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The ichnogenus *Atreipus* and its significance for Triassic biostratigraphy

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Introduction

Reptile footprint faunules from the early Mesozoic Newark Supergroup of eastern North America (Fig. 6.1) have been studied since the early 1800s. Most are from the Hartford and Deerfield basins of the Connecticut Valley; thanks to many works, particularly those of E. Hitchcock (1836, 1843, 1847, 1858, 1865) and Lull (1904, 1915, 1953), the Connecticut Valley faunules are relatively well known (although now desperately in need of revision). Long thought to be of Late Triassic age, all of the Connecticut Valley tracks come from strata above the oldest extrusive basalt flows in the Hartford and Deerfield basins and are now thought to be Early Jurassic in age. Similar Early Jurassic faunules have been more recently identified in the Newark, Culpeper, and Fundy basins (Olsen, McCune, and Thomson 1982; Olsen and Baird 1982) as well as in the Glen Canyon Group of the southwestern United States and the upper Stormberg Group of southern Africa (Olsen and Galton 1977, 1984).

Older, undoubtedly Late Triassic footprint assemblages of the Newark have received scant attention, although neither localities nor specimens are rare. Tracks from the preextrusive intervals of the Newark Basin were first reported by Eyerman in 1886, but it was not realized that these faunules were distinctly different from those of the Connecticut Valley until Baird's revisions of the assemblages in 1954 and 1957. Within the past thirty years many new footprint faunules have been found in Newark horizons of Late Triassic age, and, consequently, the composition of the older faunules has become much clearer. The purpose of this chapter is to describe an entirely new ichnogenus that is one of the most common and distinctive elements of these older assemblages, widespread in eastern North America and present as well in the European Middle Keuper.

We begin by describing the morphology and systematics of the new form and follow with a discussion of its biostratigraphic significance. Detailed locality and stratigraphic information for the material discussed in the systematic section is given in the biostratigraphic section. Finally, we attempt to reconstruct the osteology of the ichnites and try to find a likely trackmaker among known osteological taxa.

Materials and methods

All of the specimens described in this chapter are footprints, either natural casts or natural molds, not actual osseous remains of animals. We use the traditional latinized binominals for the track taxa, but the taxonomy is one parallel to that of the biological Linnaean hierarchy, not part of it. These ichnotaxa do not correspond to osteologically based fossil taxa either materially or in concept. The names are used as handles and for the classification of tracks of different morphology.

With the exception of the European form, *Atreipus metzneri*, all of the material described here comes from seven localities in the Passaic and Lockatong formations of the Newark Basin, two localities in the Gettysburg Shale in the Gettysburg Basin, one locality in the Cow Branch Formation of the Dan River Group, and one in the Wolfville Formation of the Fundy Basin (Fig. 6.2). Details of the localities are given in the section on geological occurrences and associated fossils (Appendix 2).

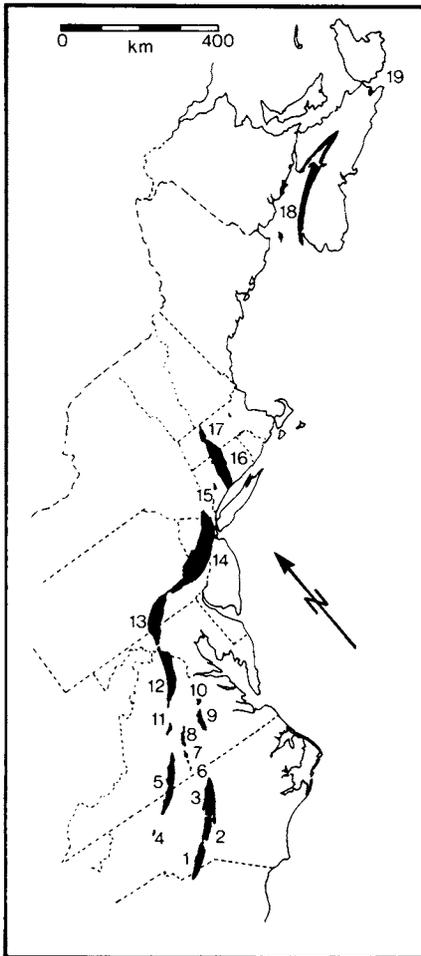
We have analyzed these footprints by preparing line drawings of all the reasonably well-preserved material and producing composites of these drawings. We define "reasonably well-preserved material" as tracks that show impressions of pads and that are not strongly distorted; thus, they are as close to the trackmakers' morphology as possible. We have purposely stayed away from the analysis of

