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Plant-insect interactions and coevolution during the Triassic in western Europe

Abstract - A review of the Triassic plant-insect interactions of western Europe is presented with some new interpretations. Several new interactions are described and discussed. This study is based on the analysis and comparison of three Triassic ecosystems which are rich in both plant and insect remains: the Grès à Voltzia (Upper Buntsandstein) of the Vosges (France) which is early Anisian, the Lower Keuper of Franconia (Germany) and the Lettenkohle of Alsace (France) which are both Upper Ladinian. Four kinds of interactions could be identified: feeding traces on plants, relations between the laying of insect eggs and host plants, parasitic relationships of galls and other growth abnormalities as well as a new fossil example of mimicry. A comprehensive account of plant-aided insect reproductive processes is given for the first time, which greatly extends the variety of fossil plant-insect interactions previously reported. Among the numerous results, the oviposition habits of the Protodonata are demonstrated, showing that they inserted their eggs in the plant tissues like the present-day endophytic Odonata. The numerous traces of their eggs in the Ladinian horsetails of Franconia (Germany) suggest moreover that this group, which was particularly flourishing in Permo-Carboniferous times, was still well established in the Triassic. The discovery of mimetic Tettigoniidae (Orthoptera) wings having an angiosperm-like venation and a leopard-like colouring led us to inquire into their significance for the process of plant-insect co-evolution. On the other hand, the floristic change in the Ladinian, with the emergence of the Cycadopsida, and the simultaneous appearance of numerous feeding traces on these new plants are evidence in favour of such a process. All these observations illustrate the dynamics of the Triassic ecosystems.

INTRODUCTION

According to biologists and ecologists studying present-day terrestrial ecosystems, knowledge of plant-insect interactions is fundamental to understanding the dynamics of the ecosystems (Gilbert, 1979). Their recognition in the fossil record is moreover essential for the study of coevolution process which affected plants and insects throughout geological time (Smart & Hughes, 1973).

In present-day ecosystems, relationships between plants and insects are very common, diversified and well studied. Most of them are related to feeding or represent associations between insects and host-plants (Southwood, 1973). Although such relationships are also known in fossil ecosystems (Scott & Taylor, 1983; Taylor & Scott, 1983; Scott & Paterson, 1984; Scott et al., 1985, 1992; Kelber & Geyer, 1989; Zhou & Zhang, 1989; Chaloner et al., 1991), they are not yet sufficiently studied. Those of the Triassic particularly have received rather little attention. Scott et al. (1992) and Donovan (1994) noted the lack of data for this period.

In the Triassic, a high diversity of insects existed in western Europe, as is evidenced by the 5300 specimens in the collection Grauvogel & Gall, from the Grès à Voltzia (Upper Buntsandstein) of the northern Vosges (eastern France), which is early Anisian (Grauvogel, 1947a; Gall, 1971). The abundant flora (Grauvogel-Stamm, 1978) associated with them suggests that inter-relationships must have occurred. In the Lower Keuper (Upper Ladinian) of Franconia in Germany, a rich and diversified flora and some insects have also been described (Kelber, 1990; Geyer & Kelber, 1987; Kelber & Hansch, 1995). The Middle Lettenkohle of Alsace (France), which is also Upper Ladinian, yielded a rich flora but no insects (Grauvogel-Stamm & Duringer, 1983; Grauvogel-Stamm et al., 1992).

Until now the plant-insect relationships which might have occurred in these ecosystems have not been studied, except in part those from the Lower Keuper of Franconia. Thus the purpose of this work is to give a full description of all the plant-insect interactions discovered in these three Triassic ecosystems of western Europe (Fig.1a-c), which at that time was located near the eastern edge of the Pangea and at the north-western border of the Tethys.

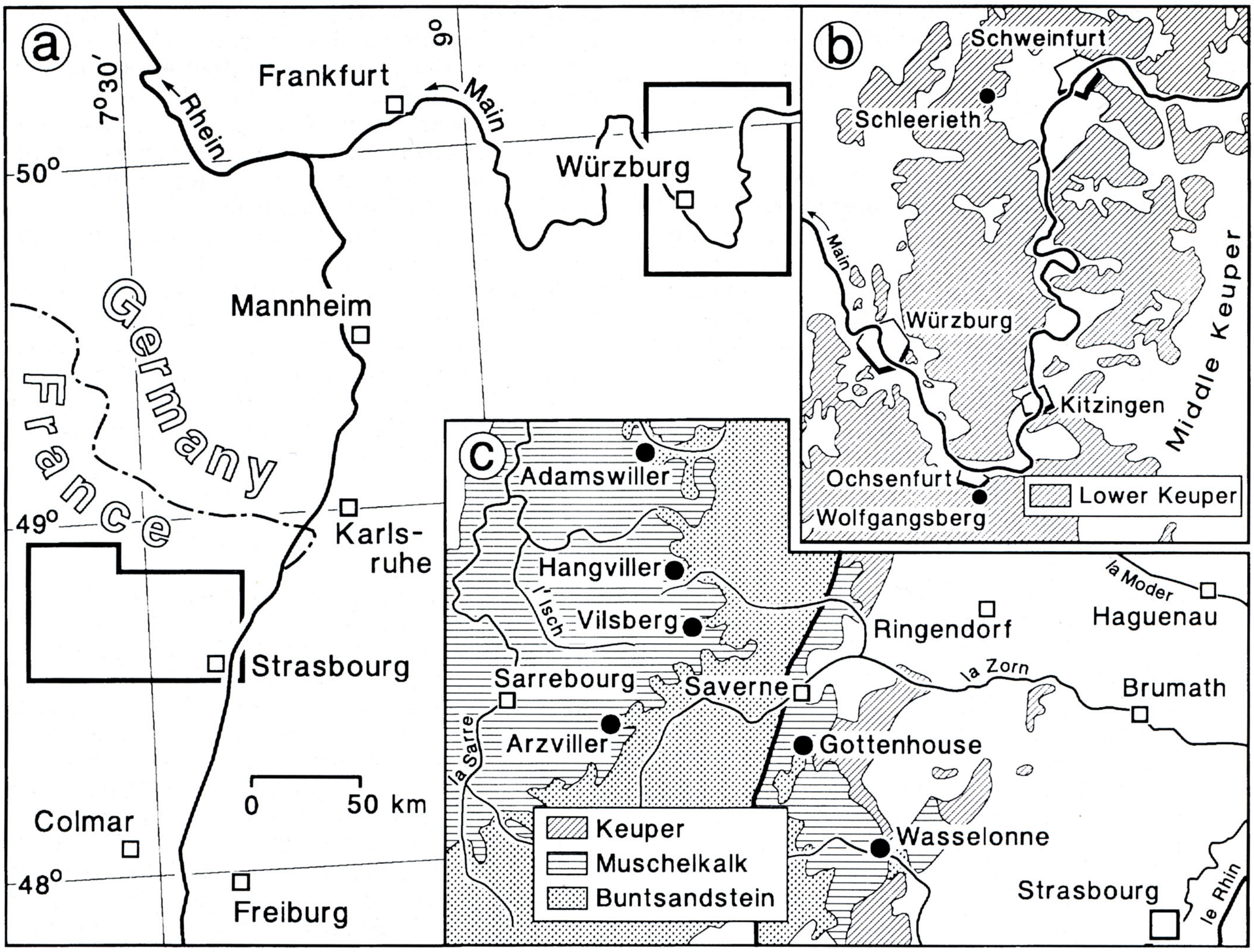


Fig. 1 - Map showing the location of the three Triassic ecosystems studied in this paper. a) overview; b) Franconia; c) Alsace and Vosges.

MATERIAL AND PREVIOUS RESULTS

An early Middle Triassic ecosystem: the Grès à Voltzia (Upper Buntsandstein) of the northern Vosges (France)

Nearly fifty years ago, Louis Grauvogel (1947a) announced the discovery of several thousands insects in the Grès à Voltzia (Upper Buntsandstein) of the northern Vosges mountains (eastern France) (Fig. 1a, c), stressing that they represented the most important portion of the fossils he found. Some of these insects have already been studied, such as the Blattodea, a Protodonata, the Odonata, the Orthoptera (study in progress) and the Mecopteroidea, including a Mecoptera, some Diptera and some representatives of the stem-groups (Grauvogel & Laurentiaux, 1952; Laurentiaux, 1953; Papier & Grauvogel-Stamm, 1995; Papier et al., 1994, 1996a, b, c; Nel et al.,1996; Krzeminski et al., 1994). The insects which have not yet been studied belong to the Coleoptera, Caloneurodea, Titanoptera, Plecoptera, Hemipteroidea with numerous Homoptera and Hemiptera, Ephemeroptera, Neuropteroidea with Megaloptera, among which are larvae of *Sialis* (the morphology of which is nearly identical with that of the modern ones, according to A. Nel) and possibly some Psocoptera and some Isoptera. Coleoptera, Orthoptera, Homoptera and Ephemeroptera are the groups best represented after Blattodea. These studies will contribute to filling the gaps in the Triassic insect diversity (Labandeira & Sepkoski, 1993).

The above insects were found associated with a flora consisting of Lycophyta (*Bustia*), Sphenophyta (*Equisetites, Schizoneura*), Filicophyta (*Anomopteris, Neuropteridium*) and Coniferophyta (*Voltzia, Aethophyllum, Yuccites, Darneya, Willsiostrobus, Sertostrobus*). The conifers form the main part of the flora (Grauvogel-Stamm, 1978, 1991; Grauvogel-Stamm & Grauvogel, 1980). The coexistence of this flora with a rich and diversified insect fauna must surely result in interactions between the two. Nevertheless, until now, only the trace of a gall has been identified (Grauvogel-Stamm, 1978; Larew, 1992). Numerous insect eggs have been reported, among which some are associated with plant remains (Grauvogel, 1947a, b; Gall & Grauvogel, 1966; Gall, 1971).

