



Desiomorphs in Amber

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Fossils from various epochs often do not easily fit into the present system of classification because they have morphological characters found in two or more extant or extinct groups, from the generic to the ordinal level. Without genetic analysis, it is difficult to determine their phylogenetic affinity and how they should be classified. We have previously referred to them as chimeras (Poinar and Poinar 2008) in the literary sense, which implies a creature combining features of two or more separate animals, such as the Greek “she-monster” with a lion’s head, goat’s body, and serpent’s tail; the part-horse, part-human centaur; or the minotaur with the head of a bull and body of a man. However, chimera now has a medical definition that makes its use confusing.

Transitional fossils imply a phylogenetic relationship (like the older terms “missing links” and “intermediate forms”) between the fossil in question and similar lineages and are often regarded as stem groups. However, morphological similarities do not always imply phylogenetic relationships because a fossil can represent a separate, unique lineage or similarities can be the result of convergence. A case in point is *Archaeopteryx*, a Jurassic vertebrate considered a “transitional fossil.” Over the years, it has been considered a winged reptile, a primitive bird, a winged dinosaur, and more recently, a link between birds and dinosaurs. However, there is no hard evidence to say it does not represent a completely separate lineage that is only distantly related to either birds or dinosaurs.

Because of the uncertainty of determining whether a fossil is truly transitional and phylogenetically intermediate between two or more separate lineages, I propose the term “desiomorph” (from the Greek *desis*, “a binding together” and *morphe*, “form or shape”) to describe fossil individuals that possess morphological characters found in two or more groups, whether fossil, extant, or a combination of both. Desiomorphs are characterized by morphology alone, without any direct implication of phylogenetic relationships. A recent vertebrate desiomorph is the 50 mya Eocene bat, *Onychonycteris finneyi* Simmons, Seymour, Habersetzer and Gunnell (2008), which has characters of modern bats as well as those of ground-dwelling mammals that used their claws to ascend trees, but is not phylogenetically transitional between these two groups.

The present work provides accounts of desiomorphs, mostly insects, encountered in amber. Even though there are rare accounts of extant insects surviving since the middle Tertiary (Hörnschemeyer et al. 2009) and some modern insect genera detected as far back as the Early Cretaceous (Poinar and Milki 2001), the great majority of insect species exist only for several million years. As one goes back in time, desiomorphs become more common and the differences between them and extant lineages become more pronounced, thus widening their systematic separation. Determining the level of difference and systematic position of desiomorphs is generally a combination of objective and subjective judgments.

The amber-embedded Tertiary and Cretaceous desiomorphs discussed below have morphological characters connecting them to two or more extant or extinct genera, subfamilies, families, or orders.

A Desiomorph at the Generic Level

The orchid bee *Paleoeglossa melissiflora* in 20-30 mya Dominican amber. New World orchid bees have attracted the attention of entomologists and botanists for their pollination activities, often being the sole pollinators for tropical orchid species. These bees are normally fairly large and often brilliantly colored with metallic markings. A pair of orchid bees in Dominican amber had characters of

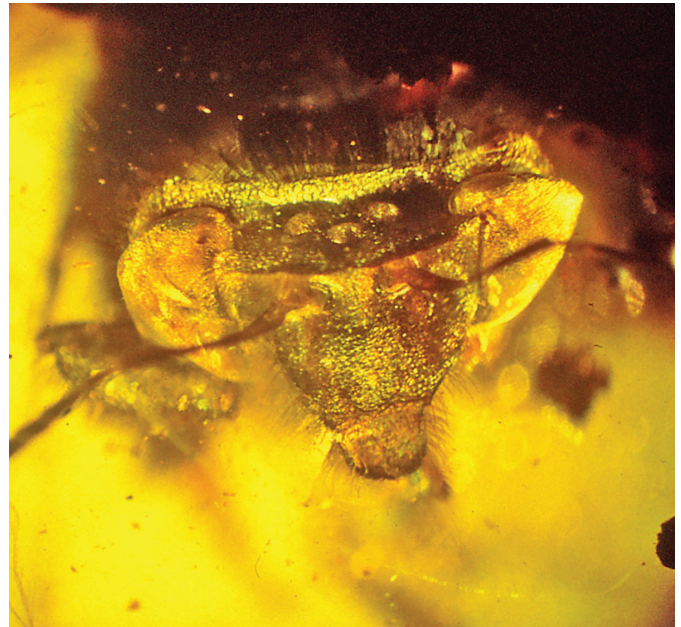


Fig. 1. The orchid bee *Paleoeglossa melissiflora* in Dominican amber.

three of the five known New World genera. *Paleoeglossa melissiflora* Poinar (1998) shared its metallic sheen with members of the extant genera *Euglossa* and *Eufresea* and its scutellar tuft with *Euglossa* and *Eulaema*. Its protruding clypeus and genal projections (Fig. 1) partly account for its placement in a new genus. Both specimens were females, and finding a pair together in amber suggests that they were collecting resin for nest construction when entrapped, a habit similar to the behavior of stingless bees that are commonly found in Dominican amber. Orchid bees have since been extirpated from Hispaniola.

