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Comparing amber fossil assemblages across the Cenozoic

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To justify faunistic comparisons of ambers that differ botanically, geographically and by age, we need to determine that resins sampled uniformly. Our pluralistic approach, analysing size distributions of 671 fossilized spider species from different behavioural guilds, demonstrates that ecological information about the communities of two well-studied ambers is retained. Several lines of evidence show that greater structural complexity of Baltic compared to Dominican amber trees explains the presence of larger web-spinners. No size differences occur in active hunters. Consequently, we demonstrate for the first time that resins were trapping organisms uniformly and that comparisons of amber palaeoecosystem structure across deep time are possible.

Keywords: Araneae; palaeoecology; palaeontology

1. INTRODUCTION

Neoecologists control for sample variation through experimental design. This is rarely possible in palaeoecological studies because of how fossils are retrieved, scarcity of specimens and the incompleteness of the fossil record (Benton *et al.* 2000). Amber provides a unique window into past forest ecosystems. It is not unreasonable to expect that different fossil resins, which differ in botanical origin, geography and geological age (Langenheim 1995), may be subject to unique biases with regard to their trapping mechanisms and the organisms they preserve. If true, then direct comparisons of the different amber faunas in an ecological context will be subject to inherent sampling problems. Such possible biases have not hitherto been analysed, primarily through a lack of sufficient amber data (Penney 2005). Miocene Dominican and Eocene Baltic ambers are well studied and a sufficiently large dataset for undertaking a pluralistic, quantitative analysis now exists. The former was produced by *Hymenaea protera* (Leguminoseae; Poinar 1991), but the botanical origin of Baltic amber remains unresolved. It was probably produced by *Agathis*-like (Araucaraceae) or *Pseudolarix*-like (Pinaceae) trees (Langenheim 2003). These two major deposits provide an opportunity for exploring whether or not differences exist in the 'trapping mechanisms' of different amber-forming resins.

Spiders are common in amber faunas, have a long and diverse geological history extending to the deep Paleozoic, although many Cenozoic spiders belong in extant families (Penney *et al.* 2003). This provides us with knowledge of their ecology through behavioural fixity/uniformitarianism (Boucot 1989), which infers that extinct organisms behaved in a similar manner to their Recent relatives at family level. Here, we test for differences in taxic composition, body size and ecological predation guild of spiders preserved in Dominican and Baltic ambers to explore whether amber-forming resins trapped organisms in a uniform manner. Such a pluralistic approach—investigating multiple aspects of inclusion-related data to document the first evidence of preferential preservation—is a rigorous method for evaluating potential differences between different ambers.

2. MATERIAL AND METHODS

Palaeontological data are scarce by their nature. New species in amber are often described from singletons and occasionally from a series of specimens, which is usually few in number. Thus, species numerical abundance data are limited, a constraint applicable to all ambers. Traditionally, analysis of terrestrial arthropod palaeocommunities has been at family level, which is a good predictor of underlying species diversity and is applied extensively as the 'higher taxon approach' by neontologists investigating distribution, ecological correlates and diversity patterns of tropical insects (Labandeira 2005). We use a similar approach. All spider species described from both Dominican and Baltic ambers were included. Families were sorted to generalized predation guilds known to occur in Recent species from the families: web spinners, hunters and ambushers (table 1). Following preliminary analysis, ecological predation guilds were further divided: funnel-web weavers, retreat-dwellers, ambush predators, mysmenids, burrow-dwellers, net-casters, nocturnal hunters, stalkers, orb-web weavers, 3D space-web weavers, sheetweb weavers and unknowns (primarily extinct families or those for which behaviour is not known). Body size for each species was taken from the holotype description (where a range was given the mean was used). The majority of holotypes are mature males. When female data were removed the significance of the results was unaltered.

