calcicoly and the modes of speciation in these groups are currently under discussion (Schilthuizen & Rutjes, 2001; Schilthuizen et al., 1999, 2002), and more exact measurements of their population structure are needed. Third, the perceived higher abundances on limestone may be artifactually raised. Limestone has a high pH, at which dissolution of shells may be retarded. Since most assessments of snail abundance are based on numbers of empty shells on the forest floor, these may be partly the result of longer persistence of shells rather than higher abundance. In this paper, we examine land-snail abundance and diversity on two limestone hills in Sabah, Malaysian Borneo, and compare these with the surrounding, non-limestone environment.

MATERIALS AND METHODS

We selected two limestone hills in Sabah, surrounded by primary forest on non-calcareous substrate (Fig. 1). Other criteria for selection were their accessibility and the availability of identified reference material. The first site (hereafter called 'Danum'), located at 4°58'26.0" N 117°48'39.3" E and 300 m asl, is a small outcrop 40 m long, 30 m wide, and 10 m high on the left bank of the Segama River, in the Danum Valley Conservation Area, approximately one km downstream from the Danum Valley Field Centre. The hill is surrounded by tall dipterocarp forest on sand- and mudstone of the Kuamut formation (Marsh, 1995). The forest in the immediate vicinity of the outcrop is somewhat disturbed because of treefalls and landslides. The malacofauna (circa 90 species) of the Danum Valley Conservation Area is well known (Schilthuizen & Rutjes, 2001; Schilthuizen et al., 2002; H. A. Rutjes & M. Schilthuizen, unpublished data).

The second site (hereafter called 'Tabin'), located at 5°18.49'N 118°44.39'E and 200 m asl (measured at the summit of the hill), is a limestone outcrop 4000 m long, 700 m wide, and 100 m high on the right bank of the Tabin River, in the Tabin Wildlife Reserve, approximately 10 km upstream from Kampung [=Village] Tidong. This hill is surrounded by sandstone of the Sebahat formation (Yin, 1985), which, upon microscopic inspection of broken surfaces, did not reveal any shell or coral fragments. The forest in this area is tall dipterocarp forest, which is, however, moderately disturbed by recent timber extraction. The malacofauna (65 recorded species) has been surveyed earlier (Schilthuizen & Vermeulen, 2002).

At Danum, the fauna was sampled in 12 plots, two of which were on limestone (the limestone hill was not large enough to accommodate more than two plots), and 10 on non-limestone substrate. In Tabin, 11 plots were sampled, six on limestone, and five on sandstone. The sampling procedure was as described earlier (Schilthuizen & Rutjes, 2001, based on methods developed by de Winter & Gittenberger, 1998). Briefly, plots of 20 x 20 m were searched for both dead and living land snails for two person-hours (in Tabin, but not in Danum, living and dead snails were preserved separately). Five litres of topsoil and litter were also collected, coarsely sieved, and enriched by flotation (which removes all heavy particles, but preserves empty shells). Microsnails were extracted by searching the dried and finely sieved samples under a dissection microscope. At each plot, circa 100 ml of soil were taken from directly underneath the topsoil. These soil samples were used for measurement of pH (according to Anderson & Ingram, 1996) and calcium carbonate content (using the protocol of Richards, 1954). Due to a laboratory error, however, the samples for Danum plots 8-12 were insufficient to do both pH and calcium carbonate analysis, so only the former was measured for these five samples. All specimens were identified to species level, except in the case of juveniles from certain genera. For several of the microsnail genera, the available taxonomy is unresolved, in which case it was impossible to assign a species name. Instead, we used numbers in the form '[genus name] sp-BO-##', which correspond to the numbering system used by one of us (J.J.V.), to indicate and voucher not-identified snail taxa from Borneo. All specimens have been deposited in the "Borneensis" collection of the Institute for Tropical Biology

