Mem. Fac. Sci. Kyoto Univ. (Ser. Biol.), 12: 119–128, Oct., 1987

Morpho-ecological Analysis on the Relationship Between Habitat and Body Shape in Adult Passalid Beetles (Coleoptera: Passalidae)

YUTAKA JOHKI and MASAHIRO KON

Department of Zoology, Faculty of Science, Kyoto University
Sakyo-ku, Kyoto, 606, Japan

(Received September 19, 1987)

Abstract The relationship between habitat and body structure in adult passalid beetles (Coleoptera, Lamellicornia) was studied. One-hundred and forty-six specimens including 20 species of the Oriental and Australian passalids were subject to measurement for analyses. Proportion of the body, such as (elytral width)/(body length) or (elytral length)/(body length), was remarkably uniform among all species examined, whereas body thickness varied greatly with species. Flattening of the body was considered as the adaptation for living under the bark of the log. In some species living in the detritus-like microhabitat, the front tibiae were flattened and widened just like the dung beetles or mole crickets, which was considered to be suitable for digging tunnels in the detritus-like material.

INTRODUCTION

Passalid beetles are often referred to by many authors as good examples of subsocial insects (Ohaus, 1900; Wheeler, 1923; Miyatake, 1959; Eickwort, 1981; Reyes-Castillo & Halffter, 1983; etc.). However, excepting their subsociality, they have little or no uniquely interesting behavioural patterns and this, coupled with their monotonous colour and shape, has led to the group being somewhat neglected by entomologists, and they are seldom referred to in the literature. Furthermore, since most species of Passalidae live in a uniform microhabitat, within a "decayed log", the relationship between habitat and body structure has not been investigated in detail and only a few authors have commented briefly on the body thickness (Schuster, 1978; Reyes-Castillo & Halffter, 1983).

In August, 1985, we observed the life mode of several passalid beetles at Sepilok and Brumas, Sabah (North Borneo), and found several kinds of morphological adaptations to special environments in adult passalids, as also seen in the carabid beetles (Sharova, 1974; Thiele, 1977). In this paper we describe the relationship between habitat and body structure in adult passalid beetles, based upon measurements of specimens and observations made in Sabah and adjacent Oriental and Australian regions.

MATERIALS AND METHODS

The number and locality of specimens of each species used for the study are summarized in Table 1. Since we restricted the species for analysis to those for which

Table 1. Number and locality of each species of Passalidae used for studies.

Subfamily[1)]	Species	No. specimens	Locality
Aulacocyclinae	*Comacupes stoliczkae*	3	Brumas (Sabah)
	Comacupes cylindraceus	1	Brumas (Sabah)
	Ceracupes arrowi	2	Taiwan
	Ceracupes sp.	3	Taiwan
	Taeniocerus bicanthatus	11	Brumas (Sabah)
	Taeniocerus platypus	8	Keningau (Sabah)
	Taeniocerus pygmaeus	6	Sepilok (Sabah)
	Aulacocyclus tricuspis	9	New Caledonia
	Aulacocyclus celebensis	3	Celebes
	Cylindrocaulus patalis	6	Japan
Macrolininae	*Aceraius laniger*	6	Mt. Kinabalu
	Aceraius grandis	14	Taiwan
	Aceraius laevicollis	13	Sabah
	Aceraius borneanus	9	Sepilok (Sabah)
	Pelopides monticulosus	5	Brumas (Sabah)
Leptaulacinae	*Leptaulax dentatus*	9	Sabah
	Leptaulax sp. 2	12	Mt. Kinabalu
	Leptaulax cyclotaenius	12	Sepilok (Sabah)
	Leptaulax planus	11	Sabah
	Leptaulax sp. 5	3	Sabah
Total	20 spp.	146	

1) For the classification of subfamilies, we followed Gravely (1918) who split the Oriental passalids into three subfamilies.

habitats and modes of living had been roughly confirmed by ourselves or others, only 146 individuals including 20 species were subject to study. Photographs of these species appear in Figure 7 at the end of the paper.