The Grès à Voltzia (Lower Anisian) corresponds to a deltaic sedimentary paleoenvironment under a semi-arid climate, along the border of a sea which occupied the German basin (Wurster, 1964; Gall 1971, 1985; Gall et al., 1977; Gall & Grauvogel-Stamm, 1993).

The specimens originate from the lower part of the Grès à Voltzia or Grès à meules of the Vosges (Fig.1a, c). They derive all from the shales which are interspersed between the lenticular sandstone bodies (Gall, 1971; Grauvogel-Stamm, 1978). The specimens are stored in the collection Grauvogel and Gall at the Geological Institute of the Université Louis Pasteur in Strasbourg (France).

Late Middle Triassic ecosystems

The Lower Keuper of Franconia (Germany)

The Lower Keuper (Upper Ladinian) of Franconia in Germany (Fig.1a,b) also provided an abundant flora, more diverse than that of the Grès à Voltzia (Kelber 1983; 1990; Kelber & Hansch, 1995). Besides common genera such as *Equisetites, Schizoneura* and *Desmiophyllum (= Yuccites* probably), there are also new plant genera such as the lycophyte *Annalepis*, the sphenophytes *Neocalamites* and *Phyllotheca*, the ferns and fern-like plants *Cladophlebis, Danaeopsis, Phlebopteris, Scythophyllum, Bernoullia, Chiropteris*, the cycadopsida *Dioonites*, *Pterophyllum*, *Taeniopteris* and conifers such as *Widdringtonites*, *Podozamites* and *Swedenborgia*. However, in contrast with the Grès à Voltzia, very few insects have been found in the Lower Keuper of Franconia. In a revision, some wings of Blattodea, Coleoptera and probably a Mecopteroidea have been described (Geyer & Kelber, 1987; Brauckmann & Schlüter, 1993).

Traces of plant-insect interactions have appeared up to now to be more numerous in the Lower Keuper of Franconia than in the Grès à Voltzia. Feeding traces on different kinds of leaves, clusters of eggs, supposedly of insects, fixed on equisetale leaf sheaths and several other unexplained traces have been described (Kelber, 1988; Kelber & Geyer, 1989). Moreover borings in a wood of the *Dadoxylon*-type (*D. keuperianum*) have been recorded from the Middle Keuper of Thuringia, north of Franconia (Linck, 1949; Mägdefrau, 1968). These wood borings have been compared to those of the present-day Anobiidae. However these Coleoptera, which only bore in dead wood, are only known since the Eocene (Carpenter, 1992).

The paleoenvironment of the Hauptsandstein-event of the Lower Keuper represents an incised fluvial drainage system, eroded during a sea-level lowstand (Aigner & Bachmann, 1992).

The specimens from the Lower Keuper of Franconia originate from greenish sandstone and siltstone at the top of the so-called Werksandstein of Franconia (Fig. 1a, b). Localities are indicated on the specimens by a number preceeded by an abbreviation: SCHL = Werksandstein quarry west of Schleerieth (Kelber, 1983, 1990, 1993); OCH = road construction B19 near the St. Wolfgang chapel, south of Ochsenfurt (Kelber, 1987). All the material is stored in the private collection Kelber, Würzburg.

The Lettenkohle of Alsace (France)

According to the French nomenclature, the Lettenkohle of Alsace represents the transition stage between the Muschelkalk and the Keuper. Its middle part was contemporaneous with the Lower Keuper of Franconia and therefore is also of Ladinian age. It yielded a similar flora in which several characteristic genera could be recognized, i.e. *Annalepis, Dioonites pennaeformis*, *Taeniopteris angustifolia* and *Danaeopsis maranteacea* (Grauvogel-Stamm & Duringer, 1983; Grauvogel-Stamm et al., 1992). It also provided a rich microflora, in which the spores of *Annalepis* (*Aratrisporites)* prevail (Duringer & Doubinger, 1985). Among the fossil plants the trace of a supposed plant-insect relationships was discovered, which can assist in the interpretation of some traces from the Lower Keuper of Franconia. However no insects have been found in the Lettenkohle of Alsace; this may be due to limited collecting of suitable material.

The paleoenvironment corresponds to a coastal marsh of the supratidal area (Grauvogel-Stamm & Duringer, 1983; Duringer & Doubinger, 1985; Duringer, 1987).

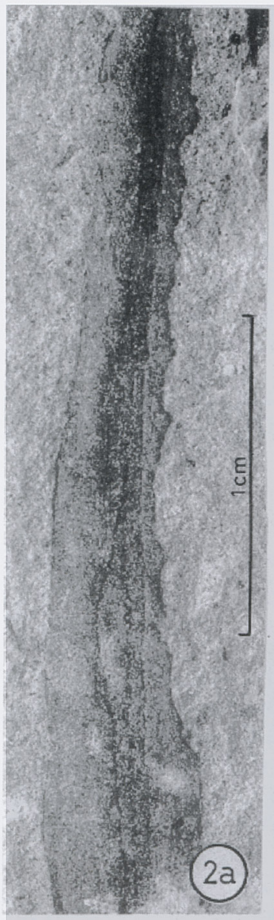
The specimens derive from the clayey marls of the Middle Lettenkohle of Wasselonne (Bas-Rhin, France) (Fig. 1a, c). They are stored in the Geological Institute of Strasbourg University.

PLANT/INSECT INTERACTIONS: DESCRIPTION AND INTERPRETATION

Phytophagous insects and food plants

Although phytophagy and specialised feeding on fresh leaves appeared rather early in the insect evolutionary history, i.e. in the late Carboniferous, it remained rather limited (Southwood, 1973). Presently, only a third of the major insect groups include phytophagous species. Phasmida represent the single insect group which exclusively contains plant feeders. The Lepidoptera is another group in which feeding is mostly on living plants. The adaptation to phytophagy met a lot of obstacles which restrained the spreading of this feeding habit (Southwood, 1973; Osborne, 1973). Most of the present-day terrestrial insect groups include indeed either carnivorous or scavenger species, or comprise species with both these feeding habits. On the 23 present-day insect groups listed by Southwood (1973), 5 are almost exclusively scavengers, 5 others almost exclusively carnivorous, whereas 9 include both scavenger and carnivorous representatives. Only 8 include plant-feeders.

In spite of the presence of some insect groups in the Grès à Voltzia of the Vosges presently known for being largely or entirely phytophagous, like the Or-


1cm
2a


1cm
2


1mm
4


4a
200µm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6
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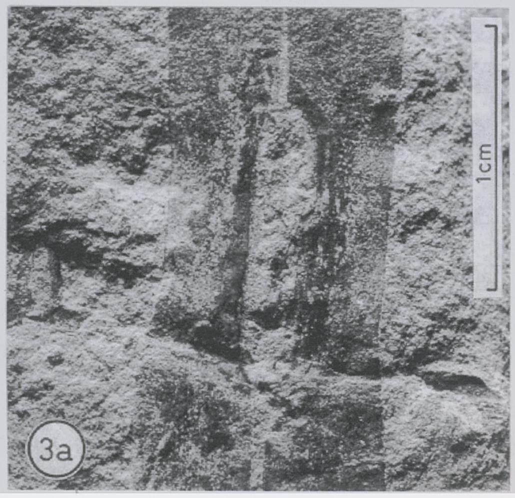
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thoptera, leaves with clear feeding traces are extremely rare in this ecosystem. The large *Yuccites* leaves never show margins marked by bite traces. The cuticle thickness possibly protected them against insect attacks.

By contrast, in the Lower Keuper of Franconia, very obvious bite traces have been described on the following two plant types, one of which also existed in the Grès à Voltzia of the Vosges (Geyer & Kelber, 1987; Kelber & Geyer, 1989; Kelber, 1990).

Feeding traces from the Lower Keuper of Franconia (Germany)

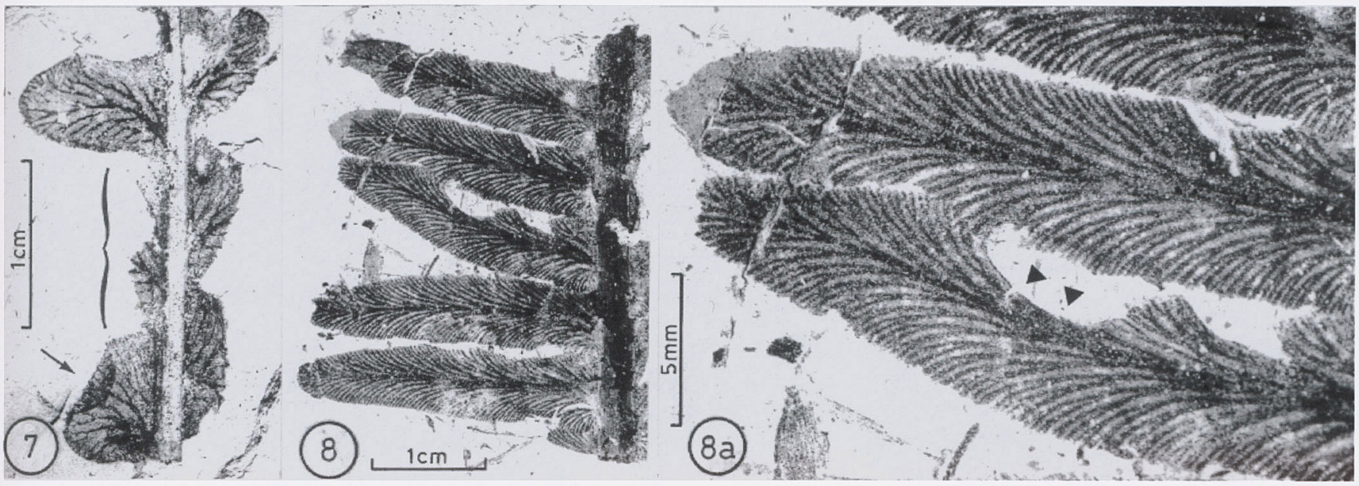
a) Marginal and non marginal feeding traces on *Schizoneura paradoxa*

Two specimens of *Schizoneura paradoxa* showing feeding traces have been found. The first one has already been described by Kelber and Geyer (1989). It consists of two fused leaves of a leaf sheath which shows an oval-shaped feeding trace along the line of junction, measuring 12 mm long and 3 mm wide (Fig. 3, 3a). The margins of the feeding trace are thickened. According to Kelber and Geyer (1989), this trace represents either a feeding gallery through which insect larvae entered to reach the parenchymatous leaf tissue or corresponds to a Blattodea feeding trace.