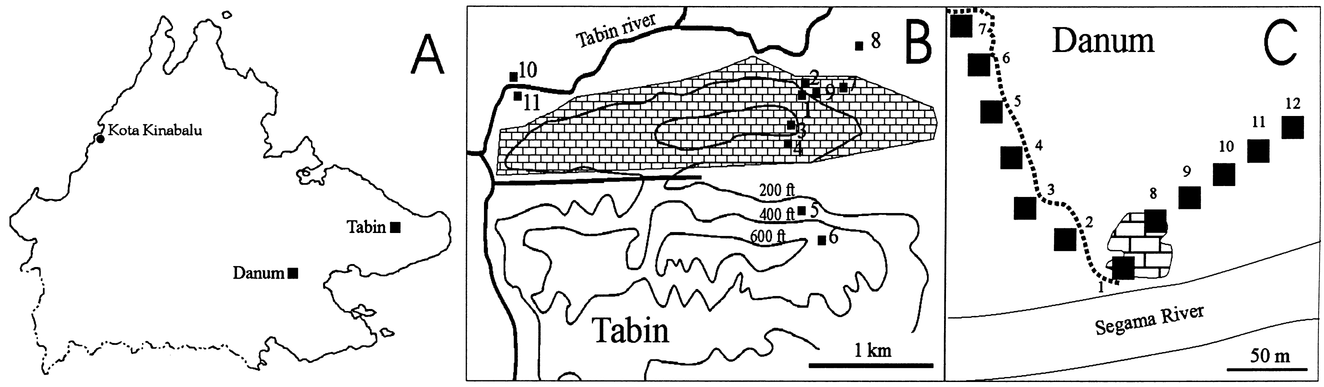

Fig. 1. Sampling localities at Danum (B) and Tabin (C), two sites in the state of Sabah (A) in northern Borneo. The limestone outcrops are indicated with brick hatching. The dotted line in Danum represents a trail.

and Conservation, Universiti Malaysia Sabah, with additional voucher specimens in the private collection of J. J. Vermeulen, Singapore.

To compare total species richness (*S*) between limestone and non-limestone plots, we performed 50 randomisations on the Tabin data (the number of limestone plots in Danum was too low) from the two plot types, and calculated *S* using the Michaelis-Menten estimator MMRuns (Raaijmakers, 1987) in the program EstimateS6.0b1 (Colwell, 2000). For large samples with few singletons, as in the Tabin data, this is an appropriate estimator (Süssenbach & Fiedler, 1999). To accommodate the unevenness in land-snail distribution (Schilthuizen et al., 2002), the patchiness parameter A was arbitrarily set to 0.5. Statistical tests were carried out either by hand or with the SPSS for Windows software package (version 7.5.1, SPSS, 1996).

To estimate the rate of breakdown of empty shells on the forest floor, we compared the numbers of live and dead individuals for the following species: *Leptopoma pellucidum* (Grateloup), *Leptopoma sericatum* (Pfeiffer), *Leptopoma undatum* (Metcalfe), *Leptopoma* juveniles, *Japonia jucunda* (Smith), *Japonia* juveniles, *Liardetia scandens* (Cox), *Liardetia* sp-BO-01, *Coneuplecta angulata* (Issel), and *Philalanka kusana* (Aldrich). All these species are tree-dwellers (Schilthuizen & Vermeulen, unpublished data), so their proportions of dead individuals should only be influenced by the rate of breakdown of empty shells, assuming similar patterns of mortality in both habitats. (In ground-dwellers, this is not necessarily the case, as they may also suffer from the low pH while still alive.)

RESULTS

In Danum, alkaline pH values were found for the two limestone plots (7.3 and 8.1). In Tabin, the six limestone plots had an average pH of 7.4 (range 7.2-7.7). Non-limestone soil was mildly acidic: the average for 10 non-limestone plots in Danum was pH 5.4 (range 4.0-7.4), and for five non-limestone plots in Tabin was 6.4 (range 5.9-6.9).

