FOSSIL INSECT EGGS AND OVIPOSITIONAL DAMAGE ON BENNETTITALEAN LEAF CUTICLES FROM THE CARNIAN (UPPER TRIASSIC) OF AUSTRIA

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ABSTRACT—Two types of evidence for insect ovipositional activity (i.e., actual egg chorions and ovipositional damage) occur on *Nilssoniopteris* (bennettitalean foliage) leaf cuticles from the Carnian of Austria and provide a rare direct insight into insect egg morphology and oviposition in the Late Triassic. The egg chorions have exclusively been found on *N. haidingeri* leaves, where they are attached to the outer surface of the abaxial cuticle; one specimen suggests that the eggs were arranged in circles. It is impossible at present to determine the affinities of the eggs; possible producers may be beetles, dragonflies, sawflies, or other allied basal Hymenoptera. Ovipositional damage occurs on *N. angustior* leaves in the form of lenticular egg impressions surrounded by a narrow, elevated margin. The impressions are visible on the ad- and abaxial cuticle, and coincide when both cuticles are superimposed, which indicates that the eggs producing these impressions were injected into the interior of the leaf. Producers of eggs that may have caused these damages are perhaps dragonflies or damselflies. The restricted occurrence of the two types of ovipositional activity suggests that some kind of host specificity existed, perhaps related to specific preferences in larval diet.

INTRODUCTION

P LANTS AND animals today display a wide variety of more or less intimate direct interactions. For example, plants serve as habitat, diet, shelter, and mating arenas for animals, and as hosts for eggs, larvae, and pupae, especially of arthropods. On the other hand, insects and several other groups of animals such as bats and birds are essential in the reproductive biology and dispersal of many plants. With this recognition of the biological and ecological significance of extant plant/animal interactions, a sound understanding of the evolutionary history of these interactions, including the roles they have played in biological and ecological processes in the past, is critical in documenting the complexity and evolution of both ancient and modern ecosystems. Moreover, fossilized plant/animal interactions may offer insights into the behavior of ancient animals and provide information on the autecology of ancient plants (e.g., Krings et al., 2003).

A wealth of information about plant/insect interactions in the fossil record has been gathered to date. However, most of the reports focus on insect damage on plants (e.g., chew marks, stylet probes, and wood borings; e.g., Labandeira, 1997, 2005), which is often easily recognizable in compression specimens or permineralizations, and on feeding specializations indicated by external insect structure such as mouthpart morphology (e.g., Labandeira and Beall, 1990). Documentation of aspects relative to the reproductive biology of ancient insects is comparatively rare. This is particularly true of egg morphology and ovipositional behavior. Although fossil insect eggs and egg remains (e.g., egg impressions or scars on plant stems and leaves) have occasionally been recorded (e.g., Grauvogel-Stamm and Kelber, 1996; Van Konijnenburg-van Cittert and Schmeißner, 1999; Béthoux et al., 2004), these structures are not normally preserved well enough to permit detailed evaluation. Ovipositional behavior is generally difficult to reconstruct based on fossils.

The Mesozoic fossil record has yielded numerous examples of plant/animal interactions in the form of damage on plants caused by phytophagous or polleniphagous insects (e.g., Kelber and Geyer, 1989; Grauvogel-Stamm and Kelber, 1996; Ash, 1997, 1999, 2005) Labandeira, 1997, 2002; Scott et al., 2004). Moreover, distinctive lenticular scars on Mesozoic plant fossils caused by ovipositor insertion of insect eggs (ovipositional scars) have been described from various stems of *Equisetites* Sternberg, 1833 and *Calamites* Brongniart, 1828; the eggs are generally interpreted as having been produced by Protodonata or Odonata (Kelber and Geyer, 1989; Grauvogel-Stamm and Kelber, 1996; Béthoux et al.,

2004; Ash, 2005). Similar ovipositional scars have been recorded for *Taeniopteris* Brongniart, 1828 leaves from the Ladinian of France and Lower Keuper of Germany, and interpreted as caused by Odonata (Grauvogel-Stamm and Kelber, 1996). *Schmeissneria* (Presl, 1833) Kirchner and Van Konijnenburg-van Cittert, 1994 leaves from the Jurassic of Germany display surface structures that have been interpreted as Odonata egg remains (Van Konijnenburg-van Cittert and Schmeißner, 1999). These latter two records are based on impression fossils and hence do not permit detailed analysis. As a result, insect egg morphology and ovipositional behavior in the Mesozoic remains poorly understood.

In this paper we provide a detailed evaluation and photographic documentation of insect eggs and ovipositional damage in the form of egg impressions on Late Triassic *Nilssoniopteris* Nathorst, 1909 emend. Pott, Krings, and Kerp, 2007 (Bennettitales) leaf cuticles from the Carnian of Lunz in Lower Austria. These fossils represent the first record for actual insect eggs and egg impressions obtained by means of cuticular analysis, and offer rare insights into insect egg morphology, ovipositional behavior, and host responses to oviposition in the Late Triassic. Although insect diversity is believed to have been high during the Late Triassic (Labandeira and Sepkoski, 1993; Scott et al., 2004; Ash, 2005; Béthoux et al., 2005; Grimaldi and Engel, 2005, p. 46) and probably akin to today (Anderson et al., 1998), no fossil insect remains have previously been documented from the Lunz paleoecosystem. Thus, the fossils presented here also represent the first record of insects from this famous Carnian paleoecosystem.

GEOLOGY, MATERIAL, AND METHODS

The fossils containing the actual insect eggs and egg impressions on bennettitalean foliage come from the area around Lunz-am-See in the Northern Calcareous Alps of Lower Austria, approximately 100 km west of Vienna, and were collected in the late 19th and early 20th centuries from several active coal mines (Fig. 1). The Lunz flora represents one of the richest and most diverse Late Triassic floras of the Northern Hemisphere and is one of the earliest Triassic plant assemblages of the Northern Hemisphere dominated by Cycadales and Bennettitales (Dobruskina, 1989, 1998).

