

The oldest plant-insect interaction in Croatia: Carboniferous evidence



Ed A. Jarzembowski

Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China; (jarzembowski2@live.co.uk)

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ABSTRACT

The feeding trace *Phagophytichnus ekowskii* VAN AMEROM, 1966 is recorded on *Taeniopteris carnotii* ZEILLER, 1888, a cycadopsid leaf, from the Lika mudstone (Upper Kasimovian-Gzhelian) of Croatia. The distribution and occurrence of this ichnogenus and species are discussed and comparison made with occurrences on *Taeniopteris angustifolia* (SCHENK, 1927) in the Upper Landinian of Germany. Recent analogues are considered of the possible producer and an orthopteroid insect is suggested.

Keywords: Pennsylvanian, Ladinian, *Phagophytichnus ekowskii*, cycadopsid, *Taeniopteris carnotii*, chewing

1. INTRODUCTION

The Carboniferous System and especially the Pennsylvanian Subsystem provides fossil evidence of the first major radiation of the winged insects, the dominant subclass of the Insecta (GRIMALDI & ENGEL, 2005). The record comprises various body- and some trace fossils found in finer-grained deltaic sediments (JARZEMBOWSKI, 1987). Insect fossils are, however, generally uncommon when compared with the abundance of plant compressions. Nevertheless, examination of the latter can reveal evidence of insect activity. In this contribution, the first discovery from the Croatian Pennsylvanian of the ichnospecies *Phagophytichnus ekowskii* VAN AMEROM, 1966, on the leaf of the cycadopsid *Taeniopteris carnotii* ZEILLER, 1888, is described and discussed. Animal folivory on leaves is known from the Croatian Miocene (ĐEREK & JAPONDŽIĆ, 2010), but this find is considerably older (c.~290 Ma).

2. GEOLOGY

The tectonic belt of Mt. Velebit and Lika is the best known and most completely developed Upper Palaeozoic outcrop in Croatia, showing more or less continuous sedimentation from the Middle Pennsylvanian (Moscovian) to the end-

Permian (Changhsinghian) (Jasenka Sremac pers. comm., 2011; JAPONDŽIĆ, KRIZMANIĆ, POLJAK & MJEDA, 2005). Upper Kasimovian-Gzhelian sediments are extensive, recording the rhythmic oscillations of sea-level fluctuation. Fossiliferous marine sediments predominate over sporadic beds of continental origin, the shoreline having never been far away. Plant compression fossils occur in grey mudstones in the Lika Region from which the trace fossil is described below. The Lika find is compared with Upper Ladinian material from Germany found in fluvial sediments and associated with a low sea-level stand (GRAUVOGEL-STAMM & KELBER, 1996).

3. SYSTEMATIC PALAEONTOLOGY

Ichnogroup *Phagophytichnidea* VASILENKO, 2007b
Ichnosubgroup *Phagophytichnida* VASILENKO, 2007b
Ichnofamily *Phagophytichnidae* VYALOV, 1975
Ichnosubfamily *Phagophytichninae* VYALOV, 1975
Ichnogenus *Phagophytichnus* van AMEROM, 1966

Remarks. *Phagophytichnus* is a long-ranging ichnogenus of marginal leaf-biting species and usually considered to be the result of insect chewing (as opposed to gastropod rasping (by land snails/slugs), RETALLACK, 2001: p. 137).

Originally referred to the Cibichnia or feeding (eating) traces, *Phagophytichnus* was then included in Praedichnia, trace fossils of predation, but more recently moved to Phagophytichnidea, feeding traces on plants (VASILENKO, 2007b), and even been given its own family, Phagophytichnidae (VYALOV, 1975). ZHERIKHIN (2003) previously placed *Phagophytichnus* in Trogichnia reserved for chew marks on plants.

Evidence that the living plant was predated is provided by a pronounced thickening (ridge) sometimes seen along the damaged margin and interpreted as callus ('scab') formation (see figure of damaged leaf of the pteridosperm *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute & Zodrow from the late Asturian of England in ATTENBOROUGH, 2005: p.167). This was previously interpreted as leaf mining (MÜLLER, 1982).