For all 146 specimens, the following six measurements were taken: (1) Body length (L), (2) Elytral length (EL), (3) Elytral width (EW), (4) Body height or body thickness (H), (5) Front-tibial length (FTL), and (6) Front-tibial width (FTW). Four kinds of ratios, EL/L, EW/L, H/EW and FTW/FTL, were then calculated and were used as indices of the body shape for quantitative analyses.

RESULTS AND DISCUSSION

Figures 1 and 2 show the distribution of EL/L and EW/L, respectively. It is obvious that these two ratios are remarkably constant regardless of species, genera and subfamilies. Even the African and New World passalids (not included in Figs. 1 and 2) were consistent with this result, which suggests that the body shape of adult Passalidae is uniform without exception throughout the world (see Fig. 3a). Arrow (1950) states that the Passalidae are a unique family, as compared mainly with the Lucanidae and Scarabaeidae, in that (a) no external difference is detectable between males and females,

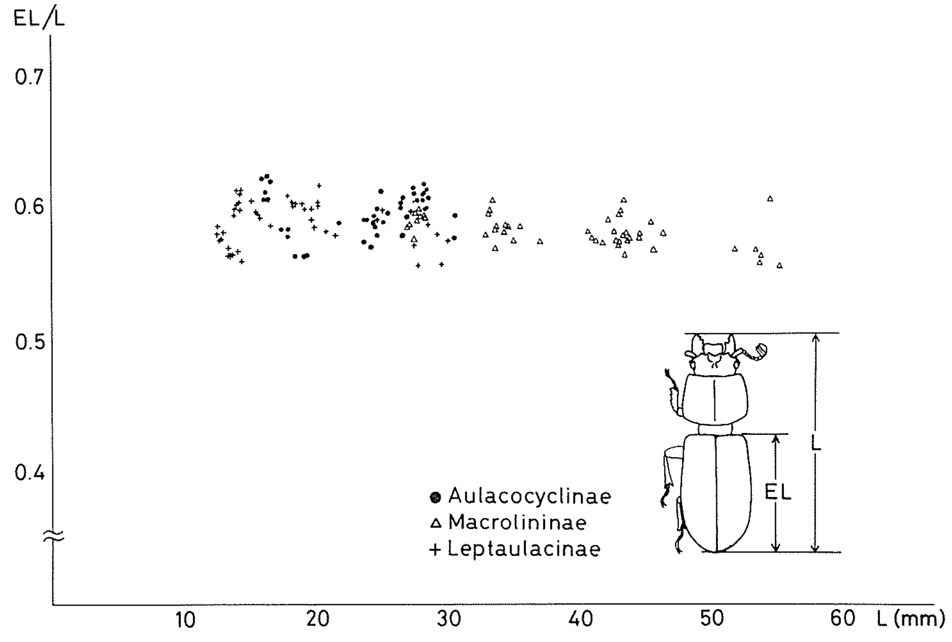

Fig. 1. Distribution of the ratio EL/L for 146 individuals of 20 species belonging to the Passalidae. Abscissa: body length

