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
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 feeding traces exhibited a “dispersed” strategy (75%) (Pl. 1, figs a-b, d-e, g-h; Pl. 2, figs a). The overall damage is distributed 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).

REFERENCES


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. Undetermined 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 development causing leaf mutation, 1 cm scale bar
h. *cf. Laburnum* sp., specimen 9781, window feeding traces, 1 cm scale bar
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