Desiomorphs at the Subfamily Level

The batfly *Enischnomyia stegosoma* in 20-30 mya Dominican amber. Bat flies (Streblidae and Nycteribiidae) feed on the blood



Fig. 2. The batfly *Enischnomyia stegosoma* in Dominican amber.

of bats and spend the greater part of their lives on their hosts, exiting only when searching for mates. A streblid bat fly, *Enischnomyia stegosoma* Poinar and Brown (2012) in Dominican amber possessed characters of two extant subfamilies (Fig. 2). The strongly compressed body and laterally flattened profemora are characteristic of the Nycterophilinae, while the fairly complete wing venation, antennal pedicel extending above the flagellum, and elongate proboscis are characteristic of the Trichobiinae. A biological character that allies the fossil with members of the Nycteribiidae pertains to its role as a vector of bat malaria. Oocysts and sporozoites of bat malaria, *Vetufebrus ovatus* Poinar (2011), were found in the gut wall and salivary glands of the fossil fly. Presently, there are no records of streblids transmitting malaria; however, representatives of at least four genera of Nycteribiidae are known vectors of bat malaria.

The ant-like stone beetle *Hapsomela burmitis* in 97-110 mya Burmese amber. A most unique desiomorph was a little beetle with its front legs equipped with 6 instead of the normal 5 segments found in all living insects (Fig. 3). While *Hapsomela burmitis* was considered an ant-like stone beetle (Coleoptera: Scydmaenidae), aside from this extra foreleg segment, it contained a combination of characters found in two extant subfamilies (Scydmaeninae and Mastiginae). These characters, along with other rather unique features, were why it was placed in its own subfamily, the Hapsomelinae (Poinar and

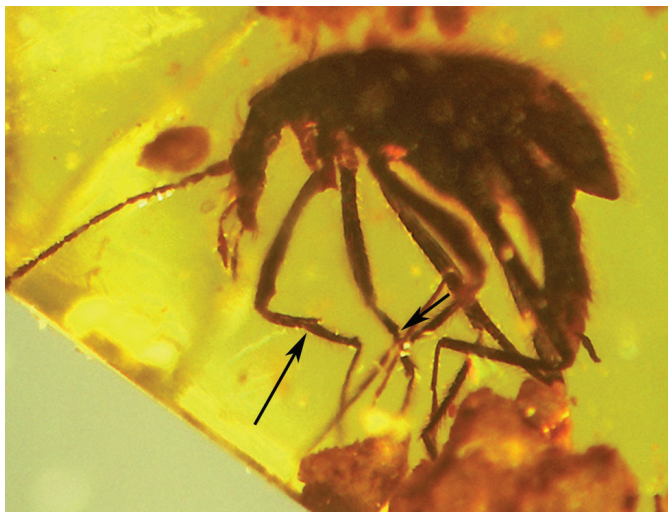


Fig. 3. The strange ant-like stone beetle *Hapsomela burmitis* in Burmese amber. Arrows show joints between patella and tibia in front legs.

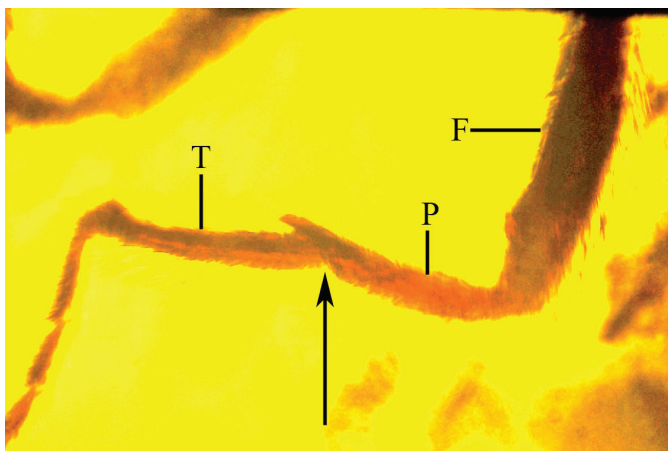


Fig. 4. Foreleg of *Hapsomela burmitis* with extra segment. F=femur; P=patella; T=tibia. Arrow shows joint between patella and tibia.

Brown 2006), but the additional segment in the front legs was the really astonishing aspect (Fig. 4). All extant insects possess legs with 5 basic segments: the coxa, trochanter, femur, tibia, and tarsus. The presence of a “patella” at the apical half of the tibia with a bend at its joint showed that this is a true dicondylic joint (allowing movement in only one direction). While myriapods, mites, and spiders possess patellae, one has to travel back to the Late Paleozoic to find insect groups with extra segments, such as members of the Paleodictyoptera, Monura, and Thysanura. Since extant scydmaenids use their forelegs to manipulate mite prey during feeding, the extra foreleg segment on *Hapsomela* probably served as a maneuvering device for securing mites, an example of functional morphology. It is unknown whether *Hapsomela*'s front legs were a resurgent ancestral character from Palaeozoic times or the result of a spontaneous mutation that occurred in this particular lineage.

Desiomorphs at the Family Level

The flat bug *Brevisensoria incrustata* in 20-30 mya Dominican amber. Termite bugs (Termitaphididae: Hemiptera) are small, flattened insects that live in the nests of termites (Fig. 5). In such a hazardous environment, intruders require good defenses. Thus, the head, thorax, and abdomen of termite bugs are merged into a hardened, smooth dorsum, analogous to the shell of a turtle. The geniculate antennae and shortened legs can be withdrawn under this protective outer case. Living in a cavern-like environment for millions of years has left termite bugs eyeless and wingless. Scientists feel that termite bugs are closely related to flat bugs (Aradidae: Hemiptera) that have distinct heads and eyes and exposed antennae.

Brevisensoria incrustata in Dominican amber has characters of both flat bugs and termite bugs, as well as a few unique features of its own. This fossil lacks eyes and wings and the dorsum forms a continuous body covering similar to termite bugs; however, the exposed antennae, longer legs, and incrustated dorsum align it with the flat bugs (Fig. 6). Its own unique characters include an unusual body shape and antennal structure. It is impossible to determine the original retreat of *Brevisensoria*. The absence of eyes, incrustated surface, and fused dorsum suggest that it inhabited a dark region



Fig. 5. The blind, wingless termite bug *Termitaradus dominicanus* in Dominican amber.

