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KARINOPTERIS, A FOSSIL PTERIDOSPERM FROM THE "PAPER" COAL OF INDIANA

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INTRODUCTION

To many people, the concept that organisms evolve seems patently absurd. The opponents of evolution have argued 1) that morphologically distinct groups of organisms (created kinds) were independently created; 2) that genealogical descent and modification can be traced within created kinds (microevolution) but not between created kinds (macroevolution); and 3) that there are no known modern or fossil taxa that are morphologically intermediate between major groups. Their argument is that evolution is simply a belief and not an experimentally supported hypothesis (that is, a theory). If evolution is presented as a simple fact without giving the students concrete examples to work with, the students may have trouble deciding if the scientific viewpoint is correct. One method of supporting the study of evolution is to have your students work with real fossils in the laboratory. A number of suggestions will be offered in this paper that will allow you to develop a laboratory exercise for your students dealing with easily obtainable fossil plant remains from the Middle Pennsylvanian of Indiana. The laboratory exercise will not require extensive field work nor an extensive fossil collection.

Central to the laboratory exercise will be the maceration of an Indiana "paper" coal and the isolation of a Middle Pennsylvanian pteridosperm, *Karinopteris* sp., from it. During the Middle Pennsylvanian, two major groups of pteridosperms existed—the Medullosaceae and the Lyginopteridaceae (Stewart, 1983; Taylor, 1981). Members of the Medullosaceae generally have several vascular bundles in the stem (they are polystelic except for the genus *Quaestora*), have longitudinal

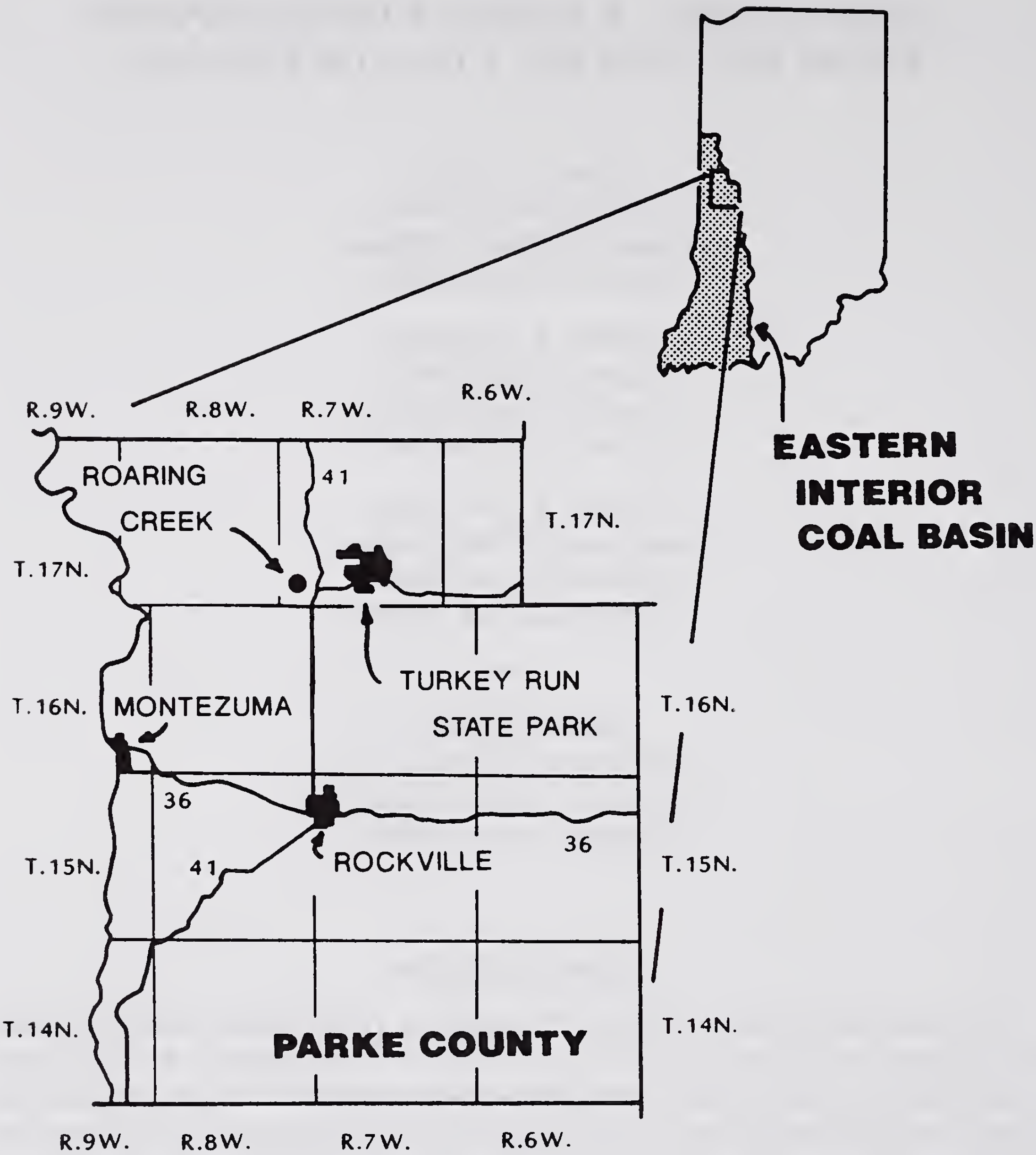

FIGURE 1. The location of Parke County and Roaring Creek in the Eastern Interior Coal Basin.

sclerotic bundles in the cortex, and have numerous traces scattered throughout the petiole. Members of the Lyginopteridaceae have a single vascular cylinder in the stem (they are monostelic), have transverse sclerotic bars in the cortex, and have one major petiolar trace after fusion. In both groups, the rachis (leaf axis) divides (bifurcates) into two major sections (a bipartite leaf). The presence of transverse sclerotic bars in the cortex indicates that *Karinopteris* has affinities with the Lyginopteridaceae, possibly to the structurally preserved *Schopfiastrum* (DiMichele, *et al.*, 1984).

A laboratory exercise based on *Karinopteris* will be unique in two ways. First, the pteridosperms (seed ferns) are completely extinct today. The last pteridosperms became extinct during the Permo-Triassic as lowland climates dried out approximately 225 million years ago. Second, although paper coals having different compositions and ages are known from Russia, Germany, France, and

Australia (DiMichele and Dolph, 1981), the paper coal of Indiana is the only reported coal of this type in the United States. As a result, your students will be working with an extinct group from a unique type of deposit.

PENNSYLVANIAN STRATIGRAPHY OF INDIANA

Rocks containing *Karinopteris* are found in west-central Indiana (Parke County) associated with coals along the eastern edge of the Eastern Interior Coal Basin (Figure 1). The Pennsylvanian rocks of the Eastern Interior Coal Basin in Indiana are confined to the following three Groups (Shaver, *et al.,* 1986):

1. McLeansboro Group (youngest Carboniferous)
   a. Mattoon Formation
   b. Bond Formation
   c. Patoka Formation
   d. Shelburn Formation
2. Carbondale Group
   a. Dugger Formation
   b. Petersburg Formation
   c. Linton Formation
3. Raccoon Creek Group (oldest Carboniferous)
   a. Staunton Formation
   b. Brazil Formation
   c. Mansfield Formation.

