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Study on the Relationship Between Species Richness and Morphological Diversity of Higher Categories in Scarabaeoidea

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Abstract: Evolutionary biology faces the important challenge of determining how to interpret the relationship between selection pressures and evolutionary radiation of species. The different biodiversity indicators highlight the disparate nature of biodiversity investigations. However, the influence of ecological factors and the specificity of taxonomic phylogeny have led to controversy over the correlation between these indicators. By combining quantitative morphology and statistical methods, here we analyze the biodiversity under the influences of phylogenetic relation factors represented by higher categories. A total of 8508 species of beetles from 1247 genera, 34 subfamilies, and 10 families of the Scarabaeoidea were selected as a test group; 70% of the family-level samples and 60% of the subfamily-level samples were selected at a proportion of 10–30% of the global described species. The taxonomic categories of family and subfamily were selected for phylogenetic representation, and the analysis of geometric morphometrics on the pronotum and elytron, which represent the major aspect of the morphology in dorsal view, was conducted. Through principal component analysis and Spearman correlation coefficient analysis, it was found that: the morphological diversity of the pronotum is higher in most groups of family/subfamily category than in the elytron; the correlation between the morphological diversity and species richness of the pronotum in the superfamily Scarabaeoidea is higher than that of the elytron; correlations between morphological diversity of the pronotum and taxa richness among sub-/families were always found to be consistent, and it was higher than it in the elytron test. This study compares the correlation between the diversity of different characters and the richness of taxa to interpret the phylogenetic impacts of biodiversity and sheds light on a fresh perspective for detailed studies of the selection pressures and formation mechanisms regulating the rise and fall of species.

Keywords: evolutionary radiation; phylogenetic relation factor; biodiversity indicator; Scarabaeoidea; geometric morphometrics

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1. Introduction

Evolutionary radiation events lead to the occurrence of biodiversity, which includes broad cladogenesis, rapid divergence, and adaptive evolution between lineages [1,2]. Different organisms have amassed extraordinary diversity in response to selection pressures [3]. Determining how diverse organisms respond to abiotic and biotic pressures becomes a significant challenge for understanding evolution [4]. The different biodiversity indicators highlight the disparate nature of biodiversity investigations [5,6], which is essential to comprehending their evolutionary strategies under the influence of ecological factors [7–11].

Among these, morphological diversity (MD) reflects biological feedback and ecosystem functionality [12], and species richness (SR) reveals the number of species in a community or area. The relation between morphological diversity and species richness has often been used to explore macroscopical patterns of biodiversity in different ecosystems [13,14]. However, due to the influence of ecological factors and the specificity of taxonomic phylogeny, the correlation between these two indicators does not always go in the same direction (positive or negative) [15–21]. For example, Gerovasileiou and Voultsiadou found that MD and SR of sponge have a significantly positive correlation in the eastern Mediterranean cave [18], Silva and Brandão found that leaf-litter ant communities in the Atlantic Forest reflected negatively correlated richness and MD with the increase in latitude [21]. In addition, Kuczynski et al. found that in European freshwater fish faunas, morphological richness was positively affected by SR in historical assemblages, but the introduction of non-native species would cause important reshuffling of assemblages [17]. The inconsistent conclusions of previous studies remind us that the relationship between these two indicators is not simple. New approaches and larger datasets might provide greater insight into this problem.

In light of the different drivers that may affect the evolutionary history of a given clade, biodiversity under different factors is probably best determined by studying individual cases. There are about 32,000 species and 2453 genera of Scarabaeoidea over the world [22]. Under the influence of strong selective pressure and long-term co-evolution, the adult scarabs have been divided into four primary feeding types: omnivorous, phytophagous, coprophagous, and non-feeding types [7]. The phytophagous and coprophagous scarabs have successfully undergone evolutionary radiation. Over a long evolutionary time, the phytophagous scarabs adapted to the differentiation of angiosperms and changes in global temperature and formed multiple clades. For the coprophagous scarabs, which are represented by Scarabaeinae and Aphodiinae, the morphological diversity of the elytron changed dramatically, indicating that there was intense niche competition among the groups. These coprophagous scarabs [23] have rapidly differentiated into about 8800 different species over the course of their evolution by occupying distinct ecological niches with specific feeding types [24,25]. The huge species richness, complicated phylogenetic relations, and divergent morphological characters between feeding-type groups make scarabs a dominant group for studying biodiversity evolution [7,26–28].

