Preservation of armoured scale insects on angiosperm leaves from the Eocene of Germany

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Of the 30 extant orders of insects, scale insects (Hemiptera: Coccoidea) have one of the best fossil records among insects that probably extends to the early Mesozoic. Most fossil Coccoidea records are of adult males which have been trapped in amber, whereas adult females are less common, probably because of their sedentary occurrence on plants. Descriptions, photos, and SEM micrographs are presented of over 250 well-preserved scale covers of adult females and nymphal stages of armoured scale insects (Hemiptera: Coccoidea: Diaspididae) which were found on dicotyledonous and monocotyledonous fossil leaves in Middle Eocene deposits from Germany. The structure of these fossil scale covers closely agrees with that of extant Diaspididae. These armoured scale insects belong to the subfamily Aspidiotinae. The age of this insect-plant association—47 to 44 million-year-old—indicates that the Diaspididae have a long history in the Palaearctic region.

Key words: Insecta, Hemiptera, Coccoidea, Diaspididae, plant-insect interactions, herbivory, parthenogenesis, Eocene, Messel, Eckfeld, Germany.

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Introduction

Insects and plants contribute substantially to the enormous biotic diversity on earth (Mitter et al. 1988). Understanding insect-host plant interactions is today a central theme in ecology (Ehrlich and Raven 1964; Thompson and Pellmyr 1991; Winkler and Mitter 2008). While there has been tremendous recent interest and active research in understanding the mechanisms and patterns of plant-insect interactions in modern ecosystems, in terms of co-evolution as one of the major processes driving diversification and speciation (e.g., Farrell and Mitter 1993; Thompson 1989, 1999a, b), their historical background is poorly understood and often limited to cursory, anecdotal snippets predominantly in the palaeobotanical literature. More recently, there have been focused examinations of the fossil record of plant-insect interactions (Scott 1991; Scott et al. 1992; Labandeira 1998, 2002, 2006a, 2007; Labandeira et al. 1994; Wilf et al. 2000, 2001; Currano et al. 2008). These and other studies document the varied ways in which plants and insects interact, and provide evidence for many of these associations in the fossil record. The feeding activities of insects that chew or mine leaves and shoots cause obvious damages. In contrast, structural damage caused by sap-sucking insects often is inconspicuous, as is the withdrawal of cell contents from plant tissues, which usually leaves the cell wall intact. Most sap-sucking insects belong to the Hemiptera. Their mouthparts house long stylets, two mandibular and two maxillary. When feeding, hemipteran insects insert the stylets into tissues of their host plant.

Scale insects (Hemiptera: Sternorrhyncha: Coccoidea) are obligatory plant parasites which are found in all terrestrial zoogeographical regions except Antarctica, being most abundant in tropical and subtropical habitats. Relationships among coccoid families are either largely unknown or alternatively not robustly supported by morphological data (Gullan and Kosztarab 1997; Cook et al. 2002).

The superfamily Coccoidea comprises 28 families that include about 7700 extant and fossil species. Koteja (2000a) summarized the records of fossil scale insects, commenting that these belonged to 6 extant families, namely Coccidae, Diaspididae, Eriococcidae, Margarodidae, Ortheziidae, and Pseudococcidae, as well as 7 additional families that were erected for only fossil species. Most fossil records (63.2%) were of species in the Margarodidae, while the number of records of species in the remaining families was low. The armoured scale insects family Diaspididae is the most diversified in number of extant species, about 2400 species (Ben-Dov and German 2005), while being the poorest in number of recorded fossil taxa (Koteja 2000b). Pampaloni (1902) was the first who recorded and described a fossil diaspidid, namely *Aspidiotus crenulatus*, which was found embedded in late Miocene Disodile rock (which is a form of “brown coal”) at Sicily, Italy. Harris et al. (2007) recorded a second fossil diaspidid (taxon not named, but referred to the subfamily Aspidiotinae) from an early Miocene leaf-bearing diatomite in New Zealand. Koteja (1990, 2000a) indicated that a few inclusions (about 30 specimens) of male Diaspididae occurred in Baltic, Dominican, and Mexican amber, none of which have been described.

