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Fossil Focus: Arthropod–plant interactions

by Ben J. Slater*[1]

Introduction:

When the geneticist and evolutionary biologist J. B. S. Haldane was asked what he could conclude about the nature of a creator from his studies of natural history, he supposedly replied that any creator must have "an inordinate fondness for beetles". Indeed, there are more species of beetle than of any other animal alive today, and as insects, beetles belong to the most diverse class of modern organisms, which includes more than two-thirds of all described species (Fig. 1).

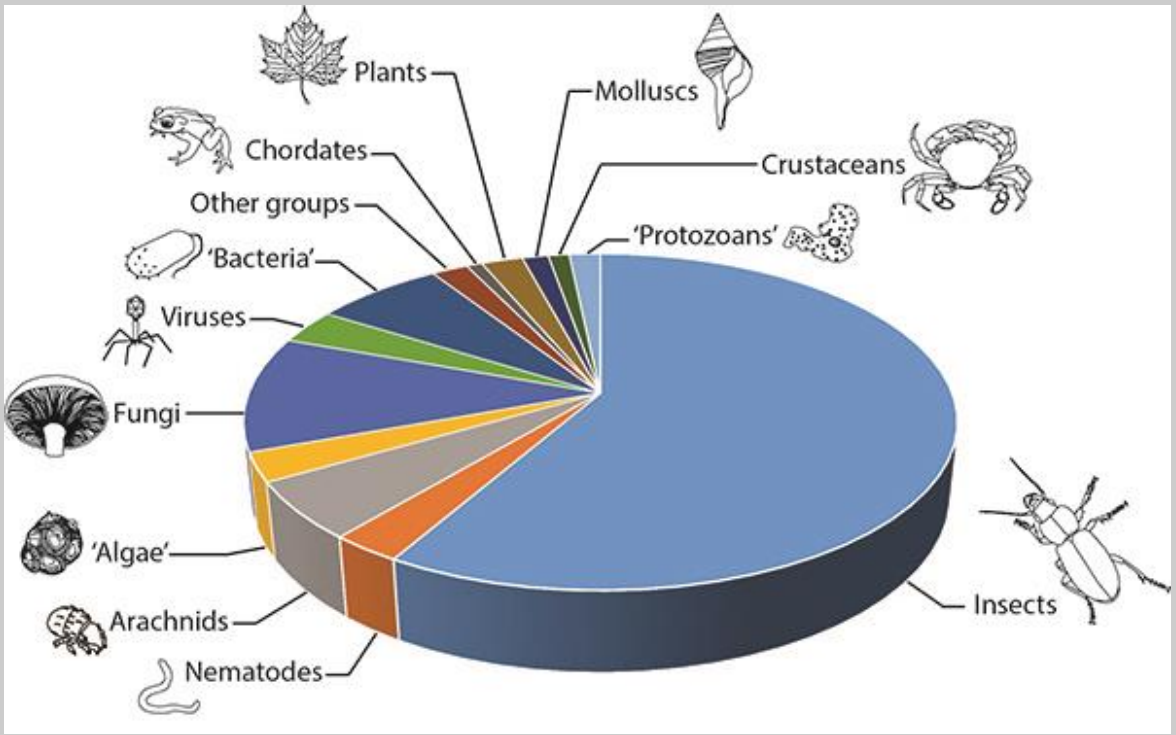

Figure 1 — Pie chart showing estimated proportions of different groups of organisms on Earth today, by numbers of species (based on data presented by Purvis and Hector 2000).

It can be said that macroscopic life is dominated by insects (and in particular beetles), but like all organisms, insects — and other arthropods, the larger phylum to which the insects belong — don't exist in isolation. Organisms are the product of their environment, which includes other living things. In the case of terrestrial arthropods, plants usually play an important part as a food source, habitat and site to mate and deposit eggs (Fig. 2). As a result, although there are perhaps only one hundredth as many species of plant alive today as species of arthropod, plants are key to modern diversity.

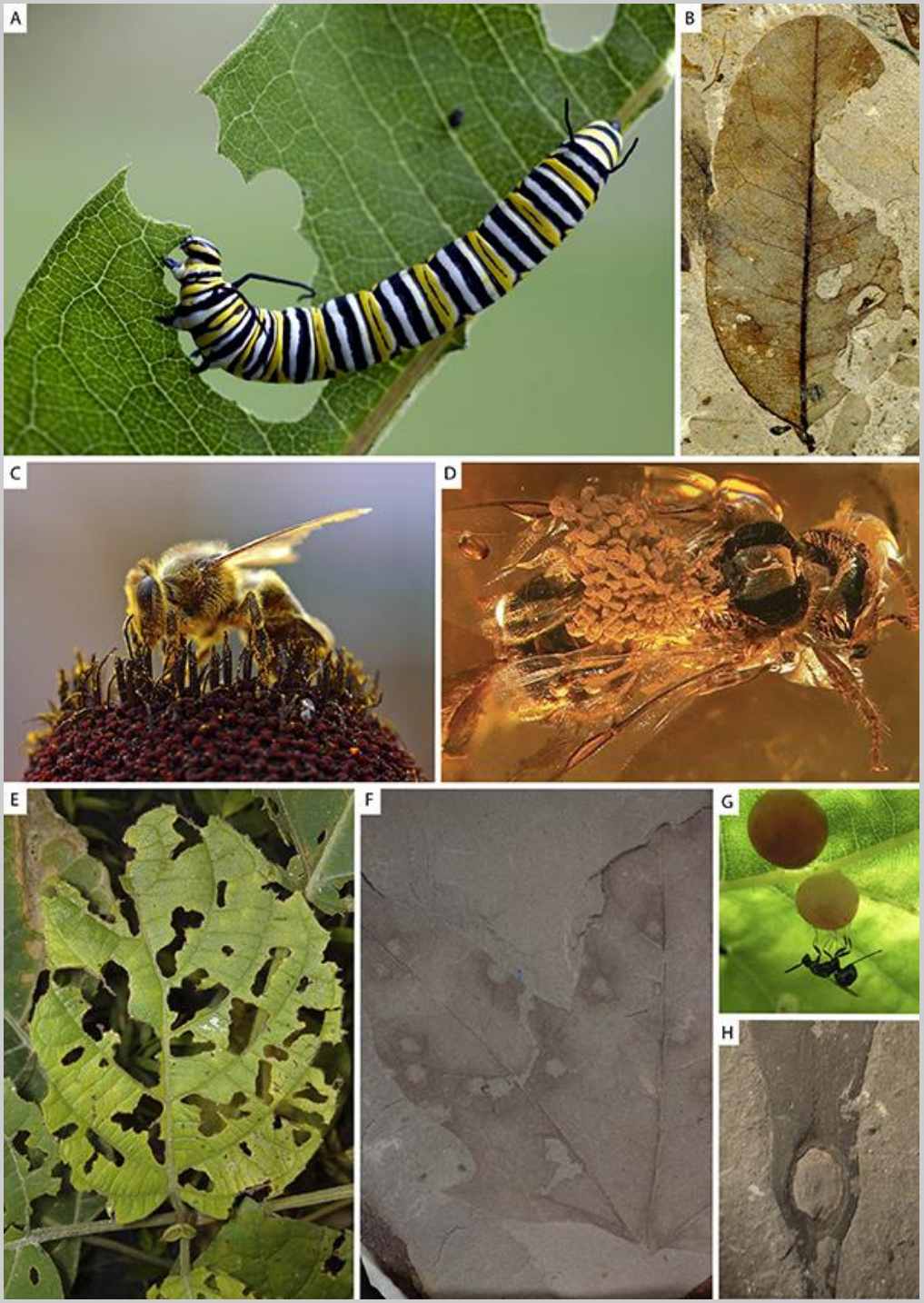

Figure 2 — Examples of arthropod–plant interactions. A. Modern marginal leaf feeding by a caterpillar of a Monarch butterfly (*Danaus plexippus*; image: National Science Foundation); B. Fossil leaf showing signs of consumption by arthropods from the Palaeocene–Eocene Thermal Maximum of Bighorn Basin, Wyoming (photograph: Ellen Currano, figured in Currano et al. 2008); C. Extant bee collecting pollen; D. Bee with cargo of orchid pollen from Miocene-age Dominican amber (from Ramírez et al. 2007); E. Modern leaf showing evidence of hole feeding (image: Wikimedia Commons); F. Fossil leaf from the Cenozoic of Japan with hole-feeding damage (photograph: Steve McLoughlin); G. Modern example of galling: a parasitic wasp is ovipositing its eggs inside the larvae of another insect developing inside a gall on the underside of an oak leaf (image: Evan Herk, Wikimedia Commons); H. Fossilized Permian example of a gall on a *Glossopteris* leaf (after McLoughlin 2011).