In this study, a large number of global scarab species (8508, c. 1/4 of known species) were selected to represent the species richness of Scarabaeoidea. This dataset included 10 scarabaeoid families and 34 subfamilies. All specimens were identified and analyzed, which reflect patterns of higher-taxon phylogenetic relation (family and subfamily). Furthermore, geometric morphometrics, a useful approach to quantitative morphology analysis, was used to evaluate the morphological diversity. Two characters, the pronotum and elytron, were employed as the foci of character tests. Thus partitioned, these data were used to explore the correlation between morphological diversity and species richness. In this study, quantitative analysis was used to quantify the morphological data of continuous characteristics, which expanded the coverage of morphological data. This study compares the correlation between the diversity of different characters and the richness of taxa to interpret the phylogenetic impacts of biodiversity, offering a fresh perspective for detailed studies of the selection pressures and formation mechanisms regulating the rise and fall of species.

2. Methods

2.1. Taxa Examined

In this study, 8508 specimens were analyzed, covering 10 families (83% of described families), 34 subfamilies (87% of described subfamilies), and 1247 genera (Table 1). The test samples used in this study were all two-dimensional images of the standard dorsal view of Scarabaeoidea insects, which were obtained from the following two sources: (1) historical accumulation of the Key Laboratory of Animal Biodiversity Conservation and Integrated

Pest Management (Chinese Academy of Sciences), Institute of Zoology, Chinese Academy of Sciences [29]; (2) studies provided by the National Knowledge Infrastructure, Web of Science, ResearchGate, and academic websites such as Google Scholar [Supplement S1]. In order to facilitate data processing and statistics, the collected documents and pictures were numbered in chronological order, and all sample image file names were assigned to reflect the specimen's family-to-species taxonomy: family, subfamily, genus, and species. Taxa richness value was obtained by counting the number of species in different test groups (Table 1) (Figure 1).

Table 1. Sampling information of test families.

Test Groups	Sampling (Described) Number of Subfamilies	Sampling (Described) Number of Genera	Sampling (Described) Number of Species
Pleocomidae	1 (1)	2 (2)	6 (50)
Geotrupidae	3 (3)	42 (70)	213 (920)
Passalidae	2 (2)	29 (64)	107 (800)
Trogidae	2 (2)	6 (6)	73 (300)
Glaresidae	1 (1)	2 (2)	52 (57)
Ochodaeidae	1 (2)	4 (10)	18 (74)
Hybosoridae	5 (5)	27 (74)	147 (573)
Glaphyridae	1 (1)	6 (10)	20 (204)
Scarabaeidae	14 (16)	1025 (1900)	6573 (27,000)
Lucanidae	4 (4)	87 (114)	1299 (1489)

2.2. Data Analysis

In this study, a certain proportion (10–30% of described species) was used to select 70% of the family and 60% of the subfamily-level samples to objectively reflect SR and MD of each category. Two characters, the pronotum and elytron, were employed as the testing characters. The pronotum and elytron are recognized as crucial components of the scarabs' body. The pronotum's morphology differs amongst groups because of the different distribution of muscles attached to the prothorax [30,31] and the foreleg's food handling habits (primarily coprophagous) [32,33]; the elytron is connected to the muscles involved in digging and hindfoot movement because of the way the mid/hind thorax is shaped [34]. These traits maintain a certain genetic correlation with other traits during the evolution of the organism as a whole but also differ from the mouthparts with their strong selective pressures from food types, which afford indirect selection to non-target traits.