Analyses employed SPSS statistics (v. 12.0.1; SPSS Inc., IL). Numbers of species per family were compared between ambers using Wilcoxon matched pairs tests, since transformations did not conform data to the requirements of normality and homoscedasity (i.e. statistical equality of variances). Chi-squared analysis was used to examine association between amber type and numbers of families in generalized predation guilds. Comparisons of specimen sizes between amber types used log transformed data and t-tests. Kolmogorov–Smirnov tests (computed and shown as Kolmogorov–Smirnov Z values) with Lilliefors significance correction were used to test for normality of size distributions. We used regression tree analysis (RTA; ANSWER TREE v. 2.0; SPSS Inc.) to explore relationships between size measurements of spiders and the factors available to classify them. It was of particular interest whether amber type would be included and if this would be only with certain ecological groups of spiders. This computer learning system divides data into classes displayed in decision trees (Lim *et al.* 2000). The decision rules for classifying observations were based on the C&RT algorithm (classification and regression trees; methods based on minimization and impurity measures; Breiman *et al.* 1984). The trees produced are hierarchical (the first split explains the most variation in the variable being explored) and the heterogeneity of nodes is defined with a deviance notion that has been interpreted as the deviance of a Gaussian model (regression tree) or multinomial model (classification tree; Breiman *et al.* 1984). Here, the continuous target variable was body size and several nominal variables (amber type, family and predation strategy) were included as the parameters to grow the tree. Cross-validation and least squared deviation measures of impurity were applied. To control the length of the tree, 'pruning' was used to remove less important splits in terms of their explained deviance. Regression trees have been considered unsurpassed as an exploratory technique or a technique used when traditional methods fail. Their strengths include acceptance of mixes of data types, the ability to examine the effects of the predictor variables one at a time, rather than just all at once and on multiple occasions (i.e. after data has been split) and ability

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Table 1. Families of spiders and numbers of species unique to and shared between Baltic and Dominican Republic ambers. (†=strictly fossil family. Predation strategies: a=ambusher, h=hunter, u=unknown, w=web spinner.)

	Baltic		shared families		Dominican Republic	
2	Baltsuccinidae$^{\dagger u}$	22	Anapidae^{w}	1	Barychelidae^{a}	1
12	Ephalmatoridae$^{\dagger u}$	1	Anyphaenidae^{h}	3	Caponiidae^{h}	1
5	Insecutoridae$^{\dagger u}$	21	Araneidae^{w}	7	Ctenidae^{h}	1
6	Protheridiidae$^{\dagger u}$	3	Clubionidae^{h}	1	Cyrtaucheniidae^{a}	1
1	Spatiatoridae$^{\dagger u}$	28	Corinnidae^{h}	5	Filistatidae^{w}	1
5	Agelenidae^{w}	33	Dictynidae^{w}	15	Lycosidae^{h}	1
1	Amaurobiidae^{w}	1	Dipluridae^{w}	2	Microstigmatidae^{h}	1
11	Archaeidae^{a}	2	Gnaphosidae^{h}	1	Miturgidae^{h}	1
2	Borboropactidae^{a}	5	Hersiliidae^{a}	3	Ochyroceratidae^{w}	2
4	Ctenizidae^{a}	39	Linyphiidae^{w}	5	Palpimanidae^{h}	1
13	Cyatholipidae^{w}	4	Liocranidae^{h}	1	Philodromidae^{h}	1
1	Deinopidae^{a}	9	Mimetidae^{h}	1	Selenopidae^{h}	2
1	Desidae?^{u}	4	Mysmenidae^{w}	2	Sicariidae^{w}	3
6	Dysderidae^{h}	10	Nesticidae^{w}	1	Sparassidae^{h}	1
5	Hahniidae^{w}	4	Oecobiidae^{w}	1	Theraphosidae^{a}	1
5	Leptonetidae^{w}	12	Oonopidae^{h}	6		
7	Pimoidae^{w}	1	Oxyopidae^{h}	1		
1	Plectreuridae^{w}	2	Pholcidae^{w}	10		
1	Synaphridae^{u}	2	Pisauridae^{h}	1		
26	Synotaxidae^{w}	40	Salticidae^{h}	16		
1	Telemidae^{w}	1	Scytodidae^{w}	3		
4	Trechaleidae^{h}	6	Segestriidae^{a}	1		
8	Zodariidae^{h}	1	Tetrablemmidae^{w}	1		
13	Zoropsidae^{h}	21	Tetragnathidae^{w}	9		
		47	Theridiidae^{w}	39		
		7	Theridiosomatidae^{w}	3		
		4	Thomisidae^{a}	2		
		17	Trochanteriidae^{h}	7		
		14	Uloboridae^{w}	2		
	24 fams (141 spp.) 5.88 spp./family		29 fams (361 and 150 spp.) 12.44 and 5.17 spp./family		15 fams (19 spp.) 1.27 spp./family	

to identify major variables and interactive effects between variables while still representing them in an easily readable fashion (Lim *et al.* 2000).