The second specimen has not been previously described and consists of an isolated leaf of *Schizoneura paradoxa* showing clear continuous marginal feeding traces on one side (Fig. 2, 2a, b). The margins of these bite traces are darker, corresponding to a wound reaction which indicates that the leaf was nibbled while alive.

As shown by these traces, only the marginal zone of both contiguous leaves and isolated leaf is damaged. The presence of tannins and lignified vascular bundles with hard walls in the central part of each leaf probably partly protected the *Schizoneura* midvein zone against the insect attacks. Indeed, as demonstrated by Grauvogel-Stamm (1978) for the *Schizoneura* of the Grès à Voltzia, each leaf of the sheath has a large central part occupied by tracheids with annular and helical thickenings and dense longitudinal black opaque strands (Fig. 4, 4a). These are more or less sinuous and spiny and resemble the articulated laticifers of the angiosperms (Fahn, 1974). These black strands which appear to be filled with an amorphous material also resemble those of the present *Equisetum* which contain tannins (Queva, 1907). According to Good (1971), they would be equivalent to the melasmatic tissue of the *Calamites* (Thomas, 1912). Tannins belong to the chemical compounds which have evolved as defence mechanisms against insects (Southwood, 1973, p.17).

Although the feeding trace observed on the specimen with two fused leaves of *Schizoneura* is marginal for each of them (Fig. 3, 3a), it in fact represents a non-marginal leaf feeding trace since the fused leaves look like a single leaf. This discovery may question



Figs.7-8 - Supposed feeding traces on *Neuropteridium* sp. pinna from the Grès à Voltzia (Upper Buntsandstein) of the Vosges. 7) Portion of a pinna showing on the left side, between two intact pinnules, one which has been strongly reduced (indicated by a bracket) probably by insect feeding. Note that the extremity of the left basal pinnule is folded, indicating that this plant was soft-textured. Arzviller (Moselle, France). 8) Portion of a pinna having a pinnule damaged along one of its margin; detail of the bite trace in Fig.8a. Gottenhouse (Bas-Rhin, France).

Figs. 2-6 - Feeding traces on plants from the Lower Keuper of Franconia (Germany). 2) *Schizoneura paradoxa* leaf showing two nibbled areas along the left margin. An enlargement of the counterpart of these zones is exhibited in Fig. 2a and 2b. Note the wide and well-delimited midvein area in these enlargements. 3) Two fused leaves of *S. paradoxa* displaying an oval-shaped feeding trace at their junction-line, enlarged in Fig.3a. 4) Anatomical structure of a *Schizoneura* leaf (peel) from the Grès à Voltzia of the Vosges (France). Note that most of its width is occupied by lignified vascular bundles and dense black strands containing probable tannins. 4a) Enlarged portion of the central zone of the leaf in Fig.4, showing the longitudinal opaque strands and the tracheids with annular and helicoidal thickenings. 5, 6) *Taeniopteris angustifolia* leaves exhibiting marginal feeding traces. Collection Kelber: 2 = specimen SCHL - 1079a; 2a, b = specimen SCHL-1079b; 3 = specimen SCHL-065; 5 = specimen SCHL-061a; 6 = specimen SCHL-1080a. Coll. Grauvogel and Gall: Fig.4, 4a, slide LG 6178. Fig.3 (from Kelber & Geyer, 1989; Kelber 1990); Fig.4, 4a (from Grauvogel-Stamm 1978); Fig.5 (from Kelber & Geyer 1989, Kelber 1990) the hypothesis of Scott et al. (1992) which states that «extensive non-marginal leaf feeding occurs firstly in the Cretaceous».

b) Marginal feeding traces on *Taeniopteris angustifolia*

Two leaves of *Taeniopteris angustifolia* from the Lower Keuper of Franconia show margins strongly damaged by insect feeding traces (Kelber & Geyer, 1989). At several places along these leaves, the lamina has been nibbled but the biting traces do not reach the midvein (Fig. 5, 6). Kelber and Geyer (1989) suggested that the darker biting outlines indicate that the tissues dried up at these places and therefore that the leaves were nibbled during the lifetime of the plant. They correspond indeed to wound reactions and could only have occurred while the plant was still alive (Scott et al., 1992).

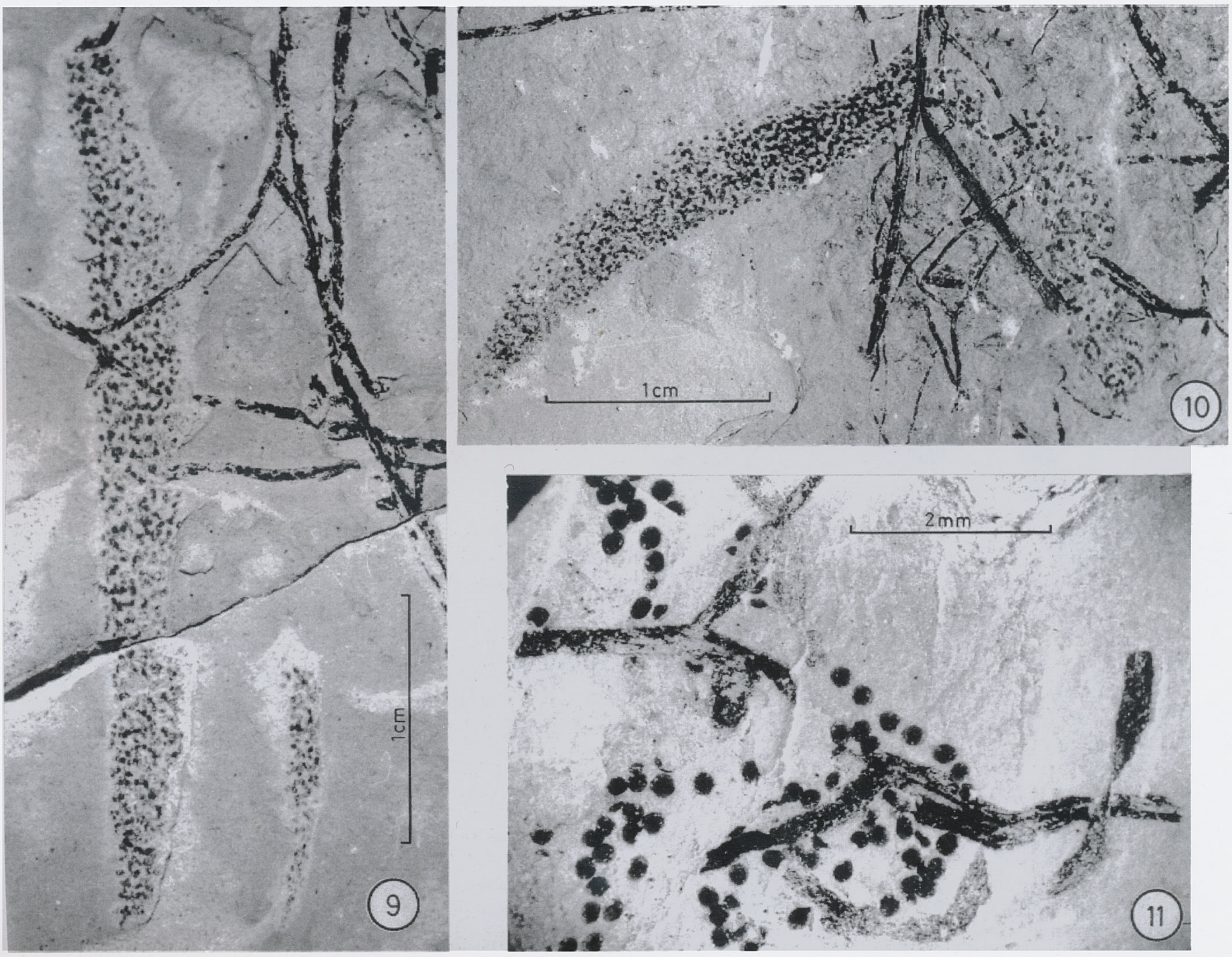
Van Amerom (1966) introduced the genus name *Phagophytichnus* for feeding traces on *Neuropteris* leaves from the Stephanian of Spain. Similar traces have also been described on *Glossopteris* and *Paripteris* leaves (Plumstead, 1963; Van Amerom & Boersma, 1971).

Feeding traces from the Grès à Voltzia of the Vosges (France)

A thorough examination of all the fossil leaves from the Grès à Voltzia in the collection Grauvogel and Gall, permitted the identification of two specimens of *Neuropteridium* which seem to show some feeding traces. One specimen which represents a portion of a pinna shows, particularly on the left side, between two intact pinnules, one which has been strongly reduced, probably by eating (Fig. 7). This plant appears to have been rather soft-textured since the extremity of the left basal pinnule is folded (arrow). However the fact that the margins of the supposed feeding trace do not show any browning suggests that this pinna was no longer alive when it was eaten.