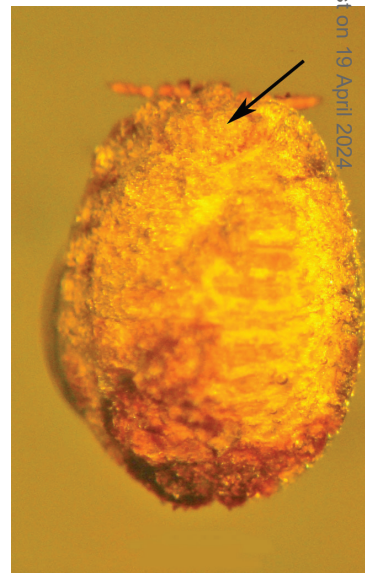


Fig. 6. The blind flat bug *Brevisensoria incrustata* in Dominican amber.

where camouflage and a defensive posture were critical, such as an animal nest (Poinar and Heiss 2011).

The primitive ant *Sphecomyrma freyi* in 90 mya New Jersey amber. One of the first amber desiomorphs reported was *Sphecomyrma freyi* Wilson, Carpenter, and Brown (1967), an Upper Cretaceous New Jersey amber fossil considered a “near-perfect link between certain nonsocial taphid wasps and the most primitive myrmecoid wasps” by possessing “a mosaic of wasp-like and antlike character states” (Wilson et al. 1967)(Fig. 7). The short, bidentate mandibles, antennal funiculi, and alitrunk (thorax and propodium) are more similar to characters of aculeate wasps, while the elongated scapes, single-segmented petiole, paired tibial spurs, and toothed tarsal claws are more like those of ants. The presence of metapleural glands, which are peculiar to most modern ants, is one of the main reasons *Sphecomyrma* was placed in the Formicidae.

The aphid *Parvaverrucosa annulata* in 97-110 mya Burmese amber. Aphids or plant lice are a very successful group, as most gardeners would agree. Aphids have a complex life cycle, and during the summer, the large wingless parthenogenetic females produce large numbers of offspring that damage plants by removing sap and transmitting plant viruses. At some point in their development, usually at the end of the growing season, winged sexual stages appear. All extant and Tertiary winged aphids possess two pairs of wings

consisting of large forewings and smaller hind wings (Fig. 8).

However, some 100 million years ago, there were aphid clades that only had functional forewings, while the hind wings were reduced to stubs or halteres (Fig. 9). The hind wings of the Cretaceous Burmese amber *Parvaverrucosa annulata* Poinar and Brown (2005) resemble the hind pair (metathoracic) of wings of male coccids. Male coccids have functional forewings, but the hind wings are reduced to rod-like structures with terminal hooks called hamulohalteres. Aphids and coccids belong to separate families in the suborder Sternorrhyncha of the order Hemiptera. The tips of *Parvaverrucosa annulata*'s stubby hind wings bear small hooks, thus making the reduced hind wings almost identical to those of coccids (Poinar and Brown 2006a) (Fig. 10). Although it has been placed with the aphids, the annulated antennae of *P. annulata* are a unique character that separates it from all fossil and extant aphids.

The unicorn fly *Cascopecia insolitis* in 97-110 mya Burmese amber. Bibionid flies (Diptera: Bibionidae), commonly known as march flies or love bugs, are noted for suddenly appearing in large mating swarms in the spring. The adults normally don't feed and the larvae mostly scavenge on plant debris. The Early Cretaceous Burmese amber *Cascopecia insolitis* (Diptera: Cascopeciidae) is a desiomorph between the Bibionidae and the extinct Mesozoic family Protopleciidae. Analyses of the fossil were based on wing venation

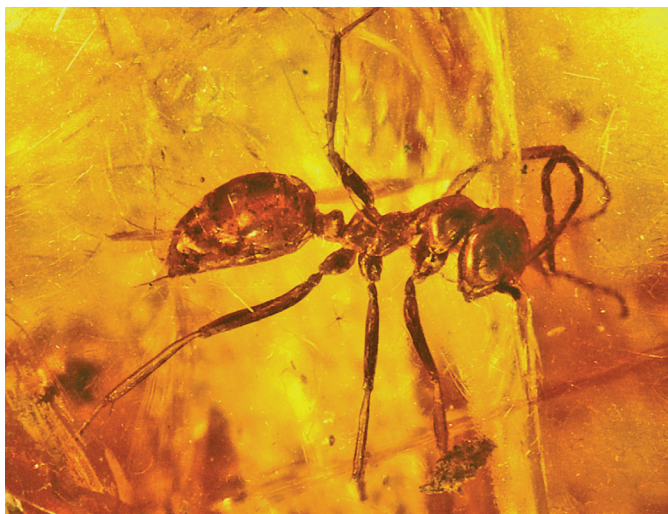


Fig. 7. Holotype (designated as worker no. 1) of *Sphecomyrma freyi* in New Jersey amber (photo by the late Frank Carpenter: specimen later accidentally destroyed at the AMNH).



Fig. 8. Fore and hind wing typical of a “modern” aphid in Dominican amber. Note smaller membranous hind wing.