Today, the flowering plants (angiosperms) are dominant components of all land-based ecosystems, except in the very north and very south of the planet. Much of the success of angiosperms seems to be derived from their intimate relationship with the insects, some of which are responsible for the pollination of plants, enabling fertilization and reproduction, often over large distances. However, this was not always so. The fossil record reveals that before the Cretaceous period (145 million to 66 million years ago), the land was dominated by other groups of plants, and terrestrial ecosystems were probably quite different. To fully understand how the close associations between arthropods and plants came about, we first need to consider their historical context — and this means consulting the fossil record.

Arthropod–plant interactions in the fossil record:

First things first, how can we recognize arthropod–plant interactions in the fossil record? Well, there are several different lines of evidence that can help with this. For instance, the morphology of the fossil arthropod, in particular its mouthparts, provides clues as to its diet (Figs 3 and 4). In general, arthropod mouthparts are adapted for slicing and chewing, piercing and sucking, sponging, siphoning or filter feeding, and knowledge of mouthpart morphology in fossil arthropods therefore helps to establish both the animal's trophic level, or position in the food chain, and its functional feeding group.

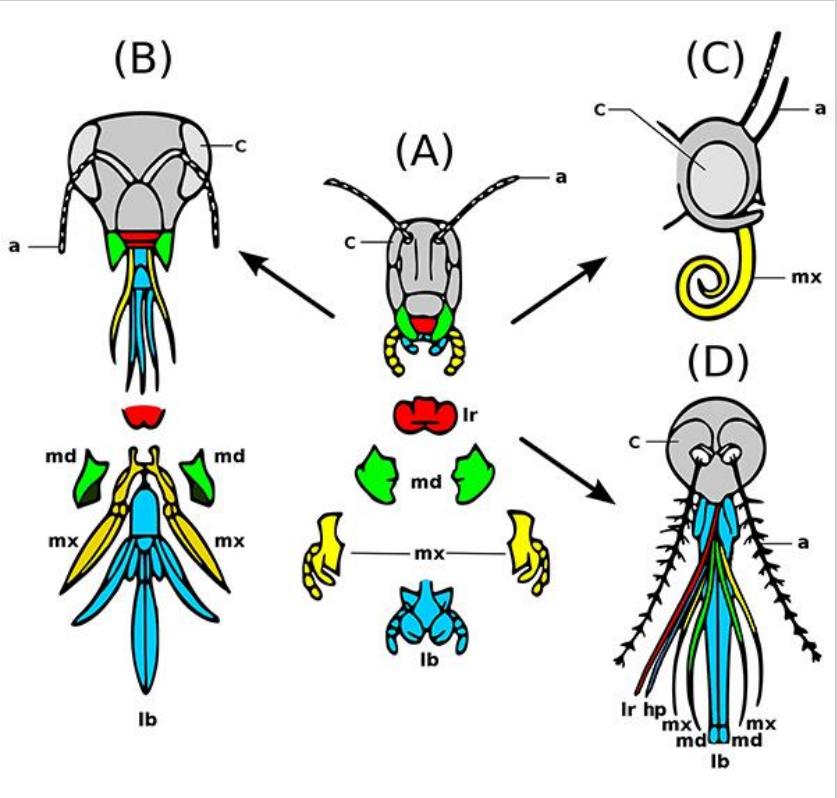

Figure 3 — The development of insect mouthparts. A. A grasshopper's primitive chewing mouthparts; B. Lapping mouthparts of a bee; C. Siphoning mouthparts of a butterfly; D. Piercing and sucking mouthparts of a female mosquito. a, antennae; c, compound eye; lb, labium; lr, labrum; md, mandibles; mx, maxillae; hp, hypopharynx.

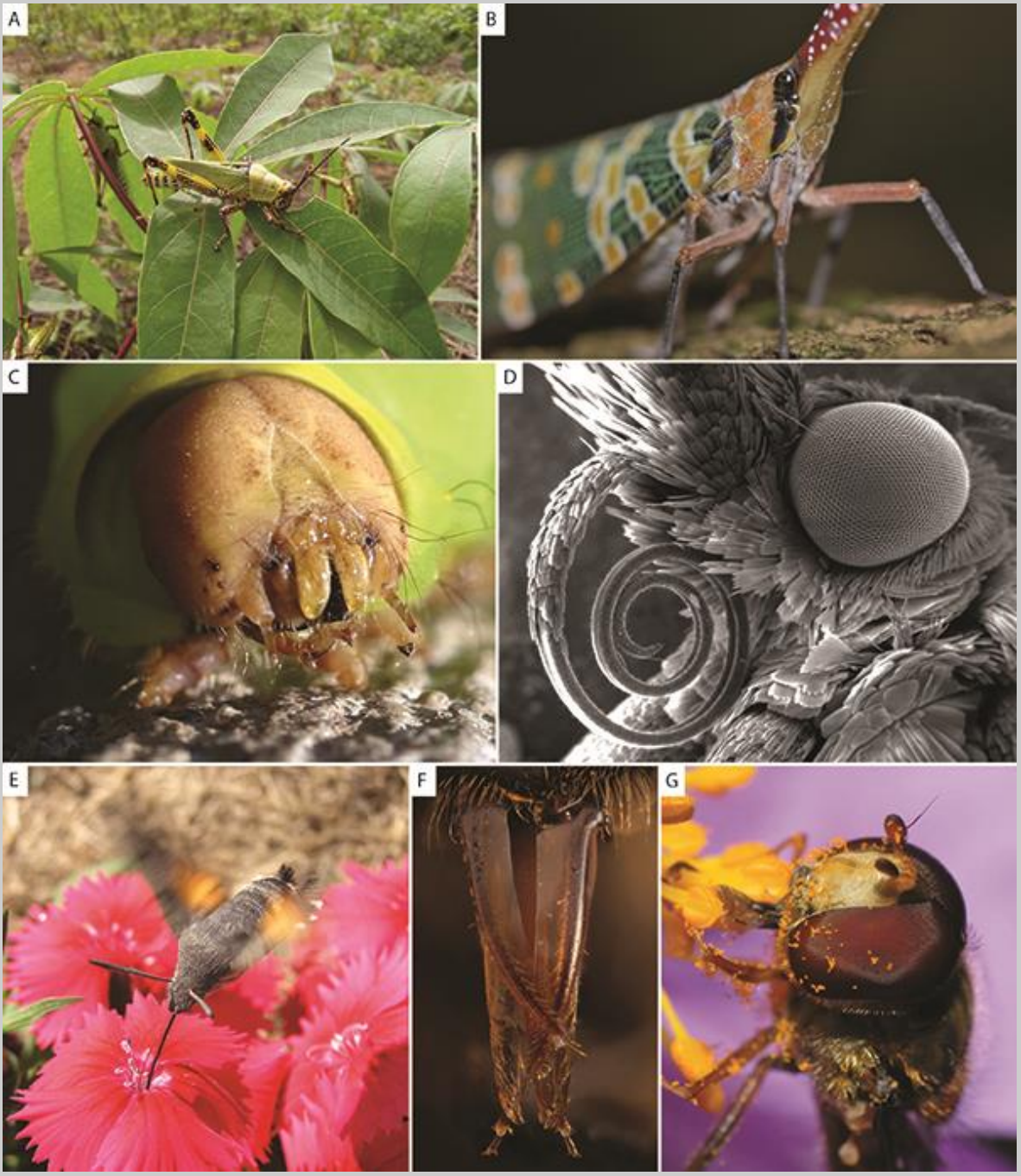

Figure 4 — Range of mouthparts in modern insects adapted for different functional feeding roles. A. Grasshopper using its chewing mouthparts to feed on the margins of a leaf (image: Christiaan Kooyman, Wikimedia Commons); B. Piercing and sucking mouthparts of a lantern bug, Hemiptera (image: Thomas Brown, Wikimedia Commons); C. Chewing mouthparts of a caterpillar (image: Tom Murphy, Wikimedia Commons); D. Scanning electron microscope image of a moth with coiled proboscis, used to siphon nectar when extended; E. Hummingbird hawkmoth using its proboscis to drink nectar; F. Lapping mouthparts of a honeybee used to drink liquid food such as nectar (image: Matt Inman, Wikimedia Commons); G. Fly with sponging mouthparts covered in pollen (image: André Karwath, Wikimedia Commons).