tracks that do not meet this criterion. The line drawings were made by tracing photographs of the tracks themselves or of inked latex or polysulfide peels of the tracks. The outlines were drawn along the surfaces of maximum change in curvature of the track. This method produces very accurate, reproducible renderings. Composites of the best material from successive tracks of single individuals (where pos-

sible) or populations were produced by visual interpolation of the superimposed track outlines.

Osteological reconstructions were developed from the composite outlines by placing joint articulations at the center of the pads. This conforms to the pedal structure of living cursorial dinosaurs (birds) (Heilmann 1926; Peabody 1948; Baird 1954, 1957) as well as to the pedal structure of crocodiles (Chapter 20) and of the largest living terrestrial reptile, the Komodo dragon (Padian and Olsen 1984).

Figure 6.1. The Newark Supergroup of Eastern North America (from Olsen, McCune, and Thomson 1982). *Atreipus* has been found in basins marked 18, 14, 13, and 2. Key to basins as follows: 1, Wadesboro Subbasin of Deep River Basin; 2, Sanford Subbasin of Deep River Basin; 3, Durham Subbasin of Deep River Basin; 4, Davie County Basin; 5, Dan River–Danville Basin; 6, Scottsburg Basin; 7, Briery Creek Basin and subsidiary basin to south; 8, Farmville Basin; 9, Richmond Basin; 10, exposed part of Taylorsville Basin; 11, Scottsville Basin; 12, Culpeper Basin; 13, Gettysburg Basin, 14, Newark Basin; 15, Pomperaug Basin; 16, Hartford Basin; 17, Deerfield Basin; 18, Fundy Basin; 19, Chedabucto Basin (= Orpheus Graben).



Systematics

Ichnofamily Atreipodidae nov.

Diagnosis. Habitually quadrupedal ichnites; pes tulip-shaped with digit three longest; manus small, digitigrade, tridactyl or tetradactyl.

Ichnogenus *Atreipus* nov.

(Fig. 6.3A–C)

Type ichnospecies. *Atreipus milfordensis* (Bock), 1952.

Included ichnospecies. The type species; *Atreipus sulcatus* (Baird 1957); *A. acadianus* nov.; *A. metzneri* (Heller 1952).

Range of Ichnogenus. Late Carnian to ?middle Norian (Late Triassic) strata of the Newark Supergroup of eastern North America.