The second specimen also shows a pinnule which is damaged on one side, alongside other intact ones (Fig. 8, 8a). The outline of the feeding trace appears to exactly follow a lateral vein. The browning which is obvious along this trace may be either a wound reaction or the remains of the vein.

As noted by Scott et al. (1992), identification of feeding traces in some leaf types can be difficult. The *Neuropteridium* leaves belong to such a type.



Figs.9-11) Egg clusters entangled in plant debris from the Grès à Voltzia (Upper Buntsandstein) of the Vosges (France). 9, 10) *Clavapartus latus*, Adamswiller (Bas-Rhin, France). 11) *Monilipartus tenuis*, Arzviller (Moselle, France) (from Gall & Grauvogel, 1966).

Insect eggs and host plants

Fossil insect eggs have rarely been described in the literature. Such traces have been discovered in all three ecosystems studied here, but are very different from each other.

Insect eggs from the Upper Buntsandstein of the Vosges (France)

Thousands of egg clusters attributed to insects have been found in the Grès à Voltzia (Upper Buntsandstein) of the northern Vosges (Grauvogel, 1947a, b; Gall & Grauvogel, 1966; Gall, 1971). These consist of a great number of eggs, often more than one thousand, each surrounded with an organic sheath. They are joined together in a mucilaginous envelope, the shape of which permits three monospecific genera to be distinguished: *Monilipartus tenuis, Clavapartus latus* and *Furcapartus exilis* (Gall & Grauvogel, 1966). Only the two first are sometimes associated with plant debris.

Monilipartus tenuis consists of eggs arranged end to end, like a string of beads, and maintained like a cord by a mucilaginous sheath (Fig. 11). The cords of eggs are distributed in irregular convolutions around a central point. These clusters contain a large number of eggs; 1500 on average and sometimes more than 3000. The eggs are oval and each measures 0.25 mm in length.

These clusters of eggs, which are mostly free are sometimes entangled in plant debris (Fig. 11). Gall and Grauvogel (1966) compared them with those of present Chironomidae in which the eggs are also enclosed in strings of jelly (Munsterhjelm, 1920; Hinton, 1981).

Clavapartus latus is another genus particularly widespread in the Grès à Voltzia which is often associated with the above. These egg clusters are subcylindrical, roll- or club-shaped and swollen at one extremity. They are 5 mm wide and 20-30 mm long. They each contain between 500 and 2000 eggs which measure 0.20 x 0.30mm. They are mostly free but sometimes they are also entangled in plant debris (Fig. 9, 10).

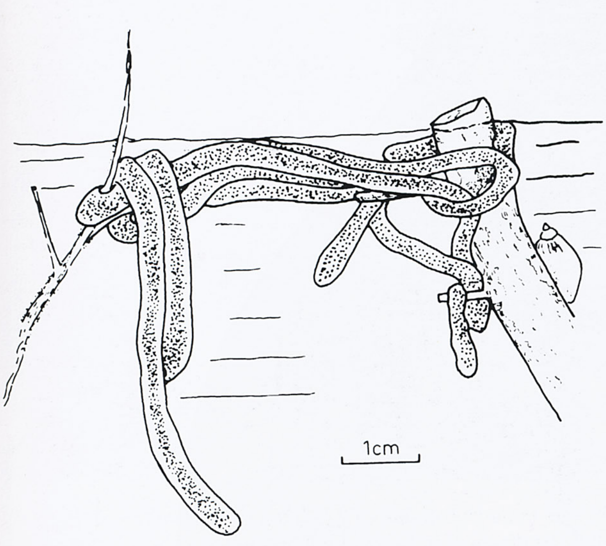


Fig.12 - Egg clusters in long strings of spumaline, fixed on plants, of the present-day Odonata genus *Tetragoneuria* (Anisoptera, Corduliidae) (redrawn from Wesenberg-Lund, 1913)

Fig.13 - Egg masses from the Lower Keuper of Franconia (Germany) adhering on a leaf sheath of *Equisetites arenaceus* (specimen OCH - 314a). Note the *Spirorbis* also fixed on this horsetail. (from Geyer & Kelber, 1987)

Gall and Grauvogel (1966) also compared these egg clusters with those of the Chironomidae and the Trichoptera. They also resemble those of some living Odonata Anisoptera. Some species like *Epitheca bimaculata* or *Tetragoneuria* (Fig. 12) (both Anisoptera, Corduliidae) lay numerous eggs embedded in long strings of spumaline which are free-floating or fixed on plants (Wesenberg-Lund, 1913a, b; Jacobs & Renner, 1988: p.147, fig. C131; Hinton, 1981). In the Grès à Voltzia an Odonata Protozygoptera existed (*Voltzialestes triasicus*), which possibly laid the egg clusters (Nel et al., 1996) attributed to *Clavapartus latus*.

These types of egg clusters, both *Monilipartus tenuis* and *Clavapartus latus*, are often found assembled together in great number, suggesting group ovipositions similar to those known in several kinds of insects (Hinton, 1981).

The association of these egg clusters with plant debris does not really represent a plant-insect interaction as it is passive and resulted from a mechanical process. It differs indeed from an interaction in which the insects choose the plants on which they are going to lay their eggs. Here, the insects have just chosen quiet water-bodies containing many plant debris.

Insect eggs from the Lower Keuper of Franconia (Germany) and the Lettenkohle of Alsace (France)

Two or more kinds of insect eggs have been described from the Lower Keuper of Franconia which differ very much from one another and also from those of the Grès à Voltzia. These are egg masses adhering to the surface of the plants and endophytic insect eggs inserted inside the plant tissues.

a) Exophytic insect eggs on *Equisetites arenaceus*

Compact egg masses without precise shape, adhering to the surface of leaf sheaths of *Equisetites arenaceus* (Fig. 13) have been described from the Lower Keuper of Franconia (Geyer & Kelber, 1987; Kelber & Geyer, 1989). The eggs, which are spherical, each measure 0.3-0.4 mm in diameter. In contrast to those of the Grès à Voltzia, no mucilaginous sheath has been observed around them. Nevertheless the fact that the eggs remain in compact masses suggests that there was probably such a sheath.

Since these egg masses are associated with numerous annelids (*Spirorbis*), which also adhere to the *Equisetites* leaf sheath, and since they do not present any traces of desiccation or rehydration, the authors concluded that probably they have been laid under water and that the plant parts carrying them did not emerge after oviposition. According to Kelber and Geyer (1989), such an oviposition occurs in an aquatic Acari (*Hydracarina*), among present-day arthropods. Some Trichoptera, like the Polycentropidae, also show this kind of oviposition habit; the egg-masses are indeed flat and irregular in outline, and are laid and cemented to the substrate under water (Wesenberg-Lund, 1913a; Hinton, 1981).

The temporary pseudoplanktic or epiphytic habit of these eggs extends the variety of plant-insect interactions (Scott et al., 1992).

b) Endophytic insect eggs in *Equisetites arenaceus*

In the Lower Keuper of Franconia, several leaf sheaths of *Equisetites arenaceus* have been described displaying numerous oval scars on their surface (Kelber 1988, 1990). The author distinguished two kinds of scars, elongate oval ones which have dimensions of between 2 x 6.5 mm and 3 x 9.5 mm and broadly oval ones ranging from 2 x 3.5 mm to 4 x 7 mm. No transitional forms between the two have been observed. They are therefore considered separately.

– Elongate oval scars: Protodonata eggs

The elongate oval, prominent scars are the most numerous and often show a high density. They are arranged in a parallel direction to one another and oriented with their long axis parallel to the stem axis

Fig.14-15 - Elongate oval scars (= supposedly endophytic Protodonata eggs) in a leaf sheath of *Equisetites arenaceus* from the Lower Keuper of Franconia (Germany). Note their longitudinal parallel arrangement in Fig. 14 thein asymmetrical shape with one extremity more tapered and the epidermis micro-ornamentation between them and on their border in Fig.15. Observe also the contiguous small circles (arrows) impressed at the surface of two contiguous scars in Fig.14a. 14, 14a = spec. SCHL-005a; 15 = spec. OCH-001. (from Kelber, 1988)

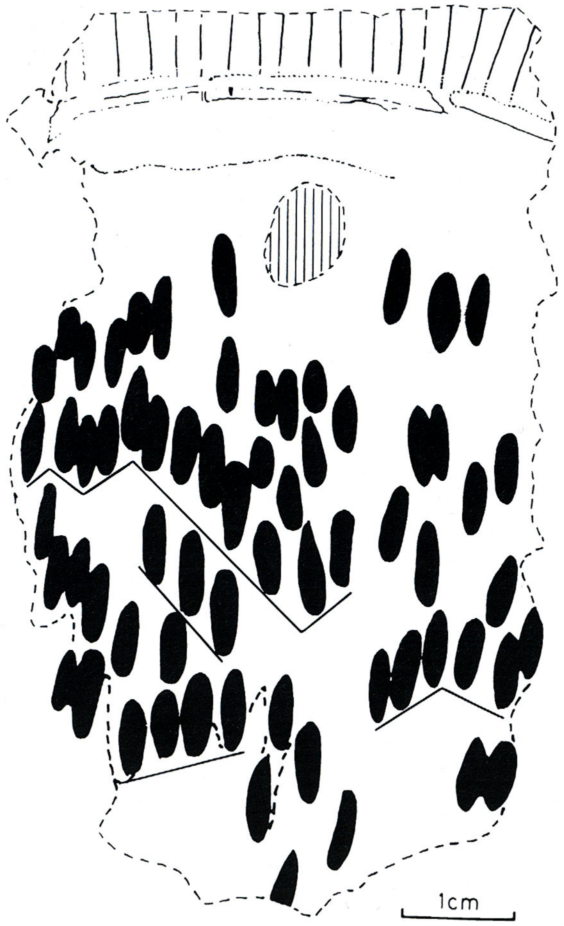


Fig.16 - Drawing of a leaf-sheath of *Equisetites arenaceus* (specimen SCHL-004a) from the Lower Keuper of Franconia (Germany) showing numerous and densely arranged elongate oval scars. Note that the laterally contiguous scars are arranged in short zigzagging lines (showed by a continuous line). (from Kelber, 1988)

(Fig. 14). Their density calculated on one of the specimens figured by Kelber (1988), figured here in Fig. 16, reaches 63 scars for a surface area of 25 cm2. On the counterpart, these scars consist of a slightly elevated, flattened and well defined oval central zone, slightly displaced toward one extremity (Fig. 14, 15). The opposite extremity is more elongated and in some specimens it is clearly tapering (Kelber, 1988, Fig. 12-14). The scars also seem all to be arranged with their tapering extremity on the same side. With their flattened area surrounded by oblique margins, they resemble a plateau with abrupt slopes. The micro-ornamentation impressed on the margins of the scars and between them is that of the epidermis (Fig. 15).