The gut contents of fossilized arthropods are occasionally preserved, and these provide direct evidence of what the organism was feeding on. Arthropod coprolites, their fossilized faeces, are vitally important for understanding the history of arthropod–plant interactions (Fig. 5). Coprolites can reveal detailed information about the diet and feeding modes of the arthropods that produced them, and about the arthropod's size. Unfortunately, it is often very difficult to assign a fossilized coprolite to a specific species, because many groups of arthropods produce rather similar looking coprolites — sometimes, particularly for isolated specimens, it is even difficult to determine whether the producer of the coprolite was an arthropod or some other invertebrate. Nevertheless, coprolites can be evidence of different trophic levels and functional feeding groups in a (palaeo)ecosystem, even in the absence of any body fossils of the organisms that produced them.

Experimental studies involving living organisms are also a powerful tool for understanding how ancient plants and arthropods interacted. Just as a palaeontologist interested in dinosaur-track formation may study modern bird footprints in a variety of sediments, so a palaeontologist interested in arthropod–plant interactions might examine examples in living species.

Another important piece of evidence about ancient arthropod–plant interactions is the presence of certain types of damage on plant fossils (Figs 2 and 6). The main types of arthropod-related damage observed on fossilized plant remains are outlined below.

External foliage feeding (EFF) is where arthropods (usually insects with chewing mouthparts) consume the outer tissues of leaves (Figs. 2A,B,E,F and 6C–E). There are several different types of EFF, including leaf-margin feeding, in which distinct scalloped shapes are created along the edges of the foliage (Figs. 2A,B and 6 C,D). Skeletonization is a type of EFF in which the outer leaf tissues are entirely consumed, leaving only the veins and midrib of the leaf. Hole feeding (Figs. 2E,F and 6E) is where a patch of leaf tissue is consumed, producing a hole in the leaf. When patches are consumed without creating a hole, this is referred to as window feeding,because it usually results in translucent window-like patches across the leaf.

Piercing and sucking is a form of herbivory found in many arthropods with mouthparts modified to pierce plant tissues and suck nutritious fluids from the leaf veins or stems. This leaves a distinct damage mark or series of piercing sites on the plant. Several lineages of arthropod have evolved piercing mouthparts, most notably the Hemiptera or 'true bugs', such as aphids, shield bugs and cicadas (Figs 4B and 7F,G). Here, the different parts of the mouth have been transformed into a proboscis specialized for piercing and sucking plant fluids (Fig. 4B).

Boring into plant tissues creates holes in the plant, in which the animal can live (Figs 5F, 6A and 8). Typically, borings occur in the woody tissues of plants (Fig. 8) or in dead plant material, where the arthropods can eat fungi and take shelter. Many borers also consume living cambial tissues, which are responsible for the growth of stems and roots; this can severely damage the host plant. Borings are produced by a wide range of arthropod groups, including oribatid mites and beetle larvae. Sometimes, borings containing coprolites are preserved in mineralized wood (Fig. 8).

Seed predation, the behaviour of consuming seeds, has a long fossil record. Fossil seeds may have a chewed hole in the husk, indicating either that an arthropod bored its way into the seed, or that a larva chewed its way out. Fossils of the seed *Trigonocarpus* (Fig. 7D) from the Carboniferous period (359 million to 299 million years ago) can exhibit signs of seed predation; fossil casts of the inside of the seed show a circular plug of protruding sediment, which indicates the position of a hole.

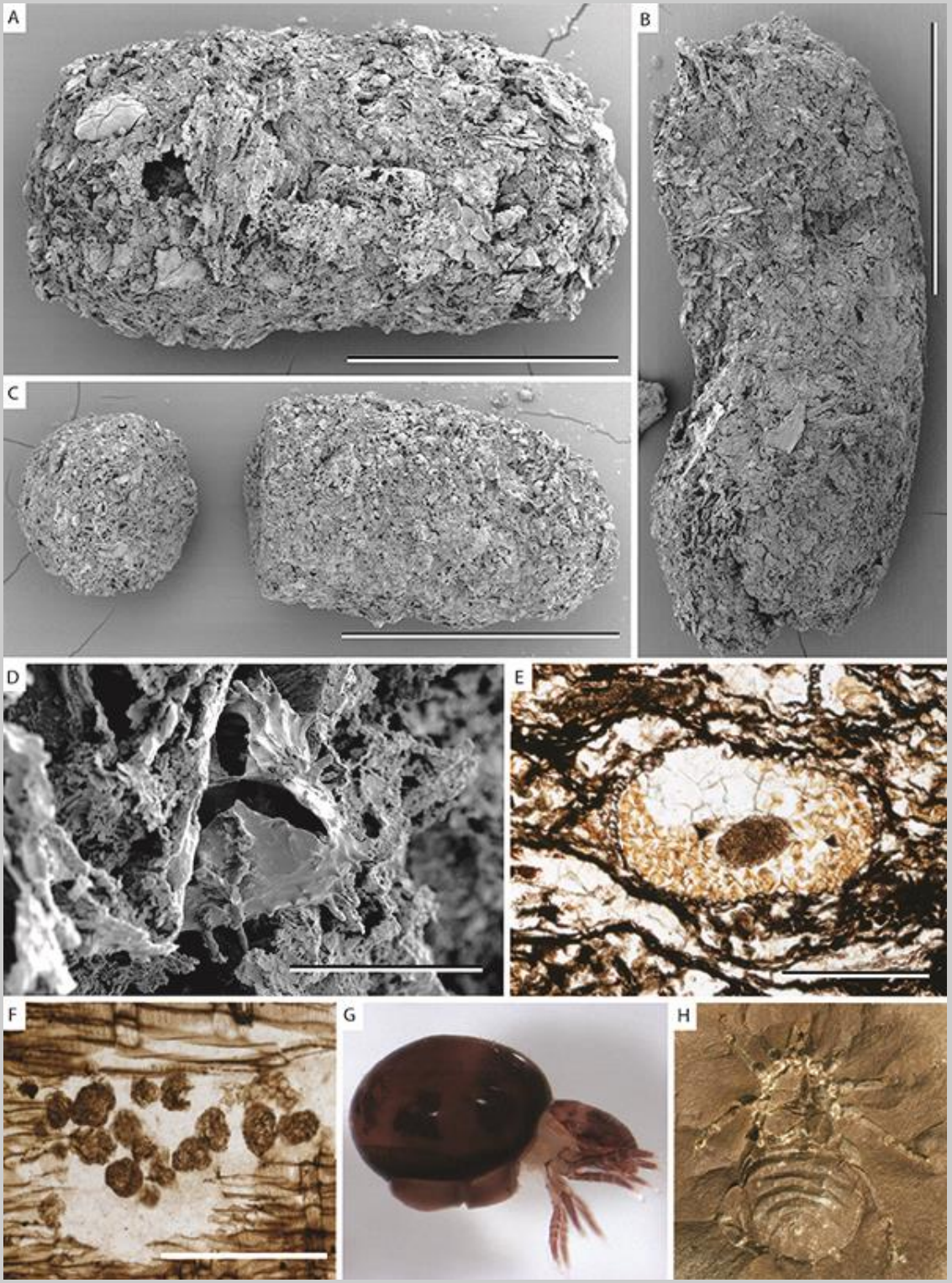

Figure 5 — Coprolites and arthropods. A–C. Scanning electron microscope images of coprolites from a silicified peat from the Permian of Antarctica. The mixed plant remains suggest they are the product of a detritivore (after Slater et al. 2012). D. Close-up showing a consumed fern spore among mixed plant debris (after Slater et al. 2012); E. Coprolite inside the spore-housing organ (sporangia) of a fern from Permian Antarctica (after Slater et al. 2012); F. Coprolites in galleries inside silicified *Australoxylon* wood from the Permian of Antarctica, possibly produced by Oribatid mites (after Slater et al. 2012); G. Modern oribatid mite; H. Trigonotarbid arachnid preserved in siderite from the Carboniferous of Coseley, England, UK (photograph: Andrew Storey). Scale bars; A = 500 µm; B = 1 mm; C = 1 mm; D = 20 µm; E = 1 mm; F = 500 µm.