Distribution. *Phagophytichnus* has been described from the Late Mississippian to the Pliocene and has a worldwide distribution (IANNUZZI & LABANDEIRA, 2008; BRUSTUR, 1997). It also represents the most common type of external foliage feeding in the fossil record (LABANDEIRA, 2006).

The inclusion of small holes in ginkgoalean foliage from the Lower Cretaceous, however, overstretches the generic limits of *Phagophytichnus* (WATSON, LYDON & HARRISON, 2001). These traces are Trogichnia or Nygmichnia (chewing or piercing marks respectively) following ZHERIKHIN (2003, tab. III), the latter not included in VYALOV (1975). Like *Phagophytichnus*, these marks are both included in Zherikhin's 'redundant' Phagophytichnia: Phyllophagichnia (leaf and petiole damage). For ease of reference, I propose to call them porichnid (from the ancient Greek poros, hole, and Latin ichnus, trace) within Vasilenko's Phagophytichnida pending a more detailed study.

***Phagophytichnus ekowskii* VAN AMEROM, 1966**

(Pl. 1, Figs. 1–2)

= *Cuniculonomus* (*Arcophionomus*) *undulatus* MÜLLER, 1982

= Damage Type 12 (LABANDEIRA, WILF, JOHNSON & MARSH, 2007)

Diagnosis: An approximately semicircular, isolated excision (cut out) of the leaf margin which is shallow or deep but less than 180 degrees of arc (LABANDEIRA et al., 2007).

Description and Measurements: The Lika trace fossil is cusped excisions (overall length c. 2 cm, width 3 mm) from the margin of the leaf of *Taeniopteris carnotii* ZEILLER, 1888 (NĚMEJC, 1936) preserved as a compression in mudstone (Pl. 1, Figs. 1A–C). It comprises 2 to 3 semicircular, asymmetrically curved, successive and separate excisions, each of which is up to 9 mm long, and all approaching the midpoint of the distance between the leaf margin and midvein.

Material (figured), locality and date: Specimen 1 (Pl. 1, Figs. 1A–C). *Registration number:* 10776. *Repository:* Geology-Palaeontology Department, Croatian Museum of Natural History. *Locality* Lika Region, east of Mt. Velebit, Croatia. *Age:* Stephanian C (late Kasimovian to Gzhelian).

Specimen 2 (Pl. 1, Fig. 2). *Registration number:* SCHL-061a. *Repository:* Kelber Collection. *Locality:* Scheerich, Franconia, Germany. *Age:* Lower Keuper, Upper Landinian.

Remarks. The Lika ichnofossil (Upper Pennsylvanian, c. 305 Ma) is of a similar size to marginal excisions on *Taeniopteris angustifolia* (SCHENK, 1927) from the late Middle Triassic (c. 230 Ma) of Scheerich, Germany (cf. GEYER & KELBER, 1987: fig. 7, lower left and KELBER & GEYER, 1989: pl. 2, figs 3, 5; also KELBER & GAYER, 1989: figs 4, 6, another specimen). One of these Triassic leaves, however, figured herein is extensively eaten (Pl. 1, Fig. 2) with successive marks (KELBER & GEYER, 1987), although a new find shows two widely spaced excisions, one comparatively small (STEINKERN, 2011). Both Carboniferous and Triassic specimens are similar in that their location is away from the midvein of the leaf and occurrence along one margin. The Triassic material has been only tentatively referred to *Phagophytichnus* (GRAUVOGEL-STAMM & KELBER, 1996), but like the Lika specimen, can be referred to *P. ekowskii*, as currently diagnosed.

In the absence of cuticular studies, *Taeniopteris carnotii* may be a cycad or a bennettite within the Class Cycadopsida Barnard & Long (cf. CLEAL & REES, 2003), and possibly a synonym of *Taeniopteris multinervis* Weiss, 1869 (Chris Cleal, pers. comm., 2012).

Distribution (range and occurrence): *Phagophytichnus* was originally based on *P. ekowskii* found on the pteridosperm *Mixoneura* Weiss (*Mixoneura wagneri* Lorenzo nec *Neuropteris praedentata* GOTHAN; CASTRO, 1997), from the Spanish Stephanian B (VAN AMEROM, 1966).

