A Comprehensive Phylogeny of Beetles Reveals the Evolutionary Origins of a Superradiation

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Beetles represent almost one-fourth of all described species, and knowledge about their relationships and evolution adds to our understanding of biodiversity. We performed a comprehensive phylogenetic analysis of Coleoptera inferred from three genes and nearly 1900 species, representing more than 80% of the world’s recognized beetle families. We defined basal relationships in the Polyphaga supergroup, which contains over 300,000 species, and established five families as the earliest branching lineages. By dating the phylogeny, we found that the success of beetles is explained neither by exceptional net diversification rates nor by a predominant role of herbivory and the Cretaceous rise of angiosperms. Instead, the pre-Cretaceous origin of more than 100 present-day lineages suggests that beetle species richness is due to high survival of lineages and sustained diversification in a variety of niches.

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which has been associated with Bostrichiformia (9, 10). All five families exhibit archaic morphological features shared only with Archostemata and Adephaga (8, 17). Their basal position was stable (always \( pp = 1.00 \)) (table S3) when trees were rooted with the neuropterid orders or only with Myxophaga or Adephaga as outgroups.

All superfamilies of Polyphaga were previously grouped into five series (4, 9), of which only the Scarabaeiformia \( ( pp = 1.00 ) \) and the Cucujiformia \( ( pp = 1.00 ) \) were strongly supported as monophyletic in this study. Staphyliniformia comprised a paraphyletic basal grade, and both Bostrichiformia and Elateriformia were polyphyletic. Relationships among the five series were poorly supported or unresolved in the consensus tree (fig. S1). Nosodendridae, usually included in Bostrichiformia near Derodontidae (4, 9) but recently associated with Scirtoidae on the basis of thoracic characters (18) instead with the nonscirtoid Elateriformia, albeit with low support (fig. S1) \( ( pp = 0.59 ) \).

Within Elateriformia, the superfamilies Burrestroidea (jewel beetles; \( pp = 1.00 \)), Dascilloidea \( ( pp = 1.00 ) \), and Elateroidea (click beetles and allies; \( pp = 0.72 \)) were supported. Our data showed that Byrrhoidae, sensu Lawrence and Newton (9), is paraphyletic, supporting the division of this clade (8) into Byrrhoidae (Byrrhididae, moss beetles; \( pp = 1.00 \)) and Dryopoidea (riffle beetles and water pennies). The Cantharidae (soldier beetles, fireflies, etc.) fell inside the Elateroidae, and our tree supported that bioluminescence arose repeatedly in beetles, in agreement with alternative feeding strategies. Restricting the comparisons to those feeding on angiosperms removes Table 1. Comparisons of species richness between clades feeding on living plants and their sister clades with alternative feeding strategies. Restricting the comparisons to those feeding on angiosperms removes contrast 4 and adds two contrasts of angiosperm- versus gymnosperm-feeding lineages within Curculionoidea and two within Chrysomeloidae [table S4; see also (5)]. Plant-feeding clades include taxa feeding mainly on rotting vegetation in contrast 7 or in recently dead wood in contrast 8, but probably >70% of species in both clades are herbivorous. Excluding the last two contrasts increases the probability under a Wilcoxon test to \( P = 0.28 \).

<table>
<thead>
<tr>
<th>Plant-feeding Diet</th>
<th>No. of species</th>
<th>Non–plant-feeding Diet</th>
<th>No. of species</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Byturidae Fruits, flowers</td>
<td>16</td>
<td>Biphyllidae</td>
<td>195</td>
</tr>
<tr>
<td>2 Langurinae Stem borers</td>
<td>800</td>
<td>Xenoscelinae</td>
<td>100</td>
</tr>
<tr>
<td>3 Chrysomeloidea Herbivorous xylophagous</td>
<td>53,442</td>
<td>Nitidulidae plus Erotylidae plus Cucujidae series</td>
<td>7743</td>
</tr>
<tr>
<td>4 Curculionoidea Herbivorous xylophagous</td>
<td>59,340</td>
<td>Brontidae plus Silvanidae plus Priesnigidae plus Coccinellidae plus Chilcinidae plus Scymnidae</td>
<td>480</td>
</tr>
<tr>
<td>5 Epilachninae Herbivorous</td>
<td>1051</td>
<td>Coccinellidae</td>
<td>3900</td>
</tr>
<tr>
<td>6 Dascillinae Roots</td>
<td>80</td>
<td>Rhipiceridae</td>
<td>57</td>
</tr>
<tr>
<td>7 Melolonthinae plus Orphinae plus Rutelinae plus Dynastinae Buprestidae Herbivorous (and saprophagous)</td>
<td>16,329</td>
<td>Cetoniinae</td>
<td>4121</td>
</tr>
<tr>
<td>8 Xylophagous, herbivorous, roots, leaf miners</td>
<td>14,000</td>
<td>Dryopoidea</td>
<td>3242</td>
</tr>
</tbody>
</table>