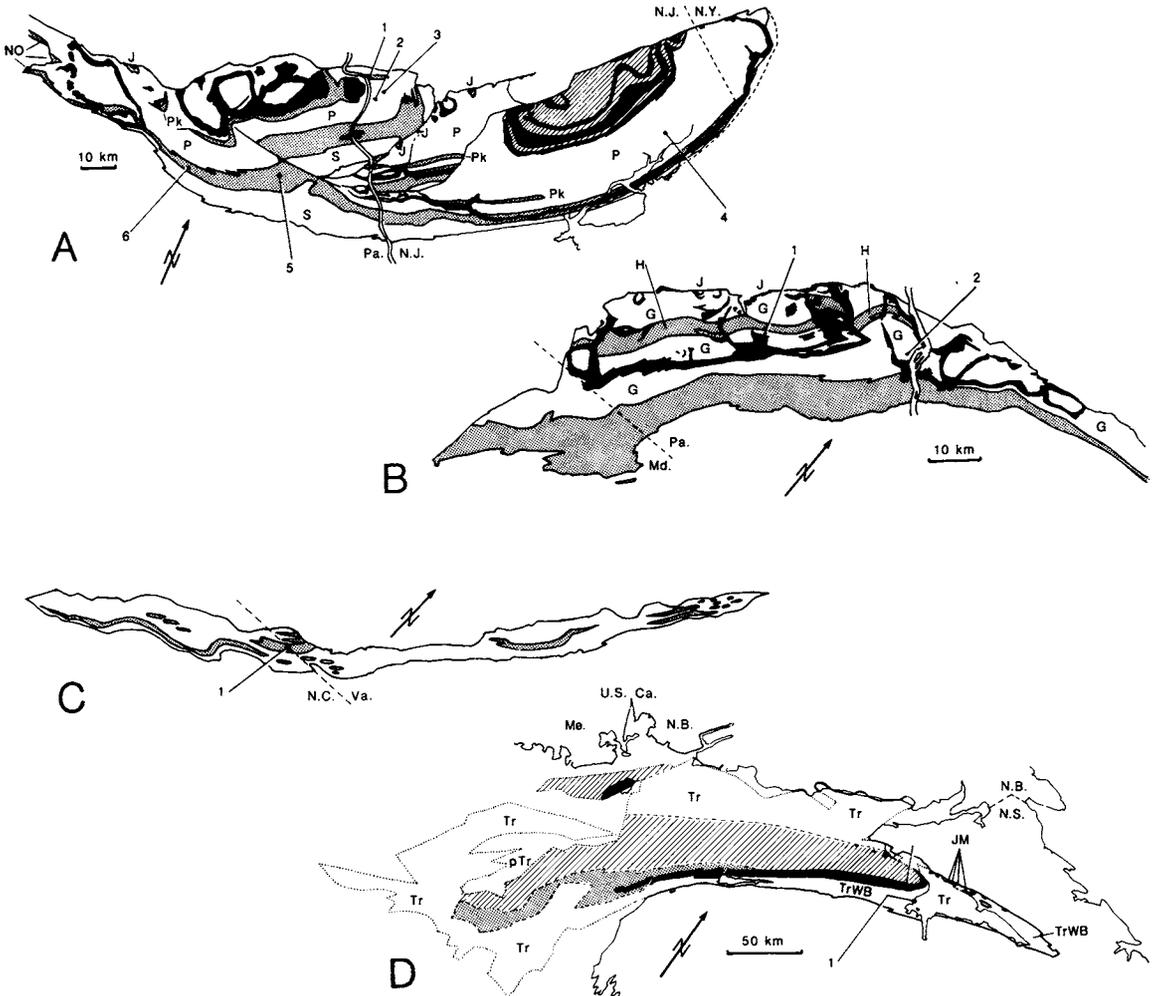
Diagnosis. As for monotypic ichnofamily. Small (9–14 cm), tulip-shaped pes impression with metatarsal–phalangeal pads of digits II and IV oval to circular and often impressed. Relative proportions very similar to those of *Grallator*. Distal phalangeal pads often indistinct from more proximal pads. Hallux not impressed even in very deep tracks. Manus digit III longest followed in length by II, IV, and I (the last impressing only in *A. acadianus*).

Etymology. Named in honor of Atreus Wanner, who uncovered many fine footprints, including *Atreipus*, in Goldsboro, York County, Pennsylvania (Wanner 1889).

Discussion

The pedes of all the ichnospecies of *Atreipus* would fit quite comfortably within the Ichnofamily Grallatoridae, as they did in the analyses of Baird (1957), were it not for the functionally tridactyl manus impressions (Figs. 6.4–6.10). Such a manus has never been described from a Newark grallatorid walking trackway, despite what must be many thousands of Newark tracks collected over the last 150 years. [The supposed “manus prints of *Anchisauripus*” reported by Willard (1940) are apparently pes imprints of a smaller individual.] The manus, in fact, is more like what might be expected in a chirotheriid. The combination of this manus with a *Grallator*-like pes is so unusual that it cannot reasonably be included in any known ichnofamily, so we erect a new ichnofamily for this distinctive ichnotaxon.

