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LEAF FEEDING TRACES FROM THE UPPER PLIOCENE FOSSIL LAGERSTÄTTE OF WILLERSHAUSEN, LOWER SAXONY, GERMANY

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ABSTRACT. The Upper Pliocene flora of the Willershausen fossil Lagerstätte was examined for leaf feeding traces. 4509 well preserved angiosperm leaves were examined. Traces were observed on 19% of leaves, a figure greater than in older Tertiary floras. Traces were treated from an ichnological perspective. "Dispersed" and "Undispersed" feeding strategies were recognised, these included; bud and feeding on developing foliage, mining, galling, continuous and interrupted marginal feeding. Gregarious and co-operative feeding on single leaves was also observed. Trace vulnerability varied dramatically between different host leaves.

KEY WORDS: Herbivory, ichnotaxonomy, trace fossils, plant-insect interactions, Tertiary, Pliocene

INTRODUCTION

The Upper Pliocene Willershausen Fossil Lagerstätte in the Harz Mountains of Lower Saxony has been known since the early part of the century. The site was used as a clay and sand pit until 1975, being declared a National Monument in 1977. The fossils are preserved in finely laminated marls interpreted as lacustrine in origin. The Willershausen lake was formed through collapse of the underlying Triassic Sandstones and dissolution of Permian evaporites (Meischner & Paul 1977). The water in the Willershausen lake was sharply stratified. Dissolution of the underlying Permian evaporites produced an anoxic and stenohaline environment excluding most life. The absence of bioturbation and inhibition of microbial activity enhanced the preservation potential of flora and fauna (Briggs. *et al*. 1977). The Willershausen biota includes more than 500 species. The fauna is dominated by crayfish and insects. The flora is dominated by hilly woodland taxa.

HISTORY AND CLASSIFICATION OF WILLERSHAUSEN FEEDING TRACES

Straus (1977) described a total of seventy different forms of leaf feeding traces from Willershausen. No quantitative data for trace abundance was collected. Three approaches were adopted for their classification. (1) The majority of the traces were attributed to modern leaf miners and gallers. Direct analogy was used to classify traces. (2) Form genera were also erected. The primary diagnostic characters in both these classifications schemes was the trace host. These appproaches only work if a trace possesses a number of unique or a combination of distinct morphological characters. Constrained host specificity and absence of identical traces created by similar or extinct tracemaker lineages was also assumed. (3) marginal, non-marginal and skeletonisation (including window feeding) traces were described as formal ichnotaxa. Ichnotaxonomy assesses the morphological the morphological characters of a trace which reflects the behaviour of the tracemaker. Ichnotaxonomy allows the frequency and diversity of leaf feeding traces to be assessed from an ethological perspective. This approach was adopted in this study.

TRACE ABUNDANCE AND FEEDING STRATEGIES AT WILLERSHAUSEN

4509 leaves from the Georg-August University Institute and Museum for Geology and Palaeontology, Gättingen were examined for traces. Traces were grouped by category into marginal (Pl. 1, figs c-g), non-marginal (Pl. 1, figs a-c) and skeletal feeding (Pl. 1, fig. h; Pl. 2, figs a-b), mining (Pl. 2, figs c-f) and galling (Pl. 2, figs g-i) traces. Traces were found on 19% of the leaves, a figure greater than that of aolder Tertiary floras examined using the same methodology (Stephenson 1991, Titchener 1998). The preservation of a number of taphonomically sensitive feeding traces, such as shallow bloch mines preserving frass (Pl. 2, fig. c), atests to the absence of extensive taphonomic filtration (Titchener