The carbonate content of soil samples was also much higher on limestone, as expected. In Danum, carbonate content for plot 1 (limestone) was 14.5%, whereas the values for plots 2-7 (non-limestone) averaged 2.6% (range 0.5%-7.2%). In Tabin, the six limestone plots had an average carbonate content of 15.9% (range 13.6%-18.8%), whereas in the five non-limestone plots it was only 2.8% (range 0.5%-5.5%).

Sampling at Danum yielded between three and 345 specimens (live snails and empty shells) per plot. In total, 632 specimens were found, representing 37 species (see Appendix). One species, *Arinia brevispira* Vermeulen, had not previously been found in the Danum Valley Conservation Area (see Schilthuizen & Rutjes, 2001). In Tabin, numbers of specimens per plot ranged from 31 to 412, for a total of 2,162 specimens belonging to 45 species (see Appendix). Of these species, only one (*Ditropopsis* sp-BO-01) had not been recorded at this locality before (see Schilthuizen & Vermeulen, in press).

At Tabin 18% of the specimens were collected alive, although this proportion varies greatly among species. For example, of 472 specimens of *Opisthostoma lissopleuron* Vermeulen, 244 (52%) were collected alive, whereas only four of 131 *Hemiplecta densa* (Adams & Reeve) were alive. The pooled Tabin data for dead versus live specimens of the eight tree-dwelling species (see Materials and Methods), are 434 dead out of a total of 472 individuals on limestone (91.9%) and 282 dead out of a total of 313 individuals on non-limestone (90.1%). The difference between these ratios is not statistically significant (χ^2-test).

Relative abundance was higher at the limestone localities. In Tabin this difference was statistically significant (P = 0.009; Mann-Whitney U test), the average number of

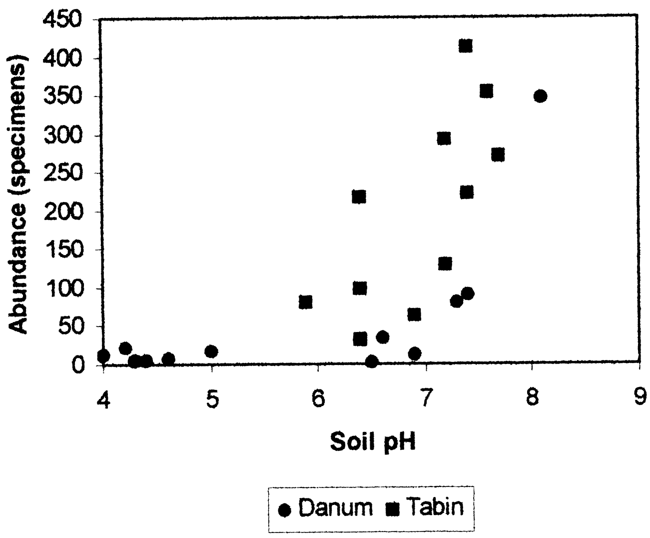

Fig. 2. Relative abundance (number of snails found per plot) against pH.

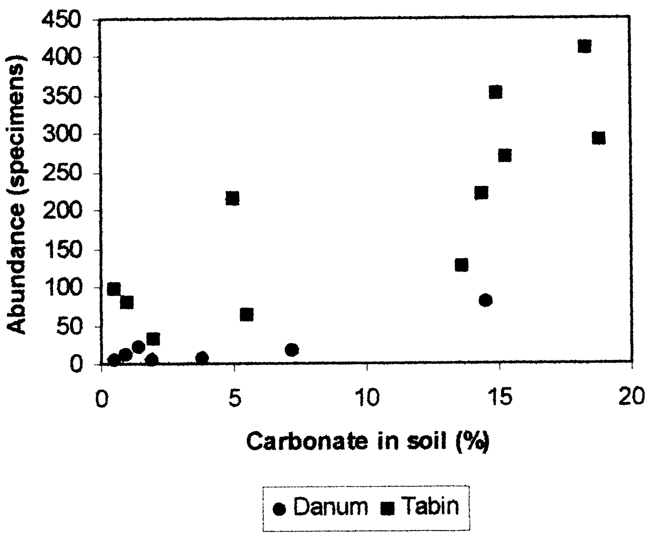

Fig. 3. Relative abundance (number of snails found per plot) against carbonate concentration.