Two curves were extracted from pronotum and elytron contours to represent their external forms. Each curve was resampled into 25 or 50 semi-landmarks (SLM) by length, respectively (Figure 2). The curves and semi-landmarks were digitized with Tps-Dig 2.05 [35]. Data files used for morphological analysis were completed by including semi-landmarks and landmarks [36] in the same data files [37–39]. Principal component analysis (PCA) and geometric modeling of mathematical spaces formed by the PC axes were used to coordinate shape variation in the whole dataset [40]. Patterns of test shape (pronotum and elytron) variation represented by the first three principal components with the largest proportion were included in this study (Figure 2).

Morphological diversity was quantified as the total Procrustes variance [41] in Morpho J 1.08.01 (Supplement S2 and S3) [42]. Correlations between pronotum and elytron morphological diversity and species/genera richness values in family category and subfamily category were analyzed via Spearman correlation coefficient based on SPSS statistical software (R27.0.1 version) [39,41,43].

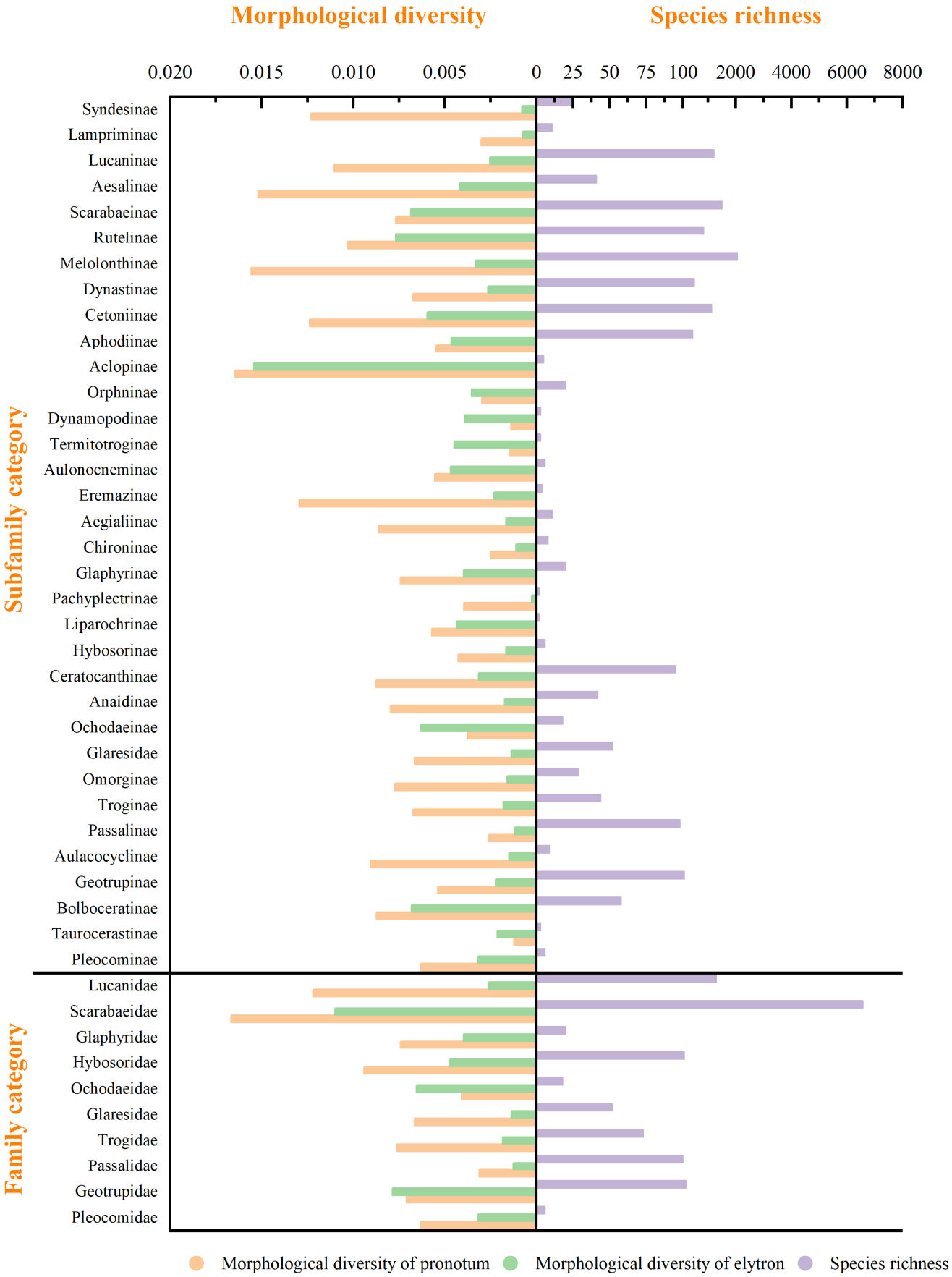


Figure 1. Morphological diversity and species richness among groups. Three parameters are shown based on phylogenetic factors.