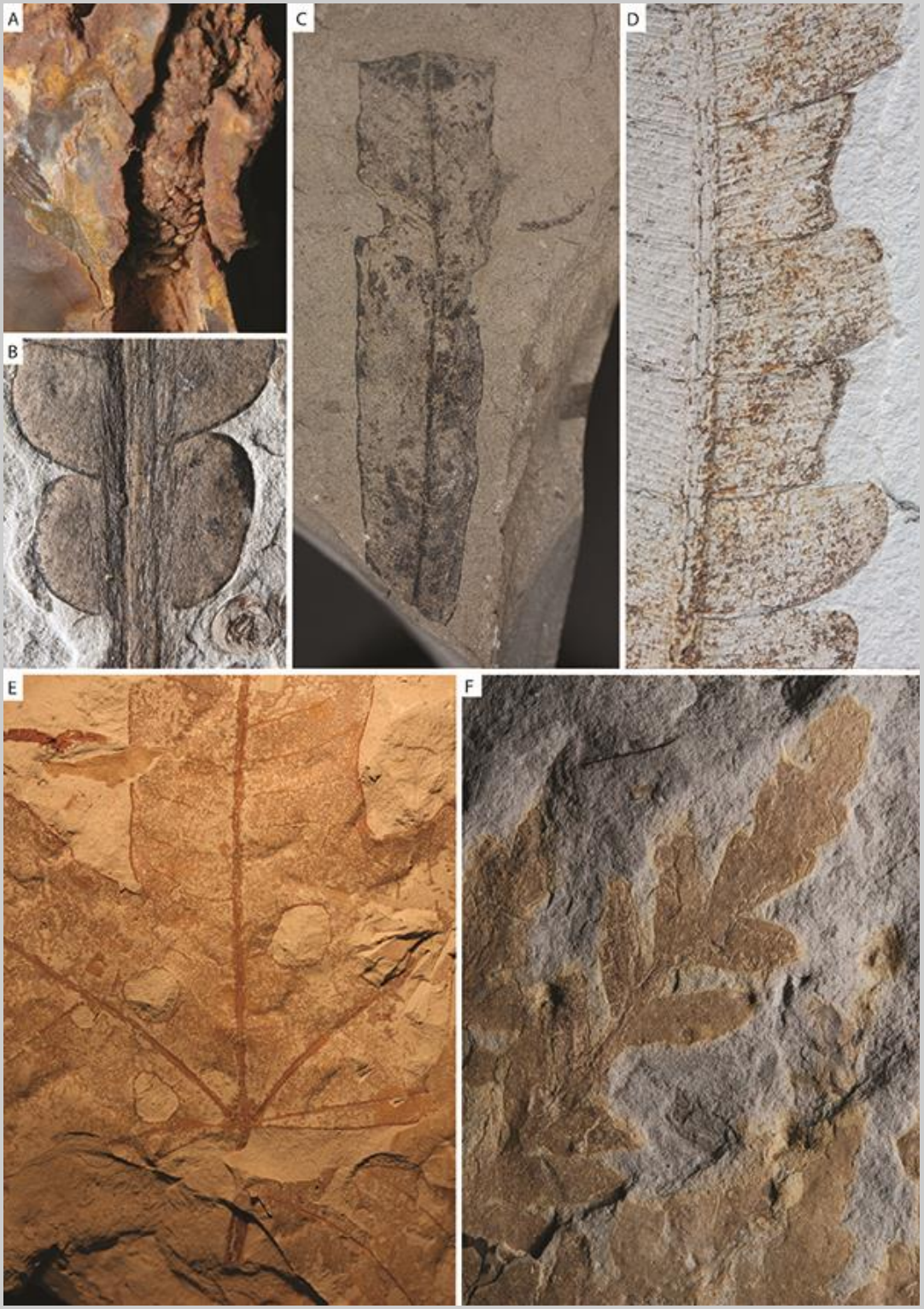

Figure 6 — Compression fossils of plants showing arthropod damage and defensive anti-herbivore adaptations. A. Chewed up debris produced by termites in petrified conifer wood from the middle Tertiary of Queensland, Australia (after Rozfelds & De Baar 1991); B. *Anomozamites villosus*, a fossil bennettite from the Middle Jurassic of China with hair defences along midrib (after Pott et al. 2012); C. Example of scalloped margin feeding on a Cenozoic fossil leaf from Japan; D. *Anomozamites villosus*, a bennettite from the Middle Jurassic of China with damage to the foliage; E. Fossil *Brachychiton* leaf from the Eocene of Anglesea, Australia, with hole damage; F. Fossil of *Pachypteris crassa* with leaf-mining damage from the Latest Jurassic of Northeast Queensland, Australia. Photographs: Steve McLoughlin.