specimens per plot being 279 (±99) against 98 (±71). In Danum, the mean difference was larger, with 213 (±187) for the two limestone plots against 21 (±24) for the non-limestone plots, but only marginally significant (P = 0.06; Mann-Whitney U test). Figs. 2 and 3 show that abundance increases with pH (R^2 of a fitted exponential trendline = 0.57; P < 0.005) and with carbonate content (R^2 = 0.65; P < 0.005) of the soil. No correlation was found between abundance in the non-limestone plots and distance from the nearest limestone (data not shown).

Total number of species per plot was significantly higher on limestone. In Tabin the average number of species per plot was 27.2 (±2.3) on limestone, and 16.2 (±3.4) on sandstone (P = 0.004; Mann-Whitney U test). In Danum, these numbers were 20.0 (±1.4) and 6.5 (±3.0), respectively (P = 0.03; Mann-Whitney U test). However, these differences are largely the result of the larger number of individuals found on limestone, as suggested when diversity is plotted against abundance (Figs. 4 and 5). Randomisations in EstimateS showed that the projected actual species richness according to the Michaelis-Menten estimator were similar: 48.6 for the limestone, and 42.9 for the non-limestone.

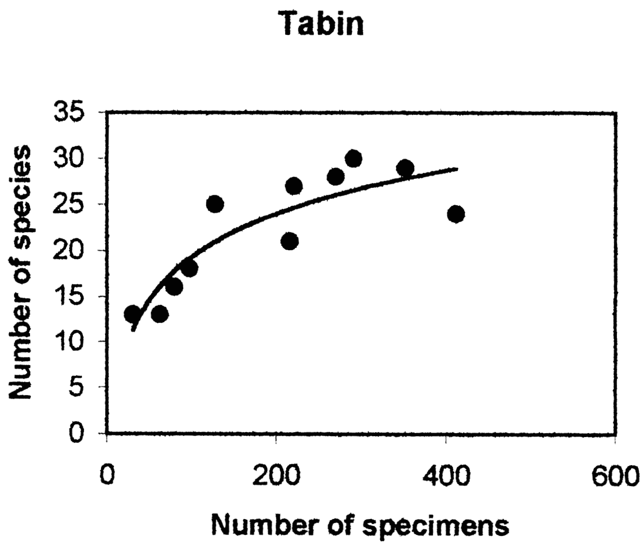

Fig. 4. Diversity against abundance for Tabin, with logarithmic trendline fitted.

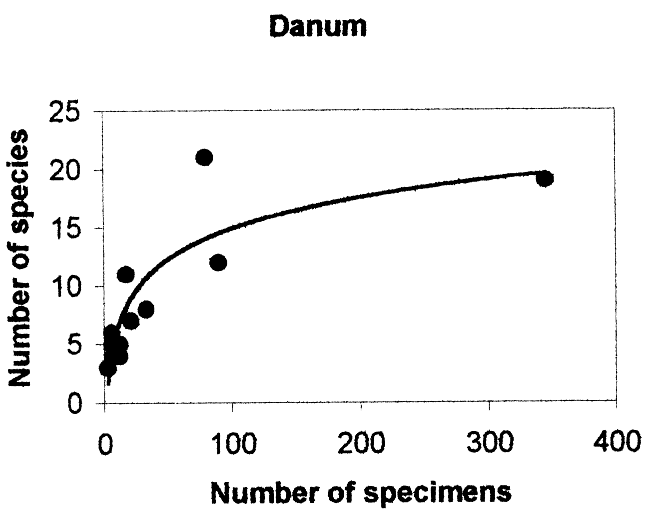

Fig. 5. Diversity against abundance for Danum, with logarithmic trendline fitted.