The fossils occur in the 'Lunzer Sandstein,' which is part of the Lunz beds. The Lunz Formation (=Lunzer Schichten) consists of sandstones at its base, followed by marine marls gradually grading upwards into terrestrial sands, shales, and coal. The coal-bearing part of the sequence is overlain by marls and displays a sandstone layer at the top. The plant fossils occur in the shales
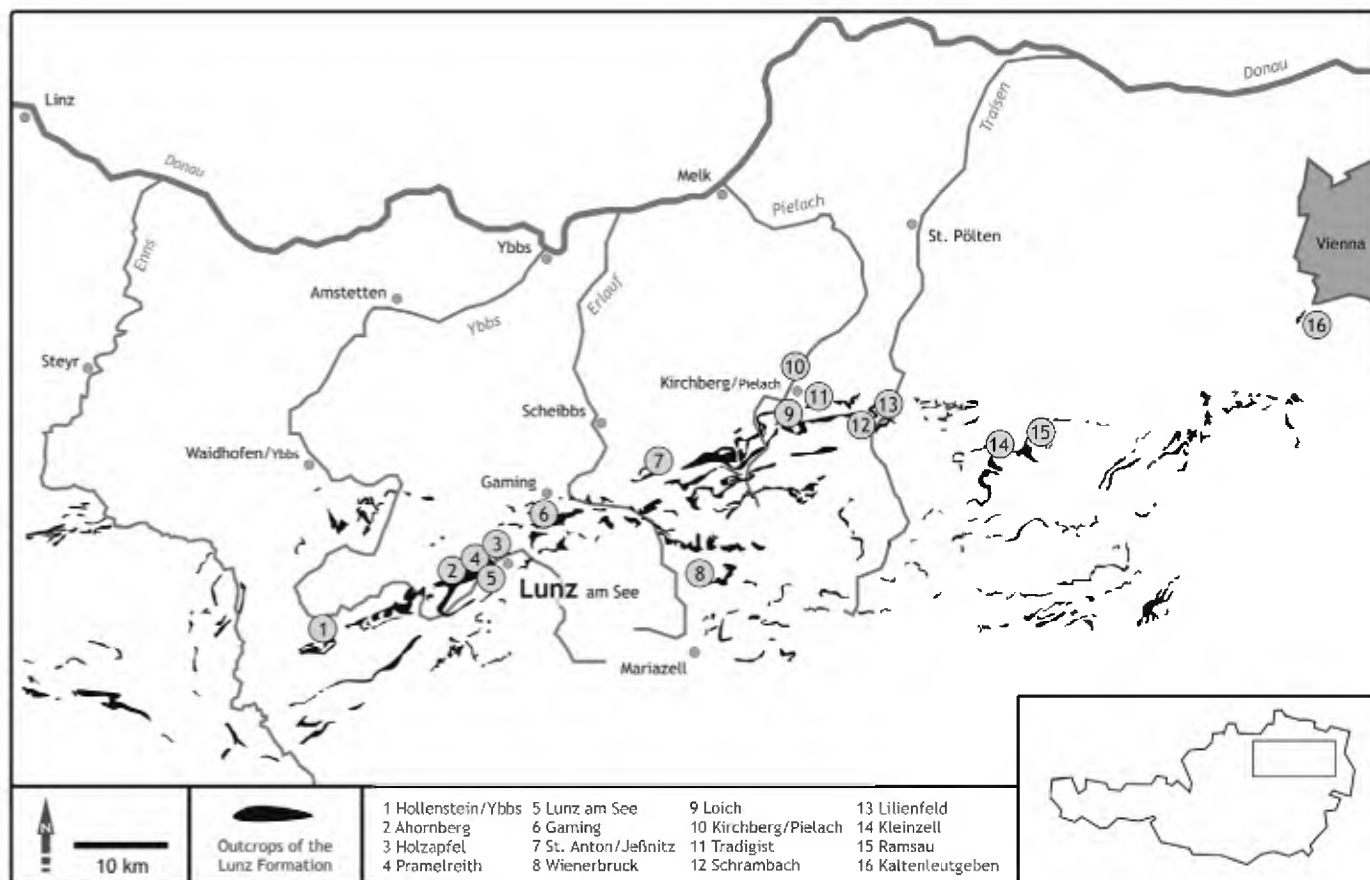
FIGURE *1*—Outcrops and locations from where the Lunz plant fossils have been collected during the 19th and early 20th centuries.

that are associated with the coal beds. Determination of the exact age of the Lunz Formation remains difficult due to the lack of adequate biomarkers such as ammonoids or conodonts. Recent studies of the Hallstatt and Reifling Intraplatform Basins (Hornung and Brandner, 2005) suggest that the Lunz Formation correlates with the upper part of the Reingraben Formation (T. Hornung, personal commun.), and thus is approximately upper Julian (Julian 2/II; Lower Carnian; c. 225 Ma) in age (Gradstein et al., 2004; Hornung, 2006).

The plant fossils from Lunz are usually preserved as compressions, often with excellently preserved cuticles. Cuticles were prepared according to procedures outlined in Kerp (1990), and Kerp and Krings (1999). Rock samples with plant remains are dissolved in hydrofluoric acid (48% HF) in order to remove the sediment. Cuticles are macerated according to standard procedure using Schulze's reagent (35% HNO_3 with a few crystals of $KClO_3$) and 5–10% potassium hydroxide (KOH). Macerated cuticles are washed in distilled water, gently dehydrated in pure glycerin, and finally mounted in permanent glycerin-jelly microscope slides. Slides are stored in the relevant museum collections; accession numbers are indicated in the figure captions.

Hand specimens were photographed with a Nikon D 100 digital camera; in order to increase contrast, cross-polarization (i.e., polarized light sources together with a polarizing filter over the camera lens) was used. Cuticles were analyzed with a Leitz Diaplan microscope and photographed with a Nikon DS-5M digital camera.

RESULTS AND DISCUSSION

The morphogenus *Nilssoniopteris* accommodates foliage in the gymnosperm order Bennettitales, an extinct group of seed plants characterized by cycad-like leaves and complex reproductive structures that was widespread and diverse in the Late Triassic and Jurassic but vanished during the Cretaceous (Kelber, 1998). A detailed description of the macromorphology, cuticles, and epidermal anatomy of the *Nilssoniopteris* species considered here can be found in Pott, Krings, and Kerp (2007). The descriptions given below of the leaf morphology and epidermal anatomy are limited to a brief summary of features significant in the context of insect oviposition.

INSECT CHORIONS ON LEAVES OF *NILSSONIOPTERIS HAIDINGERI* (STUR EX KRASSER, 1909) POTT, KRINGS AND KERP, 2007
Figures 2.1–2.2, 3.1–3.7, 4, 5.1

Leaves.—Leaves of *Nilssoniopteris haidingeri* are up to 60 cm long and 15 cm wide, almost regular broadly oval or oblong to lanceolate in outline, entire-margined or partially pinnate (Fig. 5.1). The lamina is usually coarsely divided into oppositely to sub-oppositely positioned squarish segments that insert laterally to the rachis. Numerous proximally bifurcating parallel veins enter each lamina segment and run straight to the margin. The leaves have robust cuticles. Costal and intercostal fields are distinct on the abaxial, but indistinct on the adaxial side of the leaf. Intercostal fields are characterized by epidermal cells that bear solid papillae.