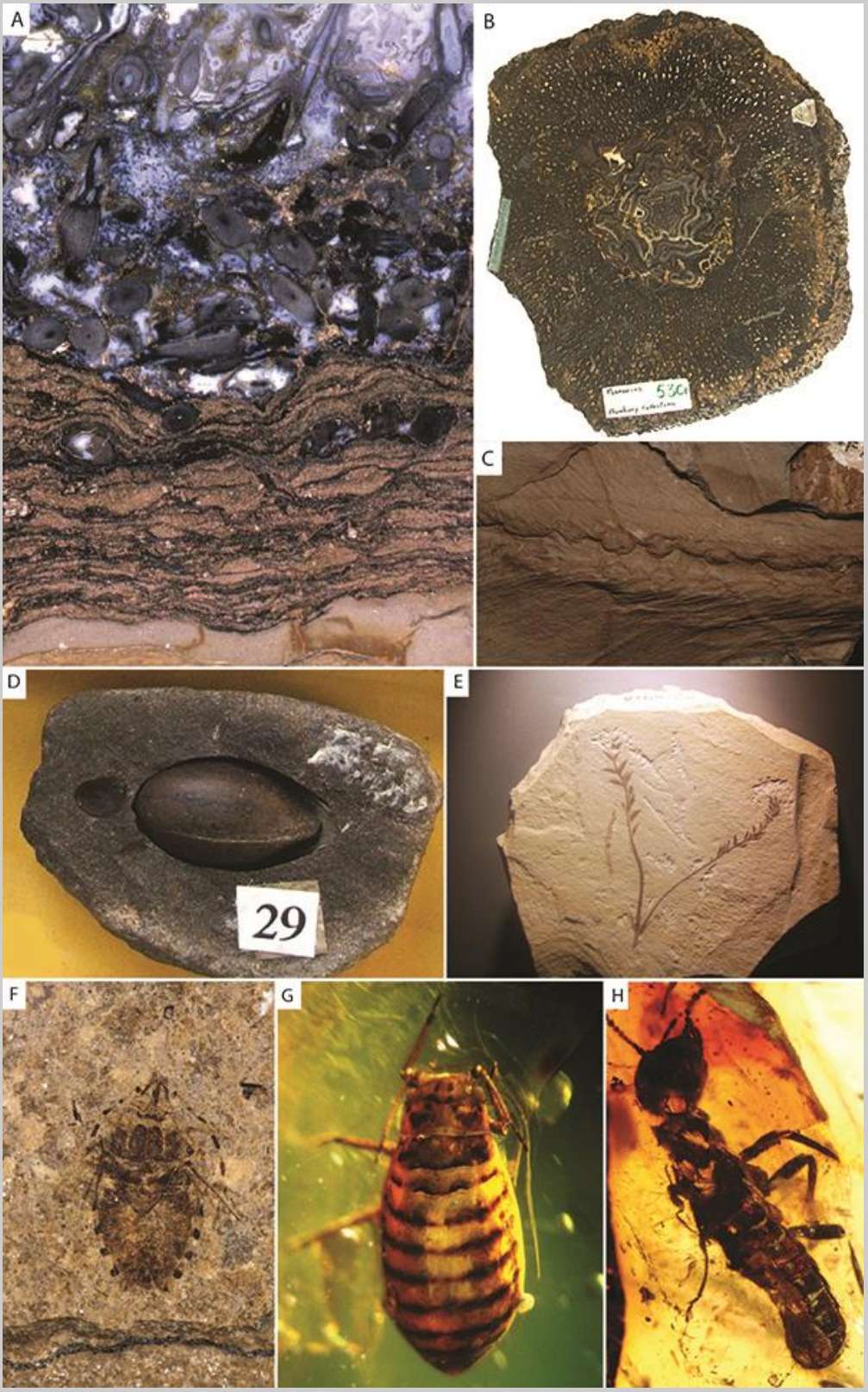

Figure 7 — Range of fossil plants and insects. A. Polished section of Rhynie Chert with plant stems; B. Polished cross-section of Carboniferous *Psaronius* trunk; C. Oviposition scars on a Permian *Glosspoteris* leaf midrib (after McLoughlin 2011); D. Carboniferous *Trigonocarpus* seed; E. *Archaefructus liaoningensis*, an Early Cretaceous angiosperm from China; F. Fossil Hemiptera from the Early Eocene of Denmark (image: Rene Sylvestersen, Wikimedia Commons); G. Aphid in Baltic amber of Eocene age (image: Anders Damgaard, Wikimedia Commons); H. Termite in amber from the Eocene of India (image: Engel, Grimaldi, Nascimbene and Singh, Wikimedia Commons).

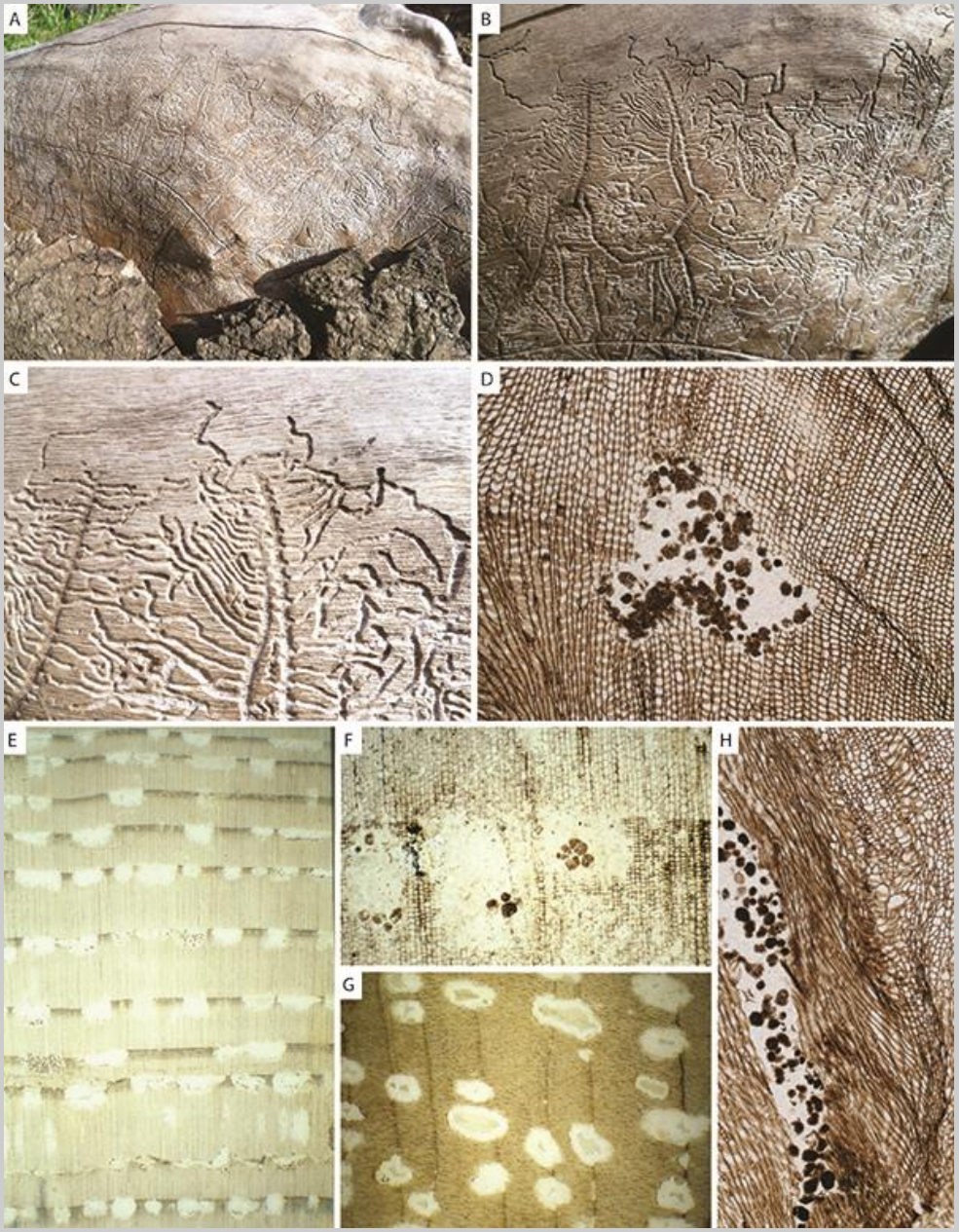

Figure 8 — Modern and fossil examples of wood boring. A–C. Modern bark-beetle (Scolytinae) galleries on a dead oak tree, Worcestershire, UK (photographs: Kristina Grinnall); D–H. Galleries filled with coprolites inside silicified *Australoxylon* stem wood and *Vertebraria* root wood of the *Glossopteris* plant from the Permian of Antarctica (after Slater et al. 2012).

Galling is a form of herbivory in which the insect induces a growth on the plant that acts as a microhabitat and food source, usually for the larvae (Fig. 2G,H and 9C). The adult insect or larva injects chemicals into the plant, which stimulate abnormal cell division. Often, the internal tissues of a gall become enriched with starch and other nutrients, which feed the growing insect. The gall protects the insect from predation. Galls take many forms, and can be recognized in fossils as swollen outgrowths on the surface or around the base of a leaf. Figure 2G shows an image of a parasitic wasp using its ovipositor — a long, piercing, egg-laying tube — to deposit eggs inside the larvae of another insect that has already developed inside a gall on the underside of an oak leaf. Hence, this demonstrates multiple layers of arthropod/plant interaction.