DISCUSSION

Our results confirm earlier claims regarding land-snail abundance on limestone (see Introduction). The abundance of specimens on the Tabin limestone outcrop was approximately twice as high as on the surrounding sandstone substrate. The difference in Danum was 10-fold, although the variance among the two limestone plots was high, and statistical significance was not reached.

The chemical analyses of soils indicated that abundances correlate positively with pH and calcium carbonate content (Figs. 2, 3). Limestone, which is chiefly composed of calcium carbonate, acts as a buffer against acidity, so high calcium carbonate content is usually accompanied by high pH; the two factors are not chemically independent. Nevertheless, they probably represent separate abiotic properties relevant to land-snails. First, shells are largely made of calcium carbonate, and although a horn-like conchiolin layer (the 'periostracum') is often present, this protective layer is often eroded at the top-whorls (Meglitsch, 1972) or not present at all (Kemperman & Gittenberger, 1988). Thus, mortality resulting from shell breakdown is likely to be higher under acidic conditions. Second, calcium carbonate availability is a limiting factor for land-snail populations, as it is required for shell growth and egg production; a positive correlation between soil calcium carbonate content and snail abundance, though possibly not universal (Barker, personal communication), has been reported frequently (e.g., Graveland et al., 1994). This is expected to be true even for snail species that are not in direct contact with the soil, such as herbivorous tree-dwellers, as calcium uptake by vegetation is much higher on karst than on non-calcareous substrates (Crowther, 1987a, b).

However, the possibility remains that shell abundances on the forest floor do not actually reflect snail population densities, but are reflective of the rate of shell breakdown on the soil. With the mildly alkaline conditions on limestone, it may be expected that empty shells persist longer there, giving rise to erroneous estimations of snail abundance. However, this possibility may be excluded because the analysis of our data on living versus dead specimens suggests that empty shells dissolve at equal rates on both substrate types. This is possibly because shells on the forest floor are dissolved more by rainwater (which is equally acidic in both types of terrain) than as a result of direct contact with the soil.

Given that snail population densities are higher on limestone, it is not surprising that diversities are higher there, too. Diversities rise, as expected logarithmically, with increasing number of collected specimens (Figs. 4, 5). As the limestone plots have the highest numbers of specimens, species richness there is highest, too. However, the fact that limestone and non-limestone plots follow the same trend, suggests that actual diversities in both types of terrain are not dissimilar. Our Michaelis-Menten randomisations for Tabin predict total diversities of 49 species for the limestone, and 43 species for the non-limestone.

Visual inspection of the lists of species shows indeed that a few species are restricted to limestone, whereas the reverse is not the case. In Tabin, the most obvious candidate for obligate calcicoly is *Opisthostoma lissopleuron*, which was a major component of the fauna in plots on limestone, but was absent from non-limestone plots. Other possible limestone-restricted species in Tabin are *Georissa bangueyensis* Smith, *Diplommatina gomantongensis* Smith, and *Diaphera wilfordi* (Dance). These species were fairly common in most (but not all) limestone plots, but always absent from non-limestone plots. Although the same was true for *Charopa* sp-BO-01, this species is not an obligate calcicole as it is regularly found on non-limestone substrates elsewhere (e.g., Schilthuizen et al., 2002). At Danum, two species may be obligate calcicoles: *Platyraphe linitus* (Godwin-Austen) and *Diaphera wilfordi*. Both were found in fairly large numbers in limestone plots but not in the non-limestone plots, and they have never been found in any of the other snail surveys on non-limestone soil in Danum (Schilthuizen & Rutjes, 2001, Schilthuizen et al., 2002). The taxonomic affiliations and biogeographic patterns of the five above-mentioned taxa are in agreement with their possible obligate calcicoly. With the exception of *Platyraphe linitus*, they belong to groups that tend to show high degrees of endemism, with species restricted to single limestone hills or clusters of limestone hills. Most notable among these is the subgenus *Plectostoma* of the diplommatinid genus *Opisthostoma* (here represented by the species *O. lissopleuron*), which forms a dominant component of the limestone malacofauna in Borneo, whereas not a single individual has ever been recorded away from limestone (Schilthuizen, 2003). In the case of the streptaxid *Diaphera*, the abundance of other snails may be the factor that determines this molluscivore's preference for limestone, rather than the availability of calcium.