The hyperdiverse Cucujiformia, representing more than half of all beetles and 90 families, was strongly supported as monophyletic (Figs. 1 and 2; \( pp = 1.00 \)). Among the seven established superfamilies, the Lyctyloidea (ship-timber beetles) was found near the base of the Tenebrionoidea (30 families; \( pp = 0.76 \)). The Cleroidea (checker beetles and allies) was monophyletic \( ( pp = 0.70 ) \) only when including the Biphyllidae plus Byturidae \( ( pp = 1.00 ) \). The latter two were formerly classified as Cucujoida10, but their association with Cleroidea is supported by genitalic characters (11). The Cucujoida, comprising 34 families, was polyphyletic, but the Cerylonid series (Figs. 1 and 2 and fig. S3) \( ( pp = 1.00 ) \) consisting of eight families (21) was monophyletic. Apart from the Sphindidae \( ( pp = 1.00 ) \), the remaining cucujoid families formed a monophyletic clade \( ( pp = 0.72 ) \) together with the species-rich Cuculonolidae and Chrysomeloida (weevils and bark beetles; \( pp = 0.73 \)) and Chrysomeloida (leaf beetles and longhorns).

Once the relationships among coleopteran families and superfamilies were established, we investigated the origins of beetle diversity. Diversification may be driven by feeding strategy, and we tested the hypothesis that feeding on plants (herbivory), and specifically flowering plants (angiosperms), explains the diversity of beetles (5). Predominantly herbivorous clades tend to contain
more species than nonherbivorous sister clades, but this difference was not significant [Table 1; one-tailed Wilcoxon test on contrasts in log (no. of species), $P = 0.13$] even when we distinguished between angiosperm and gymnosperm feeders ($P = 0.06$) (table S4). Similarly, of 21 significant shifts in diversification rate inferred with a robust equal rates null model (22, 23), only two characterize transitions between angiosperm and gymno-

Fig. 2. The phylogeny of Coleoptera at the subfamily level. The tree was selected from the 340-taxon Bayesian analysis based on maximum congruence with the majority-rule consensus (fig. S1). Posterior probability clade support values indicated at nodes $>0.5$. Approximate known species numbers in terminal taxa are given in parentheses. Black circles mark significant shifts in diversification rate of sister clades (table S5). Colored triangles mark character transitions in lifestyles inferred by parsimony optimization (see figs. S2 and S3 for details).
sperm feeders, whereas the remainder showed no association with transitions to feeding on angiosperms or seed plants (table S5). A significant increase in diversification rate was inferred near the base of the Polyphaga whether herbivorous taxa were included or excluded from the analyses (table S5). Herbivory has played a role in the diversification of some beetle lineages, but the trait per se does not explain why beetles are so diverse.

Fast diversification rates also do not explain beetle diversity. Dating the tree with fossil calibration and penalized likelihood rate-smoothing (Fig. 3 and table S6) (15), we estimated net diversification rates across terminal taxa of 0.048 to 0.068 Myear\(^{-1}\) (table S7), slightly lower than comparable measures for the angiosperms (0.077 Myear\(^{-1}\)) (24). However, more than 100 modern beetle lineages were present at the first appearance of crown-group angiosperms dated to <140 Ma on the basis of pollen records (25), and less than one-third of extant beetle species are associated with angiosperms (table S8 and fig. S3). Therefore, the extreme diversity of beetles reflects the Jurassic origin of numerous modern lineages, high lineage survival, and the diversification into a wide range of niches, including the utilization of all parts of plants. These switches into new niches occur repeatedly as, for example, the multiple shifts from terrestrial to aquatic habits in the evolutionary history of beetles, which occurred at least 10 times (Fig. 2 and fig. S2).

### References and Notes


15. Materials and methods are available as supporting material on Science Online.


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### Supporting Online Material

- www.sciencemag.org/cgi/content/full/318/5858/1913/DC1
- Materials and Methods
- Figs. S1 to S5
- Tables S1 to S8
- References and Notes
- Alignment files S1 and S2

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