3. RESULTS

Table 1 shows that of the 68 spider families represented in the two ambers, Baltic samples contained 53 families compared to 44 for the Dominican. Twenty-nine families were common to both, representing 76% of the species, although none occur in both deposits. Families common to both ambers tended to be those that contain more species. For example, families specific to Dominican amber comprised few species (1.27 per family on average, range 1–3). Whereas families in this amber that are also known from Baltic amber comprised 5.17 species per family on average, range 1–39. A similar pattern was evident for Baltic samples, with approximately double the number of species found in families common to both ambers (5.88 and 12.44 species per family, respectively). Generally, there were more species in families from Baltic amber ($Z_{68}=4.25$, $p<0.0001$) and there was no association between amber type and presence of certain behavioural guilds ($\chi_2^2=1.19$, $p=0.55$). Increased family and species richness in Baltic amber were in part due to five strictly fossil families, none of which occur in Dominican amber.

For the first time, an insight into the fossil ecology of key spider families is provided by body size data. Overall, the body size of spiders in Baltic amber was significantly greater than those in Dominican amber (comparisons made using log transformed data: $t_{654}=3.56$, $p=0.0004$; $\mathrm{mean}_{\mathrm{DomRep}}=2.66\ \mathrm{mm}\pm0.13$, $\mathrm{mean}_{\mathrm{Baltic}}=3.03\ \mathrm{mm}\pm0.07$). Three families, Dictynidae, Salticidae and Theridiidae, were represented by more than 10 species in both ambers and collectively comprised 190 species (*ca* 28% of the total data). Their prevalence in both ambers permitted a contrast of size distributions, which were positively skewed (figure 1) and differed significantly from normality in both Dictynidae (Kolmogorov–Smirnov $Z_{48}=0.183$, $p<0.0001$) and Theridiidae (Kolmogorov–Smirnov $Z_{83}=0.113$, $p=0.010$). This was not so for Salticidae (Kolmogorov–Smirnov $Z_{53}=0.095$, $p=0.200$). Visual comparisons indicate that Dominican data exhibited higher levels of positive skewness than data from Baltic amber, i.e. showed a tendency towards smaller individuals and this is highly apparent in web builders (figure 1). Both families of web-spinning spiders were larger in Baltic amber: Dictynidae ($t_{45}=6.53$, $p<0.0001$; $\mathrm{mean}_{\mathrm{DomRep}}=1.48\ \mathrm{mm}\pm0.14$, $\mathrm{mean}_{\mathrm{Baltic}}=2.99\ \mathrm{mm}$ ±0.18) and Theridiidae ($t_{78}=5.58$, $p<0.0001$;