Roselt (1954), who described similar scars on *Equisetites* stems from the Lower Keuper of Bedheim in Thuringia (Germany), interpreted them as characteristic original ornamentation and attributed these horsetails to a new species, *Equisetites foveolatus*. The scars on the Roselt specimen are smaller, measuring between 2.5 x 1.5 mm and 4.5 x 2.5 mm; this difference however is not significant. Since then two other specimens showing similar scars, measuring 4.5 x 2.5 mm, have been reported by Kräusel (1958) from the Lower Liassic of Sassendorf, near Bamberg (Bavaria, Germany). The horsetail in this case corresponds to *Equisetites muensteri* (Kelber, 1988). However, the oldest information concerning these elongate oval scars is from Heer (1877). This author described two oval scars of 6 mm long and 2 mm wide on a leaf sheath of *Equisetites platyodon* from the Lettenkohle of Switzerland and interpreted them as the elytrons of a Coleoptera (*Chrysomela*), accordingly naming this specimen *Chrysomelites rothenbachi*. Similar scars have also been described by Weber (1968) on *Neocalamites* from the Rhaetian-Liassic transitional beds of Franconia (Germany), leading the author to attribute this plant to a new species, *N. exornatus*. According to Kelber (1988, 1990), there is no doubt that these scars resulted from either an illness of the plant or an external influence such a feeding trace of insect larva or the settlement of unknown organisms.

While studying the insect oviposition habits, one of the authors (L GS) noticed that the shape and arrangement of the scars of «*Equisetites foveolatus*» strikingly resemble the oviposition of endophytic Odonata (Kumar & Prasad, 1977; Hinton, 1981; Jacobs & Renner, 1988). These authors showed that the eggs of numerous Odonata, i.e. most of the Zygoptera and some Anisoptera (the Aeshnidae and the Petaluridae), are inserted in the leaf lamina or in the stem cortex and are arranged in a parallel direction with one another, their long axis parallel to the stem axis. Furthermore, the eggs of these endophytic Odonata are elongated oval in shape with one extremity distinctly more tapered, like the scars of «*E. foveolatus*» (Fig.14, 15, 20, 21). The density of the Odonata eggs can also be very high. Thus in the species *Neurobasis chinensis* (Zygoptera, Calopterygidae), 830 eggs have been counted on a surface of 55 cm2 (Kumar & Prasad, 1977). These eggs, while being always parallel with one another, can be arranged more or less regularly. In *Platycnemis pennipes* (Zygoptera, Platycnemididae), for example, their arrangement constitutes large zigzags along the stems of water-lily (Jacobs & Renner, 1988). Similar patterns (Fig. 18, 19) have been observed in *Pyrrhosoma nymphula* and *Erythromma najas*, both belonging to the family Coenagrionidae, Zygoptera (Wesenberg-Lund, 1913b; Schiemenz, 1957). Other dragonflies, such as the Calopterygidae (*Calopteryx virgo*, Fig. 17), the Lestidae and some Coenagrionidae, lay their eggs in more or less parallel lines (Schiemenz, 1957). In *Neurobasis chinensis* (Fig. 20), their arrangement does not seem to follow a definite pattern although the female changes her place regularly during oviposition (Kumar & Prasad, 1977). In «*E. foveolatus*» described by Kelber (1988), the scar arrangement is not very regular, nevertheless it also seems to follow a certain pattern. One of the specimens figured by this author (reproduced here Fig. 16) clearly shows that the series of parallel contiguous scars are arranged in zigzagging lines, resembling very much for instance the egg arrangement of *Erythromma najas* (Fig. 19) in the flower peduncle of a water-lily (Wesenberg-Lund, 1913b). It is possible that several different females had oviposited in the same place, as observed in living endophytic Odonata, resulting in somewhat disordered zigzagging lines (Kumar & Prasad, 1977).

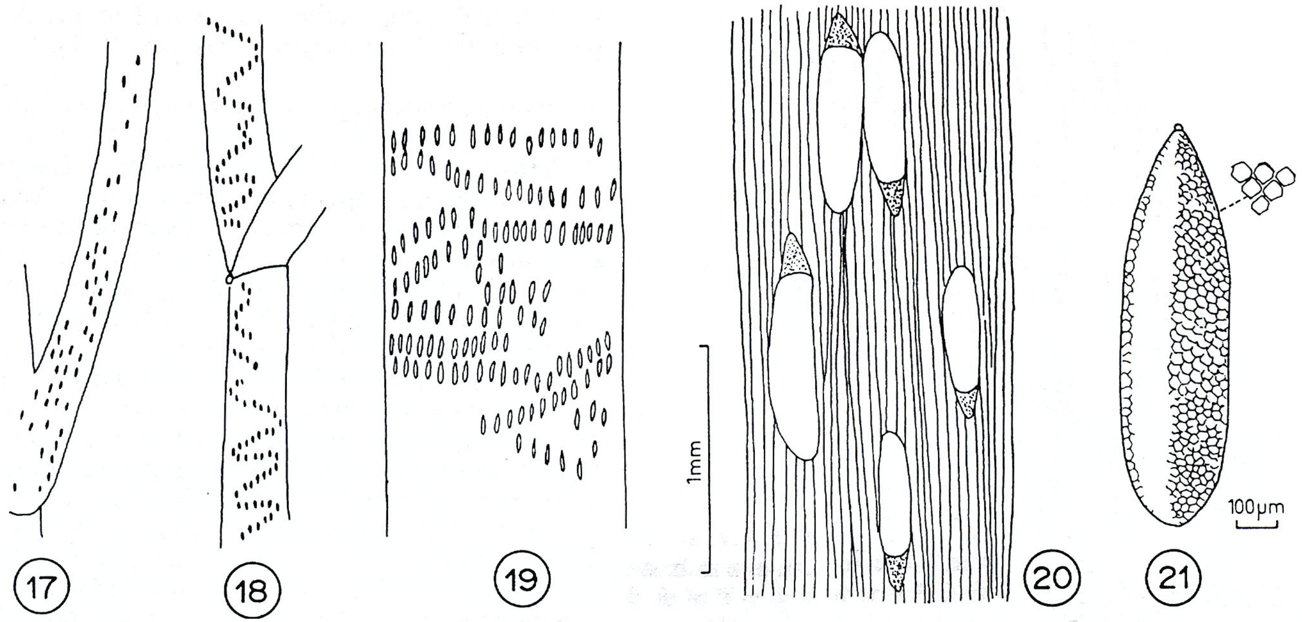


Fig.17-21 - Oviposition examples and egg detail of present-day endophytic Odonata. 17) *Calopteryx virgo* (Zygoptera, Calopterygidae): eggs arranged in longitudinal lines; 18) *Pyrrhosoma nymphula* and 19) *Erythromma najas* (both Zygoptera, Coenagrionidae): eggs arranged in large zigzags. Note that Fig.19 represents the egg arrangement in the cortex of the flower peduncle of a water-lily 20) *Neurobasis chinensis* (Zygoptera, Calopterygidae): note the asymmetrical shape of the eggs with one extremity more tapering and their arrangement parallel to the stem axis. 21) *Aeshna cyanea* (Anisoptera, Aeshnidae): detail of an egg. Note its elongate shape with one extremity more tapering and the pattern of follicular cells at its surface. Fig.17-18: redrawn after Schiemenz (1957); Fig.19: redrawn after Wesenberg-Lund (1913b); Fig.20: redrawn after Kumar & Prasad (1977); Fig.21: redrawn after Hinton (1981).

The present-day endophytic Odonata do not seem to have a preference for a specific type of vegetation. However they oviposit mostly in plants, both alive or dead, which grow in water (water-lily, *Carex*, reeds). Some species, like *Lestes sponsa* (Zygoptera, Lestidae) are known to oviposit in *Equisetes* stems (Wesenberg-Lund, 1913a, b; Schiemenz, 1957; Kumar & Prasad, 1977; Hinton, 1981; Jacob & Renner, 1988).

Another observation which, besides the characteristic shape of the scars, supports the hypothesis as to an endophytic Odonata-like oviposition, is the presence of several small circles printed on the surface of two scars figured by Kelber (1988, Fig. 21). Some of these are contiguous and measure about 0.3 mm in diameter (Fig. 14a). These small circular imprints may represent the trace of the follicular cells (Fig. 21) which is strongly marked at the surface of the eggs of the present-day, both endo- and exophytic Odonata species (Hinton, 1981).