The stratigraphic range of *P. ekowskii* was subsequently extended from the Late Mississippian to the late Triassic and the host range extended to various other pteridosperm genera including: *Autunia* Krasser, *Dicroidium* Gothan, *Glossopteris* Brongniart, *Macroneuropteris* Cleal, Shute & Zodrow, *Neuropteris* Brongniart *Paripteris* Gothan, *Odontopteris* (Brongniart) Sternberg, *Pursongia* ZALESSKY, *Triphyllopteris* SCHIMPER, and the ginkgopsid *Dejerseya* Herbst (IANNUZZI & LABANDEIRA, 2008; LABANDEIRA, 2006; LABANDEIRA & ALLEN, 2007; TROUT, LABANDEIRA & CHAPMAN, 2000; VASILENKO, 2007a). VASILENKO (2007b) recorded it (as *P. ekowskii*) on ferns and pteridosperms as late as the Cretaceous (Cenomanian), but he referred bite (chew) marks on other gymnosperms (conifers and ginkgos) to the ichnogenus *Pinovulnus* VASILENKO, although the smaller *Pinovulnus serpentiformis* Vasilenko resembles *P. ekowskii* and there may be some overlap (cf. VASILENKO, 2006, fig. 5 and Pl. 1, Fig. 1). He was evidently following ZHERIKHIN's (2003) classification based on plants rather than functional-feeding groups. As for geographic range, *Phagophytichnus ekowskii* is now worldwide (Laurasia + Gondwana), being known from Euramerica to Australasia (LOBUE & HASIOTIS, 2010; SRIVASTAVA & AGNIHOTRI, 2011; PREVEC et al., 2009). In addition, it is formally recorded on cycadopsid leaves (*Taeniopteris* species) from the Upper Pennsylvanian of Croatia and Middle Triassic of Germany herein.