Herein we record twelve new fossil Diaspididae, which are assigned to four taxa. They occur in life position, on dicotyledonous and monocotyledonous leaves from middle Eocene oil shales at Messel and Eckfeld in Germany.

Institutional abbreviations.—FIS, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany; SM. B. Me, Senckenberg Museum, botanical Messel collection; NHMM, Naturhistorisches Museum Mainz, Landessammlung für Naturkunde Rheinland-Pfalz, Mainz, Germany; PB, LS, Palaeobotanical Eckfeld collection, Landessammlung für Naturkunde Rheinland-Pfalz.

Attributes of armoured scale insects

Armoured scale insects, as other families of the Coccoidea, constitute some of the most fascinating and unusual organisms among insects, conspicuously differing from typical, commonly encountered insects, particularly in their life cycles (Gullan and Kosztarab 1997).

The adult female has a sac-like body, with functional mouthparts, spiracular system, rudimentary antennae, lacks legs, and possesses various types of wax-secreting glands and pores. The adult male on the other hand is generally a winged insect, with only one pair of wings and well-developed legs, but without mouthparts. It is an ephemeral insect, living from a few hours to one to two days. Generally, in biparental species, it is the adult female which is encountered and collected by entomologists. Besides the distinct morphological differences between female and male, their development also differs. The female develops through two nymphal instars, whereas the adult male develops through two nymphal stages, a prepupa, and a pupa. The most conspicuous feature is that the body of both sexes is covered by a detachable scale cover, from which the vernacular name “armoured scale insects” is derived. The scale cover is formed of waxy secretions in which are embedded the moults of the developing insect. Armoured scale insects are phytophagous, sucking their food resources from host-plant cells.

The taxonomy of extant Diaspididae is based almost entirely on morphological features of the adult female. These features include principally the shape and structure of various body appendages and the cuticular opening of wax glands. The shape, structure or colour of the scale covers is of minor taxonomic significance at the suprageneric level.

More details on the features of armoured scale insects are available in various chapters in Rosen (1990).

Geological setting

The Fossillagerstätten Grube Messel and Eckfeld, deposits in Germany, represent former maar lakes of Middle Eocene age (Geiseltalian) (Franzen 2005), equivalent to the earliest Lutetian Stage (Gradstein et al. 2004). Both localities are Konservat-Lagerstätten that are famous for the high-quality preservation of their fossils (e.g., Schaal and Ziegler 1992; Lutz et al. 1998). Fossil plants and insects are particularly common and diverse in these deposits (e.g., Wilde 2004; Wedmann 2005). The fossils are embedded in highly bituminous, finely laminated claystones (“oil shale”). Wappler et al. (2004) and Wedmann et al. (2007) have recently described two exceptionally well-preserved fossil insects, emphasizing the preservation potential of Messel and Eckfeld. The former “oil-shale” mine of Messel is one of the world’s best known “Fossillagerstätten” and was added in 1995 to the UNESCO list of World Nature Heritage Sites. Recent absolute dating showed that the breccia underlying the Messel sediments have an age of about 47.8±0.2 Myr (Mertz et al. 2004; Mertz and Renne 2005). Similar to the Messel locality, Eckfeld Maar also provided a highly diverse terrestrial flora and fauna (e.g., Lutz et al. 1998; Wappler 2003; Wappler and Engel 2003, 2006; Wappler et al. 2004; Wilde and Frankenhäuser 1998). Argon $^{40/39}$ dating of basalt from the diatreme breccia underlying the lake sediments at Eckfeld established its age of 44.3±0.4 Myr (Mertz et al. 2000).