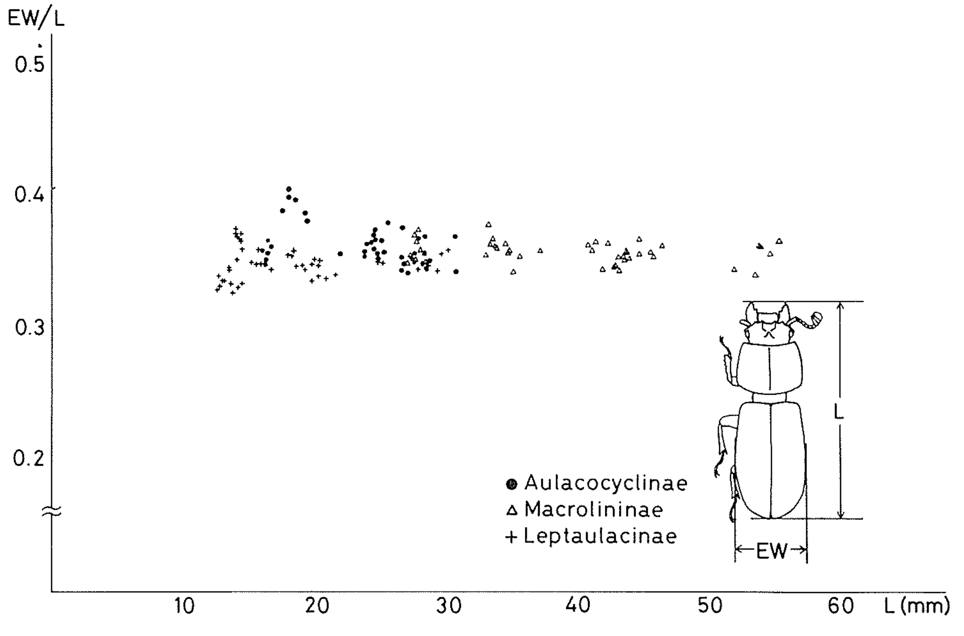

Fig. 2. Distribution of the ratio EW/L for 146 individuals of 20 species belonging to the Passalidae.

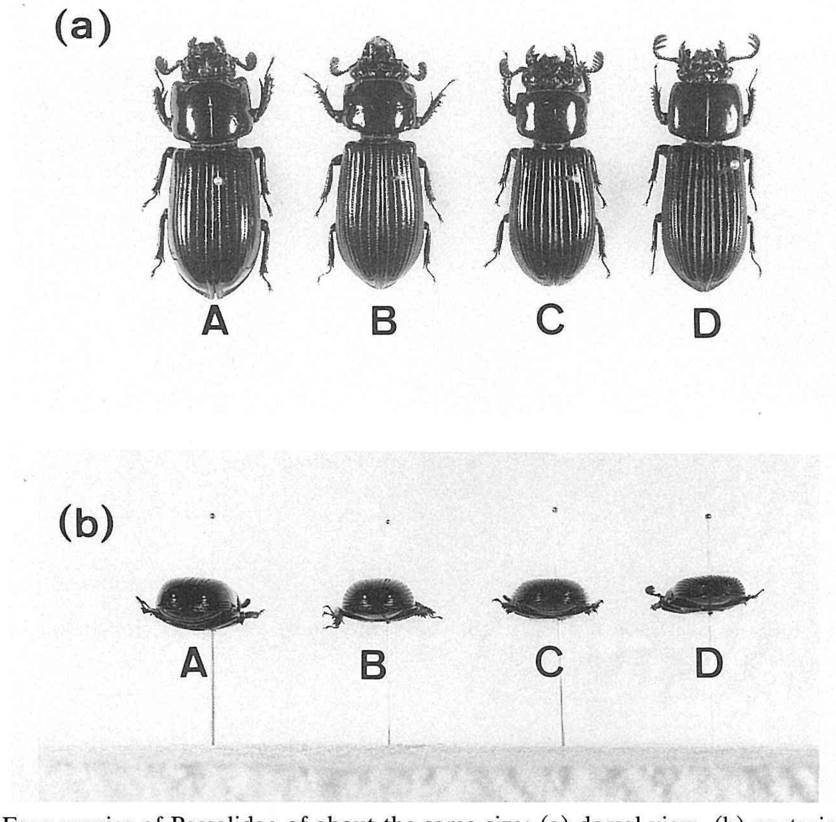

Fig. 3. Four species of Passalidae of about the same size: (a) dorsal view, (b) posterior view. A: *Comacupes cylindraceus,* B: *Protomocoelus* sp., C: *Aceraius borneanus,* D: *Leptaulax dentatus.*

and (b) there is little variation in size between each species. Our result shown in Figures 1 and 2 should be added as a third feature unique to the Passalidae. Together, these features probably contributed to the lack of interest shown in this group by coleopterologists and insect collectors.