A significant difference between the scars of «*E. foveolatus*» and the Odonata eggs lies in their respective dimensions. The eggs of present-day endophytic Odonata measure between 1.5 mm (*Lestes viridis*, Lestidae) and 1.8 mm in length (*Anax imperator*, Aeschnidae) whereas the length of the «*E. foveolatus*» scars varies between 6.5 and 9.5 mm. Those figured by Roselt (1954) are between 2.5 and 4.5 mm long. As a result, one can guess that the dragonflies originating in them were rather large and much larger than the present-day endophytic Odonata.

In the Triassic of Europe there existed a species of the Protodonata – *Triadotypus guillaumei* – whose span reached 30 to 35 cm. Its wings have been found in the Grès à Voltzia of the Vosges (Grauvogel & Laurentiaux, 1952), in the Muschelkalk of Franconia (where it was first described under the name *Handlirschia gelasii* by Reis, 1909) and in the Middle Keuper of the Alps in France (Laurentiaux-Vieira et al., 1952). All these observations suggest that this protodonate may well be the insect which made the elongate oval scars in the horsetails of the Lower Keuper of Franconia.

As a result, one can infer that this Triassic species of the Protodonata had an endophytic oviposition like the other representatives of this group which flourished in the Permo-Carboniferous (Brauckmann & Zessin, 1989). The discovery of several specimens of *Equisetites* in the Lower Keuper of Franconia containing such elongate oval scars may indicate moreover that the Protodonata were still well established in the Triassic.

The oviposition habit of the Protodonata is demonstrated and described for the first time. A previous fossil evidence of endophytic Odonata oviposition has been reported from the Upper Oligocene of Germany (Hellmund & Hellmund, 1991).

The fact that oviposition of many living endophytic Odonata occur on submerged stems and the analogies between this oviposition habit and that of the Triassic Protodonata suggest that the Triassic horsetails lived, at least periodically, with their roots in the water. This observation coincides with that of Kelber and Geyer (1989) on the egg masses adhering to the *Equisetites* leaf sheaths.

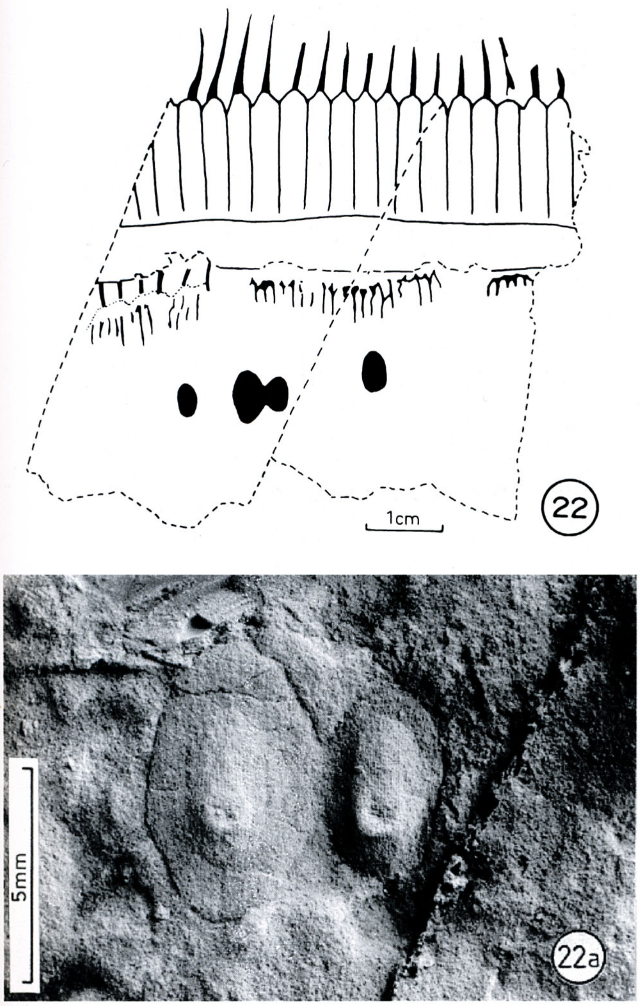


Fig.22, 22a - Drawing of the leaf-sheath of *Equisetites arenaceus* (specimen SCHL-003) from the Lower Keuper of Franconia (Germany) showing some broadly oval structure, longitudinally arranged. Note the difference in size of the contiguous structure enlarged in Fig.22a (latex cast). (from Kelber 1988).

- Broadly oval structures

On the stem of *Equisetites arenaceus* from the Lower Keuper of Franconia, Kelber (1988) noticed broadly oval scars. These are smaller and far less numerous than the elongate oval ones. They have the same arrangement, being parallel with one another and with the axis of the horsetail stem (Fig. 22, 22a). However, their shape differs in that they consist of a conical central part surrounded by a broad flat marginal area.

These scars also appear to represent eggs. However, they do not seem to correspond to endophytic Odonata eggs as these are always elongated oval in shape, with one extremity more tapering (Hinton, 1981). Another possibility is that these scars represent the trace of coccids or scale insects. The great difference in size of two contiguous scars illustrated by Kelber (1988, fig. 22, 23), represented here in Fig. 22, 22a, might support this hypothesis.The coccids are present in the Triassic (Kukalova-Peck, 1991).

c) Traces of insect eggs on *Taeniopteris angustifolia*

Among the leaves of *Taeniopteris angustifolia* from the Lower Keuper of Franconia and the Middle Lettenkohle of Alsace, are examples showing several scars in the margin of the lamina which, however, seem to differ from one another, suggesting that they have not the same origin (Kelber, 1988; Grauvogel-Stamm et al., 1992).

The scars observed on the *Taeniopteris* leaves from the Lower Keuper of Franconia are broadly oval and irregular in size and arrangement. They are slightly prominent, delimited by a furrow and underlined with weathered iron (limonite). Kelber (1988) who associated these scars with those of «*Equisetites foveolatus*», considered that they resulted from an illness of the plant or represent the trace of a plant-insect interaction. Similar scars have been observed on *Macrotaeniopteris* leaves from the Triassic of Virginia, U.S.A., in which they are considered as a result of fungal infection (Fontaine, 1883; Bock, 1969). These scars do not resemble those of the Lettenkohle which are described below.

Two of the specimens of *Taeniopteris* leaves from the Lettenkohle show several oval and regularly arranged scars in the margin (Grauvogel-Stamm et al., 1992, Pl. 13 fig. 1). These are 2 mm long and 1 mm wide, narrowly separated and arranged end to end, with their long axis parallel to the leaf margin. One of the leaves, a portion of 65 mm long and 13 mm wide, shows two series of scars, one which occupies the upper part, at right, and consists of five such scars, four of which are located very close to the leaf margin and one scar which is at half-way between the midvein and the leaf margin (Fig. 23, 23b). The other series of scars is situated in the lower part of the leaf, at left, and consists of eight scars situated approximately half-way between the midvein and the leaf margin (Fig. 23a). They are not quite parallel to the leaf margin but slightly obliquely arranged. The scars are underlined with coalified organic matter which either covers them or marks out their outlines. They are crossed more or less transversally by the lateral veins of the leaf (Fig. 23a, b). The second specimen consists of a leaf portion, 30 mm long and 13 mm wide, showing five scars situated on the same side and close to the margin (Fig. 24, 24a). In contrast with the other specimen, the scars look like ovoid bodies or depressions filled with sediment, ready to become detached.

At first glance, two interpretations of these scars appear to be acceptable:

- either they represent ovules, in which case the specimens correspond to fertile leaves or megasporophylls (1);

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(1) If these leaves with lateral oval scars of *Taeniopteris angustifolia* are really fertile ones, this would be proof that the rash and often criticized reconstruction of *Dioonitocarpidium pennaeforme* proposed by Ruhle von Lilienstern (1928) is wrong since it associates two unrelated plants (Mamay, 1976). They are, indeed, very different from the pinnate sporophylls of *Dioonites pennaeformis* which are shown associated with the sterile leaves of *Taeniopteris angustifolia* in this reconstruction. The discovery by Kelber (1990, fig. 77) of entire *Taeniopteris* leaves shows moreover that the shape of these leaves represented in this reconstruction is wrong.