Chorions.—A total of 15 small, dorsiventrally compressed chorions have been discovered on cuticles of three different *Nilssoniopteris haidingeri* specimens. All chorions display approximately the same size and morphology, which indicates that they were produced by the same kind of insect. In the following description, the micropylar end of the chorions to the leaf surface is called 'proximal tip,' while the opposite represents the distal tip; the surfaces of the chorions are termed ventral (i.e., the side oriented
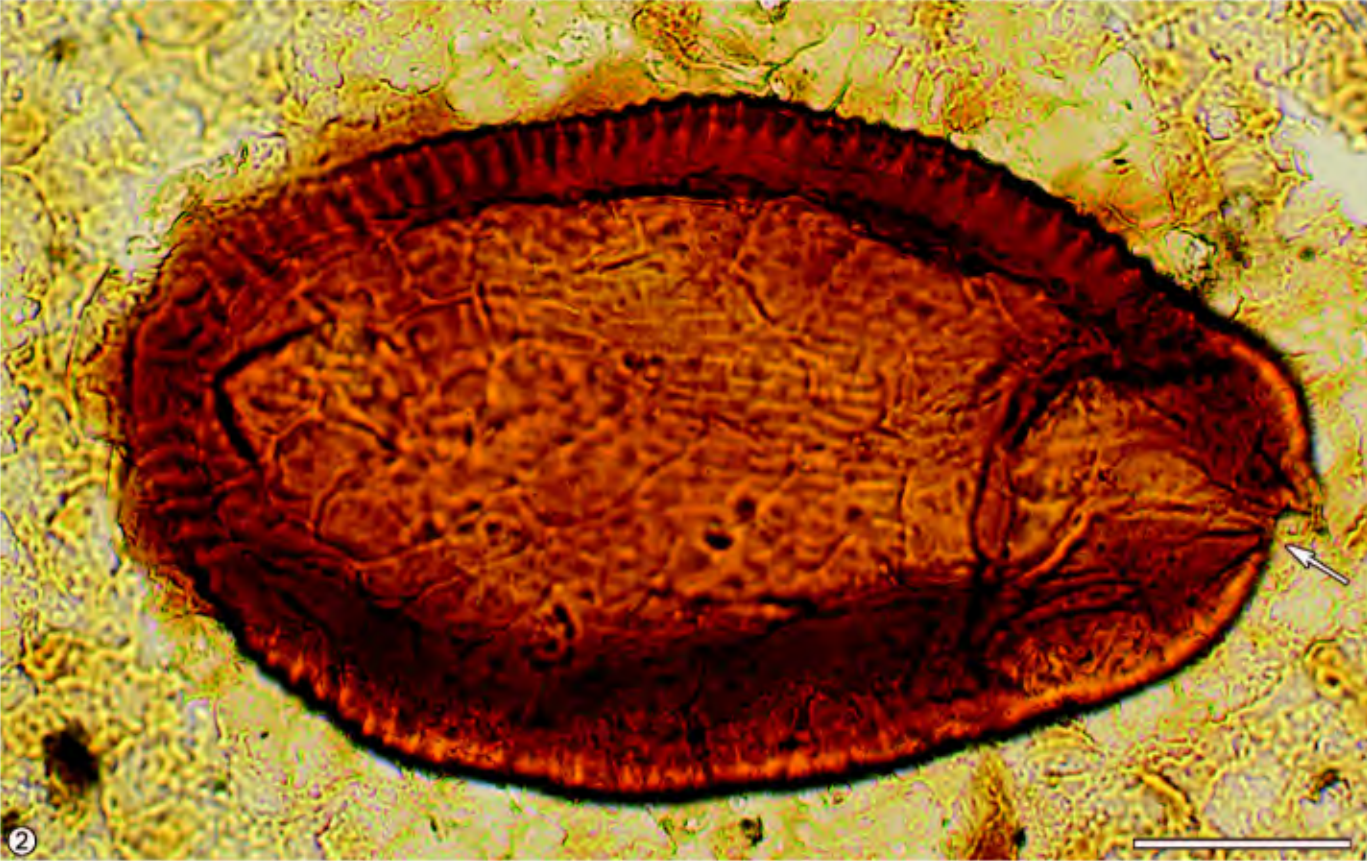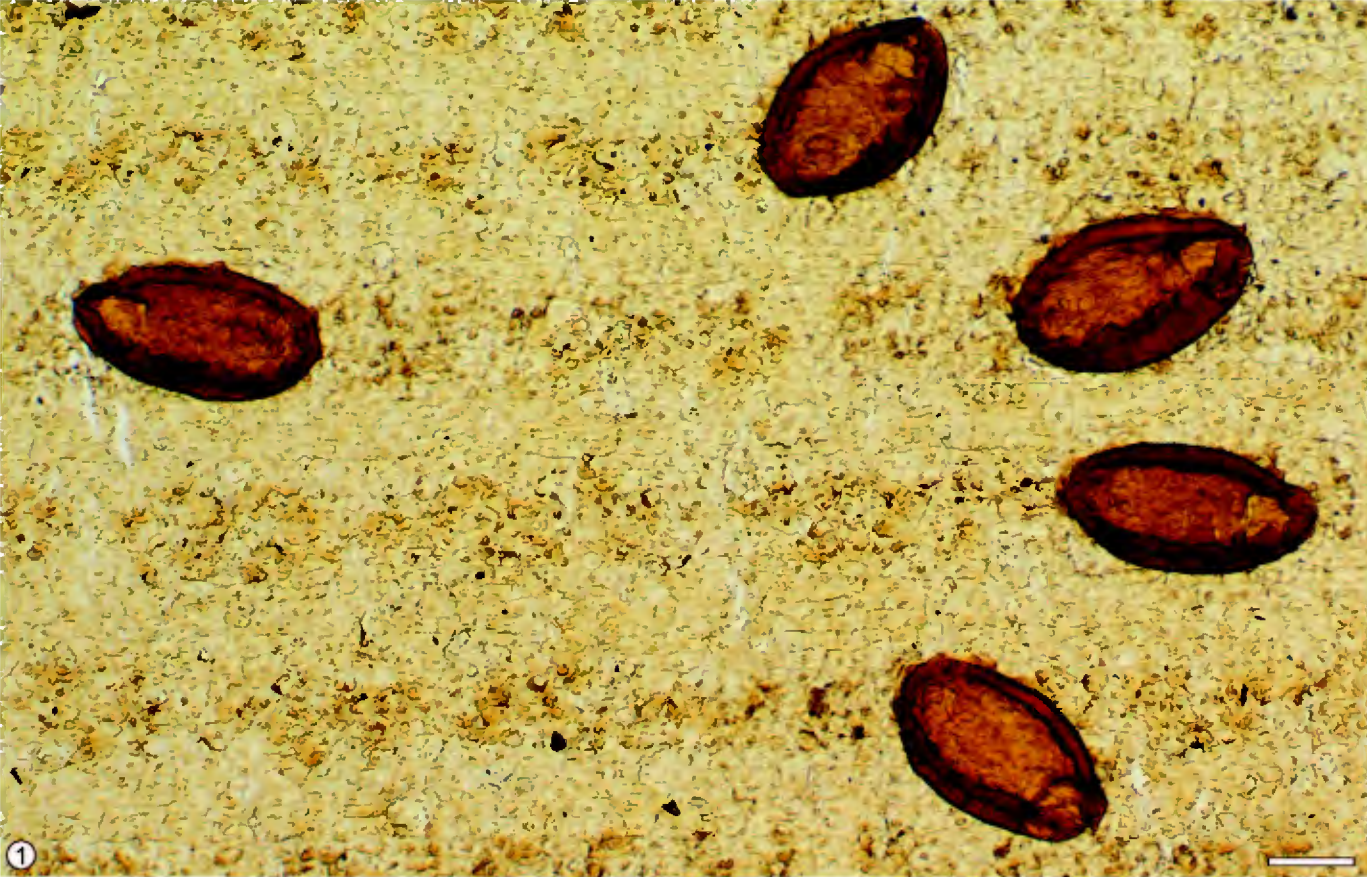
toward the leaf surface) and dorsal. The chorions are oval in outline, slightly compressed dorsiventrally, between 280 and 310 μm long and 150–180 μm wide (Figs. 2.1–2.2, 3.1, 3.3). They are attached to the outer surface of the abaxial (lower) cuticle. Eggs attached to the adaxial (upper) leaf surface have not been found to date. The chorions possess a massive lateral rim that is crenulate and characterized by prominent intercalary septae (Figs. 3.5–3.6, 4). Between the individual septae, the lateral rim shows shallow depressions (Figs. 2.2, 3.5–3.6, 4). The dorsal and ventral surfaces of the chorion are less massive (e.g., Fig. 2.2) and marked by distinct longitudinal striae that occur on the inner side of the chorion (Figs. 2.2, 3.1). The ventral side displays a near-rectangular proximal area that is thin-walled and surrounded by a stronger cutinized "wall" (Figs. 3.3, 3.3–3.4, 4). On the opposite dorsal side, the massive lateral rim is proximally interrupted and displays a distinct aperture, which is embraced by two lips formed by the lateral rim (Figs. 2.2, 3.2, 3.4, arrows, 4).

Around the lateral margins of the eggs, a narrow and incomplete ring composed of accumulated cutin occurs on the leaf surface (Figs. 2.2, 3.1, 3.3, 3.5, arrows, 4). Focusing through the objects reveals that, beneath the eggs, the papillae of the normal epidermal cells and stomatal subsidiary cells are either dissolved or the entire space between leaf surface and chorion is filled with cutin or another substance secreted by the leaf (Fig. 3.7).

The spatial distribution of the chorions on the leaf surface is preserved in one of the cuticle preparations: This specimen (Fig. 2.1) suggests that the eggs are arranged in circles of approximately 1.5 mm in diameter; all eggs are oriented with their micropylar tips towards the centre of the circle (Figs. 2.1, 3.1). Arrangement of the eggs does not concur with structural details of the leaf epidermis and cuticle (i.e., no arrangement along the veins); the eggs may occur on costal and intercostal fields (Fig. 2.1).