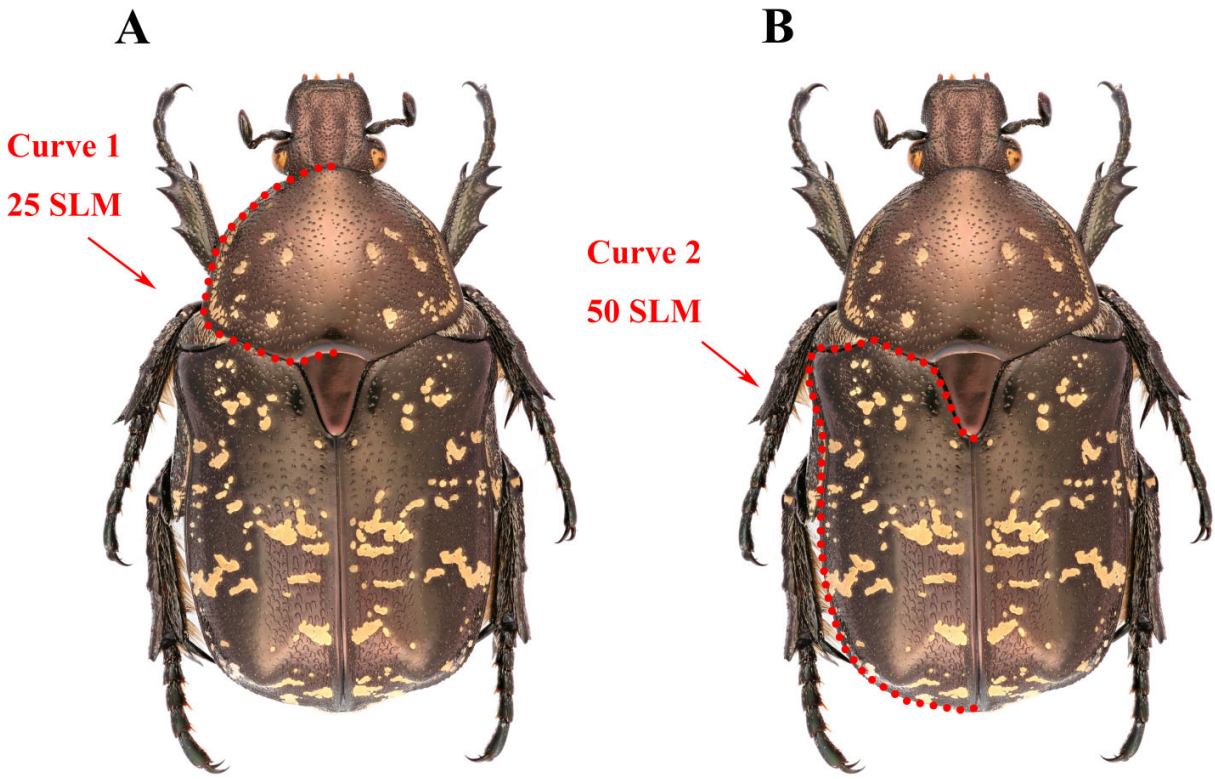


Figure 2. Semi-landmarks selection of test characters based on geometric morphometrics, *Protaetia brevitarsis* (Scarabaeoidea, Sacarabaeidae, and Cetoniinae) was selected as an example. (**A**) Pronotum (curve 1) was resampled in 25 semi-landmarks (SLM). (**B**) Elytron (curve 2) was resampled in 50 semi-landmarks (SLM).

3. Results

3.1. Species Richness Among Groups

Species richness values from 44 taxonomic groups (10 families and 34 subfamilies) are illustrated in Figure 1. In the family category, for our sample, Scarabaeidae and Lucanidae both exhibited very high species richness (6575/1299) values primarily because of their large and diverse sub-groups; Glaphyridae, Ochodaeidae, and Pleocomidae exhibited very low species richness (20/18/6) (with the species richness of the Glaresidae and Trogidae being higher (52/73) than those of all three families mentioned above). Similar patterns were also found in the subfamily category test, with most subfamilies exhibiting high species richness and relatively high genus richness values (Figure 1).

3.2. Morphological Variation in Pronotum and Elytron

The first three principal components (PCs) of the pronotum/elytron from 8508 species accounted for 88.374% and 93.167% of observed shape variation, respectively (Figure 3).

Along the positive direction of the first PC axis, the pronotum shape changed from an inverted trapezoidal to an oval outline with the retracting anterior angle and anterior margin, making the anterior angle less distinct while the posterior angle extended sharper. Along the positive direction of the second PC axis, the pronotum became diminished longitudinally and stretched horizontally with the anterior angle extending and the entire pronotum becoming markedly more inverted trapezoidal. Along the third PC axis, the entire pronotum tends to change from an inverted triangle to trapezoidal, producing a posterior angle, while the anterior angle becomes less distinct and the posterior margin shrinks inwardly.