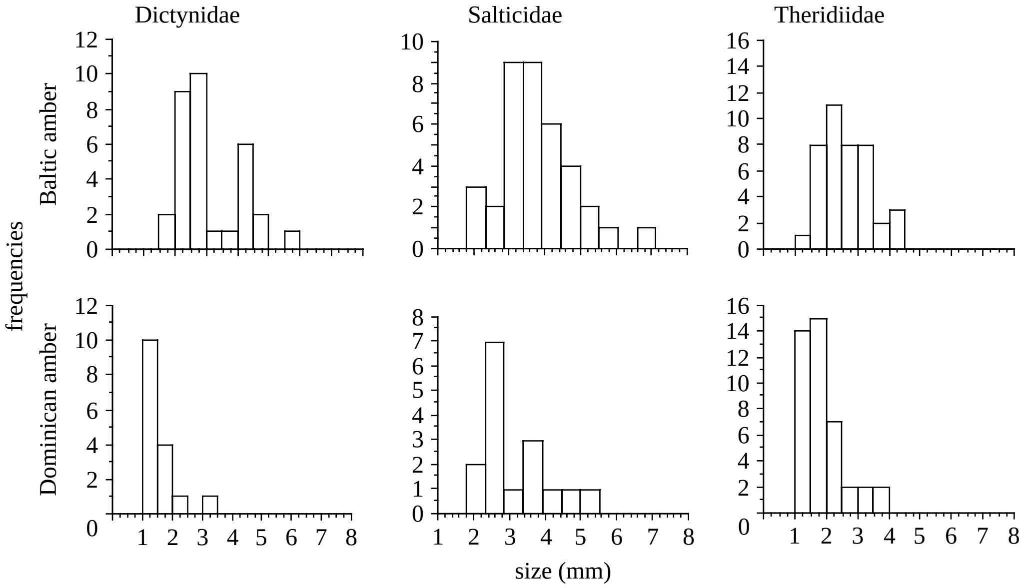

Figure 1. Body size distributions of three major spider families captured in amber extracted from the Baltic region and the Dominican Republic. Skewness values are: Dictynidae (Dominican Republic$=2.237\pm0.58$, Baltic$=0.805\pm0.41$); Salticidae (Dominican Republic$=1.046\pm0.56$, Baltic$=0.662\pm0.39$); Theridiidae (Dominican Republic $=1.611\pm0.38$, Baltic$=0.513\pm0.37$).

$\text{mean}_{\text{DomRep}}=1.81\ \text{mm}\pm0.09$, $\text{mean}_{\text{Baltic}}=2.61\ \text{mm}\pm0.12$), but Salticidae were not significantly different ($t_{51}=1.778$, $p=0.08$; $\text{mean}_{\text{DomRep}}=3.18\ \text{mm}\pm0.22$, $\text{mean}_{\text{Baltic}}=3.73\ \text{mm}\pm0.18$). Salticids are non-web building, active hunters and contained the largest individuals of these three families.

Examination of the total data using RTA highlighted differences in size of individuals between predation strategies and families, but also between different amber types (figure 2). The first split of the regression tree used predation strategy, with larger spiders belonging to groups that did not employ a web-building strategy; this group did not divide subsequently by amber source. The group containing the smaller spiders (see figure 2) were primarily aerial web-weaving spiders and contained all such guilds in the dataset. This group split twice by amber type, with larger spiders in Baltic amber and smaller spiders in Dominican amber (figure 2). All subsequent splits were, as was expected *a priori*, classifications into different family groups which varied in size and the 'pruning' function was applied to control the length of the tree. The proportion of variance explained by the final model was 55.03% and the patterns provide supporting evidence that amber type is associated with spider sizes within certain predation guilds.

4. DISCUSSION

The observed differences are in the smaller size class only (of a relatively even division of the data 41.81 and 58.19%) of the predation strategy split. This suggests that the differences are not the result of the entrapment process, because if they were, then a similar size-related split would be expected for the non-web-spinning guilds (figure 2). Therefore, either the sizes of aerial web-spinning individuals in the populations differed between the Baltic and Dominican amber forests or some aspect of the prey capture strategy permitted larger aerial web-spinning spiders on the Baltic amber-producing trees compared to Dominican amber-producing trees. The former is unlikely, given that there are no observed size differences between the non-web-spinning spiders.

If the Baltic amber producer was of pinaceous origin, as favoured by some authors (Langenheim 2003), then its morphology would differ considerably from that of the leguminous Dominican amber producer. Little is known about the gross morphology of these amber-producing trees because only small structures, such as petals, flowers, pollen and leaves are usually preserved as fossils. However, in the same way, we used comparisons with extant taxa to determine predation guilds for the fossil spider species, a comparison of related extant tree species affords a useful basis for determining the gross morphology of the extinct trees. Extant *Hymenaea* are large evergreen trees, with smooth bark and glabrous, compound leaves composed of leaflets, most of which are concentrated in the spreading crown high in the canopy. By contrast, *Pseudolarix* is a deciduous conifer, which is broadly conical, with horizontal branching and drooping branchlets along the length of the trunk and often grows as wide as it does tall; the leaves are needle-like and the bark is deeply fissured. Thus, the gross morphology of the two amber producers was very different, with the Baltic amber tree having a greater structural complexity.

Web building is an energetically costly exercise, thus web site selection is a particularly important issue for spiders. Web spinners that live in higher strata, such as trees seek optimal sites for web attachment and in this niche the architectural features of the vegetation are important factors.