Comments.—The thin-walled trapezoidal proximal area visible on the ventral side of the chorions is interpreted as the hatching aperture (e.g., Figs. 3.3–3.4, 4). The surrounding "wall" is composed of the remains of the chorion that were folded apart by the hatchling during hatching (Fig. 3.4, arrow). Presence of this feature indicates that the eggs have already hatched and only the chorions are preserved as fossils. The eggs were oriented horizontally on the leaf surface, rather than perpendicularly (i.e., standing upright) based on the fact that massive cutinization occurs around the entire outer margin (Figs. 3.3, 3.4, 3.7, 4) and in the spaces between the eggs and leaf surface. The massive cutinization beneath and around the eggs suggests that the eggs remained on the leaf surface for a longer period of time, and were gradually incorporated into the leaf cuticle. This may reflect a response of the leaf epidermis to the presence of the eggs. Alternatively, adcrustration of additional cuticular materials may have been induced by certain chemicals on the chorion in order to more firmly glue the eggs to the leaf surface during development of the hatch. The massive lateral crenulate flange with intercalary septae, along with the longitudinal striae on the inner surfaces of the dorsal and ventral sides of the chorion, supports the hypothesis that the eggs remained on the leaf for a longer period of time since they indicate that the chorions were relatively robust. Robustness of the chorions could not be explained if hatching of the larvae occurred after only a few days. Moreover, the fact that the chorions are robust strengthens the interpretation that they were deposited onto the outer surface of the leaf (Wesenberg-Lund, 1943, p. 79). The orifice embraced by lips occurring proximally

on the dorsal side (Figs. 3.2, 3.4, 4) may represent a gas-exchange device (aeropyle) for the encapsulated embryo, and/or may form part of the hatching aperture.

Affinities.—Detailed evidence for egg morphology and ovipositional behavior of ancient insects is virtually absent from the fossil record. Moreover, no insect imago or larva has been documented from Lunz to date that could provide insights into insect abundance and diversity in this Late Triassic paleoecosystem. As a result, we are confined in assessing the affinities of the chorions from Lunz to comparisons with extant insect groups for which egg morphology and ovipositional behavior have been documented, along with information about the fossil record of these extant insect groups. Assignment of the chorions to a particular insect family or genus is impossible at present. However, morphology, size, and spatial arrangement on the leaf surface permit speculation about affinities with basal Hymenoptera (i.e., Symphyta) or Coleoptera, two orders of insects that were well established and diverse by the Late Triassic (Rasnitsyn, 1969; Ponomarenko, 1977, 1992; Labandeira and Sepkoski, 1993; Grimalid and Engel, 2005).

During the Late Triassic, four major clades of insects had ovipositors capable of piercing plant tissue, particularly stems and leaves. These were the Odonata, particularly zygopteran damselflies; the Orthoptera such as phytophagous members of the Saltatoria; the basalmost clade of the Hymenoptera, the sawflies of the Tenthredinoidea; and the Coleoptera, especially some early-derived clades of the Polyphaga (Labandeira, 2006). All of these taxa have been recorded for Triassic strata, and thus may have occurred in the habitats, in which *Nilssoniopteris haidingeri* lived.

In the following paragraphs, we discuss each of these four groups and present a hypothesis with regard to the producers of the chorions based on plant damage features, ovipositor structure, and general habitat type frequented by each of the four ovipositor-bearing insect clades.

Several extant species in the basal Hymenoptera (e.g., members of the Tenthredinidae and Pamphilidae), are known to attach their eggs to abaxial leaf surfaces (Hinton, 1981, p. 705). Others, such as the Xyelidae and Tenthredinidae, have laterally compressed ovipositors with sawtooth ridges or rows of cutting denticles that are used to insert eggs endophytically (Burdick, 1961; Labandeira, 2006). The majority of the latter forms inject the eggs into leaves, rachides, and twigs. The Symphyta form the basal grade of the Hymenoptera (Rasnitsyn, 1988, 2000; Schulmeister, 2002, 2003a, 2003b; Grimaldi and Engel, 2005, p. 409). They are primitive phytophages, widespread in cool to temperate regions. The phylogenetically oldest family in the suborder Symphyta, the Xyelidae, still exists today with some 50 species; it represents one of the eight oldest insect families. Xyelidae are abundant in the fossil record; the group can be traced into the Late Triassic (Rasnitsyn, 1969; Carpenter, 1992; Grimaldi and Engel, 2005, p. 409). During the Mesozoic, xyelids apparently were more widely distributed, and occurred in distinctly warmer climates, than seen in the extant species of this family (Grimaldi and Engel, 2005, p. 410). Most extant xyelids liberate their eggs into staminate cones or needles of Pinaceae (Burdick, 1961; Blank et al., 2005), and the larvae subsequently feed on pollen or within buds (Burdick, 1961). It is possible that oviposition in cones is a derived mode, and the earliest forms generally deposited their eggs on leaves. Blank (2002) suggests that the earliest Xyelidae did not exclusively feed on pollen, but they were at best facultatively pollen-iphagous. However, no feeding traces (cf. Ash, 2005) were observed on or in any of the *Nilssoniopteris* leaves from Lunz.

FIGURE 2—Actual eggs on cuticles of leaves of *Nilssoniopteris haidingeri* (Stur ex Krasser, 1909) Pott, Krings et Kerp, 2007 (†Bennettitales). *1,* Large cuticle segment. Note the small oval eggs arranged in a circle. Slide GBA 1909/002/0250/0006 deposited in the Geological Survey of Austria, Vienna (Austria). Scale bar = 100 μm. *2,* Detail of Fig. 2.1, focusing the morphology of the eggs. Note the heavy cutinizations around the lateral margin of the egg and the well-recognizable micropyle (arrow). Scale bar = 50 μm.
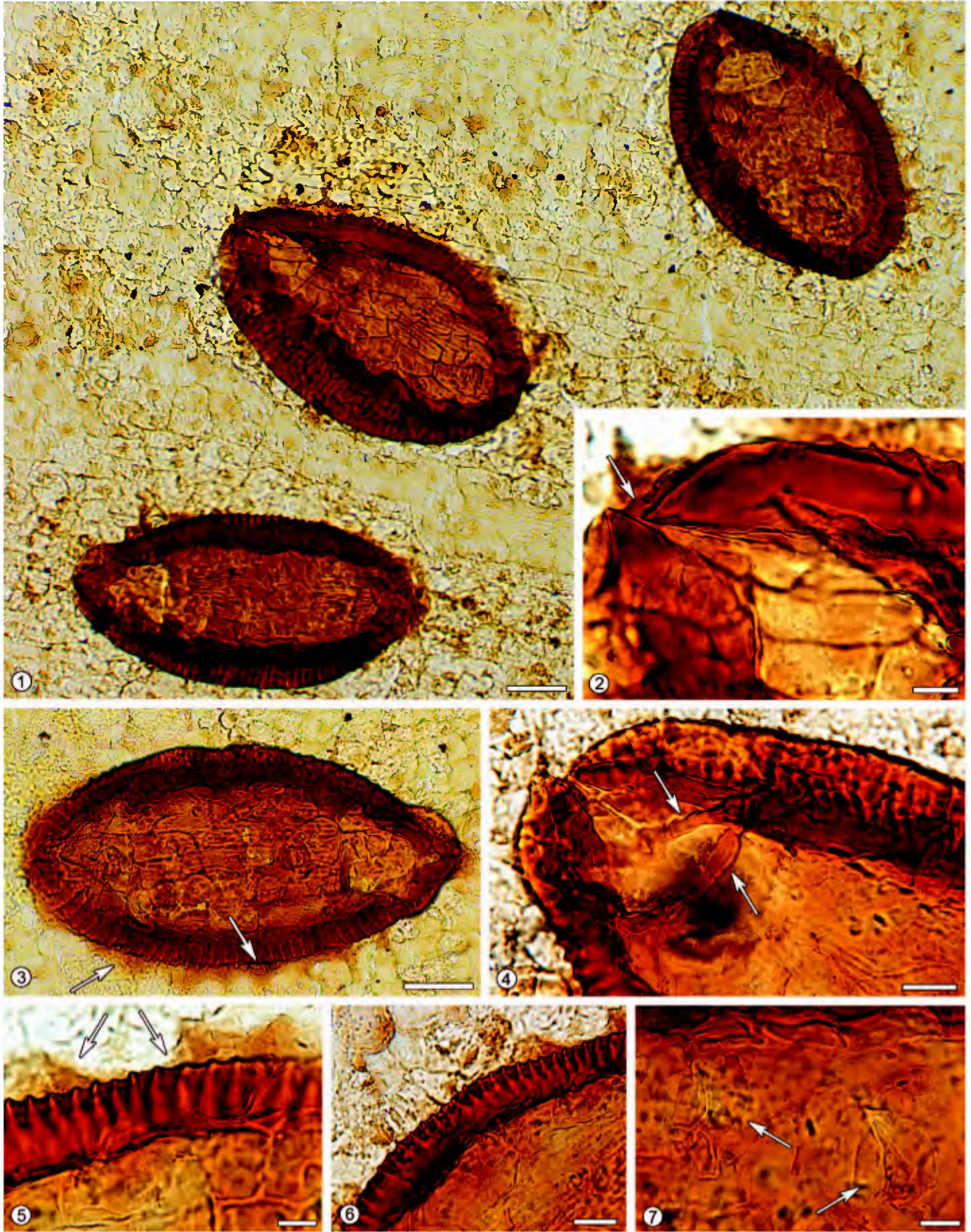
Blank (2002) also suggests that larvae of the earliest Hymenoptera did not feed endobiontically like the larvae of most derived xyelids. Eggs of some extant Xyelidae (e.g., *Pleroneura* Konow, 1897) are similar in size to the chorions from Lunz (Burdick, 1961).