Figure 4 shows the distribution of the H/EW ratio. Unlike the EL/L and EW/L, it varies greatly with species, ranging from a minimum of 0.344 (*Leptaulax planus*) to a maximum of 0.803 (*Cylindrocaulus patalis*). This suggests that there is a wide variation in body thickness, despite the uniform body shape among all species (Fig. 3a, b). Such variations correspond closely to the microhabitat of eacth species: the flattened species (e.g. *Leptaulax* spp.) live just under the bark of dead logs, while the convex group (e.g. *Taeniocerus* spp. and *Aceraius* spp.) dig tunnels in the heartwood or detritus of rotten wood, or make a gallery in the interface between the log and the ground. Flattening of the body is known to be an adaptation to living in cracks in other coleopterous families, such as the Carabidae, Cucujidae, etc. For example, the extreme flattening of the violin beetle, *Mormolyce* sp., is considered to be adaptive for seeking prey among the layers of some kinds of Polyporaceid mushrooms (Lieftinck & Wiebes, 1968), and similar adapta-

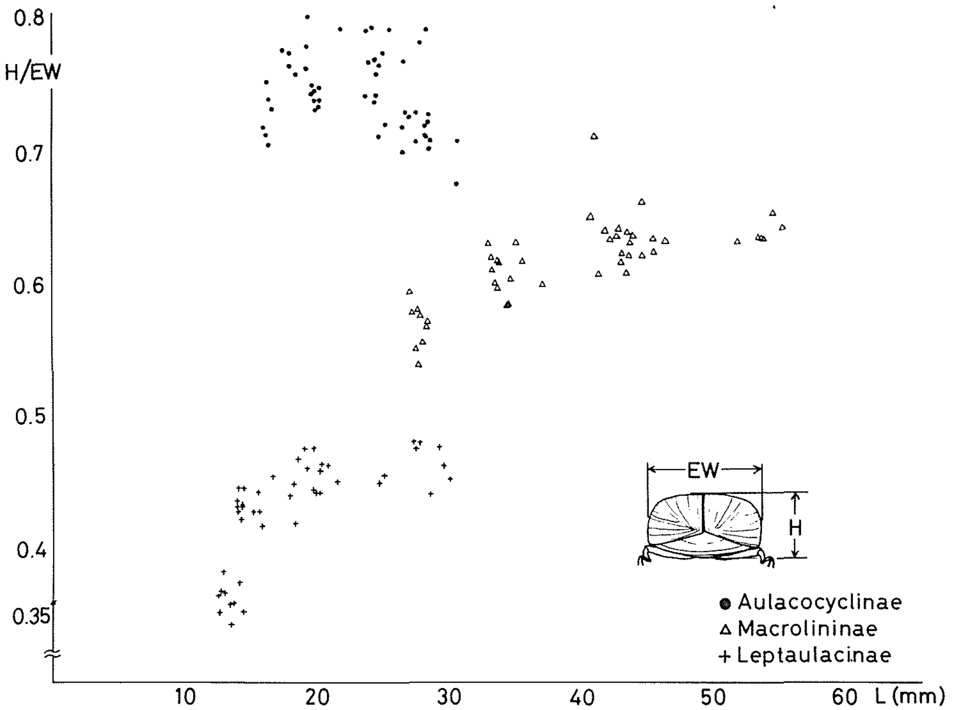

Fig. 4. Distribution of the ratio H/EW for 146 individuals of 20 species belonging to the Passalidae.

tions are seen in the carabid, *Colopodes bromeliarum,* which lives between the leaf sheaths of Bromeliaceae (Thiele, 1977), and all species of Cucujidae, which live under the bark of dead logs. The flattened groups of Passalidae, *Leptaulax* spp., live gregariously under the bark, and thus differ ecologically from the convex species, which live in a family. The sapwood just under the bark is richer in nutrition for beetles than heartwood. Some relationship may exist between life under the bark and gregariousness in *Leptaulax* spp., but it is still unknown due to the lack of detailed study.