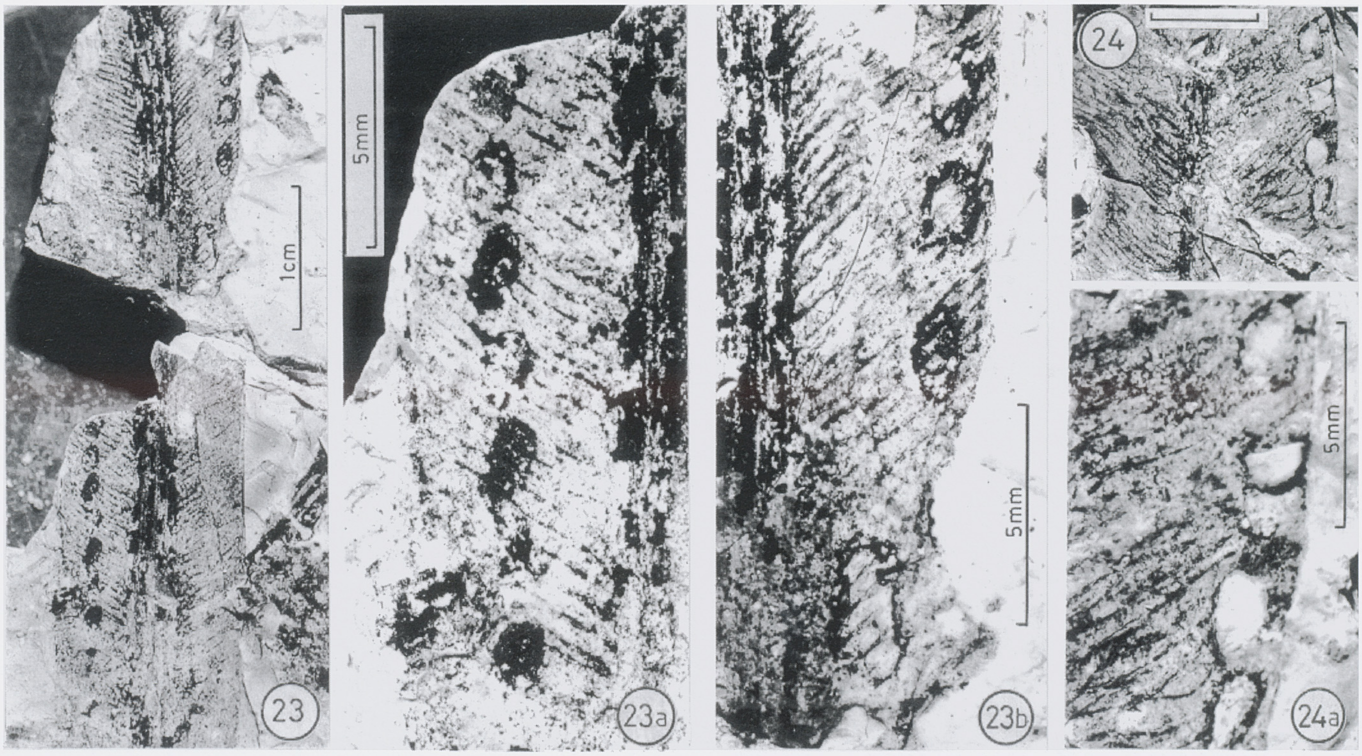

Fig.23-24 - Supposed insect eggs on or in *Taeniopteris angustifolia* leaves from the Middle Lettenkohle (Upper Ladinian) of Wasselonne (Bas-Rhin, Alsace, France). 23) Portion of a leaf showing series of oval scars longitudinally arranged on each side of the leaf. 23a) Enlargement of the scars visible on the lower part, at left, of Fig.23. Note their slightly oblique arrangement, half-way between the midvein and the margin of the leaf. 23b) Enlargement of the scars visible on the upper part, at right, of Fig.23. Note that the oval scars are close to the leaf margin; one basal scar with irregular outline is half way between the midvein and the leaf margin. Note also that they are crossed more or less transversally by the lateral veins. 24) Small portion of a *Taeniopteris* leaf showing several ovoid bodies longitudinally arranged along the leaf margin (scale = 5mm). 24a) Enlargement of the ovoid bodies seen in Fig.24.(from Grauvogel et al., 1992)

– or they correspond to the traces of fossil eggs, the specimens showing an insect-plant host interaction.

The hypothesis pertaining to «megasporophylls» in the specimens from the Lettenkohle of Alsace is based on their resemblance with fertile *Taeniopteris* leaves from the Lower Permian of Kansas (USA) attributed to *Phasmatocycas kansana* (Gillespie & Pfefferkorn, 1986). These fertile leaves indeed show contiguous ovules arranged on each side of the midvein. Nevertheless there is an ambiguity, since two kinds of arrangement have been noted by these authors. In most of the leaves, the ovules which are elongate oval and clearly display their micropylar extremity, are arranged perpendicularly to the midvein, with their long axis perpendicular to the leaf axis. These ovules are clearly attached on each side of the midvein. However, in one of the specimens (Gillespie & Pfefferkorn, 1986, Pl. 2 fig. 3) the oval scars are arranged end to end, along the leaf margin, with their long axis parallel to the leaf midvein and leaf margin, which is a quite different orientation. Gillespie and Pfefferkorn noticed this difference and wondered if these longitudinal scars represented immature ovules. This specimen differs from the others, but greatly resembles those from the Lettenkohle of Alsace.

The investigation of these specimens shows several features which seem to indicate that the longitudinally arranged oval scars or ovoid bodies do not represent the trace of ovules:

– they do not show the traces of a micropylar structure

– the arrangement of the scars is variable, either very close to the leaf margin or half-way between it and the midvein. Likewise, they are either very close to one another or more separated.

– the longitudinal orientation of the scars suggests that they have no relation with the midvein or the lateral veins and that therefore they were not vascularized like the transversally oriented ovules in *Phasmatocycas, Sobernheimia* or *Spermopteris* (Fig. 25)

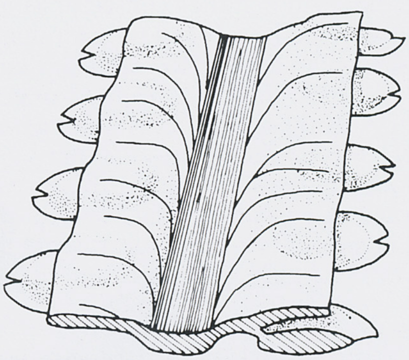

Fig.25 - Spermopteris coriacea, a pteridosperm fertile leaf from the Upper Pennsylvanian of Kansas. Note that the ovules are arranged perpendicularly to the midrib (redrawn after Cridland & Morris, 1960)

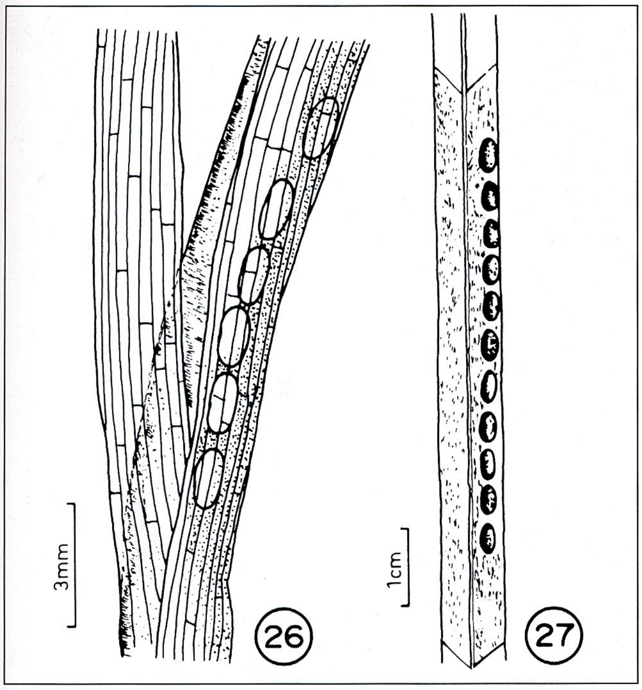

Fig.26-27 - Oviposition of present-day Dytiscidae (Coleoptera). Note the longitudinal arrangement, end to end, of the oval eggs. 26) Series of eggs of *Agabus* laid under sheathing of leaf of *Glyceria plicata* (redrawn after Hinton, 1981). 27) Series of eggs of *Colymbetes* on a *Carex* leaf (redrawn after Wesenberg-Lund, 1913).

(Cridland & Morris, 1960; Mamay, 1976; Kerp, 1983; Gillespie & Pfefferkorn, 1986).

As a result, one can speculate whether these oval scars, arranged end to end along the leaf margin, their long axis parallel to the leaf axis, might not represent the trace of insect eggs. However, the question is to determine whether these eggs were inserted in the leaf tissue or glued on their surface.

At the present-day, various kinds of insects lay their eggs in one line either in the leaf tissue or at the leaf surface. The Odonata species, *Aeshna juncea* (Aeshnidae, Anisoptera), inserts its eggs in *Carex*-leaves, arranging them in one line, end to end and parallel to the leaf axis (Jacobs & Renner 1988, p. 451 Fig. 0-9). The dimensions of these eggs are similar but the broad oval shape of those in the *Taeniopteris*-leaves does not fit with that of the endophytic Odonata eggs which are always elongate oval with one extremity more tapering. Coleoptera such as the Dytiscidae also lay their eggs in one line (Fig. 26, 27) along the leaves of aquatic plants (Wesenberg-Lund, 1913a; Hinton, 1981). Some of them (*Colymbetes, Agabus, Rhantus*) lay their eggs on dead, floating leaves whereas others (*Dytiscus, Ilybius, Agabus*) lay them inside the leaves, their long axis parallel to the leaf margin. Only the eggs of *Colymbetes* and *Agabus* have an oval shape which resembles that of the scars of the *Taeniopteris* leaves. However Dytiscidae are not known from the Triassic (Wootton, 1988). Some Mexican tettigoniids also arrange their eggs like seeds in one row along the edge of the leaves (Hinton, 1981). The resemblance in shape and arrangement of these insect eggs to ovules might be a protective device comparable to those known for several insect groups (Hinton, 1981).

The Triassic galls: cecidogenous insect-host plant interactions

The number of gall types presently known on earth is estimated to be approximately 15,000, among which 14,750 develop on angiosperms (Meyer, 1987). They are diverse and induced by a wide variety of insects (Dreger-Jauffret & Shorthouse, 1992). Fossil galls, especially older than Tertiary, are very poorly known and the cecidogenous agents generally remain hypothetical (Larew, 1992).

The oldest gall which seems to have been caused by an insect has been discovered on the Conifer *Aethophyllum stipulare* from the Grès à Voltzia (Upper Buntsandstein) in the northern Vosges, France (Grauvogel-Stamm, 1978; Larew, 1992). Further abnormal growths have been found on *Voltzia*, another widespread conifer of this ecosystem. They are described below.

Stem gall on *Aethophyllum stipulare* (conifer)

This conifer which is the only herbaceous one known, shows very clearly a spindle-shaped swelling on one of its fertile axes (Fig. 28, 28a, b). Moreover, the development of the male cone ending this axis has been strongly restrained. Compared with the normal one terminating a slender axis, which is mature and full of bisaccate pollen grains, this aborted cone remained very small but shows clearly the long delicate apices of its numerous microsporophylls. The inhibitory action of the gall was rather late as it only prevented the final ripening of this cone.

