

The possibility of ice in the cavities of the rocks is not refuted by this argument, which applies only when there is enough ice to lubricate the contacts between rocks. However, if the maria are mostly soil and rock, then Urey's delta problem remains.

A possible solution to the delta problem is the suggestion (8) that dense ash flows may carve the sinuous rills and may then be transformed into a dilute phase in which they are essentially dust-laden gas clouds. In this phase they are capable of spreading widely and dropping their load as a thin layer on the maria. Jaffe (9) has postulated the existence of such a layer for quite different reasons.

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Fossil Mycelium with Clamp Connections from the Middle Pennsylvanian

Abstract. A mycelium with clamp connections and chlamydospores has been discovered within the wood of a Middle Pennsylvanian fern. This suggests that forms extant in the middle of the Pennsylvanian had life cycles comparable to some modern Basidiomycetes.

Hyphae found in the wood of a Middle Pennsylvanian coenopterid fern *Zygopteris illinoensis* (Andrews) Baxter, have clamp connections, structures which immediately identify a mycelium as belonging to the class Basidiomycetes. The fossil hyphae are similar to extant saprophytic Basidiomycetes

(Fig. 1, compare A to G with H to K).

The numerous clamp connections formed on the fossil hyphae (Fig. 1, A and B) resemble comparable structures formed by living Basidiomycetes (Fig. 1H). The best preserved clamp connections have two septa; one within the hypha at the base of the clamp, and the second closing the clamp connection hook. Infrequently, a hyphal branching occurs from the clamp connection itself (Fig. 1C). Similar wall orientation and branching occur in extant hyphae (Fig. 1H). In some fossil material there are hyphae having clamp connections in which the hook of the clamp does not form a complete union with the

hypha (Fig. 1D). These structures resemble pseudoclamps (I) which are produced, under cytogenetic control, with common-B matings of extant basidiomycete mycelia (Fig. 1I). The fossil specimens have globose swellings which are short, unicellular portions of the hyphae characterized by rounded lateral walls which are noticeably thicker than those of the remaining mycelium. Often, septa without clamp connections occur adjacent to the area of swelling. These unicellular, swollen structures may be borne singly in a terminal position (Fig. 1G) and either singly or in chains in an intercalary position (Fig. 1, E and F). These struc-