Besides Hymenoptera, the eggs on the *Nilssoniopteris haidingeri* leaf cuticles may also have been produced by Coleoptera (beetles). Coleoptera today represent the largest order of insects. Most beetles liberate their eggs into soil, soil burrows, or wood, or attach the eggs to the abaxial surfaces of leaves (Crowson, 1981, p. 360–362). A few species are known that inject their eggs into living leaf tissues, but these are mostly members of the Phytophaga group (Cerambycidae, Chrysomelidae, Curculionidae and related lineages). Phytophagan beetles are a relatively derived group that is believed to have originated during the earlier Jurassic (Carpenter, 1992; Zherikhin and Gratshev, 1995; Gratshev and Zherikin, 2003). Thus, it is rather unlikely that they produced the eggs on *N. haidingeri*.

The Coleoptera is an ancient insect lineage, depicted by an extensive fossil record that can be traced into the late Paleozoic (Lawrence and Newman, 1982). The major radiation, however, occurred after the Permo-Triassic extinction event (Carpenter, 1992; Labandeira and Sepkoski, 1993; Grimaldi and Engel, 2005, p. 360). Many extinct groups of beetles, most belonging to the Archecoleoptera and Myxophaga, have been described based on well-preserved fossils. Some of these lineages survived the Permian/Triassic boundary and became extinct toward the end of the Jurassic (Crowson, 1981, p. 661–664; Carpenter, 1992; Grimaldi and Engel, 2005, p. 361). A comparison of the material from Lunz with the eggs and ovipositional behavior of these ancient groups of beetles is impossible because only imagines and/or larvae of these forms have been described. On the other hand, a number of extant beetle families can be traced into the Middle Triassic. For example, the earliest representatives of rove beetles (Staphylinoidea, Polyphaga group) have been recorded for the Middle Triassic (Fraser et al., 1996). Rove beetles thrive on the ground and feed on small arthropods or other soil-inhabiting animals. Although egg size and egg morphology in extant *Staphylinus* Linnaeus, 1758 (Szujecki, 1966; Hinton, 1981, p. 117) correspond well with that seen in the fossils, it is rather unlikely that these insects produced the eggs from Lunz because most extant staphylinids liberate their eggs into soil.

The Trachypachidae include six extant species, but the group was more diverse in the Late Triassic to Late Jurassic (Ponomarenko, 1977, 1992; Grimaldi and Engel, 2005, p. 366). Trachypachids are small, carabid-like animals with ancestral adephagan characters. They represent a basal sister group to the Carabidae. Trachypachid beetles live in riparian to dry habits and feed on the ground. Little is known about their biology. Nevertheless, based on the fact that they were present in the Late Triassic, and the extant species live in habitats comparable to that interpreted for the Lunz paleoecosystem, it cannot be excluded that members of this group produced the eggs on *Nilssoniopteris haidingeri*. However, the larvae of extant trachypachids usually live on the ground.

The Cupedidae (reticulated beetles) are related to the Archostemata, a taxon commonly regarded as the basal suborder of the
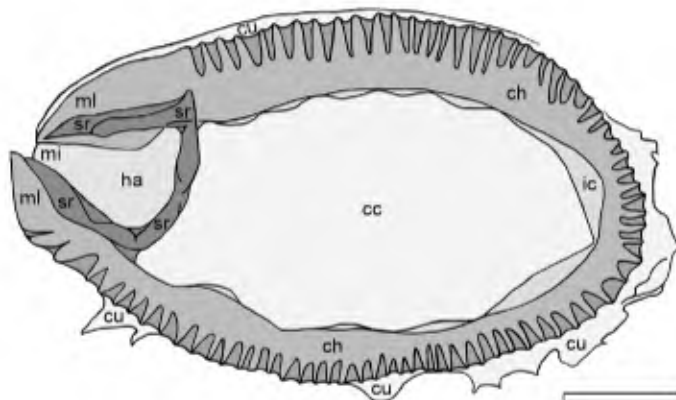

FIGURE 4—Schematic line drawing of an egg based on Figs. 2.1–2.2 and 3.1–3.7. Abbreviations: cc—central chamber; ch—chorion; cu—accumulated cutinizations around the chorion; ha—hatching aperture; ic—inner chorionic layer; mi—micropyle; ml—micropylar lips; sr—shell remains of hatching aperture folded apart during the hatching process; for details see text. Scale bar = 50 μm.

beetles (Crowson, 1962; Grimaldi and Engel, 2005, p. 363–365; Jingjing Tan et al., 2006). The extant Cupedidae represent relicts of a once diverse lineage. The fossil record indicates that the group was particularly diverse during the Late Triassic to Early Cretaceous (Carpenter, 1992). Today the reticulated beetles include some 30 species in nine genera. Larvae are wood-borers that typically live in moderately firm and dry, fungus-infested woods; adults live beneath the bark of trees or on leaves. Extant reticulated beetles occur in forests and woodland; they can be found in rainforest as well as arid grassland and open woodland ecosystems. The eggs of extant reticulated beetles (Crowson, 1962) closely resemble the fossils from Lunz with regard to size and surface structures. Unfortunately, Hinton (1981, p. 649 ff.), in his fundamental work on the biology of insect eggs, does not detail the morphology of either Cupedidae or Trachypachidae eggs.

It has variously been suggested that cupedid beetles played a major role in the reproductive biology (i.e., as pollinators) of the Bennettitales (Crowson, 1981, p. 600 and 665; Lawrence and Newton, 1982), because the diversity pattern through time of the Cupedidae seems parallel to that seen in the Bennettitales (cf. Sitte et al., 1998; Grimaldi and Engel, 2005, p. 361). Moreover, the morphology of certain flower-like bennettitalean reproductive structures (e.g., Wieland, 1916; Delevoryas, 1968; Rothwell and Stockey, 2002; Stockey and Rothwell, 2003) strongly suggests insect rather than wind pollination (Stockey and Rothwell, 2003). Interactions between bennettitaleans and cupedids were perhaps not restricted to pollination. Rather, the beetles may also have benefited from other parts of the plants (i.e., wood, leaves). This hypothesis is supported by the fact that Jurassic representatives of cupedid beetles have been shown to have lived in the wood of certain Bennettitales (Ponomarenko, 2003).