Figure 6.2. Localities for *Ateipus* in the Newark, Gettysburg, Dan River and Fundy basins. **A**, Newark Basin. Main lacustrine body is Lockatong Formation (shown in gray except as marked); Jurassic sedimentary rocks (mostly lacustrine) are shown with hatched marking. Igneous rocks adjacent to the Jurassic sedimentary rocks are extrusive flows; all others are intrusive plutons; all igneous rocks are shown in black. Localities are: 1, Perkasio Member, Passaic Formation, Milford, New Jersey; 2, Graters Member, Passaic Formation, near Frenchtown, New Jersey; 3, Members E-F, Passaic Formation, near Frenchtown, New Jersey; 4, Passaic Formation, Lyndhurst-Rutherford area, New Jersey; 5, lower Lockatong Formation, Gwynedd, Pennsylvania; 6, Weehawken Member, Lockatong Formation, Arcola, Pennsylvania. Abbreviations as follows: J, Early Jurassic extrusive flows and sediments in isolated synclines; NO, New Oxford Formation = Stockton Formation where Lockatong is absent; P, Passaic Formation; Pk, Perkasio Member, Passaic Formation; S, Stockton Formation. **B**, Gettysburg Basin. Principally gray lacustrine rocks are shown in gray; igneous rocks are shown in black. Large gray area is New Oxford Formation, which has a very large fluvial component. Localities are: 1, Gettysburg Shale, Trostle Quarry near York Springs, Pennsylvania; 2, Gettysburg Shale, near Goldsboro, Pennsylvania. Abbreviations as follows: G, Gettysburg Shale; H, Heidlersburg Member of Gettysburg Shale; J, Early Jurassic extrusive flows and sediments. **C**, Dan River Group in Dan River and Danville basins. Gray areas indicate outcrops of lacustrine Cow Branch Formation. 1 indicates position of Solite Quarry locality for *Ateipus*, Leaksville Junction, Virginia and North Carolina. **D**, Onshore and offshore Fundy Basin of New Brunswick and Nova Scotia, Canada, and the Gulf of Maine. Black areas indicate outcrops of extrusive basalts; gray areas show the offshore extent of the same basalts. Hatched lines show area of offshore extent of inferred Early Jurassic sediments (Scots Bay and McCoy Brook formations). Abbreviations are: JM, onshore outcrops of Early Jurassic McCoy Brook Formation; pTr, pre-Triassic rocks present offshore; Tr, offshore Triassic rocks; TrWB, onshore Triassic Wolfville and Blomidon formations. 1 shows the position of the Fundy Basin *Ateipus* near Paddy Island, Kings County, Nova Scotia. Maps adapted from Klein (1962), Keppie et al. (1979), Ballard and Uchupi (1980), Swift and Lyall (1968), Tagg and Uchupi (1966), Robbins (1982), Thayer (1970), Meyertons (1963), Olsen (1980a, 1984a), Faille (1973), and Nutter (1978).



Atreipus milfordensis (Bock) nov.
comb. (Fig. 6.3A)

Gigandipus (?*Anchisauripus*) *milfordensis*. Bock (1952, p. 403, Plate 43, Fig. 3) (in legend, for "No. 15210" read S488): Unit O, Perkasio Member, Lower Passaic Formation, New Jersey, early Norian of Late Triassic.

(?)*Anchisauripus gwyneddensis*. Bock (1952, pp. 406–7, Plate 44): lower Lockatong Formation, Pennsylvania, late Carnian of the Late Triassic.

Type. LC. S488, a left pes impression slightly distorted by the paratype of *Brachychirotherium parvum* (Fig. 6.4A).

Prevalus hypodigm. The type and two other imprints on the same slab; MCZ 135, 229; AMNH 1981 and 1984, all collected by John Eyerman, 1885–7. Type of *A. gwyneddensis*, ANSP 15222 (missing).