Although exposures yielding *Karinopteris* have been found throughout Parke County, Indiana, the specimens described in the literature and their geologic setting are best known from the valley of Roaring Creek. The paper coal at Roaring Creek comes from above coal C (the Upper Block Coal) in the Brazil Formation (Nelson, *et al.,* 1985). The most productive coals mined in Illinois and Indiana are found higher in the section in rocks of the Carbondale Group.

DEPOSITION AT ROARING CREEK

The exposed bedrock at Roaring Creek (7 1/2′ Wallace Quad., SW 1/4, Sec. 32, T 17N, R 7W) has been mapped by Nelson, Eggert, DiMichele, and Stecyk (1985; Figure 2). The following discussion of the deposition at Roaring Creek is taken largely from their account. The subsurface geology is currently being studied by the Indiana Geological Survey (Eggert, personal communication).

A major erosional surface (unconformity) exists in Indiana between rocks of the Mississippian and Pennsylvanian. Near the end of the Mississippian, the landscape changed gradually due to either uplift or a global sea level drop, followed by erosion of the surficial rock layers, in some places down to Devonian rocks. This created a deeply channelized surface (Bristol and Howard, 1971, 1974; Howard, 1979) in which stream aggredation occurred. Relief of up to 30 m was common on this erosional surface. Viewed from the northeast to the southwest, the Pennsylvanian topography changed from an upland to alluvial valleys and finally to a deltaic plain. Streams flowed across the area from the northeast to the southwest from a northeastern mountanous region.

A mixture of sandstones, siltstones, shales, coal, and "underclay" represent the Middle Pennsylvanian at Roaring Creek. Marine rocks have been found re-

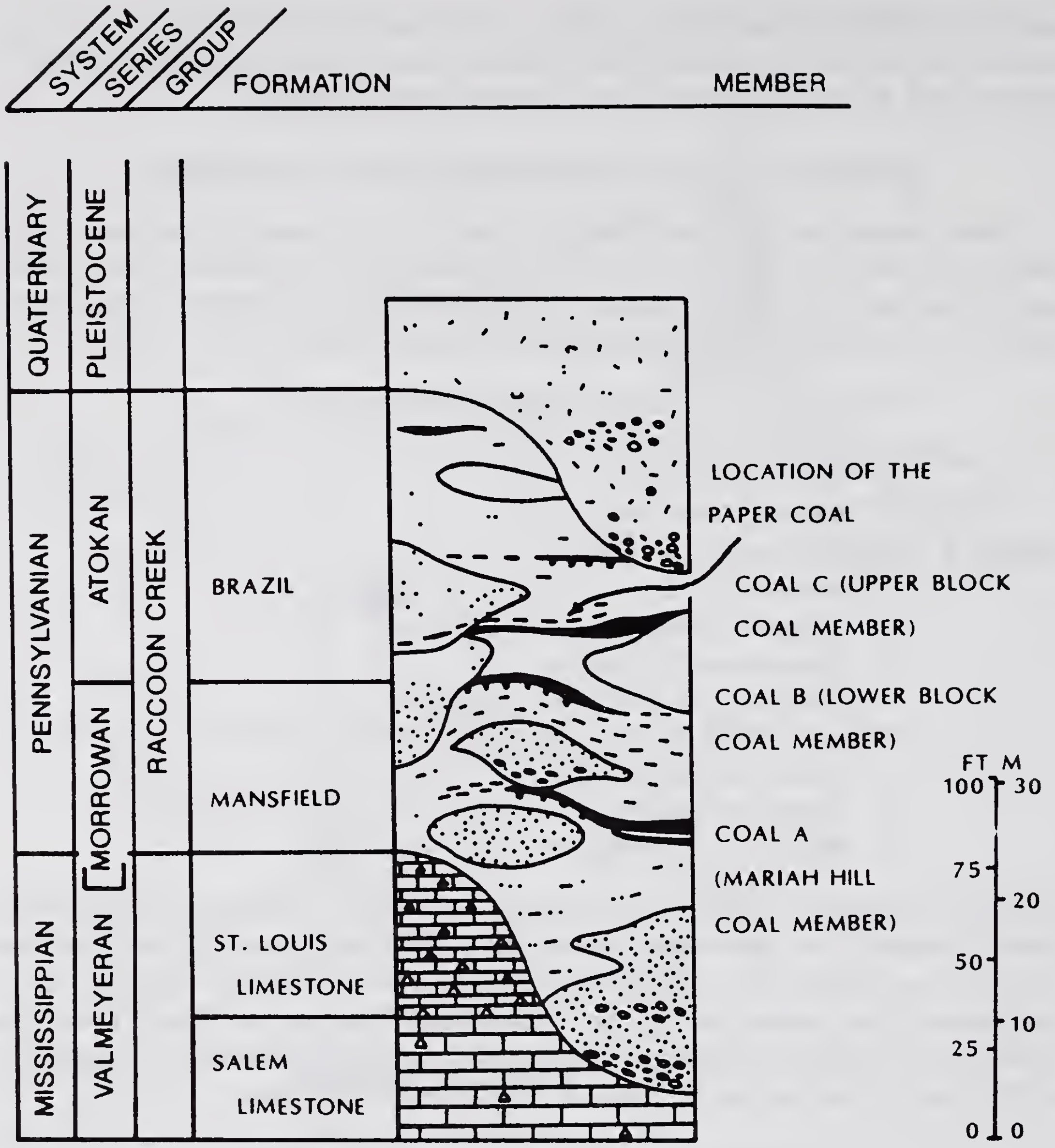

FIGURE 2. Generalized stratigraphic column from Roaring Creek (redrawn from Nelson, *et al.*, 1985).

cently (Kvale and Eggert, personal communication). The highly variable strata contrast sharply with the broad, level coal deposits formed by the younger migrating deltaic systems typical of the Middle Pennsylvanian (Carbondale Group) in much of Illinois and southwestern Indiana.

Several different depositional environments are encountered at Roaring Creek: 1) channels, 2) point bars, 3) natural levees, 4) crevasse splays, 5) floodplains (overbank deposits), and 6) swamps. In the channel sandstones, casts and coalified bark of driftwood logs are present. Crevasse splays surround upright trunks and stumps. Floodplain deposits are represented by gray shales containing numerous compression fossils. Claystone preserving rooting structures are common beneath the coal and represent ancient soils (paleosols). Alternating rooted mudstone (paleosols) and compression-containing gray shales indicate alternating periods of relative dryness and wetness.