Material and methods

The examined specimens were preserved by immersing the slabs of stone in glycerine to prevent damage by desiccation (Schaal and Ziegler 1992). All measurements were made using an ocular micrometer and are given in millimetres; structures were measured as preserved. The specimens were examined using a Leica MZ 9.5 Stereomicroscope. Photographs were made with a Leica MZ 16 Stereomicroscope, and either JVC (model KY-F70B) or Nikon Coolpix 4500 digital cameras and processed using image editing software (Adobe CS®). The scale covers were then prepared for both light microscopy (LM) and scanning electron microscopy (SEM) by removing them from the plant material with a scalpel and placing them in 99.5% ethanol, followed by a rinse of water. For LM, scale covers were embedded in synthetic resin for microsectioning, and subsequently mounted on a glass slide. For SEM, fragments were mounted on double-sided adhesive tape on an aluminium SEM stub and gold coated. SEM was performed using a CamScan MV 2300 unit operated at 15kV.

While studying the specimens listed below, we managed to detach the scale covers from the leaf surface on which they were settled. However, no remains of the body of the armoured scale insects were recovered. No modification of leaf surface was observed. The taxonomy of species and genera in extant Diaspididae is mainly based on morphological structures of the cuticle, whereas the shape, structure or colour of the scale covers is of some taxonomic significance at the suprageneric level. Since the only taxonomic feature available from the material studied was the shape and size of the scale cover, we could not assign these fossil Diaspididae to a rank below the two major subfamilies, Aspidiotinae and Diaspidinae. For a detailed description of all the available material, see our supplementary online material (http://app.pan.pl/SOM/app53-Wappler_SOM.pdf).

Systematic palaeontology

Insecta Linnaeus, 1758

Hemiptera Linnaeus, 1758

Sternorrhyncha Amyot and Serville, 1843

Coccoidea Handlirsch, 1903

Diaspididae Maskell, 1878

Aspidiotinae Ferris, 1942

Aspidiotinae gen. et sp. indet. 1

Material.—NHMM PB 2005/140, LS, FIS SM.B.Me 20246; FIS SM.B.Me 19309; NHMM PB 2005/411, LS; FIS SM.B.Me 3958; FIS SM.B.Me 19250.

Description.—The female scale cover of this species is circular, with considerable variation in diameter from 1 mm to 2.6 mm. Concentric rings, representing the scale covers excreted by first and second nymph instars, are clearly discernible (Fig. 1B). The total scale cover is surrounded with a ring (width about 250 μm), which is slightly brighter than the scale cover and elevated from the leaf surface and from scale cover surface (Fig. 1B). This ring appears not to constitute part of the scale cover, but rather belonging to the host plant. We suppose that it is a kind of reaction of the plant to the developing armoured scale insect. We could not speculate as to the colour of the scale cover. Fig. 1E is a SEM of the ventral (inner) surface of the scale cover, showing the pattern of wax secretion during the process of scale cover formation by the adult female. Fig. 1F is a cross section of the scale cover, clearly indicating the moults of nymphal stages that are incorporated within the scale cover.

Comments.—Based on the shape and size of the scale covers of the above listed two fossils, this taxon appears to be related to extant species of genera such as *Aonidiella*, *Chrysomphalus*, and *Melanaspis* (Fig. 1C, D). These genera include many extant species which are pests of various agricultural crops of great economic importance. These species are widely distributed in tropical and subtropical territories of the Nearctic, Neotropical, Ethiopian, Palearctic, Oriental, and Australasian zoogeographical regions.

Aspidiotinae gen. et sp. indet. 2

Material.—NHMM PB 1995/448, LS; NHMM PB 2005/62, LS; NHMM PB 2005/375, LS; NHMM PB 2005/456, LS.

Description.—The female scale cover of this species is circular, about 1 mm in diameter. Concentric rings, representing the first and second nymphal instars, are distinct. The "white cap" part of the scale cover is slightly whitish in hue, while the scales of second instar and adult female are brown (Fig. 1G–I). Scale covers of nymphal stages (Fig. 1J) are circular, about 300 μm in diameter. All records of this species were found on species of coryphoid-like Arecaceae (palms).