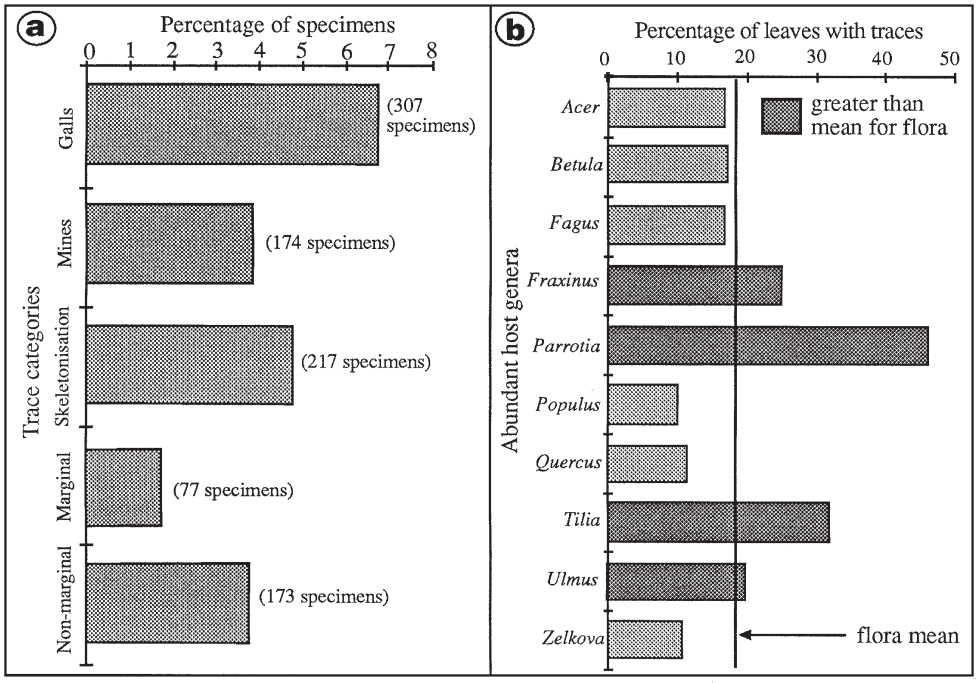

Fig. 1. **a** – Percentage of leaves exhibiting non-marginal, marginal, skeletonisation, mining and galling traces from the Göttingen collection of the Willershausen flora. **b** – Percentage of leaves exhibiting feeding traces from the ten most abundant (>40 specimens) genera from the Göttingen collection of the Willershausen flora

1998). Exhaustive collection methods also ensured a minimum of bias (see also Titchener 1998). Collection of small fragments and specimens of limited host taxonomic use were abundant. As a result cross-taxonomic host and trace variation could be examined. Non-marginal traces were most common, skeletonisation next, with galled and marginal traces occurring in similar abundance (Fig. 1a). Mined leaves were rarest (Fig. 1a). Ten host genera were present in abundance (>40 specimens) (Fig. 1b) accounting for 67% of the leaves. Hosts were observed to possess widely ranging vulnerabilities to herbivory (Fig. 1b). It is beyond the scope of this work to produce detailed and exhaustive systematic ichnotaxonic descriptions of the feeding traces observed at Willershausen (this will be undertaken by the author at a later date). Instead the feeding strategies, as reflected by trace morphology and distribution of the most important traces, are noted. The majority of the the feeding traces exhibited a "dispersed" strategy (75%) (Pl. 1, figs a-b, d-e, g-h; Pl. 2, figs a). The overall damage is distibuted across the whole leaf or a number of leaves. Explanations for this include, response to wound induced chemical changes, larval dispersal to avoid competition and predator avoidance (Titchener 1998). The effects of induced chemical defenses are evident in the form of interrupted marginal traces (Schowalter *et al.* 1986). Damage camouflage behaviour, scalloping leaf margins to produce the illusion of an undamaged leaf, is also possible (Schowalter *et al.* 1986) (Pl. 1, fig. e). Feeding on immature leaves occurs, distortion of the venation and lamina are produced as the leaf continues to grow (Pl. 1, fig. g). "Undispersed" strategies were rarer (25%). Host specificity through immunity to chemical defenses and gregarious feeding and mass attack to overcome facultative defenses are all possible (Schowalter *et al.* 1986). Gregarious and co-operative feeding in small larvae to puncture the leaf cuticle is also present (Pl. 2, fig. b).