In conclusion, this study shows that limestone habitats in Borneo do indeed support higher land-snail densities than those on other substrate types. However, diversities on limestone are similar to those in non-limestone forest, although a small number of species (perhaps two or three species per limestone locality) may be obligate calcicoles. Nevertheless, limestone hills may be considered important reservoirs for regional malacofauna. They support large populations of the species of land snails that are native to a particular area, plus a few additional limestone endemics.

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APPENDIX
Land-snails recorded in the 11 plots in Tabin and the 12 plots in Danum.

	Tab. 1	Tab. 2	Tab. 3	Tab. 4	Tab. 5	Tab. 6	Tab. 7	Tab. 8	Tab. 9	Tab.10	Tab.11	Totals	Alive
Hydrocenidae													
Georissa bangueyensis Smith	10	0	30	42	0	0	0	0	3	0	0	85	4
Georissa gomantonensis Smith	1	1	0	1	0	0	0	0	16	9	0	28	14
Georissa similis Smith	0	0	0	0	0	0	0	0	2	0	0	2	0
Helicinidae													
Sulfurina martensi (Issel)	1	0	14	2	1	0	0	0	1	12	1	32	24
Cyclophoridae													
Pterocyclos trusanensis (Godwin Austen)	27	0	13	8	12	4	0	0	19	5	0	88	3
Pterocyclos tenuilabiatus (Metcalfe)	1	0	0	1	3	1	1	1	0	1	0	9	4
Opisthoporus iris (Godwin Austen)	6	2	7	23	10	4	2	0	22	16	3	95	9
Pterocyclos/Opisthoporus juv.	2	0	13	3	0	1	1	0	2	0	1	23	1
Japonia jucunda (Smith)	7	1	1	1	1	3	1	3	1	4	0	23	2
Japonia juv.	0	3	0	1	1	1	0	0	2	0	0	8	1
Leptopoma pellucidum (Grateloup)	106	14	85	67	19	22	7	4	50	101	26	501	40
Leptopoma sericatum (Pfeiffer)	0	1	0	0	0	0	2	1	5	3	5	17	6
Leptopoma undatum (Metcalfe)	4	2	0	4	0	1	1	2	4	24	0	42	3
Leptopoma juv.	6	2	2	3	2	0	0	0	5	4	1	25	1
Chamalycaeus sp-BO-01	1	0	3	1	0	0	0	0	0	1	0	6	0
Chamalycaeus broti (Aldrich)	1	2	0	1	1	0	0	0	0	0	0	5	4
Chamalycaeus juv.	0	0	2	1	0	0	0	0	1	0	0	4	0
Alycaeus jagori von Martens	0	0	0	1	0	0	0	0	0	0	0	1	1
Ditropopsis sp-BO-01	0	0	0	0	0	1	0	0	0	0	1	2	1
Diplommatinidae													
Diplommatina rubicunda (von Martens)	0	0	0	0	0	0	0	0	1	1	0	2	1