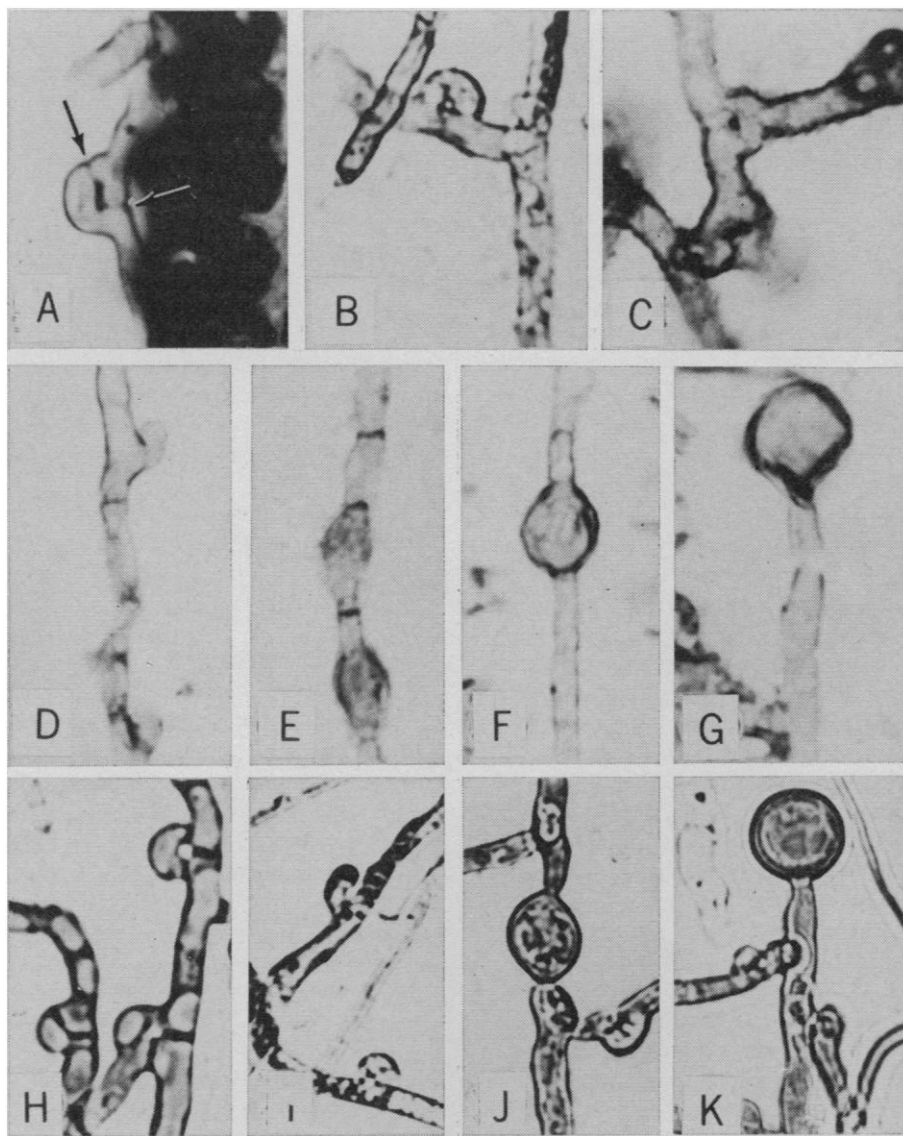


Fig. 1. Fossil specimens from the Pennsylvanian and extant structures of *Panus tigrinus* comparable to fossil forms. (A) Clamp connection with well-preserved end walls indicated by arrows. (B) Typical clamp connection and branching hypha. (C) Hypha branching from clamp connections. (D) "Pseudoclamps." (E) Chain of intercalary chlamydospores. (F) Solitary intercalary chlamydospore. (G) Solitary terminal chlamydospore. (H) *Panus tigrinus*, typical clamp connections and hypha branching from clamp connection. (I) *Panus tigrinus*, pseudoclamps. (J) *Panus tigrinus*, intercalary chlamydospore. (K) *Panus tigrinus*, terminal chlamydospore.

tures resemble chlamydospores (asexual resting spores) produced in secondary mycelia of extant forms such as *Panus tigrinus* (Fig. 1, J and K). In the extant forms the spores are either homokaryotic or dikaryotic with simple septa.

The clamp connection, a structure which insures that sister nuclei from a conjugate division of a dikaryon become separated into daughter cells, is an integral part of the basidiomycete life cycle. Because of this special function, the clamp connection is direct evidence of the existence of a secondary stage, the dikaryotic stage, in the life cycle. Furthermore, the presence of clamp connections is now thought to be a structural characteristic confined to this class (2). The observation (3) of clamp connections in the mycelium of the ascomycete *Tuber lapiceum* is not substantiated (4).

Unfortunately, the fossil record has offered little specific information about the earliest occurrence and evolution of the Basidiomycetes. There are numerous reports of Mesozoic and Tertiary Basidiomycetes, including one report of clamp connections preserved in wood from a Baltic amber sample (5). The exact age of this material has not been determined, but it is thought to range between the Late Eocene and Early Oligocene (6).