According to Larew (1992), this structurally simple gall was probably induced by an insect. At present, such stem galls are caused by Coleoptera, Cecidomyiidae (Diptera), Tenthredinidae (Hymenoptera), bacteria and fungi. Among the insects, only the Diptera and the Coleoptera are known from the Grès à Voltzia. The oldest true Diptera (*Grauvogelia arzvilleriana*) has recently been described from this formation (Krzeminski et al., 1994). The Hymenoptera, on the contrary, are not known in the Upper Buntsandstein of the Vosges. However, Symphyta (Hymenoptera) have been described from the Triassic of Asia (Rasnitsyn, 1964).

Among the Coleoptera which presently induce stem galls with swellings, there are species of the family Cerambycidae, such as *Saperda populnea* which attacks poplars and willows (Jacobs & Renner, 1988 Fig. C-49). Other modern Coleoptera such as the Buprestidae also induce stalk swellings, the species *Agrilus champlaini* on *Ostrya* (Borror et al., 1981) or *Agrilus chrysoderes* var. *rubicola* on raspberries (Meyer 1987, p. 191). Cerambycidae are not known in the Triassic but Buprestidae have been recorded from the Triassic of Australia (Carpenter, 1992).

Stem gall on *Voltzia* (conifer)

Voltzia is another conifer from the Upper Buntsandstein of the Vosges (France) on which a stem-gall has been discovered. One of the numerous collected twigs shows a rather marked swelling of the


a
b
10cm
28


1cm
28a


1cm
28b


1cm
29


1cm
30


1cm
31

stem surrounded by modified needles (Fig. 31). These needles are longer, straighter and thicker than those on the sound stem. At first glance this gall resembles the pineapple gall found to-day on the twigs of *Picea excelsa* and which is induced by two species of Adelgidae, Homoptera (*Adelges laricis, A. abietis*). In fact they differ, since in this modern gall the stem as the needle bases are only strongly swollen (Rohfritsch, 1971; Rohfritsch & Anthony, 1992).

At the present-day, nearly all the conifers are host plants for aphids whereas the pteridophytes (ferns, horsetails, lycopods), the cycads and the ginkgoales only rarely constitute host plants for these entirely plant-feeding insects (Eastop, 1973). In some aphid groups, like the Cinarinae, all the species are restricted to conifers. According to Eastop (1973), «aphids were living on the Coniferae at about the time angiosperms appeared». In the Triassic which preceded this time, conifers were widespread and often the dominant plants in the ecosystems, such as in the Grès à Voltzia. The oldest aphids (*Triassoaphis*) are known from the Middle Triassic of Australia (Evans, 1956).

Other growth anomalies on *Voltzia* (conifer)

a) Abnormal *Voltzia* twig: proliferation of buds and shoots

Among the leafy twigs of *Voltzia* originating from the Grès à Voltzia, there is a bifurcated one, in which the two branches strongly contrast one another. Whereas one branch is devoid of ramification, the other one shows a series of small lateral buds and vegetative sprouts which seem quite abnormal (Fig. 30). This anomaly suggests a growth of the witches' broom type corresponding to a loss of growth control which is generally produced by bacteria or fungi (Dreger-Jauffret, 1980; Meyer, 1987).

b) Crooked *Voltzia* twig

The apex of the *Voltzia* twigs and branches is generally straight. However among the numerous collected specimens, one shows a crook-shaped extremity with two terminal buds (Fig. 29). The twig is moreover hypertrophied. This abormality is difficult to interpret. Present-day caterpillars of the family Tortricidae (Lepidoptera) cause such abnormalities at the extremity of the conifer twigs (Jacobs & Renner, 1988) but the Lepidoptera did not exist in the Triassic (Carpenter, 1992).

Triassic Tettigoniidae (Orthoptera) and mimicry

Mimicry is another kind of plant-insect interaction (Scott & Taylor, 1983; Taylor & Scott, 1983; Scott & Patterson, 1984; Scott et al., 1992), which has been recognized in the Triassic of western Europe. The discovery in the Grès à Voltzia of the Vosges (France) of Orthoptera wings, *Triassophyllum leopardi*, which belong to the family Tettigoniidae, possibly to the sub-family Pseudophyllinae, raised the question of their adaptive resemblances to plants (Papier et al., in press). These new Orthoptera wings combine two features, a specialized vein arrangement and a characteristic colour pattern, which, both seem to be mimetic.

The venation of *T. leopardi* resembles that of the present-day Tettigoniidae of which the forewings are similar to angiosperm leaves. Like in these plants, the reticulate venation consists of areoles and veinlets ending blindly in them. Moreover, due to its central position, the radial vein looks like the midvein of a leaf.

The colour pattern which consists of black, irregular, multilobate stains inside of each areoles is another very striking feature of these wings, probably more apparent than the angiosperm-like venation.

These two supposed mimetic features led us to inquire into the model and mimicked leaves. None of the plants which have been found in the Grès à Voltzia (Grauvogel-Stamm, 1978; 1991; Grauvogel-Stamm & Grauvogel, 1980) shows a venation resembling that of an angiosperm-like plant. Likewise, none of the pollen grains of the palynological association from the Grès à Voltzia of the Vosges, France (Adloff & Doubinger, 1969), resembles that of an angiosperm. Although some paleobotanists suggest that the flowering plants already appeared in the Triassic, there is no clear evidence for this and it is generally admitted that they arose in the Cretaceous (Crane, 1993; Stewart & Rothwell, 1993; Taylor & Taylor, 1993; Doyle & Donoghue, 1993; Palmer, 1994). Therefore one can wonder about what is the significance of these mimetic features whereas the model (angiosperm) does not yet seem to exist.

Fig. 28-31 - Galls and other growth abnomalities from the Grès à Voltzia of the Vosges (France). 28) *Aethophyllum stipulare*, an herbaceous Conifer showing two male cones, one mature and normally developed (arrow a), enlarged in Fig.28a, and the other which is aborted (arrow b) as a result of a stem gall (enlarged in Fig. 28b) Arzviller (Moselle, France) (from Grauvogel-Stamm, 1978). 29) Crooked twig of *Voltzia*, another Conifer from the Grès à Voltzia. Hangviller (Moselle, France). 30) Bifurcated *Voltzia* twig of which one branch bears a proliferation of vegetative buds and shoots, resembling a witche's broom. Arzviller (Moselle, France). 31) *Voltzia* twig showing a strong swelling on its stem and a modification of its needles which probably represents a stem gall. Vilsberg (Moselle, France).

CONCLUSIONS

Fossil evidence of plant-insect interactions exists from the Silurian and their diversifications are known to occur in the early Devonian, late Carboniferous and mid-Cretaceous (Scott et al., 1992). The oldest evidences concern mainly feeding on plants.The earliest record of wood-boring traces comes from the early Carboniferous and those of leaf eating and leaf mining are from the late Carboniferous. Although most of the other links between plants and insects, for example shelter and reproduction, are presumed to have existed from the Carboniferous, they are known mostly from the Cretaceous when angiosperms appeared.

As noted in the literature, there is an absence of data for plant-insect interactions in the Triassic. The study presented here greatly contributes to filling this gap. It shows that the insect-plant interactions in the Triassic of Europe were already well diversified 230-240 million years ago and that most of them resemble those of the present day. As demonstrated in this paper, herbivory traces, mimicry, relations between insect reproduction and host plants and interactions between gall inducing insects and host plants already existed in the Triassic. Evidence of both endophytic and exophytic insect oviposition is documented, for the first time, showing the role played by fossil plants in fossil insect reproduction. Until now, only the role played by insects in the evolution of plant reproduction through pollination was known. These data strongly increase the known diversity of fossil plant-insect relationships.

Like today, the plant-insect interactions played a major role in the dynamics of the fossil ecosystems. The great differences between the styles of interaction noticed in the Triassic ecosystems studied here lead us to enquire into the reasons for their distinctiveness. The interactions observed in the Upper Buntsandstein of the Vosges (France) mostly consists of galls and abnormal growths induced by insects in the plants whereas the Lower Keuper of Franconia (Germany) and the Middle Lettenkohle of Alsace (France) contain mainly evidences of leaf-feeding and plant-aided insect reproduction. It is moreover surprising that the outcrops which contain numerous insects do not provide any feeding traces on the associated plants and that those which yielded obvious feeding traces bear nearly no insect remains. Likewise, it is enigmatic that the outcrop which afforded a Protodonata wing does not contain any traces of their endophytic oviposition and that those which gave numerous traces of their eggs did not yield any specimen of this giant dragonfly. Nevertheless, comparison of the paleoentomofauna and plant-insect interactions of these ecosystems, in the light of present-day insect oviposition habits, permits the thesis that the Protodonata were still well established in the Triassic.

The lack of clear herbivory traces in the Grès à Voltzia may suggest that the phytophagous insects were not autochtonous. The fragmentary state of most of the insects would also corroborate this hypothesis. However, the presence of remains as fragile as Blattodea exuvias, for example, seems to demonstrate the contrary. Possibly some insects were autochtonous whereas others were not. Another possibility is that both scavenger and carnivorous insects prevailed in the Grès à Voltzia and that the number of phytophagous insects increased in the Keuper. The floristic change in the Ladinian, characterized by the emergence of the Cycadopsida, and the simultaneous appearance of numerous feeding traces on these new plants also suggest a process of plant/insect co-evolution. These plants developed attraction mechanisms which forged several links with the insects, such as feeding and shelter for the eggs in *Taeniopteris angustifolia*. On the other hand, the appearance of mimetic Orthoptera (Tettigoniidae) having wings with angiosperm-like venation and leopard-like colouring led us to inquire into the significance of these mimetic features for the process of plant-insect co-evolution. All these observations illustrate the dynamics of the Triassic ecosystems but they also show their complexity and the difficulties of interpretation.

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