Diplommatina gomantongensis Smith	0	1	0	6	0	0	2	0	17	0	0	26	0
Diplommatina soror Vermeulen	0	0	0	0	0	0	2	0	0	0	0	2	0
Opisthostoma lissopleuron Vermeulen	11	137	152	57	0	0	53	0	62	0	0	472	244
Arinia stenotrochus Vermeulen	0	0	21	34	0	0	4	1	0	6	8	74	0
Arinia turgida Vermeulen	0	0	0	0	1	0	0	0	0	0	0	1	0
Arinia brevispira Vermeulen	0	0	10	19	1	0	0	0	1	0	2	33	0
Vertiginidae													
Ptychopatula orcula (Benson)	1	2	1	0	0	0	0	0	0	0	0	4	0
Subulinidae													
Lamellaxis clavulinus (Potiez & Michaud)	0	1	0	0	1	0	0	0	1	0	0	3	1
Lamellaxis gracilis (Hutton)	0	4	1	0	0	0	0	0	0	0	0	5	0
Streptaxidae													
Diaphera wilfordi (Dance)	0	0	3	10	0	0	1	0	3	0	0	17	6
Charopidae													
Charopa sp-BO-01	0	5	0	0	0	0	9	0	1	0	0	15	0
Charopa sp-BO-02	2	1	0	0	0	0	2	0	0	0	0	5	0
Endodontidae													
Philalanka kusana (Aldrich)	0	2	0	0	0	0	3	0	1	1	2	9	1
Euconulidae													
Liardetia scandens (Cox)	4	2	3	1	9	11	1	0	0	1	9	41	4
Liardetia sp-BO-01	1	3	4	4	0	1	1	1	1	13	0	29	1
Coneuplecta angulata (Issel)	3	0	0	0	0	2	0	0	0	0	0	5	0
Helicarionidae													
Helicarion spec.	0	0	0	4	0	2	0	0	6	0	0	12	0
Geotrochus kinabaluensis (Smith)	6	3	1	13	5	7	3	3	3	0	0	44	7
Geotrochus bongaoensis (Smith)	1	0	0	2	0	0	0	0	0	0	0	3	0
Ariophantidae													
Hemiplecta densa (Adams & Reeve)	29	3	9	12	15	10	16	6	26	4	1	131	4
Quantula subconsul (Smith)	16	7	18	15	6	3	5	0	14	4	0	88	2
Microcystina sp-BO-01	3	5	11	3	2	0	4	1	2	0	0	31	0
Microcystina sp-BO-03	0	2	1	0	0	0	2	0	0	2	0	7	0
Macrochlamys tersa (Issel)	1	0	0	0	0	0	0	2	0	0	1	4	2
Trochomorphidae													
Videna metcalfei (Pfeiffer)	3	1	1	5	5	0	0	0	0	0	1	16	3
Videna froggatti (Iredale)	1	0	1	0	0	0	1	2	6	2	0	13	1
Videna juv.	0	1	0	0	0	0	0	0	0	0	0	1	0
Bertia brookei (Adams & Reeve)	0	1	0	1	0	0	0	0	1	0	0	3	0
Camaenidae													
Amphidromus martensi Boettger	1	1	1	5	0	2	1	0	3	1	0	15	1
Trachia pudica (Godwin Austen)	2	10	0	0	2	0	2	4	1	0	0	21	0
Chloritis kinabaluensis (Kobelt)	12	1	4	1	1	4	1	0	8	1	1	34	0
Total specimens	270	221	412	352	98	80	128	31	291	216	63	2162	396
Total species	28	27	24	29	18	16	25	13	30	21	13		