Another morpho-ecological feature of Passalidae is seen in the front tibiae of several species. In *Taeniocerus* spp. from Sabah, *Ceracupes arrowi* from Taiwan, and *Aulacocyclus celebensis* from Celebes, the front tibiae are flattened and widened and equipped with lateral teeth (Fig. 5), just like the dung beetles (Scarabaeidae) and the mole crickets (Orthoptera, Gryllotalpidae). Consequently, these passalids have a higher ratio of FTW/FTL than other species, as shown in Figure 6. *Taeniocerus* spp., *Ceracupes arrowi* and *Aulacocyclus celebensis,* all belonging to the subfamily Aulacocyclinae, show some similarity in their life styles, all living in the detritus-like microhabitat out of the wood. *Taeniocerus bicanthatus* was found living in the interface between the log and the ground (Kon *et al.,* 1985; Kon & Johki, 1987); *Ceracupes arrowi* was confirmed by us to live in detritus among the rhizomes of epiphytic ferns of the family Aspleniaceae (Johki & Kon, 1986); *Aulacocyclus celebensis* is also said to live among the rhizomes of some ferns (M. Toyama, personal comm.). Their flattened and widened front tibiae are therefore considered as a "shovel" used for making a gallery in such detritus-like

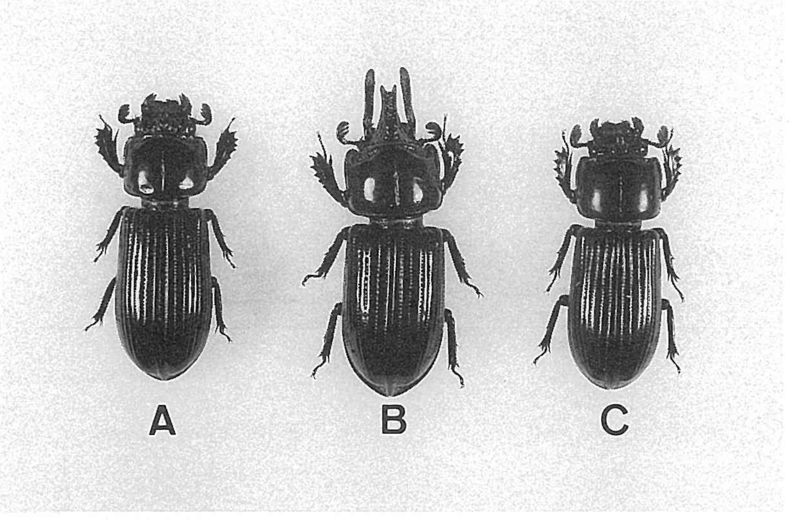

Fig. 5. Three species of Passalidae with flattened and widened front tibiae. A: *Taeniocerus bicanthatus,* B: *Ceracupes arrowi,* C: *Aulacocyclus celebensis.*