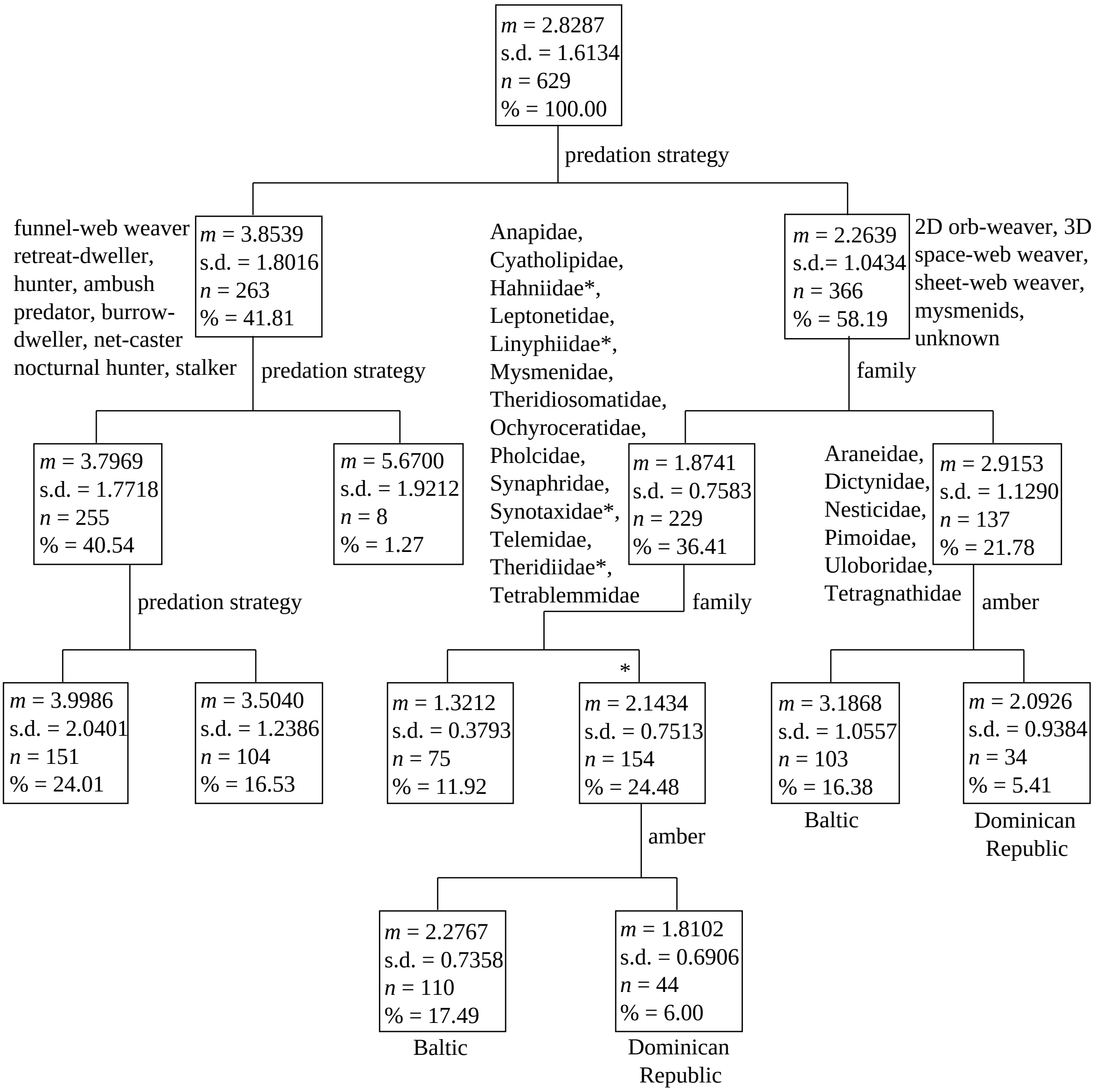

Figure 2. Dendrogram showing a hierarchy of main predictors of spider size as modelled by regression tree analysis. The strongest predictor of size (first split) separates the dataset by predation strategy into larger non-web and smaller web spinners. Only the web spinners are ultimately classified by amber source (shown on the right-hand branch of the dendrogram).

Effects arise not only from variations in the availability of supports for web anchorage and space for the web capture area, but also from the provision of retreats, microclimate and prey availability (Wise 1993). It has been demonstrated experimentally that body size of arboreal web-spinning spiders is larger in more structurally complex habitats, as defined by needle density and branching complexity (Halaj *et al.* 2000). Thus, we conclude that the greater structural complexity of the Baltic amber-producing tree compared to the Dominican amber producer, favoured larger aerial web-spinning spiders. We believe that the observed size differences in aerial web-spinners, but not the other predatory strategies, are related to this rather than to resin entrapment-related biases. It follows, that the original resin entrapment processes in the Baltic and Dominican amber forests were operating physically as traps in a similar manner and that they are directly comparable in this respect.

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