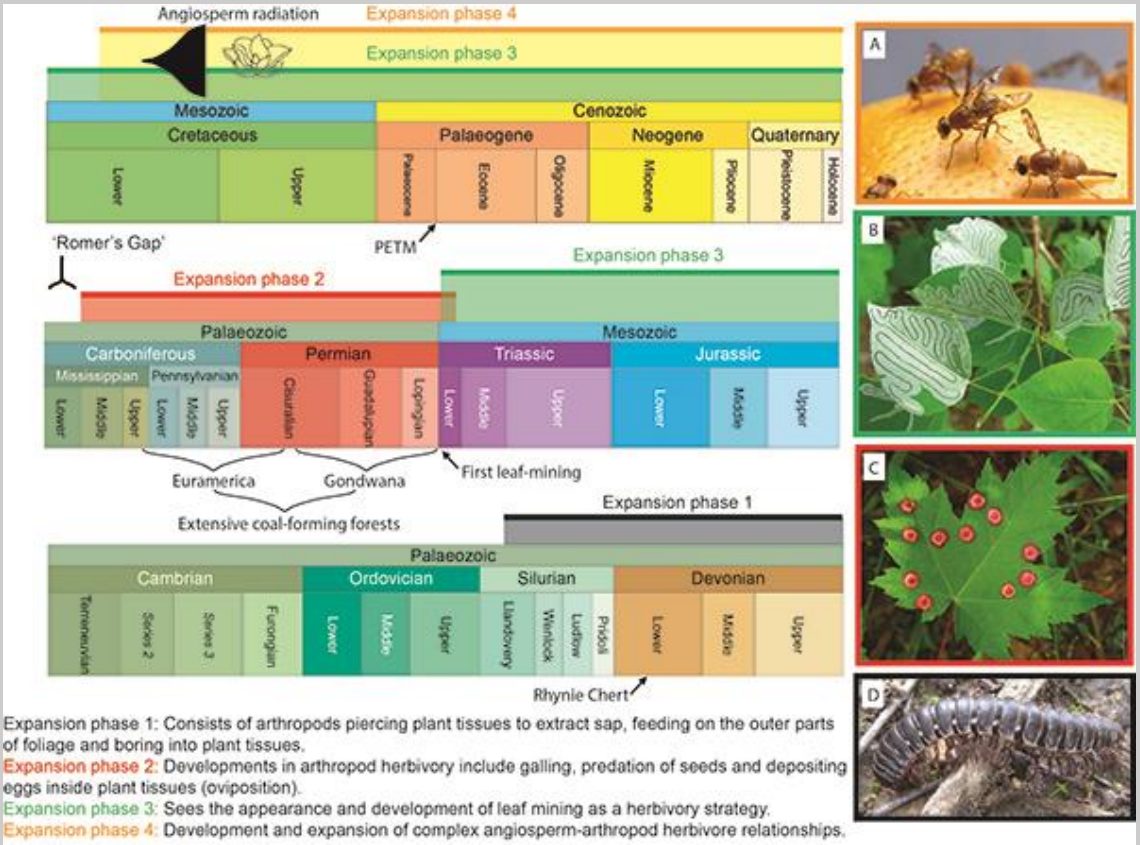

Figure 9 — The four phases of plant–arthropod-herbivore expansion in the fossil record identified by Conrad Labandeira (Labandeira 2006). 'Romer's Gap' is a period in the early Carboniferous identified by the palaeontologist Alfred Romer, from which very few fossil tetrapod or arthropod fossils are known. It may represent an interval of low atmospheric oxygen concentrations. A. Image of Mexican fruit flies feeding; B. Leaf-mining trails on *Populus tremuloides* leaves from British Columbia, Canada (photograph: Jason Hollinger, Wikimedia Commons); C. Leaf galls or petiole galls produced by mites on *Acer rubrum* (photograph: Jason Hollinger, Wikimedia Commons); D. Millipede from Mozambique (photograph: Tom Rulkens, Wikimedia Commons).

Endophytic oviposition is the practice of laying eggs inside plants (Fig. 2G). A range of insects use their ovipositor to insert the eggs inside plant tissues, affording them some protection and often depositing them close to a food source. Oviposition scars can be recognized on fossil leaves and stems, sometimes as a series of small holes along the leaf midrib or plant stem (Fig. 7C).

Leaf mining, in which insect larvae tunnel through leaf tissues (Figs 6F and 9B), first appeared in the earliest Triassic period (250 million to 200 million years ago; Fig. 9). Following endophytic oviposition (described above), the hatched larvae feed on the most nutritious tissues of the leaves between the outer layers of waxy cuticle; this has the advantage of ensuring that they are not exposed to predators. The patterns developed by different leaf miners can be quite distinct, and so leaf mines are readily recognizable in well-preserved compression fossils (Fig. 6F). Some plants have evolved to avoid leaf miners by developing leaf patterns that fool adult insects into thinking that the leaves have already been fed on.

Pollination is a mutually beneficial interaction, in which an animal transports pollen between the reproductive structures of different plants, and is rewarded with nutrition — either consuming a portion of the pollen, or drinking nectar provided by the plant. Pollination may have begun with

arthropods feeding directly on spores (sporivory) or pollen (pollenivory), and accidentally dispersing them. If a proportion of the spores or pollen could survive digestion, or became entrapped in the hairs and carapace of the arthropod, then sporivory and pollenivory may have become beneficial to the plant. Spores and pollen are common components of fossilized arthropod coprolites (Fig. 5D,E), although it is not always clear whether these were consumed passively when the animals fed on dead plant litter and detritus (detritivory), or actively through sporivory or pollenivory. True pollination can be identified in fossils by the shape and structure of fossil insect mouthparts and through the presence of plant structures such as nectaries and flowers.

Geological history of arthropod–plant interactions:

Conrad Labandeira, a palaeontologist specializing in arthropod–plant interactions, described four distinct phases in the historical development of arthropod herbivory (Fig. 9). The first phase consists exclusively of feeding, boring and piercing or sucking on external foliage. The second phase includes the development of oviposition, galling and seed predation. Phase three involves the development of leaf mining in the earliest Triassic. The fourth phase began in the Early Cretaceous and continues to the present, and includes the expansion of species-specific relationships between insect herbivores and their flowering-plant hosts. In all cases, there is a significant lag between the development of new organs/tissues in plants and the first appearance of arthropod damage to them. This means that considerable time was required for arthropods to develop adaptations for exploiting these new plant resources.

Some of the earliest evidence of arthropods interacting with plants comes in the form of coprolites from Silurian (around 443 million to 419 million years) rocks in the Welsh borderlands and Gotland in Sweden. These coprolites contain a variety of spores and other plant fragments, which were probably produced by detritivores living among the earliest terrestrial plant communities. Detritivorous arthropods that are thought to have been present in terrestrial ecosystems at this time include myriapods (such as millipedes) and mites; other modern arthropod detritivores such as terrestrial isopods (woodlice) did not reach the land until much later. Coprolites containing plant spores are particularly common in these deposits; however, this might reflect preservational biases, because the material that makes up the walls of plant spores and pollen is extremely durable and lends itself to fossilization.

Our most complete glimpse into the early world of arthropod–plant interactions comes from a remarkable rock deposit from the Early Devonian period (around 410 million years ago): the Rhynie Chert. This famous site in Aberdeenshire, Scotland, preserves the remains of entire ecosystems of plants, arthropods and other animals, many of which have been exquisitely fossilized in three dimensions, including cellular details of plant tissues. The organisms were living in an environment populated with volcanically charged hot springs, similar to Yellowstone National Park today. When the mineral-rich volcanic waters spilled out from hot pools, they entombed the surrounding plants and animals in silica. Over time, as the sediments were buried, this silica turned to chert, an extremely stable and hard glass-like rock, in which the remains of this ecosystem were preserved (Fig. 7A).

When thin sections of the Rhynie Chert and nearby Windyfield chert are studied under the microscope, evidence of a number of different arthropod–plant interactions can be observed, including a range of coprolites, body fossils of arthropods (sometimes including gut contents) and lesions in the plant stems where the arthropods had pierced into the xylem tissues. The Rhynie Chert also contains some of the

earliest evidence of the interactions between non-arthropod invertebrates and plants, in the form of exquisitely preserved nematode worms infesting the plant *Aglaophyton major*. The palaeoecosystem preserved at Rhynie exhibits several trophic levels and significant numbers of predatory arthropods. This level of complexity could suggest that the terrestrial ecosystem had been developing for a long time before the Early Devonian, but had not been preserved in the fossil record.

By the Carboniferous period, arthropod–plant interactions had become more varied. Our information on Carboniferous arthropod–plant interactions is more detailed than that for other time periods, in part because the fossils are buried in rocks that have long been dug up to extract coal in Europe and North America, and also because of the abundance of coal balls that preserve plant debris with exceptional cellular detail. In addition to this, nodules of the iron-based mineral siderite from sediments of this age contain excellent fossils of many terrestrial arthropods that inhabited lowland forests.