At Roaring Creek, the swamp deposits are represented by coal seams that vary greatly throughout their extent. The three major seams are found throughout the area (Nelson, *et al.,* 1985). However, there may be some minor seams that are discontinuous. Swamps in this area of Indiana during the Middle Pennsylvanian were geographically restricted and short lived. They were subject to influxes of clastic material and erosion by stream channels. The floras are probably late Westphalian C in age, which places them in a wetter interval of the Pennsylvanian (Phillips and Peppers, 1984). Most coal seams formed on the delta plain or in coastal swamps further to the west. In Indiana, the coal seams formed along the extreme upper margin of the delta plain.

Three coals (coals A (Mariah Hill), B (Lower Block), and C (Upper Block); Figure 2) crop out in the valley of Roaring Creek and its tributaries. The ages of these coals were determined by biostratigraphic techniques based on miospore analysis (Peppers, 1979a, 1979b, 1982). The maximum thickness of coals A and B is about 0.9 m and the maximum thickness of coal C is about 0.6 m. The coal seams are not constant in elevation but may change elevation by as much as 9 m in a lateral distance of 30 m to 40 m. These differences probably resulted from a combination of differential compaction of the sediments before lithification, an irregular depositional surface in the area, and the activities of contemporaneous stream channels.

INDIANA PAPER COAL

Paper coal is found above coal C (Upper Block Coal equivalent) at some points along Roaring Creek. The texture and appearance of the paper coal will vary depending on the relative amounts of shale and cuticle present and on the amount of weathering that has occurred. Unweathered paper coal may vary from black to deep maroon in color. The clastic (shaley) component may form as much as fifty percent of the unweathered paper coal, giving it a distinct shaley cleavage. When the unweathered paper coal is split, large fragments of *Karinopteris* are visible along the bedding planes. At a weathered exposure, the papery texture will be obvious at the rock surface. Most of the clastic component will have weathered out, and the rock surface will feel like soft cloth. Cuticle exposed on the weathered surface may vary from deep brown to golden brown in color.

The paper coal consists primarily of the cuticle of the pteridosperm vine, *Karinopteris* (DiMichele, *et al.,* 1984). Previously, these cuticular fragments had been identified as *Sphenopteris bradfordii* (Neavel and Guennel, 1960) and *Eusphenopteris* (DiMichele and Dolph, 1981). When more specimens became available, their affinity with *Karinopteris* and not with *Sphenopteris* or *Eusphenopteris* became obvious.

Because cuticle is a biopolymer which is highly resistant to decay, it can be selectively concentrated in subaerially exposed plant litter (peat). The peat that lithified into coal C must have been exposed to the air at isolated sites within the original coal swamp. This exposure was responsible for the formation of the paper coal. The concentration of *Karinopteris* in the paper coal does not indicate that a monotonous stand of this pteridosperm covered the study area. *Karinopteris,* by virtue of having the thickest, most resistant cuticle of the plants in the area, was selectively concentrated during subaerial exposure of the peat. Cuticles of the other plants decayed on exposure.

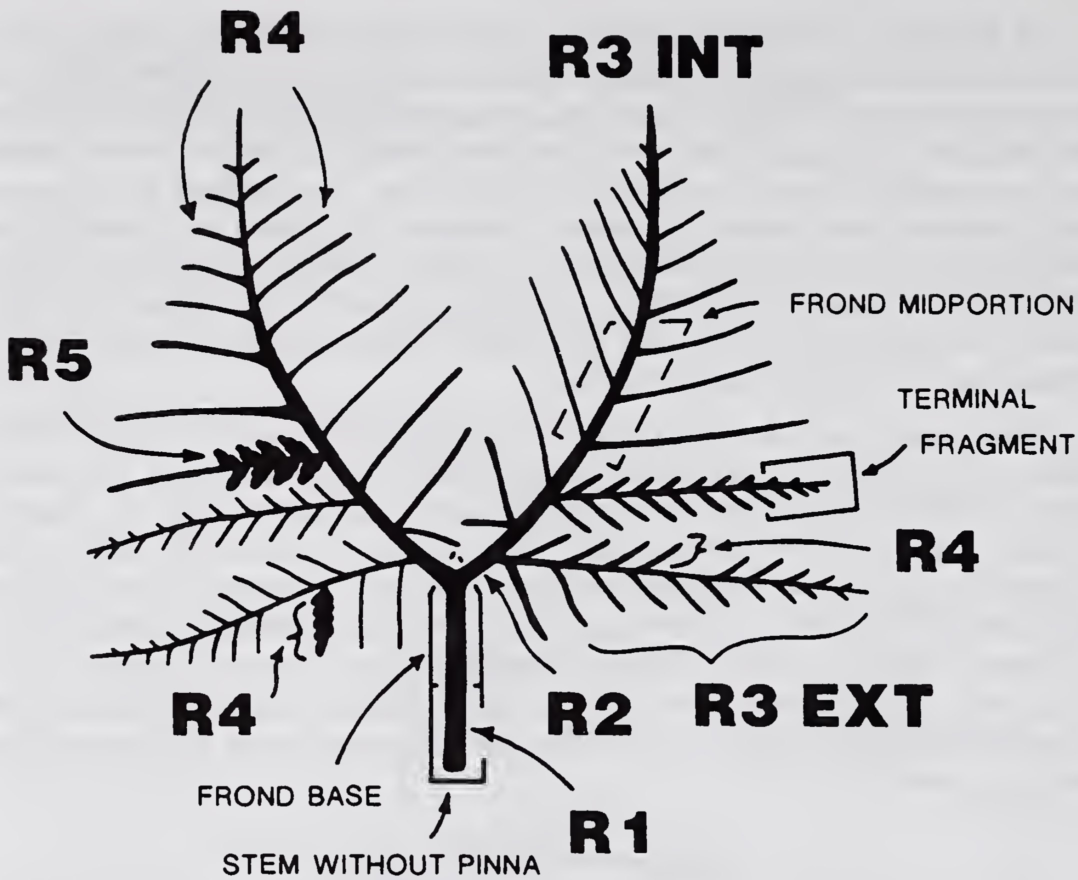

FIGURE 3. A stylized representation of the K-type frond of *Karinopteris* (redrawn from Gastaldo and Boersma, 1983a).

Nevertheless, the abundance of *Karinopteris* is unusual, because lycophytes (tree-sized relatives of modern club mosses) tended to dominate in the Euramerican peat-accumulating swamps of the Early and Middle Pennsylvanian. During the Middle Pennsylvanian in the Illinois Basin, lycophytes accounted for approximately three-fourths of the total peat volume (Phillips, Peppers, and DiMichele, 1985). Therefore, the flora from the paper coal at Roaring Creek has very little in common with typical Middle Pennsylvanian coal swamp floras found further to the west.