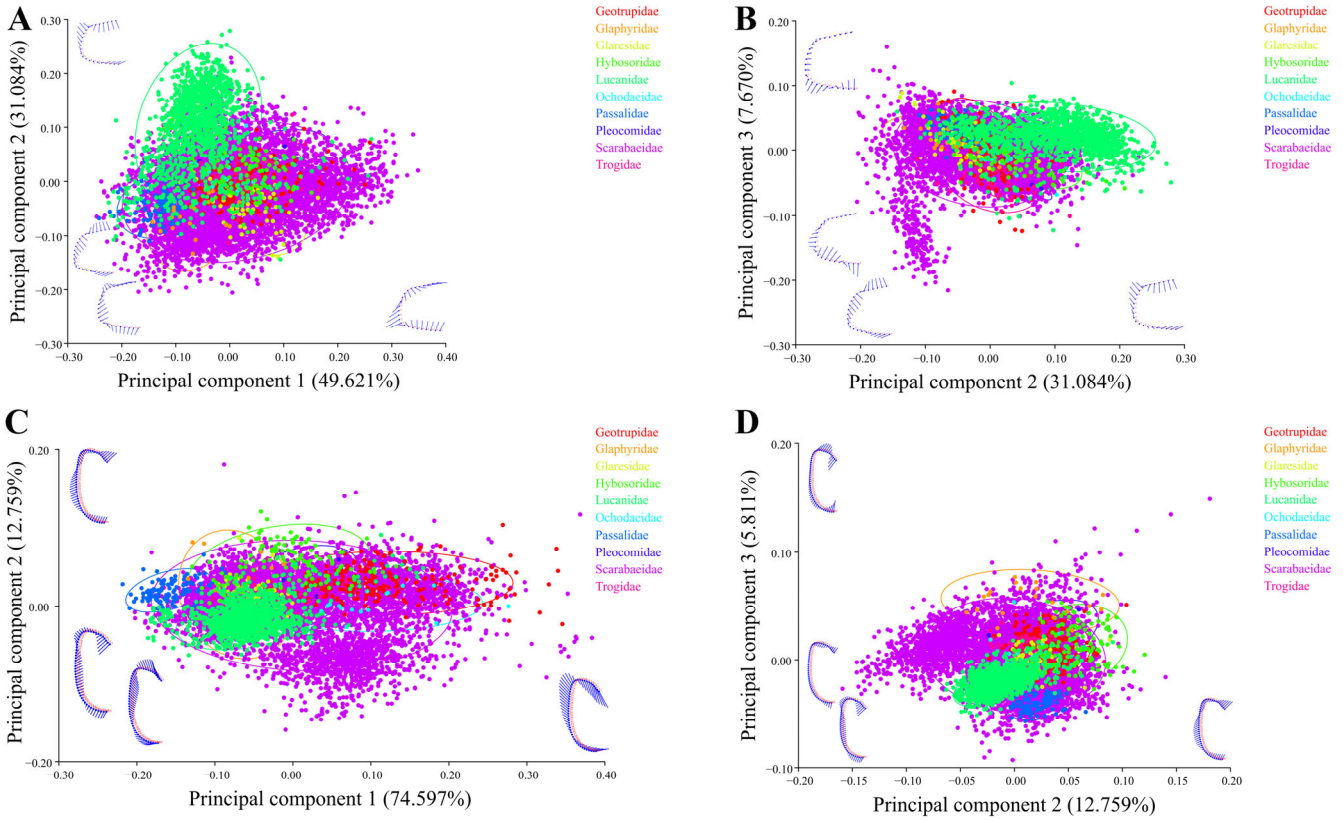


Figure 3. Principal component analysis on family level: the first three principal components of pronotum (88.374%) and elytron (93.167%) were selected to represent shape variation. (**A**) Variation in test pronotum in space built by PC1 and PC2. (**B**) Variation in test pronotum in space built by PC2 and PC3. (**C**) Variation in test elytron in space built by PC1 and PC2. (**D**) Variation in test elytron in space built by PC2 and PC3.

Along the positive direction of its first PC axis, the elytron becomes laterally wider with the anterior angle becoming larger, while the lateral margin and posterior margin shrink inward, making its trace a smooth curve. Along the positive direction of the second elytron PC axis, the anterior margin stretches outward and the posterior margin shrinks inward. The entire elytron stretches horizontally and shrinks longitudinally. Along the positive direction of the third elytron PC axis, the anterior margin shrinks inward, producing an anterior angle. At the same time, the posterior margin shrinks inward and the entire elytron stretches longitudinally and shrinks horizontally.

3.3. Morphological Diversity Among Groups

Morphological diversity of both the pronotum and elytron among the 10 families and 34 subfamilies reflects the influence of phylogenetic factors. The Scarabaeidae exhibited both the highest morphological diversity (Suppl. 2 and 3) and species richness (Figure 1), while the Passalidae was found to have the lowest relative morphological diversity (Figure 1).

However, the relationship between morphological diversity and species richness was not always consistent. The Passalidae exhibited high species-richness values despite their fairly low morphological diversity (Figure 1). The Ochodaeidae, with a comparatively small number of test species (18), were found to have the third highest pronotum diversity.

In the test of 34 subfamilies (Figure 1), results similar to the family test were obtained. Morphological diversities of certain subfamilies were also found to lack a strong association with species richness. The Aclopinae were found to have the highest pronotum and elytron

diversity, despite their low species richness (5) in our sample. Similarly, with 449 species included in our sample, the Aphodiinae were found to have fairly low pronotum diversity.