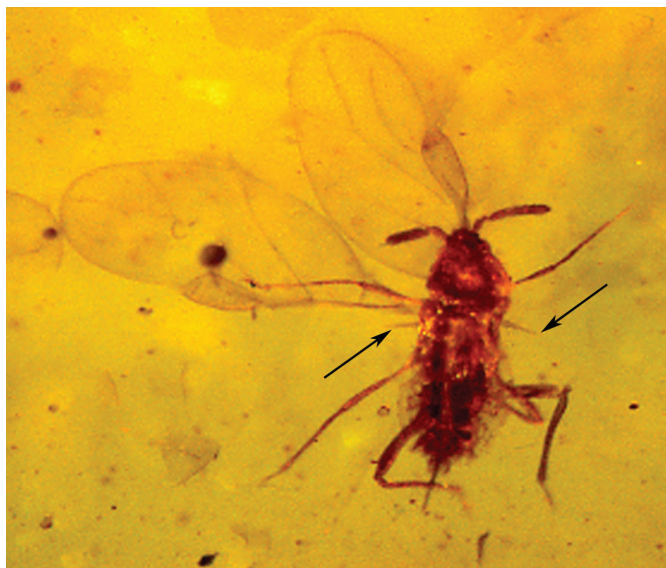


Fig. 9. The two-winged aphid *Parvaverrucosa annulata* in Dominican amber. Arrows show reduced haltere-like hind wings.

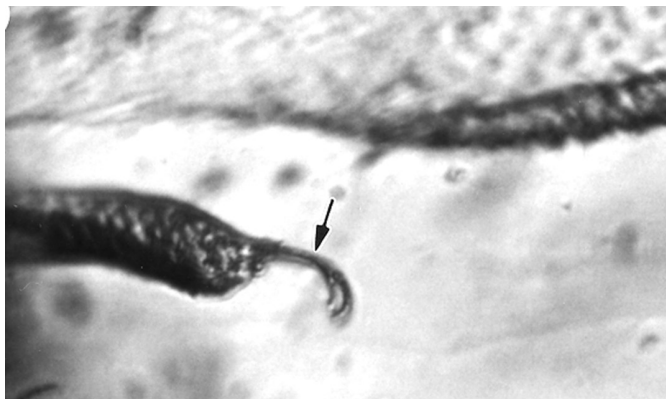


Fig. 10. Detail of hooks (arrow) on the end of the haltere of *Parvaverrucosa annulata* in Dominican amber.

comparisons because most Mesozoic Diptera are known only from isolated wings. Wing venation within the Bibionomorpha is fairly conserved, so using venational patterns to assign fossils to extant or extinct clades (pterotaxonomy) is generally dependable. The wing venation of *Cascoplecia insolitis* fell between the extant genus *Plecia* (Bibionidae) and the Mesozoic genus *Protoplecia* (Protopleciidae).

Since *Cascoplecia* was complete, body characters could also be used in determining its systematic placement. The strange S-shaped antennomeres, elongate palps, and head protuberance bearing ocelli placed *Cascoplecia* apart from any extant or extinct member of the Bibionomorpha (Poinar 2009) (Fig. 11).

The weevil *Anchineus dolichobothris* in 97-110 mya Burmese amber. A small but significant weevil in Burmese amber, *Anchineus dolichobothris*, had a combination of character traits of three extant and one extinct weevil families. The 7-jointed funicle and bifid claws resemble members of the Apionidae, while the geniculate antennae with loosely three-segmented antennal clubs are characters of the Nanophyidae. The antennae inserted on the sides of the rostrum,



Fig. 11. Head of the unicorn fly *Cascoplecia insolitis* in Burmese amber.



Fig. 12. The primitive weevil *Anchineus dolichobothris* in Burmese amber.

tarsi with divaricate claws, and leveled and subequal abdominal ventrites are characters of the Caridae. The 11-segmented, loosely clubbed antennae, well-developed eyes, and lateral carina of the pronotum are characters of the Late Jurassic family Eobelidae. This above combination of characters, as well as the loose antennal club, vertical mandibles, and deep insertion of the unguitactor plate into the pretarsus (resulting in a lobed fifth segment), justified placing this weevil in its own family (Poinar and Brown 2009).

Using functional morphology to determine the biology of *Anchineus*, the bi-lobed tarsi and robust claws indicate an arboreal existence, while the long rostrum and vertical mandibles suggest it fed on and oviposited in stems, buds, or soft fruits (Fig. 12).

The primitive crane fly *Dacochile microsoma* in 97-110 mya Burmese amber. The curious *Dacochile microsoma* possesses character states found in both the Psychodidae (Bruchomyiinae) and the Tanyderidae (Poinar and Brown 2006b). While the proportion of the palpal segments, immaculate wings lacking an anal lobe, and a short Rs vein align *Dacochile* with the Bruchomyiinae, the presence of an m-m cross vein, serrated mandibles, setae between the ommatidia, and two segmented cerci and the absence of flagellar ascoids align it with the Tanyderidae (Fig. 13).

A row of heavily sclerotized, thorn-shaped processes (spines/spurs) on the inside of the hind tibiae and first two tarsal segments of *Dacochile* suggest it may have hung from vegetation by its hind legs to wait for passing prey. This behavior of hanging from plants has been noted in the New Zealand *Tanyderus forcipatus*.

The serrated mandibles of *Dacochile* (Fig.14) are another tany-

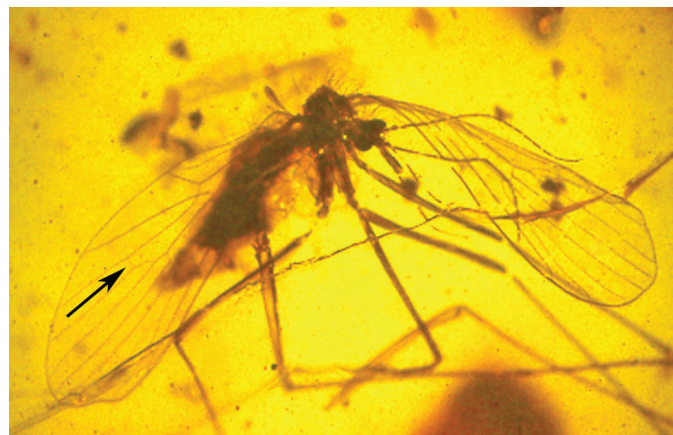


Fig. 13. The primitive crane fly *Dacochile microsoma* in Burmese amber. Arrow shows m-m crossvein, a key character of the Tanyderidae.