Other plant fossils are found in small numbers along with *Karinopteris* in the paper coal (DiMichele, *et al.*, 1984). These fossils include the lycophytes, *Lepidodendron aculeatum* and *Sigillaria brardii;* the sphenophytes (relatives of the modern scouring rush), *Calamites carinatus* and *Sphenophyllum* sp.; the pteridophyte, *Pecopteris miltonii;* the gymnosperms, *Alethopteris ambigua* (? *davreuxii*) and ? *Neuropteris obliqua;* and numerous small pteridosperm ovules. The fossil plant association supports the lithological conclusion that deposition was taking place along the coal-swamp margin. *Sigillaria* and *L. aculeatum* were characteristic of clastic, lowland areas and were rare in coal swamps. *Calamites* was most common in aggradational areas, probably along stream or lake margins (Oshurkova, 1977) and in parts of the swamp where peat was subaerially exposed (DiMichele, Phillips, and Peppers, 1985). *Alethopteris* and *Neuropteris* are foliage types characteristic of medullosan seed ferns. *Pecopteris* leaves are indicative of the presence of the marattialean tree ferns. Both the medullosan seed ferns and the marattialean tree ferns were most abundant and diverse in drier and microtopographically higher environments (clastic wetlands) than the coal swamps (Gastaldo, 1987).

A higher diversity flora is indicated by the results of spore and pollen (palynological) analysis of the coal associated with *Karinopteris*. Approximately 90 species of spores were recorded from the Roaring Creek coals (Peppers, 1979a, 1979b). The most abundant spores are associated with the arborescent lycophytes and marattialean tree ferns (DiMichele and Dolph, 1981). Because pollen and spores can be transported great distances in the air before deposition, they present a much broader picture of regional vegetational composition than the plants recovered from the paper coal.

PROCEDURE

The plant remains preserved in the Indiana paper coal consist almost entirely of the fragmentary cuticles of *Karinopteris*. Little cellular material remains except for transverse, sclerotic bars in the stems and rachises of *Karinopteris*. Although some specimens can be removed directly from a bedding plane without chemical treatment, the following steps should be followed when removing *Karinopteris* from the surrounding coal and shale matrix (DiMichele, *et al.,* 1984):

1. Immense the sample in 5% KOH until the cuticles separate. This may take several weeks depending on the amount of material being macerated. (You may have some difficulty deciding when to rinse your specimens (Step 2), because the KOH turns jet black when added to the paper coal.)
2. Rinse for 5 days in gently running water.
3. Place in 5-10% H_2O_2 (suproxal) for at least one hour. Superoxyl is purchased as a 32% solution. When added to the macerate, a highly exothermic reaction occurs. This reaction should be monitored carefully, especially if a higher strength solution is used. It is preferable to use a fume hood, rubber gloves, apron, and goggles, when handling superoxyl. The total time in superoxyl will vary depending on how weathered the material is.
4. Rinse in gently running water for 48 hours.
5. Remove the cuticles that have separated and place any aggregated material back into KOH.

These steps dissolve any vitrain (coaly material) present, disrupt the clastic (shaley material) matrix, and release the cuticle. Then:

6. Hand separate the cuticle under a dissecting microscope.
7. Dehydrate the cuticle using a graded alcohol series, suspend the cuticle in your mounting medium's solvent, and mount the cuticle onto glass slides of appropriate size. No staining is necessary. The alcohol dehydration should be carried out very slowly to prevent the material from becoming folded and brittle. As an alternative, the material can also be mounted in a water soluble mounting medium such as KARO.
8. Store the excess cuticle in a 1:1:1 mixture of distilled water, glycerol, and absolute alcohol (100% ETOH).

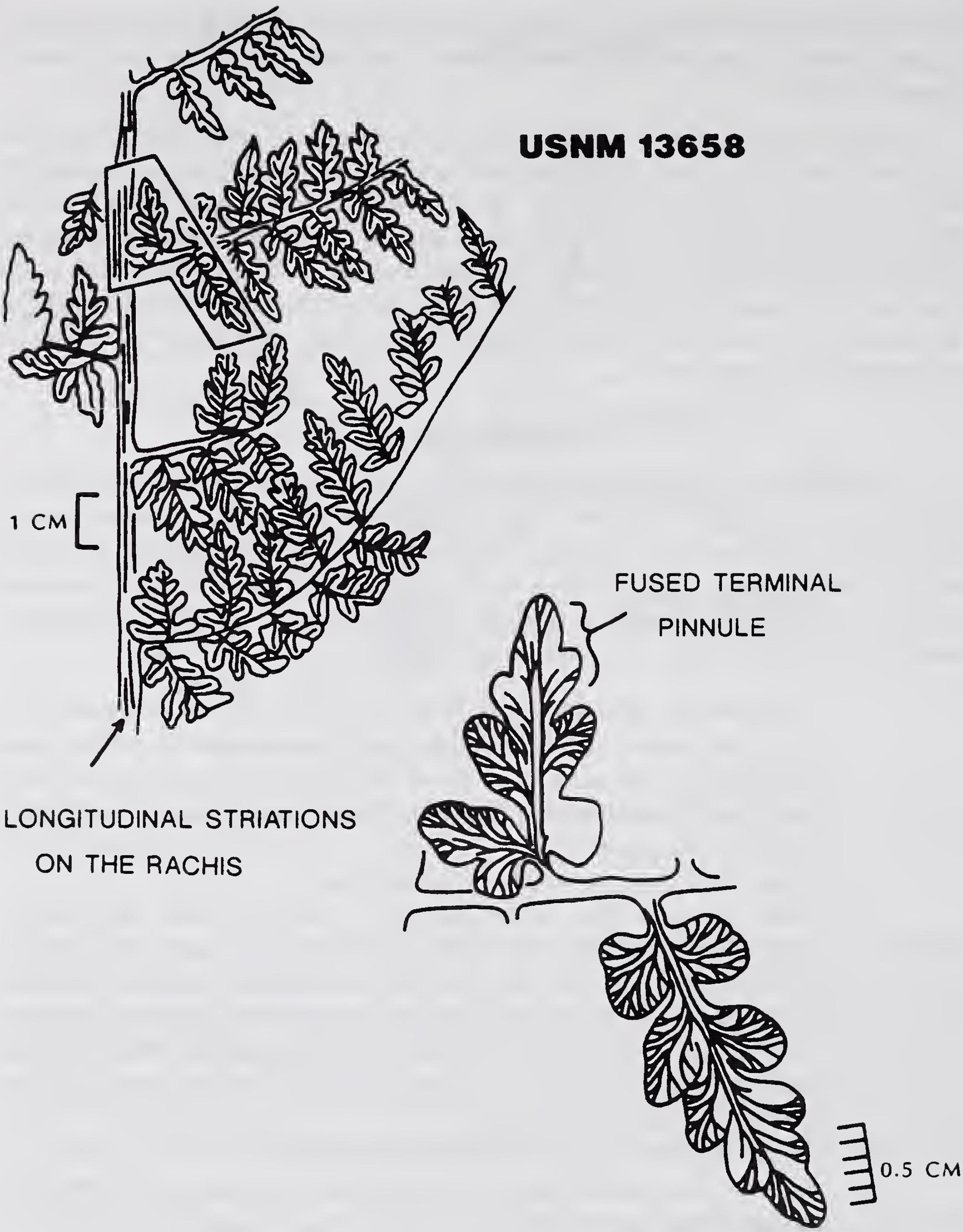

FIGURE 4. A line drawing showing a small portion of the frond of *Sphenopteris pottsvillea* (United States National Museum Specimen 13658).