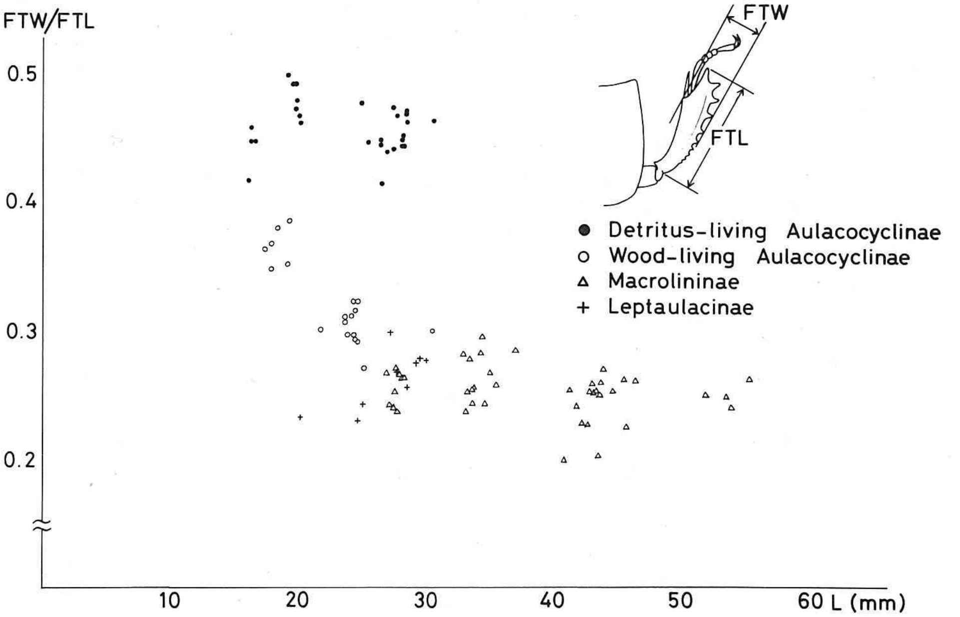

Fig. 6. Distribution of the ratio FTW/FTL for 108 individuals of 16 species belonging to the Passalidae.

materials, as in the famous examples of the dung beetles (Heinrich & Bartholomew, 1979) and mole crickets (Chapman, 1969; Richards & Davies, 1977).

Even in the wood-living species of Aulacocyclinae, the front tibiae are relatively