Comments.—Extant scale insects (Coccoidea), including extant armoured scale insects (Diaspididae), frequently infest host plants of the family Arecaceae (Ben-Dov and Miller 2007). Among 2384 extant species of Diaspididae, 153 species have been recorded from species of Arecaceae. The armoured scale species *Comstockiella sabalis* (Comstock, 1883), and *Parlatoria blanchardi* Targioni Tozzetti, 1892, have been reported exclusively from species of Arecaceae. The pit-scale family, Asterolecaniidae, includes the genus *Palmaspis*, with 32 species, all of which develop only on palms. The monogeneric family Phoenicococcidae, contains one species, namely, *Phoenicococcus marlatti* Cockerell, 1899, which develops on about 12 species of Arecaceae.

Aspidiotinae gen. et sp. indet. 3

Material.—FIS SM.B.Me 3468. An incomplete preserved pinnate leaf ("feather-leaved") of a lepidocaryoide palm, most probably belonging to the genus *Phoenicites*; found in Messel pit near Darmstadt, Hesse, Germany.

Description.—We observed on lower surface of one leaf about 120 circular scale covers, diameter 0.317–0.439 mm. The smaller size of the scale covers, and the structure of its concentric rings, as compared to Aspidiotinae gen. et sp. indet. 2, suggest that Aspidiotinae gen. et sp. indet. 3, includes the scale covers of nymphal stages that we regard as belonging to a separate species. The crowded population (Fig. 1K) resembles heavy infestations of the extant species *Parlatoria blanchardi* Targioni Tozzetti, 1892 (Fig. 1L), which is a common pest of date palms in North Africa and the Middle East (Ben-Dov and Miller 2007).

Comments.—Palms constitute one of the most familiar and most easily recognized plant families. They are distinguished from most other angiosperms by distinctive leaves, or fronds, and they constitute one of the few monocotyledonous plant families with arborescences (Howard et al. 2001). Palms are essentially tropical plants, of which about 75% of the species occur within rainforest (Dransfield 1978). Additionally, there is a marked dissimilarity between the palm floras of the Old and New World. The lepidocaryoid palms (resembling the Messel specimen) are Old World taxa, except for *Lepidocaryum*, *Mauritia*, and one species of *Raphia* in the New World (Tomlinson 1979).

The Arecaceae, of all identifiable monocotyledons, display the richest fossil records, as revised by Harley (2006). By the late Cretaceous, all major palm fossil categories are present. Therefore it seems unsubstantiated that insect-palm relationships are so little known and reported in the fossil record be-