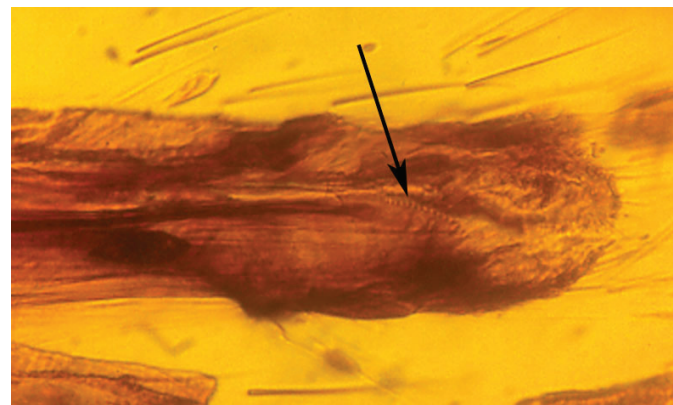


Fig. 14. Serrated mandibles (arrow) of *Dacochile microsoma* in Burmese amber.

derid character and give some indication of the feeding habits of the fossil. A piercing-sucking habit and preying on invertebrates or vertebrates may have provided its major means of obtaining nourishment.

The shore bug *Palaeoleptus burmanicus* in 97-110 mya Burmese amber. Shore bugs (Hemiptera: Saldidae) represent a family of small insects that favor damp or wet habitats, such as streams, lakebeds, ocean beaches, or bays. An intertidal shore bug that is common along the Pacific coast is *Saldula laticollis* (Fig. 15), a predator capable of surviving short periods of immersion in seawater. A shore bug in Early Cretaceous Burmese amber (Fig. 16) had some characters found in modern saldids as well as in the related family, Leptopodidae. While the body shape, rostrum length and antennal structure of *Palaeoleptus burmanicus* are saldoid features, the position of the ocelli, rostral spines, and profemur armature are leptopodid characters. Aside from these shared characters, *Palaeoleptus* has such a unique forewing venation that it was placed in its own family (Poinar and Buckley 2009).

The asymmetrical genital plate directed to the left side of the body suggests that *Palaeoleptus* practiced side-by-side mating, similar to the condition in saldids.

The mantidfly *Doratomantispa burmanica* in 97-110 mya Burmese amber. Mantidflies (Mantispidae: Neuroptera) are strange neuropterans with large raptorial forelegs similar in form and function to those of the unrelated praying mantises. A mantispid, *Doratomantispa burmanica*, in Early Cretaceous Burmese amber (Fig. 17) not only possessed characters found in all four extant subfamilies (Calomantispinae, Symphrasinae, Drepanicinae, and Mantispinae) of mantidflies, but also exhibited a wing character found in the related thorny lacewings (Rhachiberothidae) (Poinar and Buckley 2010). The character shared with the thorny lacewings was the arrangement of short supporting rods (trichosors) along the wing margin. Most mantispids lack trichosors, or if they are present, they are usually reduced and only occur along the wing tips. Thorny lacewings not only have numerous trichosors along most of the wing margin, but there is only a single trichosor between the veinlets. This is the exact condition found in *Doratomantispa* (Fig. 18).

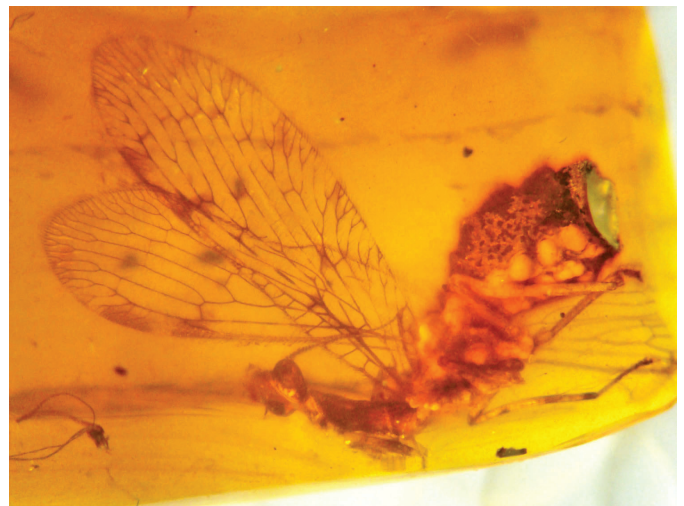
An ecological feature of *Doratomantispa* that could function as a desiomorphic character is the presence of spherical-sub spherical bodies of a possible rickettsial pathogen in its abdomen (Fig.17).