	Dan. 1	Dan. 2	Dan. 3	Dan. 4	Dan. 5	Dan. 6	Dan. 7	Dan. 8	Dan. 9	Dan.10	Dan.11	Dan.12	Totals
Cyclophoridae													
Platyraphe linitus (Godwin Austen)	14	0	0	0	0	0	0	3	0	0	0	0	17
Opisthoporus birostris (Pfeiffer)	15	1	0	0	1	1	1	9	0	0	0	0	28
Japonia juv.	0	2	1	0	0	0	1	0	0	0	0	0	4
Leptopoma sericatum (Pfeiffer)	1	0	0	0	2	0	0	0	0	0	0	0	3
Diplommatinidae													
Diplommatina soror Vermeulen	0	1	0	1	0	0	0	3	0	0	0	0	5
Diplommatina whiteheadi Smith	0	0	0	0	0	1	0	0	0	6	10	0	17
Diplommatina sykesi Vermeulen	6	1	0	0	0	0	0	38	1	0	0	0	46
Diplommatina cf. *centralis* Vermeulen	0	0	0	0	0	0	0	0	0	1	0	0	1
Arinia paricostata Vermeulen	9	3	0	0	0	0	0	221	4	0	1	1	239
Arinia brevispira Vermeulen	0	0	0	0	0	0	0	1	0	0	0	0	1
Arinia stenotrochus Vermeulen	0	0	0	0	0	0	0	2	0	0	0	0	2
Subulinidae													
Lamellaxis clavulinus (Potiez & Michaud)	4	0	3	0	0	0	1	3	0	0	0	0	11
Lamellaxis gracilis (Hutton)	0	0	0	2	10	3	0	0	0	0	54	0	69
Clausiliidae													
Phaedusa filicostata filialis (von Martens)	0	0	0	0	0	0	0	4	0	0	0	0	4
Streptaxidae													
Diaphera wilfordi (Dance)	0	0	0	0	0	0	0	7	0	0	0	0	7
Endodontidae													
Philalanka kusana (Aldrich)	1	4	2	0	0	0	0	17	0	0	1	0	25
Charopidae													
Beilania philippinensis (Semper)	0	0	0	0	0	0	0	1	0	0	0	0	1
Charopa sp-BO-02	0	0	0	0	1	0	0	0	0	4	3	1	9
Charopa sp-BO-01	0	0	0	0	0	0	0	0	6	3	1	0	10
Euconulidae													
Liardetia sp-BO-01	2	0	0	1	0	0	0	14	0	7	6	1	31
Liardetia scandens (Cox)	1	0	0	0	0	0	0	0	0	0	0	0	1
Coneuplecta microconus (Mousson)	1	0	0	0	0	0	0	0	0	0	0	0	1
Coneuplecta angulata (Issel)	1	0	0	1	1	0	0	0	0	0	0	0	3
Helicarionidae													
Helicarion spec.	1	0	0	0	5	2	0	0	0	0	0	0	8
Ariophantidae													
Hemiplecta densa (Adams & Reeve)	4	0	1	1	0	0	1	0	0	1	2	0	10
Everettia spec. “banded”	1	0	0	0	0	0	0	0	0	0	0	0	1
Everettia spec. “large”	7	1	0	0	1	0	1	9	1	0	1	0	21
Quantula spec.	0	1	0	0	0	0	0	0	0	0	0	0	1
Microcystina sp-BO-01	2	1	0	0	0	0	0	1	0	10	8	0	22
Microcystina sp-BO-03	0	1	0	0	0	0	0	6	0	0	1	0	8
Microcystina sp-BO-04	2	0	0	0	0	0	1	4	0	0	0	0	7
Macrochlamys tersa (Issel)	0	0	0	0	0	0	0	0	0	1	0	0	1
Trochomorphidae													
Videna metcalfei (Pfeiffer)	4	1	0	0	0	5	0	1	0	0	2	0	13
Camaenidae													
Trachia pudica (Godwin Austen)	1	0	0	0	0	0	0	0	0	0	0	0	1
Chloritis kinabaluensis (Kobelt)	1	0	0	0	0	0	0	0	0	0	0	0	1
Chloritis spec.	0	0	0	0	0	0	0	1	0	0	0	0	1
Ganesella acris (Benson)	2	0	0	0	0	0	0	0	0	0	0	0	2
Total specimens	80	17	7	6	21	12	6	345	12	33	90	3	632
Total species	21	11	4	5	7	5	6	19	4	8	12	3	