K-TYPE LEAF ARCHITECTURE

A paper comparing the leaf architectures of two similar seed fern form genera, *Mariopteris* and *Karinopteris*, was published by Gastaldo and Boersma (1983a). A detailed discussion of *Mariopteris'* leaf architecture, their M-type frond (leaf), does not concern us here. However, an understanding of the leaf architecture of *Karinopteris*, their K-type frond (Figure 3), is very important to the following discussion. (The orders of karinopteroid rachial branching are normally placed in quotation marks to distinguish *Karinopteris* from *Mariopteris*. Because *Mariopteris* is not discussed in this paper, the quotation marks have been omitted.)

A primary rachis (R1) arises from the stem of the liana. Petiolar pinnules (pinnules located on the primary rachis (R1)) are not present as they are in some closely related form genera such as *Eusphenopteris* (Gastaldo, 1988). The primary rachis bifurcates (divides into two parts) to form two secondary rachises (R2). Each secondary rachis bifurcates after a short distance to form two tertiary rachises (R3). The inner tertiary rachises (R3 interior) are more strongly developed than the outer tertiary rachises (R3 exterior). Visually, the frond is divided into two distinct halves, each a mirror image of the other. Therefore, *Karinopteris* is bipartite. The tertiary rachises (R3) will bear laminate quaternary rachises (R4) and, in some cases, laminate quintuplicate rachises (R5). Each laminate rachis forms a pinna. In *Karinopteris*, each pinna bore sphenopteroid, lobate pinnules.

METHOD OF INTERPRETING *KARINOPTERIS* FROND FRAGMENTS

The most important reason for studying *Karinopteris* is that the students gain first hand experience in working with a fossil, the direct evidence of evolution. The experience may consist solely of removing material to make a single prepared slide (an approach best suited for elementary and middle schools) or it may involve reconstructing a typical frond based on the analysis of a wide range of material (an approach best suited for secondary schools and colleges). In the interest to time, some instructors might prefer to prepare the specimens themselves and only allow the students to reconstruct a typical frond.

The specimens of *Karinopteris* from the Indiana paper coals are quite fragmentary. Four types of material can be isolated (DiMichele, *et al.*, 1984): terminal frond segments, frond midportions, frond bases showing the bifurcating rachises, and stems and rachises without pinnae. These portions are blocked out on Figure 3 to allow for easy correlation between fragments and frond portions.

A comparison of the material with the reconstruction in Figure 3 should make it possible to identify the portions of the frond from which your specimens were derived. These placements can be made by determining the diameter of the largest axis of each fragment and then arranging the specimens from those having the smallest diameter to those having the largest diameter.

The terminal frond segments average about 1 mm in diameter (ranging from 0.3 mm to 2.0 mm in diameter). These terminal frond segments often can be identified by the presence of spine-like projections, which may have aided in supporting the liana in the upper level of the forest canopy (DiMichele, *et al.*, 1984). Fragments (1.5 mm to 5.6 mm in diameter) bearing lateral axes (ranchises between 1.1 mm to 2.0 mm in diameter) are from the center of the frond (frond midportions). Bifurcating rachises are rare. When found, the primary rachis averages 4.5 mm in diameter (ranging from 2.0 mm to 4.7 mm in diameter), and the secondary rachises above the bifurcation average 3.1 mm in diameter (ranging from 1.3 mm to 7.3 mm in diameter). Axes having transverse, sclerotic bars and lacking pinna may represent either the stem of the liana or the lower portion of a primary rachis. These fragments are normally between 0.75 cm and 2.0 cm in diameter. Unfortunately, if you rush your maceration, you can artificially strip a rachis of its lateral appendages, making its placement within the frond very difficult.

A study of *Karinopteris* points out the problems paleobotanists and paleontologists face when working with fragmentary fossil remains. Some fossils can be

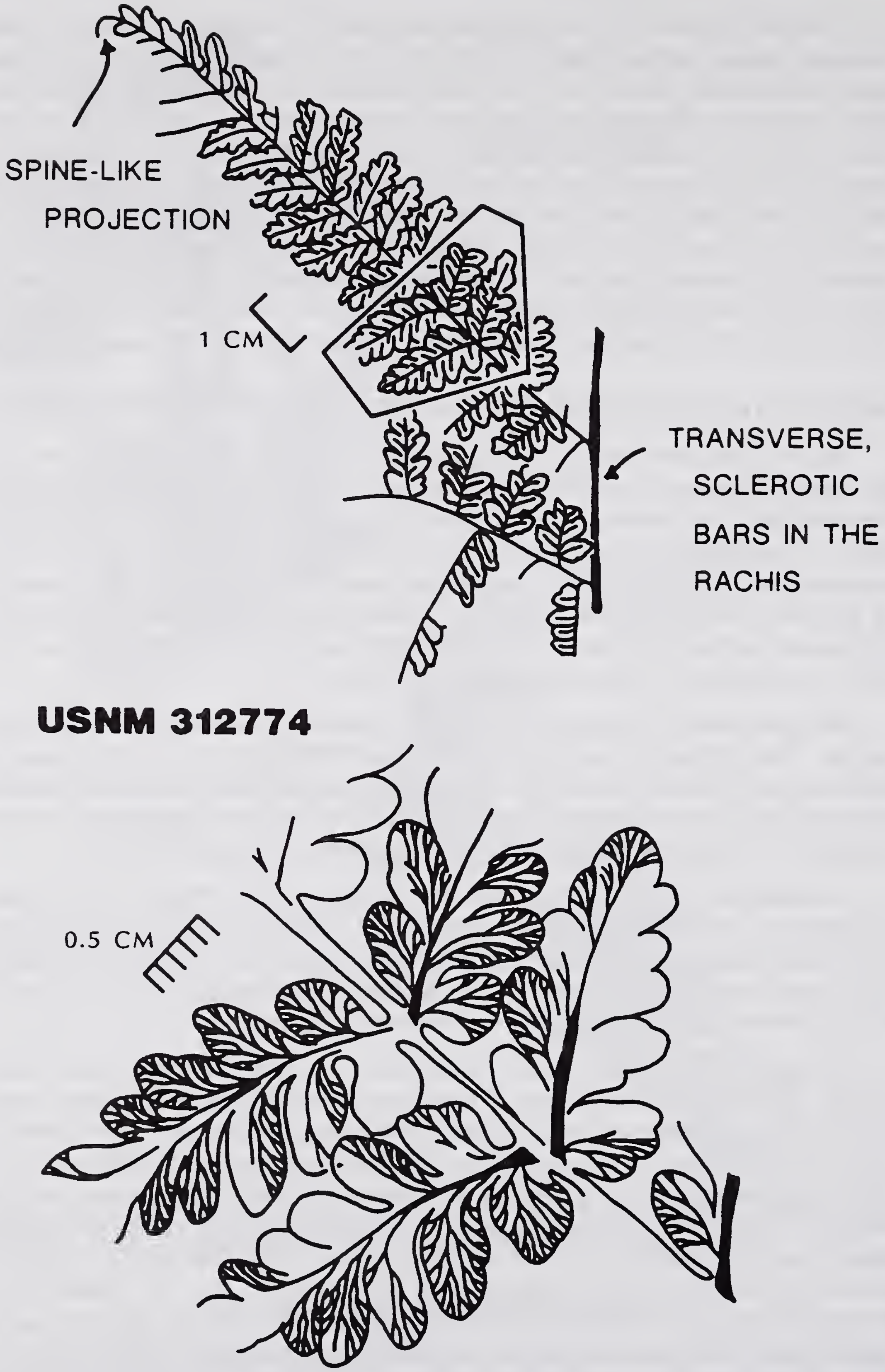

FIGURE 5. A line drawing showing a small portion of the frond of *Karinopteris soubeiranii* (United States National Museum Specimen 312774).