Other possible producers of the eggs include dragonflies. Most modern odonatan taxa, particularly zygopterans such as the Coenagrionidae, insert eggs into plant tissue with laterally compressed

FIGURE 3—Actual eggs on cuticles of leaves of *Nilssoniopteris haidingeri* (Stur ex Krasser, 1909) Pott, Krings et Kerp, 2007 (†Bennettitales). *1*, Detail of Fig. 2.1, focusing on some of the eggs. Scale bar = 50 μm. *2*, Close up of hatching aperture and micropyle (arrow) embraced by two lips. Slide GBA 1909/002/0250/0006 deposited in the Geological Survey of Austria, Vienna (Austria). Scale bar = 10 μm. *3*, Details of Fig. 2.1, showing the morphology of the eggs. Note heavy cutinizations around the lateral margin of the eggs (arrow). Scale bar = 50 μm. *4*, Close up of hatching aperture with putative shell remains folded apart by the hatching embryo (arrow). Slide GBA 1909/002/0250/0006 deposited in the Geological Survey of Austria, Vienna (Austria). Scale bar = 20 μm. *5*, Close-up, focusing on the crenulate margin. Arrows indicate heavy cutinizations around the margins of the chorion. Slide GBA 1909/002/0250/0006 deposited in the Geological Survey of Austria, Vienna (Austria). Scale bar = 10 μm. *6*, Structure of crenulate margin, overview. Slide GBA 1909/002/0250/0006 deposited in the Geological Survey of Austria, Vienna (Austria). Scale bar = 50 μm. *7*, Two stomata (arrows) that occur in the leaf epidermis beneath one of the eggs. Slide GBA 1909/002/0250/0006 deposited in the Geological Survey of Austria, Vienna (Austria). Scale bar = 10 μm.
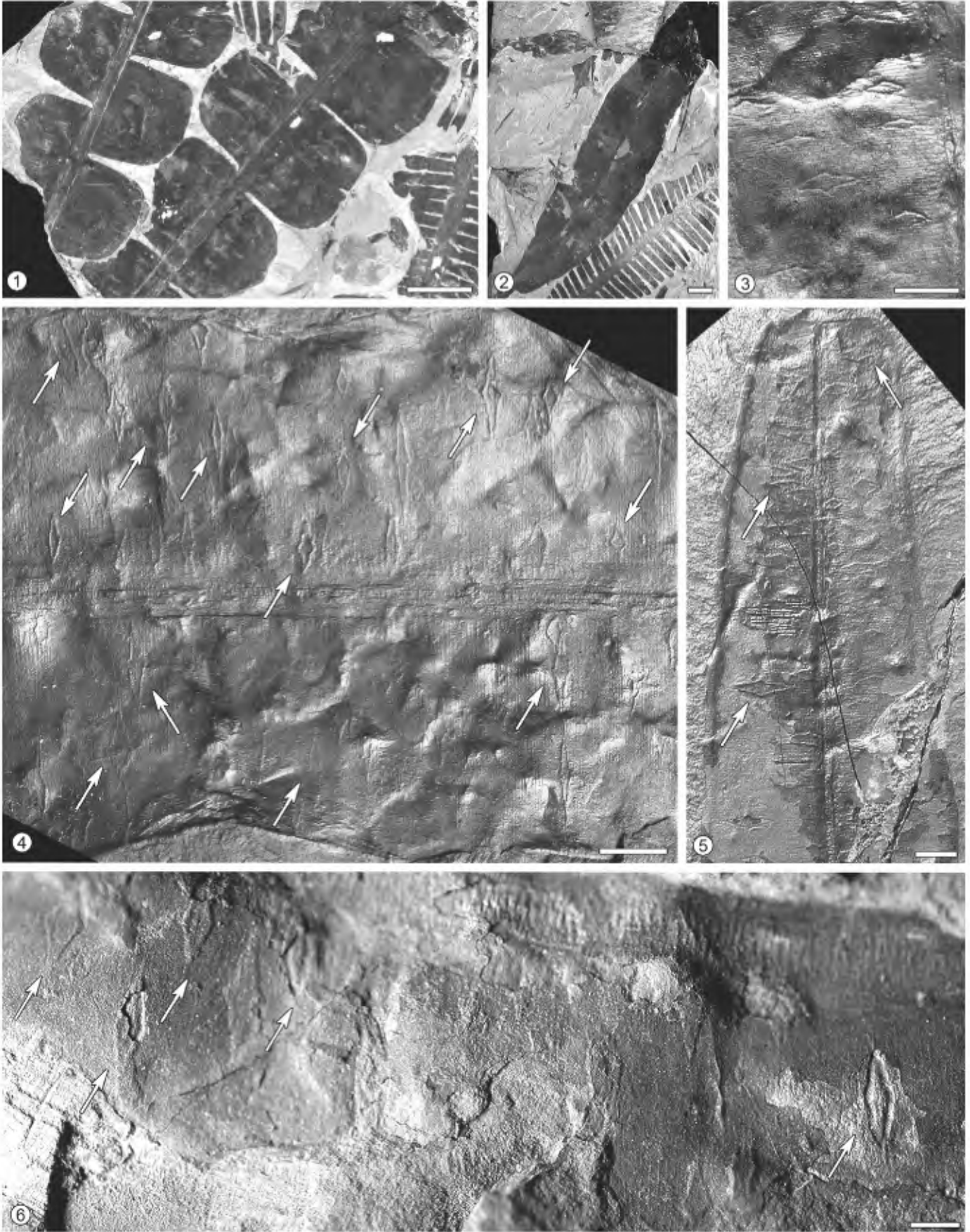
sawtooth ovipositors that superficially resemble that of tenthre-dinids (Labandeira, 2006). The eggs are inserted either completely into plant tissue, foliar or stem, or partially with about half of the egg emergent. A few groups in the Anisoptera, however, attach their eggs to plant surfaces. Eggs partially inserted or attached to surfaces usually leave characteristic ellipsoidal to ovoidal marks surrounded by callus or other scar material, with disorganized tissue within, often appearing as a shallow crater (Labandeira, 2002). The shape and general appearance of the chorions is similar to that of exophytic Odonata. Endophytic eggs are typically more elongate (roughly four times longer than wide) and often slightly curved. The chorion from Lunz appear to have only a single terminal micropyle, assuming the dorsal structure alluded to is in fact an aeropyle or related to the hatching process; its position is certainly very different from the micropyle in modern odonatan eggs. In all extant Odonata, the eggs have at least two terminal or subterminal micropyles, and the more plesiotypic taxa have numerous micropyles (e.g., Sahlén, 1994, 1995). Hatching usually involves complete or nearly complete separation of a terminal 'cap,' not a longitudinal split. No odonatan eggs have been described that have a lateral crenulate flange as seen in the chorions from Lunz. Finally, arrangement of the eggs in a partial circle (Fig. 2) is not typical of the modern Odonata species laying eggs externally on leaves; these are most often deposited in irregular masses (Corbet, 2004, p. 36). Eggs inserted into plant tissue usually are much larger (i.e., 1.5 to 2.0 mm long) than the eggs from Lunz, but eggs produced by species that deposit onto plant surfaces typically are only about 0.5 mm long (Schiemenz, 1957), and thus similar in size with the eggs from Lunz. In addition, the arrangement of the eggs in circles adds support to the hypothesis that dragonflies produced the eggs (Wesenberg-Lund, 1943, p. 70–71). Some, but not all, endophytic species, including some Lestidae (Matushkina and Gorb, 2000) place their eggs in a radial pattern, but neither the morphology nor position on the leaf suggests that the eggs from Lunz were endophytic.

Chorion size, morphology, and ovipositional marks surrounded by callus or other scar material with disorganized tissue, along with the insect groups present during the Late Triassic, it is possible to speculate that a cupedid or related beetle most likely produced the chorions on *Nilssoniopteris haidingeri*.