In addition, morphological diversity was also found to vary with the character of features tested. The changing trends of characters and species richness values were not always highly associated (Figure 1). For example, the elytron diversity of the Lucanidae was low despite its high pronotum diversity. In the subfamily test, the Syndesinae were found to exhibit a high pronotum diversity but a fairly low elytron diversity.

3.4. Relationship Between Morphological Diversity and Species Richness

Spearman correlation analysis was conducted on SR and MD of test families /subfamilies, and the relationship between SR and MD was obtained. (Table 2). The results showed that MD was significantly correlated with the SR of family/subfamily based on pronotum
($p = 0.014/p = 0.007$, both of which were lower than 0.05). However, there was no correlation between SR and MD of the family/subfamily based on elytron ($p = 0.223/p = 0.162$, both greater than 0.05). In addition, the Spearman correlation coefficients between SR and MD based on pronotum and elytron of family/subfamily were higher (r = 0.685/r = 0.273) than that of subfamily (r = 0.418/r = 0.175).

Table 2. Spearman correlation coefficient between morphological diversity (MD) and species richness (SR) in different test taxa.

	Family		**Subfamily**	
	r	***p***	**r**	***p***
MD of pronotum	0.685	0.014 *	0.418	0.007 **
MD of elytron	0.273	0.223	0.175	0.162

* indicates significant correlation ($p < 0.05$). ** indicates very significant correlation ($p < 0.01$).

4. Discussion

In this study, we compared the species richness and morphological diversity in the pronotum and elytron of 8508 scarab species using geometric morphometric and statistical analyses. The influence of phylogenetic factors on the correlation between morphological diversity and species richness was examined quantitatively. Results showed that the phylogenetic factor correlations were found to be statistically significant.

This is the first study to examine the relationship between morphological diversity and species richness in Scarabaeoidea. The role of phylogenetic factors on the associations between pronotum and elytron shape variation with taxonomy and an important aspect of ecology were revealed in the context of quantitative analyses. Different morphologies are associated with diverse functional aspects of niches [44,45] and both the evolution and development of taxa. These account for the variable morphological characteristics of scarabs [7,37]. Biological diversity can be quantified in terms of species richness and morphological diversity [46], both of which are dependent on ecological variability and species interactions [47,48]. As a result of selection-based feedback due to the variability of ecological factors, new forms emerge as a result of biological evolution [49]. This phenomenon can be found in some other groups as well. For example, the special galeas of stag beetles adapt to relatively fixed food, but their conservative diets do not affect the diverse morphological changes in their pronotums, which play an important role in their ability to raise their heads while raising opponents with their mandibles [50]. More conservative external morphologies and decreased morphological diversities have been found in coprophagous scarab groups (e.g., Scarabainae) [51], presumably because of their specialization. Although they have various alternative food sources, such as vertebrate carrion, invertebrate carrion, fungus, and plant pieces. Those feedings are not always a primary strategy [24]. The variety of the external forms that characterize phytophagous (e.g., Cetoniinae and Melolonthinae) and omnivorous groups (e.g., Hybosoridae) arise as a result of coevolution with their diverse diets. These well-understood principles account

for the shape diversity exhibited by scarabs' pronotum and elytron in coprophagous, non-feeding, phytophagous, and omnivorous groups. In addition, our sample of phytophagous scarabs was found to exhibit a very high pronotum diversity but fairly low elytron diversity, which implies that the pronotum is under more direct selection pressure from diverse environments and surrounding ecological factors, presumably as a consequence of playing an important role in the structuring of the muscle systems responsible for leg locomotion. The elytron's role is mainly one of protecting the beetles' abdomen, and so its requirement for environmentally mediated shape adjustment is far less pronounced than that of the pronotum.