A recent review lists the oldest known occurrences of mycelial specimens ascribed to the Basidiomycetes (7). However, most specimens are poorly preserved remains from the Pennsylvanian and are of uncertain affinities. Some, such as *Excipulites* Geoppert, consist of structureless spots on various kinds of Paleozoic foliage (8). Others, such as *Pseudopolyporus carbonicus* Hollick (9) and *Dactyloporus archaeus* Herzer (10), although grossly resembling Basidiomycetes, lack pertinent cellular detail. Another possible basidiomycete, *Archagaricon bulbosum* Hancock & Atthey, is illustrated as a branching mycelium having intercalary swellings but lacking definitive basidiomycete features (11). *Polyporites bowmanni* Lindley and Hutton has been identified as a fish scale (12). *Teleutospira milloti* (13) is often cited as a rustlike basidiomycete from the Carboniferous. However, published illustrations do not convincingly demonstrate this. The best preserved rustlike material is *Anthracomycetes cannallensis* Renault, which has branching mycelial strands with terminal conidia-like spheres (14). Poor preservation and absence of

definitive structures in previously described Pennsylvanian forms makes it impossible to regard any of these as indisputable Basidiomycetes. Thus, the presence of the Basidiomycetes in the Paleozoic has remained an open question (15).

These fossil specimens provide the first convincing evidence of Basidiomycetes in the Paleozoic Era. The presence of clamp connections in the fossil material does not support recent suggestions that this structural feature indicates an advanced phyletic position and is of relatively recent origin among the Basidiomycetes. Apparently saprophytism arose among the Basidiomycetes much earlier than has been supposed. The presence of clamp connections and saprophytism are thought to be features of advanced Basidiomycetes (15). If one wished to support this supposition, the occurrence of these features in Middle Pennsylvanian time should place the origin of the Basidiomycetes considerably earlier.

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References and Notes

1. Pseudoclamps are identified in living hyphae by the presence of a nucleus which is trapped within the incomplete clamp connection. The structures present in the fossil specimens, although lacking nuclei, are best interpreted as pseudoclamps rather than immature normal clamp connections since production of these latter structures occurs in an extremely short time. It is highly improbable that intermediate stages of such a brief developmental process would be preserved.
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Hoabinhian: A Pebble-Tool Complex with Early Plant Associations in Southeast Asia

Abstract. The term "Hoabinhian" has been applied to "mesolithic" assemblages from all parts of mainland Southeast Asia. Recent excavation in north Thailand has yielded the first associated carbon-14 dates and provided evidence for the early (about 7000 B.C.) domestication of plants in Southeast Asia.

The term "mesolithic" has been applied (1) to a number of prehistoric, Southeast Asian assemblages thought to be artifacts of post-Pleistocene food collectors. On mainland Southeast Asia the term "Hoabinhian" is almost synonymous with mesolithic. Until recently Hoabinhian assemblages have been ill defined and undated (2).

In attempting a local sequence which would bracket the transition between the Hoabinhian and early food-producing in at least one area (3), I located Spirit Cave (4), a small limestone rock-shelter (20°N by 98°E) approximately 60 km north of the Thai provincial center of Mae Hongson, northwest Thailand.

The central shelter, located 600 m up the face of a limestone cliff overlooking a part of the Salween drainage system, has a floor area of approximately 25 m². Surface and subsurface animal disturbances were encountered. The general stratigraphic layers, however, formed distinct horizons over the total excavated area. A 1.5-meter grid was constructed over the shelter floor; 1-meter squares were excavated, with natural strata as units of vertical control. Balks (50 cm) were left in place until all squares had been excavated; they were then lifted to provide intersecting profiles across the deposit. Owing to internally complex stratigraphy and local ash lensing several squares were excavated in 8 to 12 layer units. All "excavation layers" were then correlated across the site (Fig. 1).

Five general layers are represented in the Spirit Cave deposit, and we may speak of this overall layer stratigraphy and soil horizons together. Each layer in Fig. 1 has differing soil characteristics. Layers 2 to 4 may represent one cultural group with the different soil horizons representing varying occupational patterns. The interface between layer 2 and layer 1, and layer 1 itself, both evidence a culture contact situation.

Layers 4, 3, 2a, and 2 may be