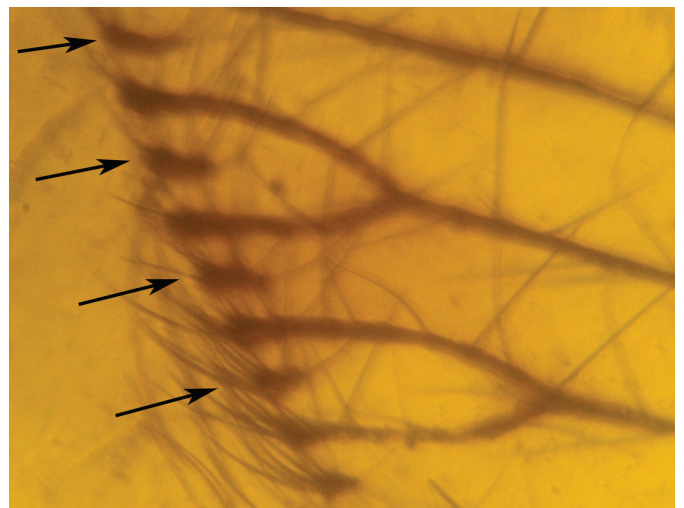
Fig. 15. An intertidal shore bug *Saldula laticollis* along the Oregon coast.



16. The shore bug *Palaeoleptus burmanicus* in Burmese amber.



17. The mantidfly, *Doratomantispa burmanica* in Burmese amber. Note the white, spherical bodies in the abdomen, which indicates a rickettsial infection.

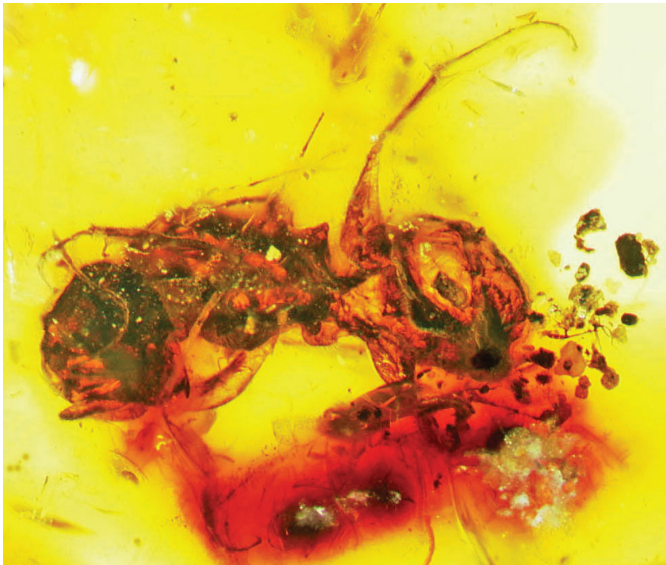


18. Trichosors (arrows) on the wing margin of *Doratomantispa burmanica* in Burmese amber.

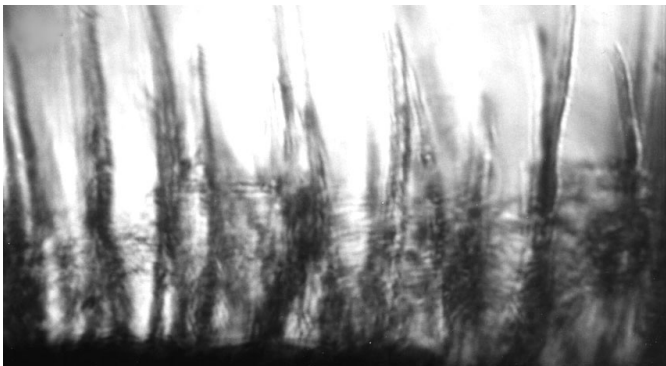
While such infections are not known in extant mantispids or thorny lacewings, they have been reported in chrysopid neuropterans. Female heterostigmatid mites (Khaustov and Poinar 2011) adjacent to the wings and body of *Doratomantispa* presented another interesting aspect of this fossil. Phoretic mites have not been reported on any extant Neuroptera.

The primitive bee *Melittosphex burmensis* in 97-110 mya Burmese amber. *Melittosphex burmensis* (Apoidea: Melittosphexidae) represents an extinct lineage of bees with some wasp-like characters. It provides important insights into the transition from predatory crabronid wasps to pollen-collecting bees. Its mixture of bee- and wasp-like features makes it an ideal desiomorph and explains why it was placed in a new sister family to the modern bees.

In general shape, *Melittosphex* resembles a small andrenid or halictid bee, and like modern bees, it is covered with branched hairs over most of its body (Fig. 19). While its wing venation is more bee-like than wasp-like and the branched hairs (Fig. 20) separate it from all apoid wasps, *Melittosphex* possesses two mid-tibial spurs and a slender hind basitarsus, which are basic features of apoid wasps. Autapomorphic features are large, clearly tridentate mandibles, slender hind legs, and prominent tubercles on the propodeum (Danforth



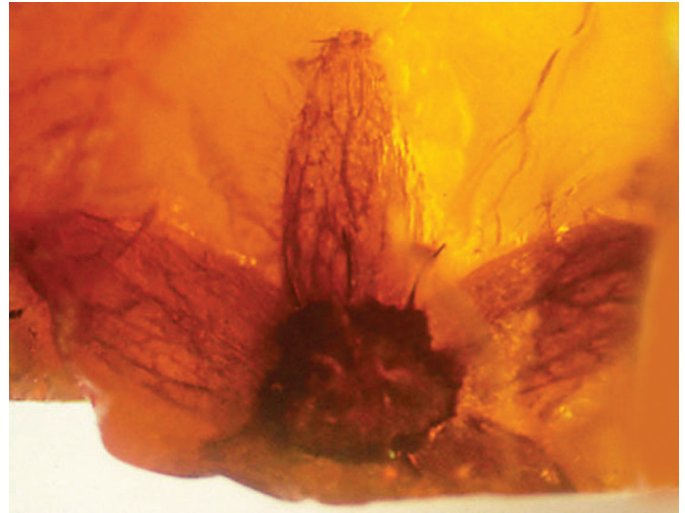
19. The primitive bee *Melittosphex burmensis* in Burmese amber.