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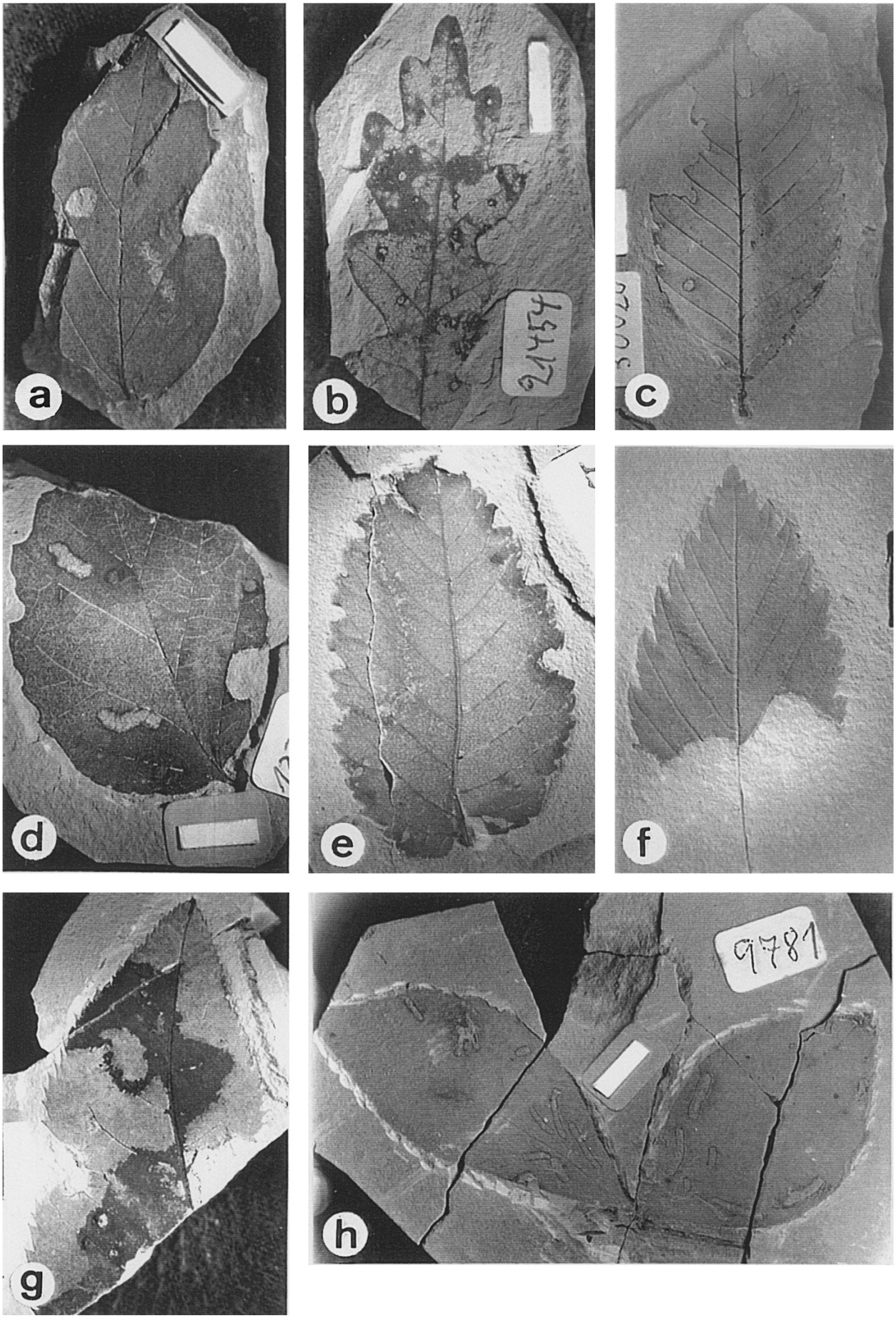
PLATES