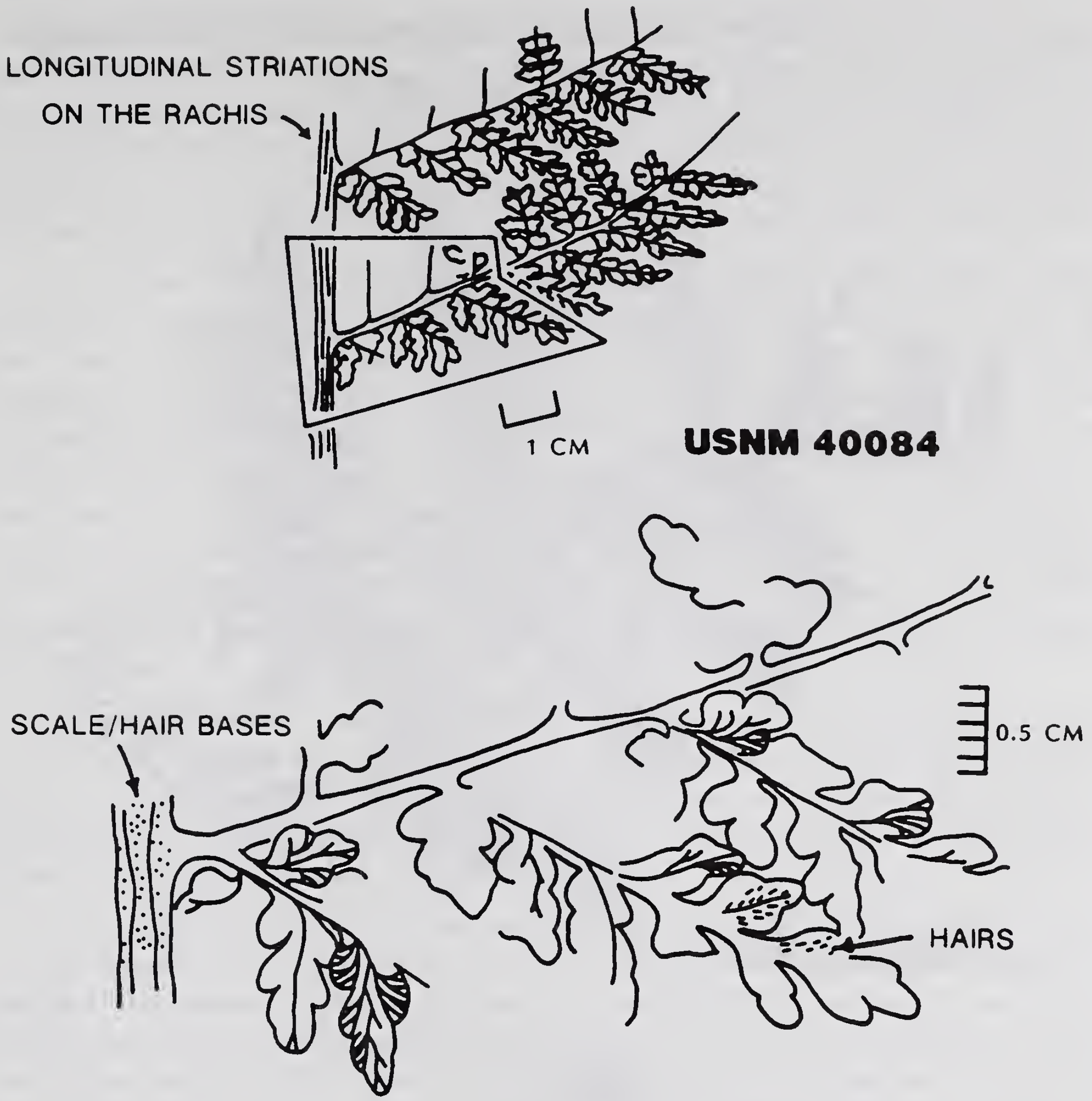

FIGURE 6. A line drawing showing a small portion of the frond of *Eusphenopteris paddocki* (United States National Museum Specimen 40084).

retrieved whole; for example, snail shells or pollen grains. Other fossils can be retrieved only in a very fragmentary state; for example, land plants and vertebrates. Only by carefully studying the specimens and developing methods for inferring position within the complete organism can the form of the original plant or animal be reconstructed.

A DICHOTOMOUS KEY

Most students are familiar with the traditional concept of the genus and species. When working with plant fossils, paleobotanists don't always know what the entire plant looked like. Pinnate fronds, such as those of *Karinopteris*, become fragmented (disarticulated) prior to burial and preservation. Rarely are large portions of fronds found intact (e.g., Gastaldo, 1988; White, 1943). Due to fragmentation, it is often difficult to match the separate parts of a frond with their true parent. Only when large specimens or large suites of specimens preserving various aspects of the parent are encountered can the many parts be placed together to form a complete frond. In order to classify the disarticulated parts