One fossil that has been the subject of much attention is *Psaronius* (Fig. 7B), a tree-sized marattialean fern from the Carboniferous tropics of Europe and North America and Lower Permian rocks of China. Detailed studies of the fossilized tissues of this plant have revealed traces of arthropod damage, as well as coprolites associated with all organs of the tree fern. This indicates that a variety of different arthropods were reliant on this plant. A similar range of interactions has been identified in the fossilized remains of the *Glossopteris* plant from deposits of Permian age (around 299 million to 252 million years ago). *Glossopteris* grew in Permian wetlands of the Southern Hemisphere and was a very different plant to *Psaronius*; despite these differences, a similar guild of herbivores and detritivores was apparently present in both.

Throughout the Mesozoic era (around 252 million to 66 million years ago), arthropod–plant interactions became increasingly sophisticated. The first definitive fossils of leaf-mining appear in sediments from the earliest Triassic. During the Triassic (around 252 million to 201 million years ago) and Jurassic (around 201 million to 145 million years ago) periods, arthropods targeted an ever-expanding range of plants, including the bennettitaleans, ginkgoopsids and cycads. The Jurassic was also a time of radiation in insects, particularly beetles, 'true bugs' and flies. It saw the first occurrence in the fossil record of the Lepidoptera (butterflies and moths), which later became major consumers and pollinators of many plants. Finally, fossil scorpionflies from the Jurassic have mouthparts that indicate that they probably fed on nectar-like substances, and therefore probably acted as pollinators. Some of the earliest plant–insect pollinator relationships may have been developed in this group.

The radiation of angiosperms in the Cretaceous period ranks among the most significant changes ever in the terrestrial biosphere. The complex suite of interactions between angiosperms and their insect pollinators and herbivores generated a hyperdiversity of species that radiated throughout the Cretaceous and into the Cenozoic era (from around 66 million years ago to the present). The rise of angiosperms occurred in tandem with a diversification of specialized pollination agents in insects, and also the origins of the social insects (wasps, ants, bees, termites and some aphids), many of which are known from fossils occurring in amber (Figs 2D and 7F,G,H). Remarkably preserved charcoalified fossils from the Early Cretaceous of Portugal have revealed the structure of some of the earliest flowers; the diversity of such floral structures increased during the Cretaceous (Fig. 7E) and continued to radiate throughout the Cenozoic. Within this geological era, the Paleocene–Eocene boundary was a particularly interesting period for insect–plant interactions. An interval of significant climatic change, the

Palaeocene–Eocene Thermal Maximum 56 million years ago marks the beginning of the Eocene, with multiple lines of evidence (from studies of geochemistry, fossils and sediments) pointing to a period of rapid global warming sparked by an abrupt increase in the concentration of greenhouse gases in the atmosphere. Significantly, plant fossils from the earliest Eocene are distinguished by an increased abundance of instances and types of herbivory-related damage (Fig. 2B). This intensification of herbivory was possibly driven by the increased concentrations of atmospheric carbon dioxide, which reduced the nutritional value of the plant material. This meant that larger volumes of plant tissue had to be consumed to obtain the required nutrition.

Plant adaptations to arthropods:

Throughout history, plants have responded to arthropod herbivores by evolving defences. Among the most widely used are chemical defences such as toxins that are concentrated in the plant tissues or exuded onto the plant surface to poison or otherwise deter herbivores. Plants have even developed complex chemical-based defences that attract predators of the insect herbivores. The evolution of such defences cannot be inferred easily from the fossil record; however, some specific damage types can at least indicate the presence of chemical anti-herbivory defences (Fig. 10). Plants also deter arthropod herbivores by increasing the amount of indigestible materials in their tissues, such as lignin and silica, which can wear down arthropod mandibles.

Mechanical defences can include structures such as thorns, which discourage browsing by mammals or other large herbivores; smaller spines or even hairs can help to deter arthropods (Fig. 6B). Trichomes are small hairs or protrusions that are found on many parts of fossil and living plants, and can function as mechanical defences (Fig. 11C). Sticky substances are secreted from some trichomes, and these can interfere with grazing arthropods' mouthparts and locomotion. In the extreme cases of carnivorous plants such as sundews (Fig. 11D), butterworts and *Roridula*, these adaptations have helped to turn the tables on the arthropods, allowing the plant to trap and feed on the animal.

Some plants use mimicry to deceive would-be herbivores: passion flowers, for example, produce small growths that resemble butterfly eggs to dupe female butterflies into thinking that eggs have already been deposited and the plant would be an unsuitable site for their young. Such structures are potentially identifiable in fossil plants.

Other forms of arthropod–plant interactions:

Plants are not just food sources and hosts for arthropods. They have harnessed insects as their pollination couriers, and many plants are totally reliant on species-specific pollinators for their reproduction. These insects are in turn completely dependent on their plant partners for nutrition. Mimicry is also an important interaction between the two groups; insects often resemble leaves, twigs and other organs of a plant as camouflage to avoid predators (Fig. 11A,B). Conversely, some plants have evolved to resemble insects: for example, bee orchids resemble female bees in colour, shape and scent, tricking male bees to land on them and carry their pollen (Fig. 11E,F). Fossil examples of mimicry include remarkable specimens of Jurassic scorpionflies from China that closely resemble fossilized *Ginkgo* tree leaves in the same deposits, and Jurassic lacewings with wings resembling pinnate leaves.