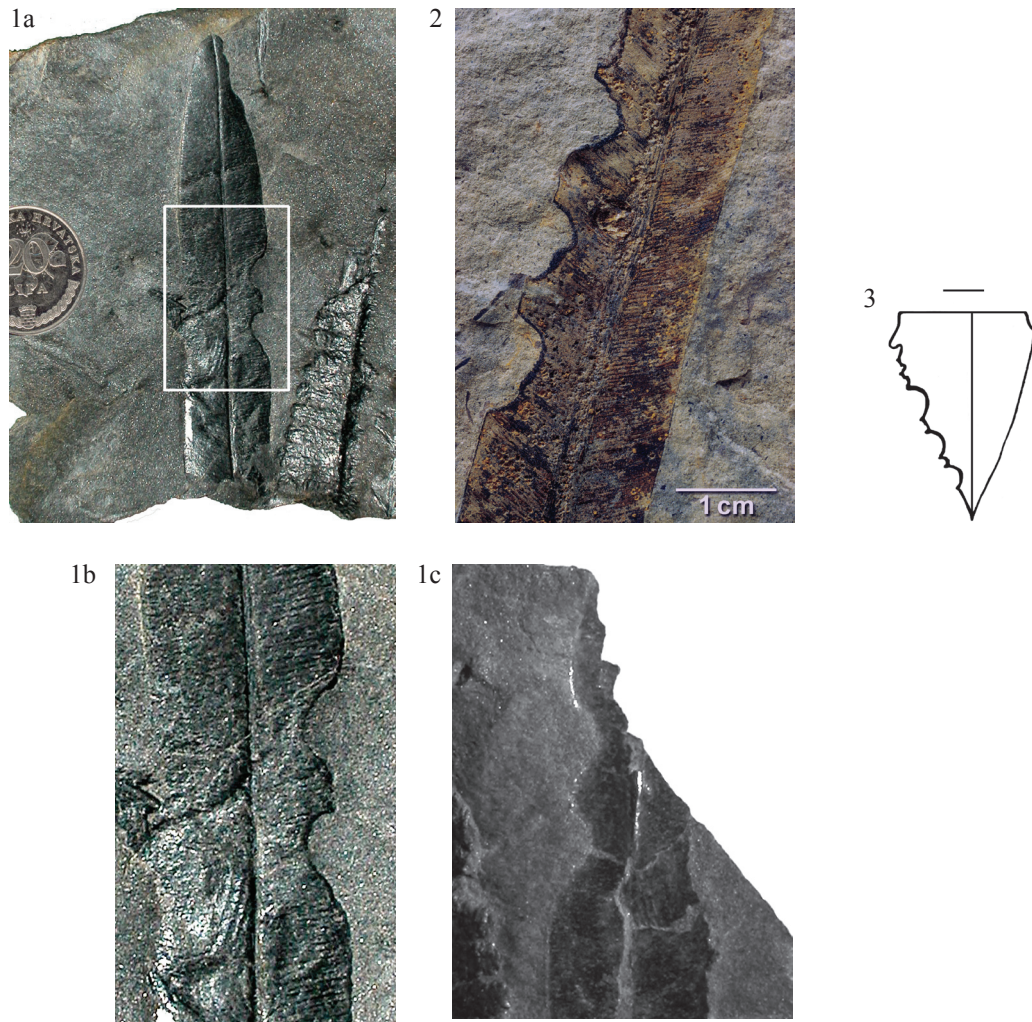


PLATE 1

Phagophytichnus ekowskii on *Taeniopteris carnotii*, Lika.

1a – part, middle right. The undulation in the leaf margin (top right) is sedimentary. Scale: 20 lipa coin, 18 mm diameter;

1b – close up of part in a;

1c – close up of counterpart.

2 – *P. ekowskii* on *Taeniopteris angustifolia*, SCHEERICH. Note callus formation.

3 – *Psophus stridulus* on *Taraxacum officinale*, recent. Scale line, 1 cm. Redrawn after KAZAKOVA (1985).

Attribution: LABANDEIRA et al. (2007) attributed this isp. to protorthopteran/stem-orthopteroïd insects, whilst allowing that other mandibulate (jaw-bearing) arthropods might be involved (diplopod millipedes), whereas GU, BÉTHOUX & REN (2011) stressed a preference for carnivory in these insect groups. GEYER & KELBER (1987) and KELBER & GEYER (1989) considered that holometabolous insects, especially the caterpillars of Lepidoptera (moths and butterflies) could also be responsible for this isp. as well as orthopteran (grasshoppers and crickets). Body fossils of Lepidoptera are known by the Lower Jurassic and Hymenoptera (sawflies, ants, bees and wasps), which also have a caterpillar larva, are known by the Upper Triassic although Orthoptera are known from the Pennsylvanian onwards (JARZEMBOWSKI, 2003). Millipedes are not considered to be a significant defoliator to-

day but orthopteran are a large and diverse order with herbivorous and carnivorous forms (KEY, 1970). A bush cricket-like insect may therefore have been responsible for the feeding damage on European *Taeniopteris*, although it is unlikely to be always the same species due to a significant time gap (~c. 75 Ma) between the Lika and Scheerich leaves, and an unknown stem-holometabolan might be involved. BECK & LABANDEIRA (1998) also recognised orthopteroïd damage on *Taeniopteris* sp. from the Early-Middle Permian of the USA differing from *P. ekowskii* in including leaf holes as well as marginal feeding, but supported by the presence of vein strands as produced by recent short-horned grasshoppers. The latter are also present in chew marks on leaflets of *Anomozamites villosus* POTT, McLOUGHLIN, WU & FRIIS, 2012, a newly described cycadopsid from the Middle Jurassic of

China (pers. obs.). Examination of the Lika leaf under magnification was however inconclusive, revealing irregularities along the margin, but also embedding in an obscuring, grainy matrix (but see gross cf. below).