EGG IMPRESSIONS ON LEAVES OF *NILSSONIOPTERIS ANGUSTIOR* (STUR EX KRASSER, 1909) POTT, KRINGS AND KERP, 2007
Figures 5.2–5.6, 6.1–6.8

Leaves.—Leaves of *Nilssoniopteris angustior* (Fig. 5.2) are oblong to lanceolate in outline, up to 30 cm long and 5 cm wide. The lamina is usually entire-margined and inserts laterally to a prominent rachis. Numerous basally bifurcating parallel veins enter the lamina and run straight to the margin. The leaves have delicate to massive cuticles; an alternation of stomatiferous and non-stomatiferous areas occurs on the abaxial side. Stomata occur sporadically in adaxial lamina areas close to the midrib. Stomata and subsidiary cells of the abaxial lamina are arranged in rows that alternate with non-stomatiferous bands of cells; however, this alternation is irregular and does not concur with the venation pattern.

Impressions.—Of the 65 specimens at hand of *Nilssoniopteris*

angustior, 22 specimens are marked by one to several regularly rhomboidal impressions (Fig. 5.3–5.6), which are 3–6 mm long and 1–2 mm wide. Impressions may occur on the adaxial (upper) and abaxial (lower) side of the leaf. However, in compressions that expose the adaxial side of the leaf, the impressions are surrounded by a narrow raised margin, and hence clearly demarcated from the surrounding epidermis (Fig. 5.3–5.5), while impressions on the abaxial side lack this feature (Fig. 5.6). The impressions are consistently oriented parallel to the lateral veins and perpendicular to the rachis (Fig. 5.3–5.5). They usually occur near the rachis (Fig. 5.5–5.6), but impressions close to the leaf margin have also been found (Fig. 5.4).

Cuticle preparations of individual impressions and vicinity reveal that the impressions congruently occur on both the adaxial and abaxial side (Fig. 6.1), i.e., ad- and abaxial imprint areas coincide when both cuticles are superimposed. However, ad- and abaxial impressions display characteristic structural differences (Fig. 6.1–6.6), which are especially well recognizable in the mirror-inverted imprint shown in Fig. 6.1 (grey and white arrows). On the adaxial side, the leaf cuticle is distinctly thinner along the margin of the impression, which is also recognizable in the compression specimens (e.g., Fig. 5.4), whereas the central region of the impression area is normally cutinized (Fig. 6.3, 6.5). Cell forms and sizes, as well as spatial arrangement of the epidermal cells, correspond to those seen outside the imprint area, and the individual epidermal cells within the impression area are not unnaturally distorted (Fig. 6.5). Delicateness of the cuticle along the margin of the adaxial impressions often causes tearing of the cuticle (Fig. 6.1, grey arrow). On the other hand, the abaxial imprint area is characterized by a considerably thinner cuticle within the rhomboid (Fig. 6.1, white arrow, 6.2, 6.4). A narrow band consisting of heavily cutinized epidermal cells marks the border line of the impression area (Fig. 6.4, 6.6). Close to this marginal scar, the epidermal cells within the imprint area are distinctly deformed (Fig. 6.6); the general epidermal cell pattern, however, is not affected.

Comments.—The impressions described here are structurally similar to the rhomboidal impressions or lenticular scars documented on *Schmeissneria* leaves from the Lower Jurassic of Germany by Van Konijnenburg-van Cittert and Schmeißner (1999). These authors interpret the impressions as egg impressions. However, detailed analyses of the leaf cuticle and epidermal anatomy within and outside of the imprint area, have not been provided because these fossils are preserved as impressions. Nevertheless, based on the corresponding in basic structure and spatial arrangement between the impressions described here and the structures detailed by Van Konijnenburg-van Cittert and Schmeißner (1999), we interpret the impressions on *Nilssoniopteris angustior* leaves from Lunz as impressions caused by insect eggs. With regard to the lenticular shape, prominent marginal scar and comparatively flat center, and arrangement parallel to venation, the impressions from Lunz are similar to impressions seen on various leaves from the Upper Triassic Molteno Formation (South Africa), and on glossopterid leaves from the Clouston Farm Site (Permian) in South Africa.

The fact that the impressions are visible on both surfaces of

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FIGURE 5—Leaves of *Nilssoniopteris haidingeri* (Stur ex Krasser, 1909) Pott, Krings et Kerp, 2007, and *Nilssoniopteris angustior* (Stur ex Krasser) Pott, Krings et Kerp, 2007 (†Bennettitales). *1, Nilssoniopteris haidingeri*, Specimen NHM 2006B0008/0042; deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 10 mm. *2, Nilssoniopteris angustior*. Specimen NHM 1887/I/0009; deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 10 mm. *3, 4–5*, Rhomboidal impressions on leaves of *Nilssoniopteris angustior*. View from the adaxial side, showing the raised outer margins of the imprint areas. Specimens NHM 1884/0015 (Fig. 5.3), and NHM 1884/0015 (Fig. 5.4), deposited in the Museum of Natural History, Vienna (Austria), and GBA 1909/002/0185 (Fig. 5.5), deposited in the Geological Survey of Austria, Vienna (Austria). Scale bars = 5 mm (Fig. 5.3, 5.4), and 10 mm (Fig. 5.5). *6*, Rhomboidal impressions on *Nilssoniopteris angustior*. View from the abaxial side; carbonaceous material removed. Specimen RUU 17895 deposited in the Laboratory of Palaeobotany and Palynology, Utrecht (The Netherlands). Scale bar = 5 mm.

the leaf, and coincide when both cuticles are superimposed, indicates that the eggs were deposited into the interior leaf tissues. Moreover, one specimen suggests that insertion of the eggs into the leaves occurred from the abaxial side: Several circular injuries, 70–300 μm in diameter, occur in the cuticle close to the impressions (Fig. 6.7–6.8). These injuries may have been caused by an insect ovipositor (cf. Wesenberg-Lund, 1943, figs. 63–65). Each of the injuries is surrounded by heavily cutinized epidermal cells (Fig. 6.8), which likely represent a post-trauma wound response of the leaf (i.e., wound callus formation).

The abnormal shape of the epidermal cells within the abaxial impression area is indicative of mechanical distortion as a result of oviposition or egg growth. Moreover, the plant cuticle within the abaxial impression area became considerably thinner in response to the presence of the eggs in the interior. The mechanisms underlying the alteration of the cuticle thickness cannot be determined. It is possible that certain chemicals exuded from the eggs, or injected during oviposition, have dissolved part of cuticle. This may eventually have facilitated hatching of the naiads or larvae. However, leaf surface openings produced by the escaping larvae, or evidence for larval feeding activity in the interior of the leaves, have not been observed. The heavily cutinized marginal scar, which occurs around the abaxial impression areas (e.g., Fig. 6.4) may represent a form of defense reaction of the plant, or was produced by the plant to protect and stabilize the epidermis in this area of the leaf (Peeters, 2002).

Affinities.—Van Konijnenburg-van Cittert and Schmeißner (1999) attribute the egg impressions on *Schmeissneria* leaves from the Lower Jurassic of Germany and on leaves of various plants from the Carnian of South Africa, respectively, to the Odonata (dragonflies and damselflies). This is based primarily on the characteristic distribution pattern and macroscopic appearance of the structures. However, since the Triassic and Jurassic impressions are larger (i.e., 0.8 × 3 mm in diam.) than those caused by extant members in the Odonata, they are interpreted as having been caused by representatives in this group of insects that were larger than the extant species. The egg impressions from Lunz correspond well to those described by Van Konijnenburg-van Cittert and Schmeißner (1999).