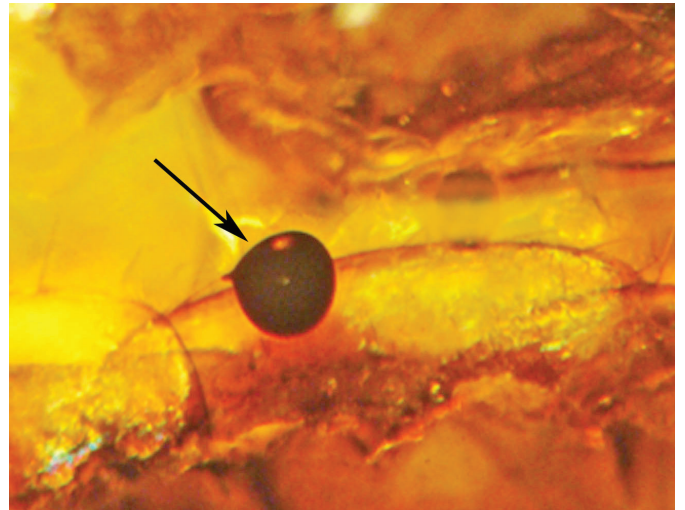
20. Branched hairs on body of *Melittosphex burmensis*.

and Poinar 2011). The small size of *Melittosphex* correlates with the small flowers that have been recovered from Burmese amber. These Early Cretaceous flowers, which represent diverse plant families, only range from 1-6 mm in diameter (Chambers et al. 2010) (Fig. 21).

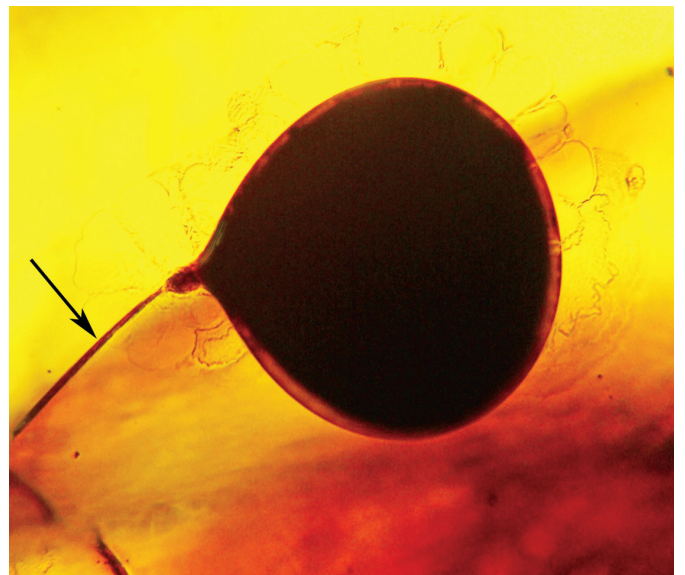
The eugregarine *Primigregarina burmanica* in 97-110 mya Burmese amber. Gregarines are extremely diverse protozoan parasites that infect invertebrates, especially annelids and arthropods. Many parasitize insects, especially cockroaches, grasshoppers, and other members of the Dictyoptera. The first fossil gregarine, *Primigregarina burmanica*, occurred adjacent to a cockroach in Burmese amber that had been attacked by a predator and had its midgut ripped open, thus exposing the contents (Poinar 2010). This action revealed the epimerate and gametocyst stages of the gregarine and showed that cockroaches harbored these parasites in the Early Cretaceous (Fig. 22). The fossil shares characters with both of the extant families Monoductidae and Gregarinidae. While the single sporoduct on the gametocyst (Fig. 23) aligns the fossil with members of the Monoductidae, the large spherical gametocyst and non-pronged epimerate are characters of the Gregarinidae. The short inverted neck of the epimerite is a unique character of *Primigregarina*. Evidence of spore expulsion from the gametocyst in the gut of the cockroach host is another unusual character. Normally, gametocysts dehisce after being passed from the body of the host and the time between capture and becoming embedded in the resin would seem to be too short for the formation of a spore duct with spore release.



21. Flower of *Tropidogyne pikei* in Burmese amber. This is one of the small flowers that females of *Melittosphex* could have visited. The flower diameter is slightly over 5 mm.



22. Part of a predated cockroach showing a gametocyst of the eugregarine protozoan *Primigregarina burmanica* (arrow) in Burmese amber.



23. Sporoduct (arrow) emerging from the gametocyst of *Primigregarina burmanica* in Burmese amber.

Desiomorphs at the Ordinal Level

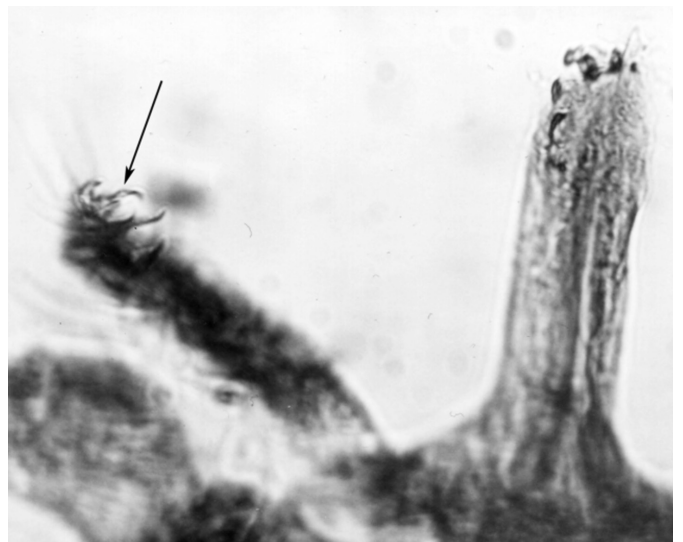
Velvet worms in 20-30 mya Dominican amber and 40-50 mya Baltic amber. Velvet worms of the Subphylum Onychophora are enigmatic invertebrates with a unique accumulation of characters. At first appearance, they resemble annelids with legs, but their affinity (which is still somewhat of a mystery) seems to lie with the arthropods. As predators, their singular method of prey capture employs the use of a slimy secretion propelled toward the victim from a pair of head papillae. The slime ensnares the prey, which is then consumed. All extant velvet worms have an apical non-retractable foot portion at the base of their legs. This foot portion bears a terminal pair of claws and well-defined pads with associated papillae. However, the foot portion is absent on a pair of velvet worms found in Baltic and Dominican amber (Poinar 2000).