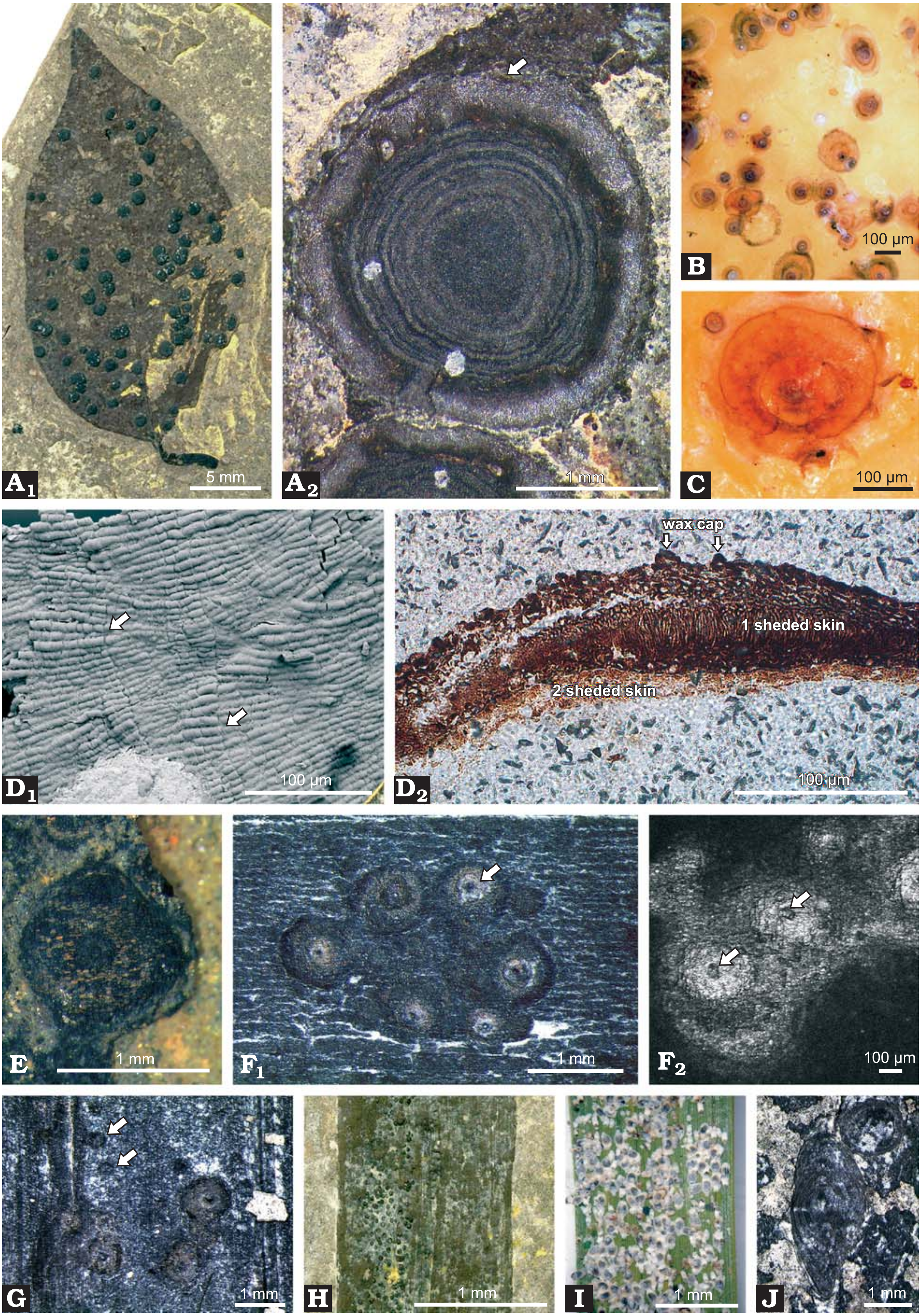
A1
5 mm
A2
1 mm
B
100 µm
C
100 µm
D1
100 µm
wax cap
1 sheded skin
2 sheded skin
D2
100 µm
E
1 mm
F1
1 mm
F2
100 µm
G
1 mm
H
1 mm
I
1 mm
J
1 mm

Table 1. Geological records of Diaspididae (updated from Koteja 1990, 2000a, 2001; Koteja and Ben-Dov 2003; Harris et al. 2007). Abbreviations: * Koteja (2000: 212, 2001: 51) referred to this material but did not name it. Diaspididae are represented by numerous inclusions. ** Koteja (1990: 153) indicated that at least 30 specimens of armoured scale insects were found in Tertiary amber deposits. *** Armoured scale insects occur on dicotyledonous and monocotyledonous leaves. It must be noted that the gender assignment of some of these fossil specimen may be problematic. **** Koteja (1990) noted that although formally unassigned, this fossil definitely belonged to the Diaspididae, very likely resembling a species of *Lepidosaphes*. ***** Putative scale structures preserved on coryphoid Arecaceae from the uppermost Cretaceous (Late Maastrichtian) of the Denver Basin, Colorado, USA (personal communication Conrad C. Labandeira 2007; Labandeira et al. 2007), and convex, circular scales marks on the stem of the equisetalian *Balenosetum candlewaxia* (see Labandeira 2006b: fig. 39) and *Zonulamites elandensis*, on the leaves of the conifer *Heidiphyllum elongatum*, and the seed fern *Dicroidium dubium* from the Triassic of South Africa.