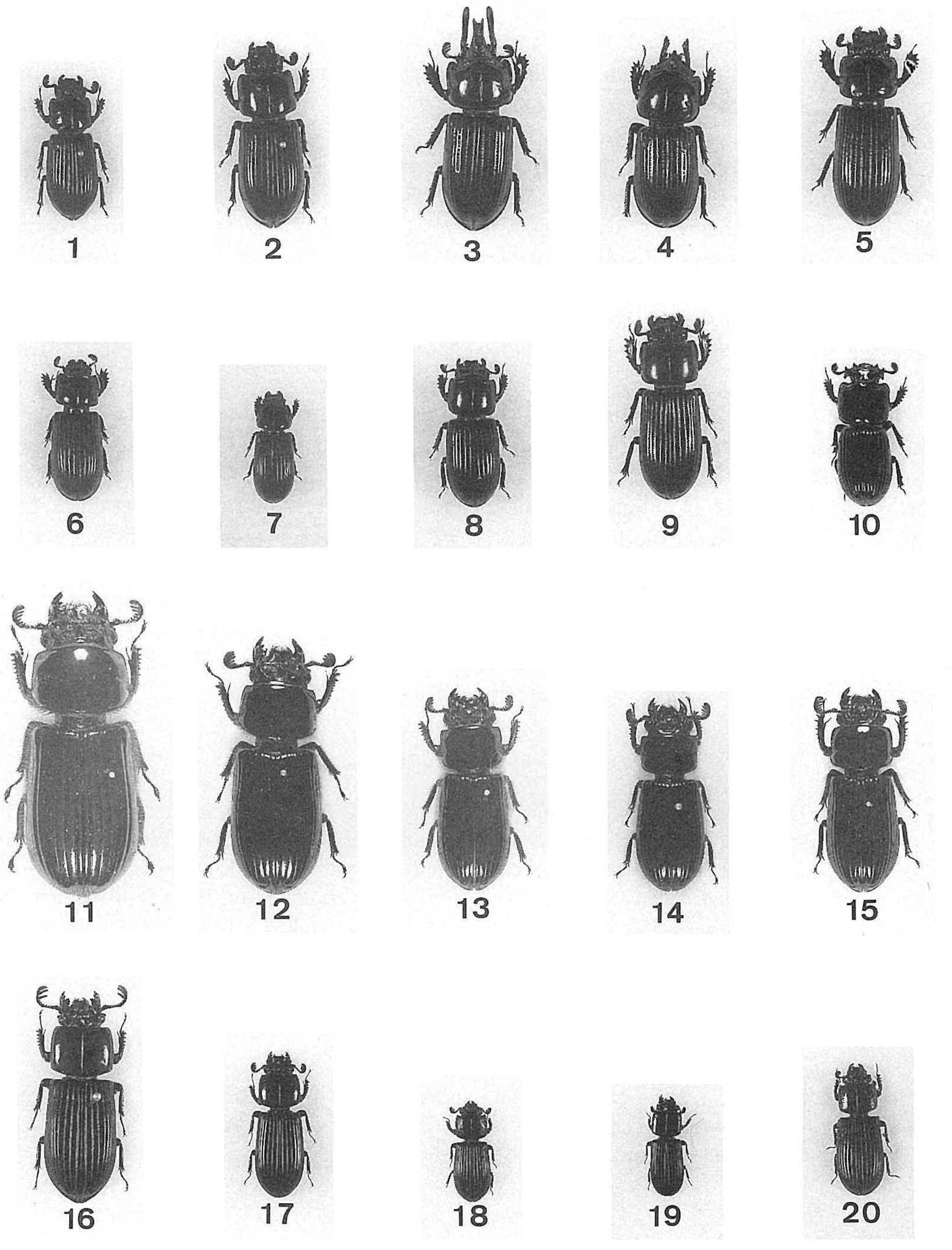

Fig. 7. Species of Passalidae used in the morpho-ecological analyses. 1: *Comacupes stoliczkae*; 2: *Comacupes cylindraceus*; 3: *Ceracupes arrowi*; 4: *Ceracupes* sp.; 5: *Taeniocerus bicanthatus*; 6: *Taeniocerus platypus*; 7: *Taeniocerus pygmaeus*; 8: *Aulacocyclus tricuspis*; 9: *Aulacocyclus celebensis*; 10: *Cylindrocaulus patalis*; 11: *Aceraius laniger*; 12: *Aceraius grandis*; 13: *Aceraius laevicollis*; 14: *Aceraius borneanus*; 15: *Pelopides monticulosus*; 16: *Leptaulax dentatus*; 17: *Leptaulax* sp. 2; 18: *Leptaulax cyclotaenius*; 19: *Leptaulax planus*; 20: *Leptaulax* sp. 5.

wider than the species of Macrolininae and Leptaulacinae (Fig. 6), which corresponds to their living in more-decayed wood than do members of the other two subfamilies. Conversely, all species of the Macrolininae and Leptaulacinae have slender, cylindrical front tibiae. Their mandibles look far stronger and seem suitable for crunching through hard wood.

A similar morphological adaptation to detritus-living is seen in the New World passalid, *Ptichopus angulatus,* which is found in the detritus below the nest of the leaf-cutter ant, and has wide front tibiae (Reyes-Castillo, 1970). Furthermore, Schuster (1978) reported that several species of New World Passalidae are found in detritus-like microhabitats, such as under cow manure, among the roots of epiphytic Bromeliaceae, under stones, and in the guano of bats and oilbirds on the cave floor. Although he did not refer to the front tibiae of those passalids, they probably have wide tibiae as apparatus for digging detritus.

Due to the large number of species showing a wide variety of habitats, foods and life forms, extensive morpho-ecological studies have been performed on the Carabidae (e.g. Sharova, 1974 ; Thiele, 1977). However, due to preconception of coleopterologists that passalid beetles lived in a uniform and monotonous microhabitat, such studies have never been performed on the Passalidae. However, our observations and those by a few entomologists have shown clearly that the microhabitat diversity of passalid beetles is much greater than hitherto expected. In the Oriental region, there had been no report on the ecology of Passalidae since the brief notes made by Gravely (1914). Hopefully, further discoveries of microhabitat diversity in passalid beetles will stimulate further morpho-ecological studies of this interesting group.