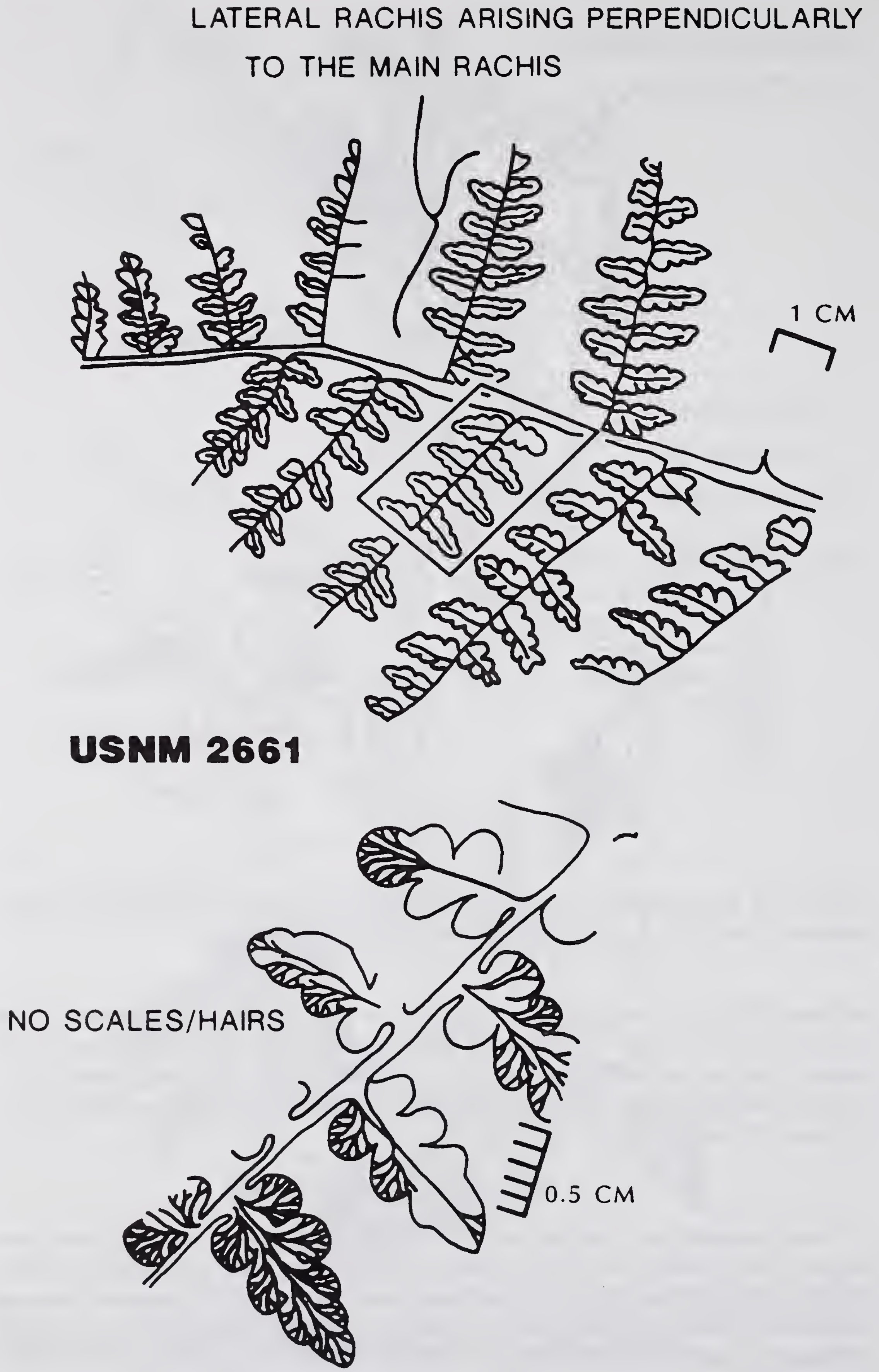

FIGURE 7. A line drawing showing a small portion of the frond of *Eusphenopteris lobata* (United States National Museum Specimen 2661).

unassignable to any known taxon, the International Rules of Botanical Nomenclature provides for a category called the form taxon. Form taxa may be used at any rank in the classificational hierarchy (e.g., a form family). *Karinopteris* is a form genus of pteridosperm foliage, and *K. soubeiranii* represents a specific type of karinopteroid foliage. The characteristics used to define the taxon are those that are most prevalent and shared by the parts that one wants to systematize.

In addition to preparing their own slides of *Karinopteris*, the students could construct a small dichotomous key for identifying the foliage of a number of pteridosperm species. Line drawings of *Sphenopteris pottsvillea* (White) Gastaldo & Boersma, *Karinopteris soubeiranii* (Zeiller) Boersma, *Eusphenopteris lobata* (White) Gastaldo & Boersma, and *E. paddocki* (White) Gastaldo & Boersma are provided. These species were originally part of the form genus *Mariopteris* as diagnosed or interpreted by White (1900, 1943), and their new assignments are based on a reexamination of White's specimens that was carried out by Gastaldo and Boersma (1983a, 1983b). The specimens illustrated are housed in the United States National Museum of Natural History (Smithsonian Institution, Washington, D.C.) and are real. None of the characteristics depicted are falsified.

Fragments of these species all share a number of similar characteristics (Figures 4-7). Within the major dichotomies of the rachis, the frond is bipinnate. At the tip, the pinnules are borne directly on the main rachis (R2). The pinnules alternate along the rachis and arise at an oblique angle. A single vein enters the pinnules and dichotomizes several times before reaching the pinnule margin.

The fronds also differ in a number of significant ways. In *Karinopteris soubeiranii* (Figure 5), the petiole and rachises are crossed by transverse bars. In addition, the pinnae near the tip of the main rachis (R2) as well as the rachis tip itself are elongated as spine-like projections. The axes of the remaining three species are longitudinally striated and lack the spine-like projections. In *Sphenopteris pottsvillea* (Figure 4), the terminal pinnule is fused with the subadjacent pinnules. In *Eusphenopteris paddocki* (Figure 6), scale/hair bases are present on the rachises. The pinnules of *E. paddocki* are all pubescent. Finally, *Eusphenopteris lobata* (Figure 7) differs from *E. paddocki* by having the lateral rachises inserted perpendicularly on the side of the main rachis toward the frond apex. There is no evidence for scale/hair bases on *E. lobata*.

Based on these differences, any number of dichotomous keys, such as the two given below, can be developed:

1. Rachis crossed by transverse bars; terminal pinnules end in spine-like projections . . . . *Karinopteris soubeiranii*
1. Rachis longitudinally striated; spine-like projections lacking 2

2. Terminal pinnule fused to subadjacent pinnules . . . . *Sphenopteris pottsvillea*
2. Terminal pinnule free 3

3. Scale/hair bases present on rachis; pinnules pubescent . . . . *Eusphenopteris paddocki*
3. Scale/hair bases absent; not pubescent . . . . *E. lobata*

or

1. Scale/hair bases present on rachis; pinnules pubescent .... *Eusphenopteris paddocki*
1. Scale/hair bases absent; not pubescent 2
2. Rachis crossed by transverse bars; terminal pinnules end in spine-like projections.......... *Karinopteris soubeiranii*
2. Rachis longitudinally striated; spine-like projections lacking 3
3. Terminal pinnule fused to subadjacent pinnules .... *Sphenopteris pottsvillea*
3. Terminal pinnule not fused to subadjacent pinnules .... *Eusphenopteris lobata*

The specimens of *Karinopteris* found in Indiana have not been assigned to an individual species (DiMichele, *et al.,* 1984). The above keys can be modified to identify the Indiana specimens by replacing *Karinopteris soubeiranii* with *Karinopteris* sp.