Epoch	Locality	Gender		Fossil type	Taxon
		♂	♀		
Late Miocene	Syracuse province, Sicily, Italy		1	compression	*Aspidiotus crenulatus* (Pampaloni date)
Middle Miocene	Dominican amber, Hispaniola, Dominican Republic	*		inclusion**	not assigned
Middle Miocene	Mexican amber, Chiapas, Mexico	1	1	inclusion**	not assigned
Early Miocene	Foulden Hill, Otago, New Zealand		14	compression	Aspidiotinae gen. et sp. indet.
Middle Eocene	Eckfeld maar, Germany		46***	compression	Aspidiotinae gen. et sp. indet. present contribution
Middle Eocene	Messel maar, Germany		>214***	compression	Aspidiotinae gen. et sp. indet. present contribution
Middle Eocene	Baltic amber, Baltic	2****		inclusion**	not assigned
Late Maastrichtian	Denver Basin, Colorado, USA	*****		compression	not assigned
Late Triassic	Molteno Formation, South Africa	*****		compression	not assigned

cause multitude of different insect families use palms as a reliable source of food (Howard et al. 2001; Labandeira et al. 2007). One reason could be that the insect fauna of about 85% of palm genera is completely unknown (Lepesme 1947) and knowledge of insect-palm relationships is overwhelmingly derived from studies of three economically important palms, oil palm (*Elaeis guineensis*), coconut (*Cocos nucifera*), and date palm (*Phoenix dactylifera*), and not from wild palms (Howard 2001). There may be other reasons particular to palm anatomy or biology, but they are conjectural. These include (1) that the thicker adaxial ("upper") wax layer on most fronds is more difficult for insects to penetrate than equivalent layers in other plants; (2) that for insects using nectar or pollen, most palm species flower only during a limited time interval of the year, restricting the spectrum of available pollinators; (3) in the absence of cambium or bark, palms are not attacked by cambium borers or bark beetles; and (4) roots of palms are not a prime target of attack by arthropods because they are not centres of carbohydrate storage (see Howard 2001).

The majority of fossil palms cannot be determined below family level, due to lack of distinctive morphological variations in foliar organs. This is especially correct regarding the genus *Phoenicites*, to which very likely belong the fossil specimens recorded here. Read and Hickey (1972) redefined the fossil genus *Phoenicites* and suggested that *Phoenicites* should, henceforth, be reserved or applied to non-*Phoenix*-like pinnate leaves.

Aspidiotinae gen. et sp. indet. 4

Material.— NHMN PB 2005/140, LS. An incompletely preserved, dicotyledonous leaf found at Eckfeld Maar near Manderscheid, Eifel Mountains, Germany; middle Eocene (middle Lutetian, ELMA Geiseltalian, MP13, 44.3 ± 0.4 Myr).

← Fig. 1. Scale covers of female and nymphal stages of armoured scale insects on dicotyledon and monocotyledon fossil leaves from the middle Eocene (44–47 Myr) Messel and Eckfeld maar fossil sites. **A**. FIS SM.B.Me 20426; A_1, complete preserved leaf of undetermined dicotyledon (microphyll), with about 70 scale covers; A_2, concentric rings, representing the first and second nymph instars, covers surrounded with a ring (white arrow). **B**. *Aonidiella aurantii* (Maskell, 1878). Mainly known as an important pest of *Citrus*. **C**. Single scale of *Aonidiella aurantii* (Maskell, 1878) on grapefruit. **D**. FIS SM.B. Me 19309; D_1, SEM micrograph of scale cover surface structure revealing secretionary pattern during the process of scale cover formation (black arrows indicating the position of first and second nymph instars); D_2, microsection of a single female scale cover clearly showing the moults of nymph stages incorporated in the scale cover. **E**. NHMM PB 2005-62, LS. Female scale cover in 3D preservation on a palm leaf. **F**. NHMM PB 2005-456, LS. Female scale cover in 3D preservation on a palm leaf; F_1, showing "white-cap" secretion of the first instar (white arrow); F_2, showing "white-cap" secretion of the first instar (white arrow) under laser scanning microscope. **G**. NHMM PB 1995-448, LS. Female scale covers with putative immature stages (white arrows). **H**. FIS SM.B.Me 3468. Crowded population of armoured scale insects of a fossil palm leaf, resembles heavy infestations of the extant species *Parlatoria blanchardi* Targioni Tozzetti, 1892. **I**. Heavy infestations of the extant species *Parlatoria blanchardi* Targioni Tozzetti, 1892 on *Phoenix dactylifera* in Israel. **J**. NHMM PB 2005-140, LS. Elongated scale situated on the main vein, which does not resemble scale covers of any extant species.