The impressions from Lunz are up to 5 times larger than those described by Van Konijnenburg-van Cittert and Schmeißner (1999). Taking this into account, it is likely that they were produced by still larger members in the Odonata. Two suborders of the Odonata are known from the Triassic: the Archizygoptera, which survived the Permian/Triassic boundary, and the Triassolestoidea (Anisozygoptera), which first appeared in the Late Triassic (Carpenter, 1992). Both groups are extinct today. The latter group is related to the extant damselflies and characterized by a transversely elongate head and absence of epiprocts in adults (Grimaldi and Engel, 2005, p. 184). Extant damselflies inject the eggs into leaves of aquatic plants or plants overarching inshore waters

(Wesenberg-Lund, 1943, p. 70–71; Hinton, 1981, p. 486 ff.). Several species in the Odonata (e.g., emerald damselflies of the genus *Lestes* Leach, 1815) exclusively inject the eggs into plants growing above or outside the water (e.g., *Alisma* Linnaeus 1753 species) (Wesenberg-Lund, 1913). After hatching, the naiads drop into the water. Eggs of extant Odonata are considerably smaller than the eggs outlined by the impressions on *N. angustior* from Lunz. Nevertheless, the mode of oviposition displayed by extant Odonata, along with the typical spatial arrangement of the eggs, may suggest that the egg impressions from Lunz have been caused by eggs belonging to Odonata (Schiemenz, 1957; Wesenberg-Lund, 1943, p. 70–71; Hinton, 1981, p. 486 ff.; Hellmund and Hellmund, 1996; Corbet, 2004, p. 21–22; Van Konijnenburg-van Cittert and Schmeissner, 1999). However, it cannot be ruled out that the damages have other origins, but pupae or mining is less likely because evidence for mines or other external damage is lacking in the hand specimens as well as in the cuticles.

These egg impressions provide additional information regarding the ecology of the plants producing *Nilssoniopteris angustior* foliage: the hatching naiads of dragonflies have to reach water immediately to complete development, which implies that these plants have grown near inshore waters, perhaps with branches or leaves overhanging the water surface.

DISCUSSION AND CONCLUSIONS

Insect eggs and/or egg impressions have variously been described from the Mesozoic fossil record. However, evidence based on cuticular analysis has not been produced to date. The material presented here provides the first detailed documentation of fossil insect eggs and egg impressions based on cuticle preparations.

It is impossible at present to determine the affinities of the eggs and egg impressions from Lunz, due primarily to the fact that detailed information on the morphology and distribution on/in leaves of other fossil and extant insect eggs is rare. The material at hand demonstrates that insect eggs liberated onto or into leaves characteristically affect the structure of the plant surface, especially with regard to cuticle thickness. Such characteristic alterations in cuticle thickness may be used in future studies to detect insect oviposition activity from plant cuticles, even if the eggs themselves are not preserved, and thus provide an innovative means to gather data about the composition and ecology of ancient ecosystems.

The fossils from Lunz also demonstrate that different modes of oviposition can be reconstructed based on how the presence of the eggs has affected the leaf cuticle. The coinciding ad- and abaxial impressions on leaves of *Nilssoniopteris angustior* (Fig. 6.1) suggest that insect eggs were placed into interior leaf tissues by an insect with an elongate ovipositor or abdomen as seen in extant dragonflies (Wesenberg-Lund, 1943, p. 70–71, figs. 56–57). Circular injuries occurring in the abaxial cuticle may have been inflicted by a penetrating long ovipositor (Fig. 6.7–6.8).

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FIGURE 6—Ovipositional damage on leaf cuticles of *Nilssoniopteris angustior* (Stur ex Krasser) Pott, Krings et Kerp, 2007 (†Bennettitales). *1,* Overview of a large cuticle segment. The cuticle segment is opened with the interior side up; for orientation background columns are given, indicating (from left to right) right adaxial cuticle (grey); central vascular bundle (white); left adaxial cuticle (grey); leaf margin (white); left abaxial cuticle (grey); central vascular bundle (white); right abaxial cuticle (grey). The grey and white arrows indicate mirror-inverted imprint areas on the adaxial (grey arrow, inner area of the imprint torn off) and abaxial cuticle (white arrow); black arrows indicate additional imprint areas on the adaxial cuticle). Slide NHM 1884/0015/0003 deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 1 mm. *2,* Abaxial cuticle, showing a rhomboidal imprint characterized by a weakly cutinized inner and normally cutinized outer area. Slide NHM 1884/0015/0016 deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 100 μm. *3,* Adaxial cuticle, showing a rhomboidal imprint; note the differences in cuticle thickness. Slide NHM 1884/0015/0007 deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 200 μm. *4,* Abaxial cuticle, showing a rhomboidal imprint. Detail of the inner area and heavily cutinized margin of the imprint area. Slide NHM 1884/0015/0003 deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 100 μm. *5,* Close up of a detail of Fig. 6.3. Scale bar = 50 μm. *6,* Detail of a rhomboidal imprint, showing the epidermal cell pattern with distorted cells and heavily cutinized outer margin. Slide NHM 1884/0015/0003 deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 50 μm. *7,* Abaxial cuticle, showing a rhomboidal imprint (arrow) and a circular injury perhaps caused by an insect ovipositor. Note the wound-callus formation around the damaged area. Slide NHM 1884/0015/0002 deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 100 μm. *8,* Close-up on one of the circular injuries in the leaf surface. Slide NHM 1884/0015/0002 deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 50 μm.

Wound callus formation around the injuries indicates that the surfaces were pierced while the leaf was alive. On the other hand, the eggs deposited onto the abaxial leaf surfaces of *N. haidingeri* (Fig. 2.1–2.2) are suggestive of an insect that did not pierce the leaf surface for oviposition, and thus might have had a reduced ovipositor. If these eggs were not preserved, the characteristic alteration of the abaxial cuticle in the form of massive cutinizations beneath and around the eggs would still document deposition of the eggs onto the abaxial leaf surface.

It is interesting to note that the eggs and egg impressions on *Nilssoniopteris* seem to display host-specificity. During the last two years, we have analyzed cuticles of all taxa of Cycadales and Bennettitales from Lunz based on a large sample set consisting of approximately 2,500 cuticle preparations of about 350 leaves of 10 species of the genera *Pterophyllum, Nilssoniopteris, Nilssonia,* and *Pseutoctenis* (Pott et al., 2007a, 2007b; Pott, Krings, and Kerp, 2007; Pott, Van Konijnenburg-van Cittert et al., 2007). However, egg impressions were found exclusively on leaves of *N. angustior* (Fig. 5.2), while the eggs only occur on cuticles of *N. haidingeri* (Fig. 5.1). It is possible to envisage that this host-specificity reflects certain preferences in larval diet or differences in the spatial (topographical) distribution of the host plants. For example, the hatch of extant Odonata that emerges from eggs deposited outside the water immediately drops down into the water where the naiads further develop (Corbet, 2004, p. 69–71); naiads that fail to reach the water shortly after hatching will perish after only a short period of time. Therefore, successful reproduction in Odontata requires that the eggs are liberated on plants that grow close to open water. If the impressions on *N. angustior* were produced by Odonata eggs, these plants must have grown in close proximity to a body of water. Assuming a cupedid origin of the actual eggs on leaves of *N. haidingeri,* those plants may have grown elsewhere but accessible for arboreal or ground beetles. Host plant specificity is stated to have been manifest in all possible degrees in herbivorous beetles (Crowson, 1981, p. 585).

Although cuticular analysis is long since known to represent a valuable means of extracting biological information from compression fossils that is useful in taxonomy but also important with regard to paleobiological and paleoecological considerations, cuticular analysis has rarely been applied in the decipherment of plant/animal interactions. The results presented here document that fossil cuticles may provide features with regard to the reproductive biology of ancient insects such as egg morphology, spatial arrangement of eggs, modes of oviposition, and host-specificity. Because compression fossils are much more abundant than permineralizations, they represent a copious source of information about plant/insect associations (e.g., Anderson et al., 1998; Scott et al., 2004; Labandeira, 2005). This source, however, has remained largely untapped to date. The cycadophytes from Lunz may serve as template for future studies of ancient insect activities on foliage based on fossil cuticles.

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