OUTCOMES

A number of valuable student outcomes can result from working with specimens of *Karinopteris*:

1. This experiment will allow the students to replicate studies of the reconstruction of *Karinopteris.* Their work will show that scientific inquiry is repeatable. The original author's hypothesis, the nature of the bipartite frond and its architecture, can be tested and retested with the same or nearly the same results.
2. The students will see that evolutionary theory has a strong empirical basis. Evolution is not an idea or a belief. It is a viable working hypothesis that is supported by an abundance of actual fossilized specimens of ancient life forms.
3. The rules of biological nomenclature can be discussed and the concept of form taxa can be introduced. Paleobotanists have a tendency to emphasize disarticulation and to give separate names (form taxa) to each disarticulated part. In comparison, disarticulation has not been enshrined by the vertebrate paleontologists. They have no form taxa. Should a tooth and femur, previously standing as two distinct taxa, be found to go together, they are placed in the same taxon. The principle of priority is applied, and they are given one name. This practice had not been followed in paleobotany Students should be made aware of the advantages and distadvantages of each approach.
4. The development and function of a taxonomic key can be introduced or reinforced.
5. Leaf architecture (frond morphology) and terminology can be studied. A knowledge of the appropriate terminology will provide the students with one of the tools necessary to test the hypothesis that the leaves of *Karinopteris* are constructed in a bipartite pattern.

LITERATURE CITED

Bristol, H.M. and R.H. Howard. 1971. Paleogeologic map of the sub-Pennsylvanian Chesterian (Upper Mississippian) surface in the Illinois Basin. Ill. St. Geol. Surv. Circ. 458, 14 pp.

__________ and __________. 1974. Sub-Pennsylvanian valleys in the Chesterian surface of the Illinois Basin and related Chesterian slump blocks. *In:* G. Briggs (Ed.), *Carboniferous of the Southeastern United States*, Geol. Soc. Am. Spec. Paper 148: 315-335.

DiMichele, W.A. and G.E. Dolph. 1981. Guidebook to Pennsylvanian plant localities. AIBS Field Trip 2, Paleobot. Sec. Bot. Soc. Amer., 8 pp.

__________, M.O. Rischbieter, D.L. Eggert, and R.A. Gastaldo. 1984. Stem and leaf cuticle of *Karinopteris:* Source of cuticles from the Indiana "paper" coal. Amer. J. Bot. 71(5): 626-637.

__________ and T.L. Phillips. 1985. Arborescent lycopod reproduction and paleoecology in a coal-swamp environment of Late Pennsylvanian age (Herrin Coal, Illinois, U.S.A.). Rev. Palaeobot. Palynol. 44: 1-26.

__________, __________, and R.A. Peppers. 1985. The influence of climate and depositional environment on the distribution and evolution of Pennsylvanian coal-swamp plants. *In:* B.H. Tiffney (Ed.), *Geological Factors and the Evolution of Plants,* pp. 223-256, Yale University Press, New Haven.

Gastaldo, R.A. 1987. Confirmation of Carboniferous clastic swamp communities. Nature 326(6116): 869-871.

__________. 1988. Evidence for the frond architecture of *Sphenopteris pottsvillea* (White) Gastaldo and Boersma. J. Paleontol. 62(6): 981-992.

__________ and M. Boersma. 1983a. A revision of Early Pennsylvanian species of *Mariopteris* from the Appalachian Region. I. *Karinopteris, Mariopteris,* and the "pottsvillea complex." Rev. Palaeobot. Palynol. 38: 185-226.

__________ and __________1983b. A reinvestigation of Early Pennsylvanian species of *Marinopteris* from the Appalachin Region. II. *Eusphenopteris* and *Sphenopteris.* Rev. Palaeobot. Palynol. 38: 227-247.

Howard, R.H. 1979. The Mississippian-Pennsylvanian unconformity in the Illinois Basin—Old and new thinking. *In:* J.E. Palmer and R.R. Dutcher (Eds.), *Depositional and Structural History of the Pennsylvanian System of the Illinois Basis, Part 2,* Field Trip No. 9, 9th Int. Congr. Carb. Strat. Geol., pp. 34-43.

Neavel, R.C. and G.K. Guennel. 1960. Indiana paper coal: Composition and deposition. J. Sed. Petrol. 30(2): 241-248.

Nelson, W.J., D.L. Eggert, W.A. DiMichele, and A.C. Stecyk. 1985. Origin of discontinuities of coal-bearing strata at Roaring Creek (basal Pennsylvanian of Indiana). Int. J. Coal Geol. 4: 355-370.

Oshurkova, M.V. 1977. The principles and methods of facies-paleoecological studies of continental deposits containing plant remains. Paleontol. J. 2: 233-241 (Translation of Paleontol. Zh. 2: 105-114).

Peppers, R.A. 1979a. Coal palynology: Roaring Creek coals. *In:* D.L. Eggert and T.L. Phillips (Eds.), *Guidebook to Environments of Plant Deposition—Coal Balls, Paper Coals, and Gray Shale Floras,* pp. 54-60, 9th Int. Congr. Carb. Strat. Geol. Guidebook, Field Trip B.

__________. 1979b. Development of coal-forming floras during the early part of the Pennsylvanian in the Illinois Basin. *In:* J.E. Palmer and R.R. Dutcher (Eds.), *Depositional and Structural History of the Pennsylvanian System of the Illinois Basin,* pp. 65-72, 9th Int. Congr. Carb. Strat. Geol. Guidebook, Field Trip 9.

__________. 1982. Palynology of coals along Roaring Creek. *In:* D.L. Eggert and T.L. Phillips (Eds.), *Environments of Deposition: Coal Balls, Cuticular Shale* *and Gray Shale Floras in Fountain and Parke Counties, Indiana,* pp. 14-19, Indiana Geol. Surv. Spec. Rep. 30, 43 pp.

Phillips, T.L. and R.A. Peppers. 1984. Changing patterns of Pennsylvanian coal-swamp vegetation and implication of climatic control on coal occurrence. Int. J. Coal Geol. 3: 205-255.

———, ———, and W.A. DiMichele. 1985. Stratigraphic and interregional changes in Pennsylvanian coal-swamp vegetation: Environmental inferences. Int. J. Coal Geol. 5: 43-109.

Shaver, R.H., C.H. Ault, A.M. Burger, D.D. Carr, J.B. Droste, D.L. Eggert, H.H. Gray, D. Harper, N.R. Hasenmueller, W.A. Hasenmueller, A.S. Horowitz, H.C. Hutchison, B.D. Keith, S.J. Keller, J.B. Patton, C.B. Rexroad, and C.E. Weir. 1986. Compendium of Paleozoic rock-unit stratigraphy in Indiana—a revision. Ind. Geol. Surv. Bull. 59, 203 pp.

Stewart, W.N. 1983. Paleobotany and the evolution of plants. Cambridge Univ. Press, New York, 405 pp.

Taylor, T.N. 1981. Paleobotany: An introduction to fossil plant biology. McGraw-Hill Book Company, New York, 589 pp.

White, D. 1900. The stratigraphic succession of fossil floras of the Pottsville Formation in the southern Anthracite Coal Field, Pennsylvania. 20th Annu. Rep. U.S. Geol. Surv., pp. 749-930.

White, D. 1943. Lower Pennsylvania species of *Mariopteris, Eremopteris, Diplotmena,* and *Aneimites* from the Appalachian region. U.S. Geol. Surv. Prof. Paper 197C:1-140.