Plate 1

a. *Parrotia* sp., specimen 12231, non-marginal feeding trace, 1 cm scale bar
b. *Quercus praeerucifolia* Straus., specimen 21454, non-marginal feeding traces, 1 cm scale bar
c. Undetemined host., specimen 30020, continuous marginal trace and two non-marginal traces, 1 cm scale bar
d. *Parrotia* sp., specimen 13386, semi-circular marginal trace and skeletonisation, 1 cm scale bar
e. Undetermined leaf., specimen 23389, interrupted marginal trace, 1 cm scale bar
f. *Zelkova* sp., specimen 38482, leaf partially stripped to the midrib, 1 cm scale bar
g. Undetermined leaf., specimen 11710, marginal trace created during leaf developement causing leaf mutation, 1 cm scale bar
h. cf. *Laburnum* sp., specimen 9781, window feeding traces, 1 cm scale bar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c
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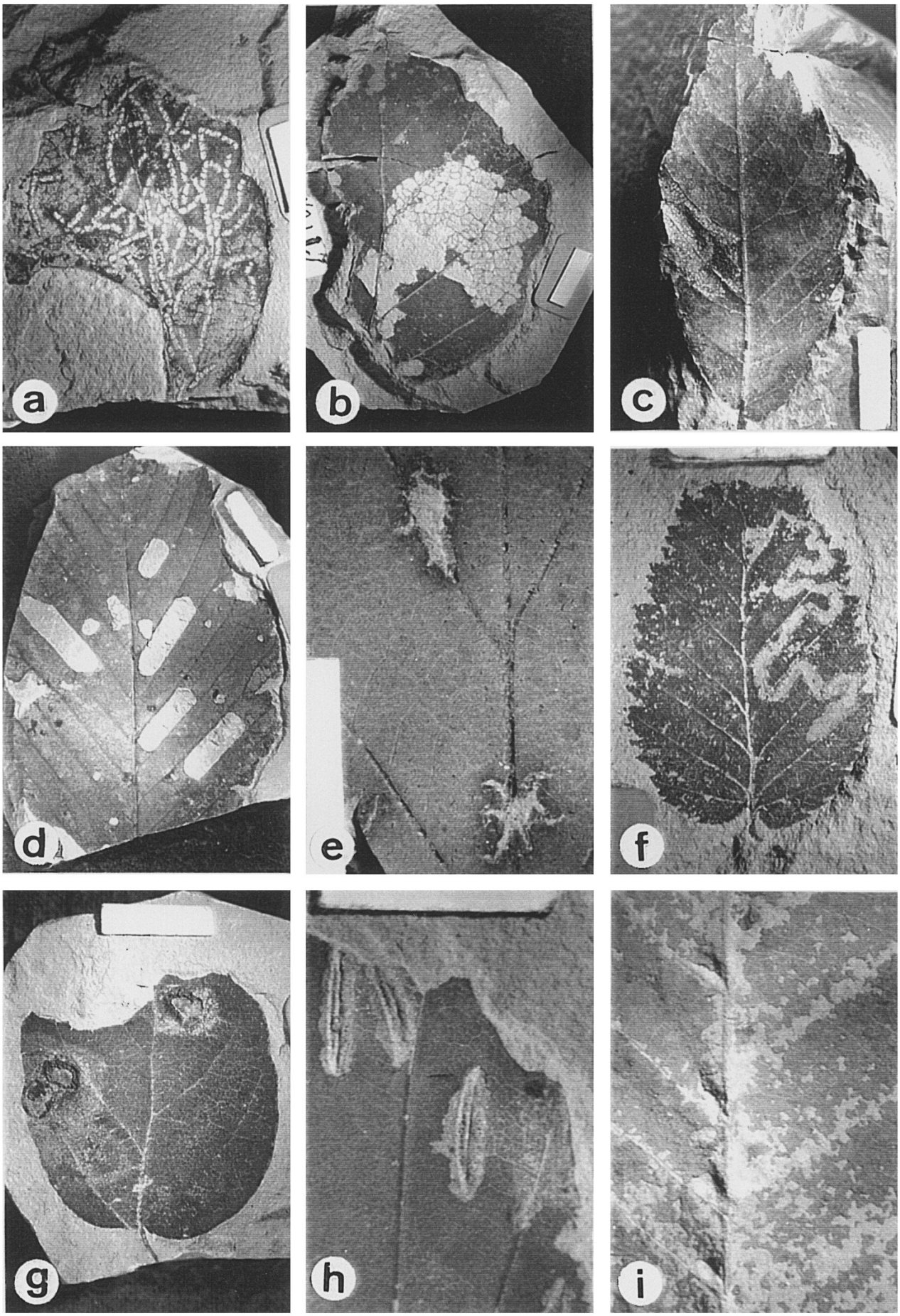
Plate 2

a. *Parrotia* sp., specimen 10626, “dispersed” skeletonisation, 1 cm scale bar
b. *Parrotia* sp., specimen 21482, “undispersed” skeletonisation site of co-operative feeding?, 1 cm scale bar
c. *Zelkova* sp., specimen 24175, blotch mine with mass of frass arranged centrally, 1 cm scale bar
d. *Fagus* sp., specimen 21926, trace of an abscissed or mechanically destroyed blotch mines, 1 cm scale bar
e. *Sorbus torminalis* L., specimen 12724, frass free digitate leaf mines, 1 cm scale bar
f. *Carpinus orientalis* Mill., specimen 22763, frass free sinuous mine with a slightly expanded terminal chamber, 1 cm scale bar
g. *Parrotia* sp., specimen 13156, three leaf galls, 1 cm scale bar
h. *Fagus* sp., specimen 21979, three leaf galls, 1 cm scale bar
i. *Alnus* sp., specimen 3201, paired axil galls, 1 cm scale bar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