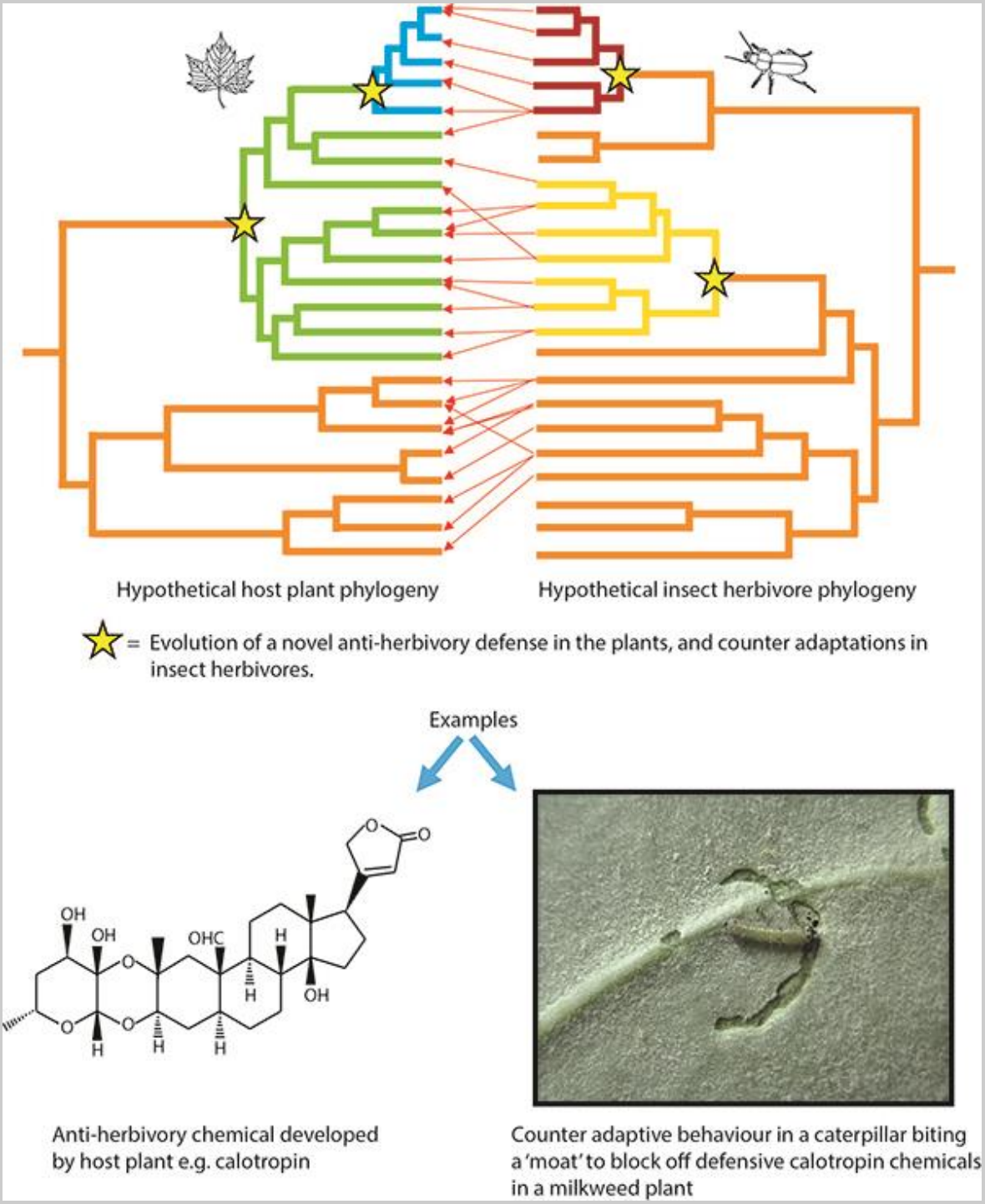

Figure 10 — A hypothetical 'escape and radiate' example of coevolution, with a host-plant evolutionary tree, or phylogeny, on the left and an insect-herbivore phylogeny on the right. Red arrows: insect species feeding on a particular host. Stars: the origin of a novel anti-herbivory defence (in plants) or counteradaptations to overcome these defences (in insects). Different colours represent radiations with the new adaptations. Speciation occurs first in the plants and then in the insect herbivores (based on Ehrlich & Raven 1964 and Futuyma & Agrawal 2009).

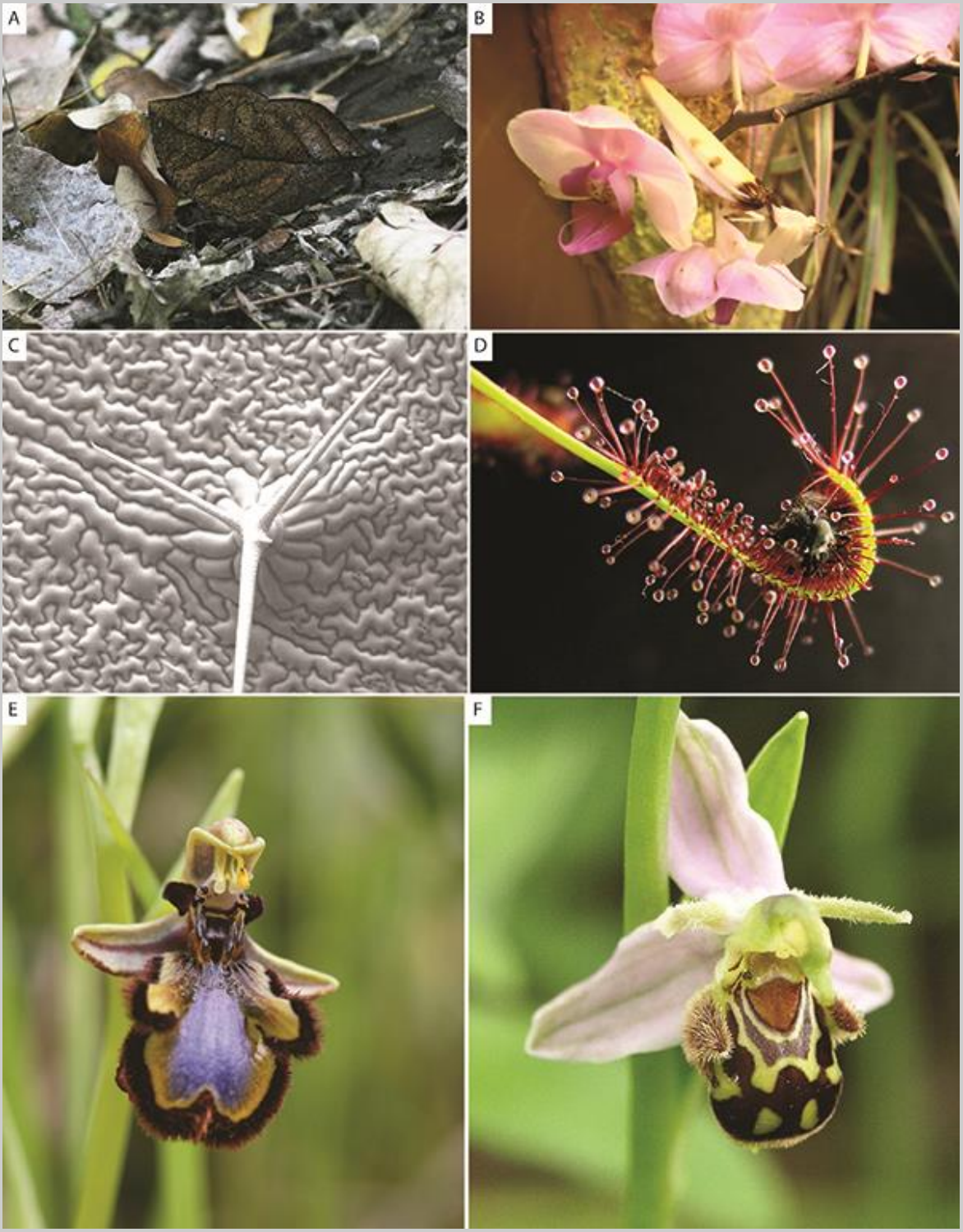

Figure 11 — Other forms of arthropod–plant interactions. A. Orange oak leaf butterfly with wings resembling dead leaves for camouflage from predators (image: Robert Lawton, Wikimedia Commons); B. Flower mantis resembling orchid flowers for camouflage from prey (image: Philipp Psurek, Wikimedia Commons); C. Scanning electron microscope image of a trichome on the surface of *Arabadopsis* plant (image: Emmanuel Boutet, Wikimedia Commons); D. Sundew trapping a fly (image: Noah Elhardt, Wikimedia Commons); E. Mirror orchid from Mallorca, which mimics the appearance and pheromones of female of a particular wasp species, to encourage pollination by males (image: Hans Hillewaert, Wikimedia Commons); F. Bee orchid, mimics the appearance and pheromones of the female bee *Eucera* to encourage pollination by males (image by BerndhH, Wikimedia Commons).

Significance:

The fossil record of arthropod–plant interactions can help us to answer some important questions on the processes that govern the formation of new species. In 1964, the entomologist and demographer Paul R. Ehrlich and the botanist and environmentalist Peter H. Raven proposed a model of coevolution that went some way to explaining the high species diversity seen in herbivorous insects (Fig. 10). The premise of this 'escape and radiate' coevolution model is that as plants evolve novel anti-herbivory defences such as new chemical compounds, the plants are relieved of herbivory pressures, allowing them to 'escape' and radiate as a clade – developing many more species. In time, insect herbivores evolve counter-adaptations to these defences in an arms race that allows the insects to radiate and exploit these new host-plant resources. There is some evidence to support this model, because plant groups that have convergently evolved certain chemical defences often contain more species than groups that have not, and herbivorous clades of insects are usually more diverse than their non-herbivorous sister clades. The fossil record could help us to further investigate such evolutionary processes. If the escape and radiate model is accurate, then after plant radiations in the fossil record we would expect to find a stepwise radiation of herbivorous insects. Fossils can give us data on the first occurrence of certain features, and calibration points for comparing the evolution of plants and insects. If very specific types of feeding damage can be found on certain fossil plants, for example, this could help us to identify when particular feeding strategies evolved. By studying coprolites and arthropod damage, we can reconstruct patterns and changes in herbivory, and identify arthropod functional feeding groups even without body fossils. Coprolites and gut contents might also help palaeontologists to reconstruct ancient food webs, giving us a much richer picture of what ancient ecosystems were like. The fossil record of arthropod–plant interactions is an invaluable resource that can be used to better understand the history of life on land, and how the complex web of modern biodiversity arose.

Suggestions for further reading:

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