4. RECENT ANALOGUE

Grasshoppers and caterpillars are unrelated insects but share mandibulate (basic chewing) mouthparts. Modern lepidopteran (butterfly) caterpillars are known to defoliate some cycads, such as the Cycad Blue (*Theclinesthes onycha* HEWITSON) in Australia. Cycads are no longer native to Europe, but I have often observed caterpillars feeding on angiosperms in southeast England. The caterpillar's numerous paired legs are used to hold on to the leaf, often tenaciously. As in other mandibulate insects, the paired jaws are orientated beneath the anterior part of the head capsule and the edge of the leaf is harvested in a sideways cutting motion. The head moves progressively forwards and downwards, sometimes obliquely, to obtain purchase and then access to fresh tissue. This would produce a curved excision as seen on the fossil leaves. Slight body movements coupled with a break in feeding, often due to a disturbance, result in an excision with subordinate cuspules evident (cf. KELBER & GEYER, 1989: fig. 4; also, GRAUVOGEL-STAMM & KELBER, 1996: fig. 6). The insect may resume feeding, or move on allowing wound reaction (callus) tissue and subsequent drying out to form a thickening inside the damaged margin as seen on fossils (e. g. Pl. 1, Fig. 2). My observations on bullace (*Prunus insititia* L.) point to this thickening of the callus being a gradual process, taking weeks to form a feature prominent enough to be readily seen on compression leaves. This could explain the apparent absence of callus in *P. ekowskii* in JARZEMBOWSKI (2004: pl. 1, fig. 3).

Bush crickets are less easy to watch, but such a great green 'grasshopper' fed on lettuce showed broadly similar chewing behaviour (MICHAËL, 2011). GANGWERE (1966) discussed feeding in more derived orthopteroids (acridiid grasshoppers): interestingly, some of the chew marks produced by the rattle grasshopper (*Psophus stridulus* (L.)), a recent forbivorous European species, show a comparable outline to the Lika fossil (Pl. 1, Fig. 3). Modern land snails, such as *Helix aspersa* (Müller), can also form marginal incisions and holes in leaves by rasping downwards and sideways with their radulae. Terrestrial molluscs are scarce in the Carboniferous-Triassic of Europe, but have been found in Middle Pennsylvanian nodules with plants and insects in the Upper Silesian Coalfield and in the Middle/Upper Pennsylvanian of the English Midlands, investigated during IGCP 469 (STWORZEWICZ, SZULC & POKRYSZKO, 2009). Where known, the affinities of Carboniferous European snails (ellobioid and *Cerion*-like, loc. cit.) suggest that they fed on detritus or non-vascular plants by analogy with recent thorn and peanut snails rather than the leaves discussed herein. The situation is similar in the Late Pennsylvanian of North America, such as at Joggins, in Newfoundland, also investigated during IGCP 469 (FALCON-LANG, BENTON, BRADDY & DAVIES, 2006; molluscan detritivory rather

than folivory (leaf feeding) was also suggested by SOLEM & YOCHELSON, 1979). In the absence of slime trails and coprolites, stereo-electron microscopy on well-preserved fossil plants may help to distinguish the work of biting mandibles from rasping radulae in future studies.

5. CONCLUSION

Phagophytichnus ekowskii provides fossil evidence for a long- and wide-ranging, generalised feeder with low host specificity, principally on pteridosperm leaf margins. GRAUVOGEL-STAMM & KELBER (1996) considered *Phagophytichnus* on *Taeniopteris*, however, as part of a novel insect-plant interaction on Mesozoic Cycadopsida following the Permo-Triassic extinction event. The Lika find shows that the *Phagophytichnus-Taeniopteris* association is considerably older, dating back to the late Palaeozoic (Upper Pennsylvanian). Insects are otherwise unknown from the Croatian Carboniferous and this discovery also helps to fill a gap in the Pennsylvanian record of southeast Europe. Its rarity is, however, not surprising because *Taeniopteris* was likely more resistant than pteridosperms to insect attack due to the cycadopsid's tougher cuticle and well-developed resin glands (BECK & LABANDEIRA, 1998). In contrast, the hirsute leaves of *Macroneuropteris* may have only slowed down chewing (ATTENBOROUGH, 2005, figure p. 167).

IGCP 575 is concerned with environmental change at the Middle/Upper Pennsylvanian transition. The Lika Flora needs to be examined further to determine the extent of insect herbivory, the current data predicting higher rates of pteridosperm folivory by insects unless carnivory was widespread. A search for associated fauna may provide clues to a more precise identification of the consumer.

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