In our study, the pronotum of Cetoniinae showed higher morphological diversity than that of Scarabaeinae, which may be due to the fact that Cetoniinae needed to fly and land more times during the feeding flight, and the flight path was more complex [52]. This puts more selective pressure on the flight muscles and pronotum. As a trait of great significance to the beetle's flight and feeding, hind wing features reflect the evolution of the whole body and mid thorax morphology [53,54]. To reveal the relationship between morphological changes and behavior and feeding preference in scarabs, the morphology of hind wing venations should be considered in further study.

In addition, the pronotum of Scarabaeinae showed a higher morphological diversity, which is probably because digging behavior requires more forefoot muscles, putting the pronotum under more selective pressure among burrowing beetles. Scarabaeinae evolved a more arched and shortened body to bury dung balls under the ground, while some Aphodiinae scarabs evolved an elongated shape during the evolution of dwelling behavior in feces and anthills [23]. These differences are mainly caused by behavioral and niche differences and are reflected in the quantified morphological information.

The phylogenetic factors were found to explain the observed correlation between the morphological diversity of the pronotum and elytron and the species richness of scarabs to a certain extent. In this study, complex and irregular relations existed in different groups on the entire family category and subfamily category due to scarabs' diverse habits and the quite different coevolution of test characters. Scarabaeidae was found to exhibit the highest species richness and morphological diversity, a result that can be explained by the variety of its habitats, from rainforest to desert, and its taxonomic richness [55]. Low elytron shape diversity was found in the test of Passalidae, which are adapted to live in the tunnels of rotten wood. A total of 3 species of Diphyllostomatidae have been recorded worldwide; its small population and basal characters determined that this group was relatively conservative [24], leading to its very low external morphological diversity. The Hybosoridae are a large, diverse, and globally distributed family of c. 573 species and 74 genera. Its diversified food habits, which include fresh corpses, small insects, or fungi [56], are associated positively with its high pronotum diversity of morphology, despite only 147 species being included in this study. Meanwhile, based on our spearman correlation analysis results, the correlation of morphological diversity to species richness in the subfamily category test was found to be not as good as that exhibited by the family category. In this study, our inconsistent results showed that the factors affecting these correlations are complex and diverse, with phylogenetic factors exhibiting high correlations between species/genus richness and morphological diversity to some extent. Additionally, some of the high-ranking traditional taxonomic categories (e.g., sub-/families) are artificial phylogenetically and so were not formally tested in the phylogenetic analyses [55,57,58]. In this case, the results of this study could be slightly changed if the classification system of Scarabaeoidea is modified in the future. It would be interesting to make additional tests following the stable classification of Scarabaeoidea in the future based on comprehensive sampling and phylogenetic analyses.

5. Conclusions

As a large and diverse group, the Scarabaeoidea was found to have a varied morphological appearance of pronotum and elytron. Procrustes PCA revealed that this variation

reflects associations with various constraining factors. Coprophagous groups exhibit specialized external forms despite their fairly stable habits. The phylogenetic factors were found to reveal strong associations with species/genus richness and morphological diversity. Influenced by niche and coevolution, the species/genus richness and morphological diversity values did not always display consistent family category and subfamily category relations. Nonetheless, there remain many limitations in our results. Our phylogenetic factor analyses revealed only a small fraction of the impact these factors may have on the correlation between species/genus richness and morphological diversity. In addition, present limitations on the composition of our test sample for dimorphic groups make our results less generalized, and perhaps less stable, than they might have been otherwise. These issues can be addressed when more complete samples become available.

In future studies, more traits, for example, hind wing venation, as an important trait for feeding and flight behavior, should also be considered to improve our understanding of morphological diversity and richness, and more parts or ecological factors should be included to explore which aspects of the morphology are more meaningful for explaining the correlation between morphological diversity and species richness.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16120721/s1, Supplement S1. Studies provided by National Knowledge Infrastructure, Web of Science, ResearchGate, and academic websites such as Google Scholar. Supplement S2. Morphological diversity (MD) of test characters in the family test. Supplement S3. Morphological diversity (MD) of test characters in the subfamily test.

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