Even though the Dominican amber *Tertiapatus dominicanus* (Fig. 24) and Baltic amber *Succinipatopsis balticus* (Fig. 25) are terrestrial, possess a ventral mouth, and have numerous simple legs and slime-secreting head papillae, they both lack clawed footpads. Simple legs lacking footpads with claws are also characteristic of Paleozoic onychophorans.

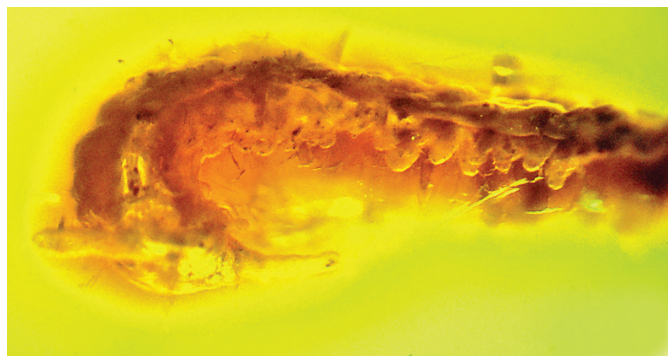
The hard tick *Cornupalpatum burmanicum* in 97-110 mya Burmese amber. Ticks are rare as fossils, but both hard (Ixodidae) and soft (Argasidae) ticks have been found in amber deposits. The oldest records of hard ticks are in Early Cretaceous Burmese amber, and one of these has features of a desiomorph (Poinar and Brown 2003). While resembling modern ticks in most characters (Fig. 26), the first instar larva of *Cornupalpatum burmanicum* possesses palpal claws (Fig. 27). Such armature is lacking on all extinct and extant ticks, but terminal or subterminal palpal claws occur in members of the mite groups Opilioacarida, Holothyrida, and Mesostigmata. The function of the palpal claws on *Cornupalpatum* is unknown, but because the fossil is immature, it is doubtful the claws would be



26. The hard tick *Cornupalpatum burmanicum* in Burmese amber.



27. Anterior end of *Cornupalpatum burmanicum* in Burmese amber. Arrow shows claws on tips of palps.



24. The Dominican amber onychophoran *Tertiapatus dominicanus*.



25. The Baltic amber onychophoran *Succinipatopsis balticus*.

related to mating behavior. They were probably used to assist the tick in attaching to a host.

Summary

While these desiomorphs reveal the long geological past of certain invertebrate clades, it is difficult to determine how many are stem groups and represent transitional fossils and how many are separate, unique lineages that share characters as the result of convergence. As aforementioned, morphological characters can be misleading in determining whether a particular organism is a true transitional fossil.

Darwin cited the absence of “innumerable transitional forms” as a major problem with his theory of phyletic evolution. While the number of fossils has increased greatly since Darwin’s time, his comment on the “extreme imperfection of the fossil record” still applies in large part today. One of the difficulties in deciding if desiomorphs represent actual transition fossils is our lack of knowledge of the biology of the fossils, especially if there are no characters that indicate functional morphology. If closely related to an extant clade, one can deduce the biology of a fossil by using the principal of behavior fixity, which infers that the behavior, ecology, and climatic preferences of fossil organisms will be similar to those of their present-day descendants at the generic, and in some cases, the family level (Boucot and Poinar 2010).

Desiomorphs are among the most intriguing topics in paleontology, and questions about their lifestyle, disappearance, and classification will occupy us for years to come. They show the inadequacy of our present system of classification in dealing with ancient invertebrates and give us a time zone for the appearance and extinction of ancient lineages.

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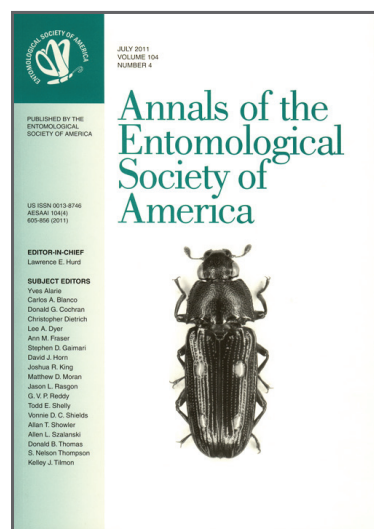
Dr. George Poinar, who received his higher education from Cornell University, has been studying life forms in amber since 1975, shortly after he joined the Entomology Department at the University of California, Berkeley. Travels to the Baltic area, Dominican Republic, Mexico, Alberta, Canada and New Zealand gave him an opportunity to collect amber firsthand from various depositional sites. His early retirement at Berkeley offered an opportunity to transfer to Oregon State University where he continues to study amber inclusions from around the world.

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