Acknowledgments

We thank Dr. K. Morimoto of Kyushu University, Dr. M. Miyatake of Ehime University, Mr. H. Ota of Kyoto University and Mr. M. Toyama for their valuable suggestions. We also thank Mr. T. Mori, Mr. Saikeh Bin Lantoh, Mr. Momin Binti and other all staff of Entomological Section of the Forest Research Centre, Sabah, for their valuable advice and help for our field work. Thanks are due to the staff of the Sabah Softwoods Sdn. Bhd. for providing accommodation for us and permission to conduct surveys in the plantation area at Brumas. We thank Drs. M. Hori and R. Iwata, and Messrs. H. Arimoto, T. Ito, A. Kato, K. Matsuda, T. Ochi, T. Ohbuchi, M. Ohgaki, T. Shimomura, M. Tanaka, K. Urata and M. Yagi, for offering the invaluable specimens used in this study. Special thanks are due to Prof. Dr. T. Hidaka for giving us an opportunity to conduct the research in Sabah, and to Dr. M. Matsui, Mr. T. Hikida, Dr. M. Ishii, Dr. K. Sakurai, Mr. H. Fujii and Mr. K. Abe for warm companionship and assistance during the survey. This work was supported by a Grant-in-Aid for Scientific Research (Overseas Scientific Survey) from the Ministry of Education, Science and Culture, Japan, No. 60041037 (1985) and No. 61043033 (1986).

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Appendix. List of Passalidae collected in Sabah, 1985.

Species	No. collected	Locality[1]	Date	Way of collection[2]
[Aulacocyclinae]				
1. *Comacupes stoliczkae*	4	BMS	Aug. 24	Wood
2. *Comacupes cylindraceus*	1	BMS	Aug. 25	Wood
3. *Taeniocerus bicanthatus*	1	BMS	Aug. 21	Road
	2	BMS	Aug. 25	Wood
	11	BMS	Aug. 26	Wood
	12	BMS	Aug. 27	Wood
[Macrolininae]				
4. *Aceraius tricornis*	1	KDS	Jul. 31	Light
5. *Aceraius perakensis*	1	KDS	Jul. 31	Light
6. *Aceraius laevicollis*	1	SPK	Aug. 5	Light
	1	BMS	Aug. 18	Light

(Continued)

(Continued)

	1	BMS	Aug. 21	Light
	2	BMS	Aug. 23	Wood
	1	BMS	Aug. 24	Walk
	2	BMS	Aug. 25	Wood
	1	BMS	Sept. ?	Wood
	1	BMS	Sept. 20	Light
	3	BMS	Oct. 2	Light
	6	BMS	Oct. 17	Light
7. *Aceraius borneanus*	1	SPK	Aug. 10	Light
	1	SPK	Aug. 17	Wood
	22	SPK	Aug. 18	Wood
8. *Pelopides monticulosus*	1	BMS	Aug. 18	Road
	1	BMS	Aug. 24	Wood
	1	BMS	Oct. 2	Light
9. *Macrolinus latipennis*	2	SPK	Aug. 13	Wood
10. *Ophrygonius singapurae*	1	SPK	Aug. 8	Walk
[Leptaulacinae]				
11. *Leptaulax dentatus*	1	SPK	Sept. 15	Light
12. *Leptaulax cyclotaenius*	3	SPK	Aug. 4	Wood
	2	SPK	Aug. 14	Wood
	14	SPK	Aug. 17	Wood
13. *Leptaulax planus*	2	SPK	Aug. 3	Light
	1	SPK	Aug. 7	Light
	2	SPK	Aug. 15	Light
	1	SPK	Aug. 18	Light
	2	BMS	Aug. 23	Wood
	68	BMS	Sept. 23	Light
	1	BMS	Sept. 24	Light
	1	BMS	Sept. 25	Light
	1	BMS	Sept. 26	Light
	1	BMS	Oct. 17	Light
14. *Leptaulax* sp. 5	1	BMS	Aug. 18	Light
	2	BMS	Aug. 26	Wood
	2	BMS	Sept. 23	Light

1) BMS: Brumas, KDS: Kundasang (Mt. Kinabalu), SPK: Sepilok.
2) Wood: from the log or rotten wood, Road: dying on the roadside, Light: collected by the light-trap, Walk: walking on the road or on the log.

著者： 常喜　豊・近　雅博，〒606　京都市左京区北白川追分町　京都大学理学部動物学教室.