Description.—We observed on the leaf surface three oval-elongate scale covers (1.77–2.3 mm wide, 3.1–3.2. mm long) (Fig. 1M). These elongated scale covers were placed on the same leaf next to five circular scale covers (diameter about 1.53 mm), which are here assigned to Aspidiotinae gen. et sp. indet. 2. Unlike the circular scale covers that are distributed sparsely over the leaf, the elongated scale covers are restricted to the main vein and secondary veins. It seems likely that these scale insects fed directly from the leaf veins.

Comments.—The elongated shape of these scale covers does not resemble scale covers of extant species. It is remarkably different from *Lepidosaphes*. The structure and arrangement of concentric rings on the scale cover appear to indicate that they belong to adult females and not males.

Discussion

Taxa in the suborder Sternorrhyncha of the Hemiptera are quite ancient and originated during the transition from the Permian to the Triassic. The Coccoidea (scale insects) as a whole probably stems from the Late Triassic and through the Jurassic. Nevertheless, the origin and early history of Coccoidea has been discussed by various authors, recently by Shcherbakov (2007), albeit their origins are still unknown from the fossil record. Even in the absence of earlier Mesozoic fossil scale insect occurrences, the mere presence of distinct scale damage types during the Late Triassic indicates that the coccoid lineage (not necessarily the modern families) also was present during this period (Table 1). More recent periods of radiation affected the archeococcoids (Othezioidea) and neococcoids (Coccoidea). Interestingly, the radiation of scale insects coincides nicely with the period in which angiosperm diversity increased dramatically, with a trend of basal families ("archaeococcoids") in Cretaceous amber and diverse neococcoids by the Early Eocene (Koteja 1988, 2000a; Grimaldi and Engel 2005). Many fossils of scale insects have been described, most of which appeared in a series of papers by Koteja (1984, 1990, 2000a, b, 2001, 2004), based almost entirely on male coccids fossilised in amber. Female armoured scale insects are not known from Baltic amber (see Koteja 1990, 2000a).

For scale insect impressions, however, the fossil record is at the first glance comparatively sparse, most probably because the female is sedentary and the males are ephemeral and minute, which partly could explain the paucity of scale insect impressions. However, the occurrence of over 250 well-preserved scale covers of adult female and nymphal stages of armoured scale insects on dicotyledonous and monocotyledonous fossil leaves, together with a variety of coccids on palms during the latest Cretaceous in the Denver Basin of Colorado, support the hypothesis that scale insect impressions are much more abundant in the fossil record than previously believed because in most cases the scale insect damage on plants remains unreported (personal communication, Conrad C. Labandeira 2007). The exploration of scale insect damage on plants is imperative, no matter how seemingly futile, and will play an important, albeit somewhat more limited role in understanding scale insect evolution and may eventually prove to be critical for understanding the earliest origin of coccoids.

Derived members of the Aspidiotinae occur during the Middle Eocene, however, indicating that the more basal divergences in the neococcoids must have taken place earlier in the Palaeocene or Latest Cretaceous.

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