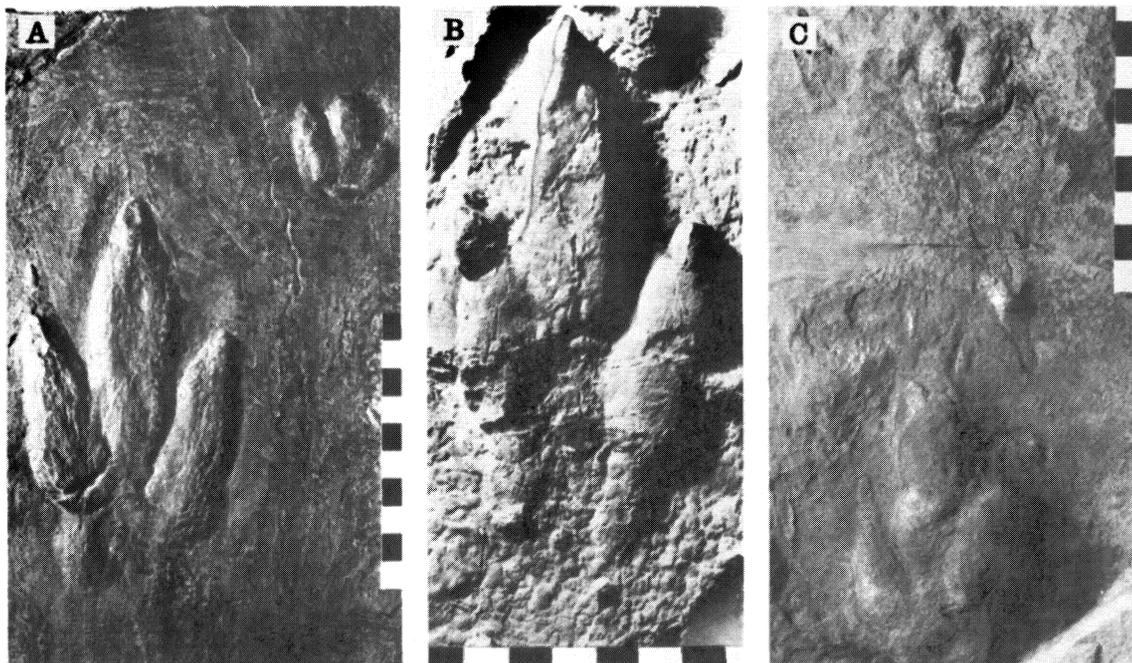
Distribution. Late Carnian and early Norian of the Late Triassic in the Newark, Gettysburg, and Dan River basins of the Newark Supergroup.

Locality of type. Clark Brothers quarry, 1.5 km north of the Delaware River Bridge at Milford, Hunterdon County, New Jersey.

Referred material. Additional material from the abandoned Clark Quarry: a slab with several quadrupedal trackways (PU 18581), manus–pes sets

(PU 23486) and miscellaneous tracks (PU 23649) collected by D. Baird and Robert M. Salkin in 1963; manus–pes sets from the base of member F of the Passaic Formation (PU 23640), from Nishisakawick creek 4.7 km east of Frenchtown, New Jersey, collected by P. Olsen in 1984; isolated pes impression from the lower division (G) of the Graters Member (YPM 7554) from Little Nishisakawick Creek, Frenchtown, New Jersey, collected by P. Olsen, 1971; two overlapping trackways from the lower Passaic Formation (YPM 9960) near Rutherford, New Jersey, collected by Larry Black in 1969; quadrupedal trackways from the Gettysburg Shale of the Gettysburg Basin from near Goldsboro, York County, Pennsylvania, collected by Atreus Wanner (Wanner 1889) in 1888 and accessioned by the United States National Museum, but later lost (Baird 1957); trackways from the Trostle Quarry near Bermudian Creek, Bermudian Springs, Pennsylvania, Adams County, Pennsylvania, collected by Elmer R. Haile, Jr., 1937 (Stose and Jonas 1939) including CM 12081 and 12087; isolated manus–pes set (YPM 9961) from the long trackway from lower Lockatong in cut of Schuylkill Expressway at Arcola, Pennsylvania, collected by P. Olsen and Cynthia Banach in 1983; latex peel (YPM 9962) of large slab of poor trackways from the upper member of the

Figure 6.3. Examples of the three recognized species of *Atreipus* from the Newark Supergroup: A, Latex cast of right manus–pes set of *Atreipus milfordensis* from the middle Gettysburg Shale, Trostle Quarry, Adams County, Pennsylvania (CM 12081). B, Natural cast of right pes of *Atreipus sulcatus*, the type specimen from the lower Passaic Formation of Milford, New Jersey (MCZ 215). C, Natural cast of right manus–pes set of *Atreipus acadianus*, from the upper Wolfville Formation of Paddy Island, Kings County, Nova Scotia (PU 23635). Scales in cm.



Cow Branch Formation of the Dan River Group, Solite Corporation Quarry, Leaksville Junction, Virginia and North Carolina.

Diagnosis. *Atreipus* in which digits II and IV of the pes are nearly equal in their forward projection, with the bases of the claws of II and IV lying almost opposite the crease between the first and second phalangeal pads of digit III. Digit I of manus not impressed.

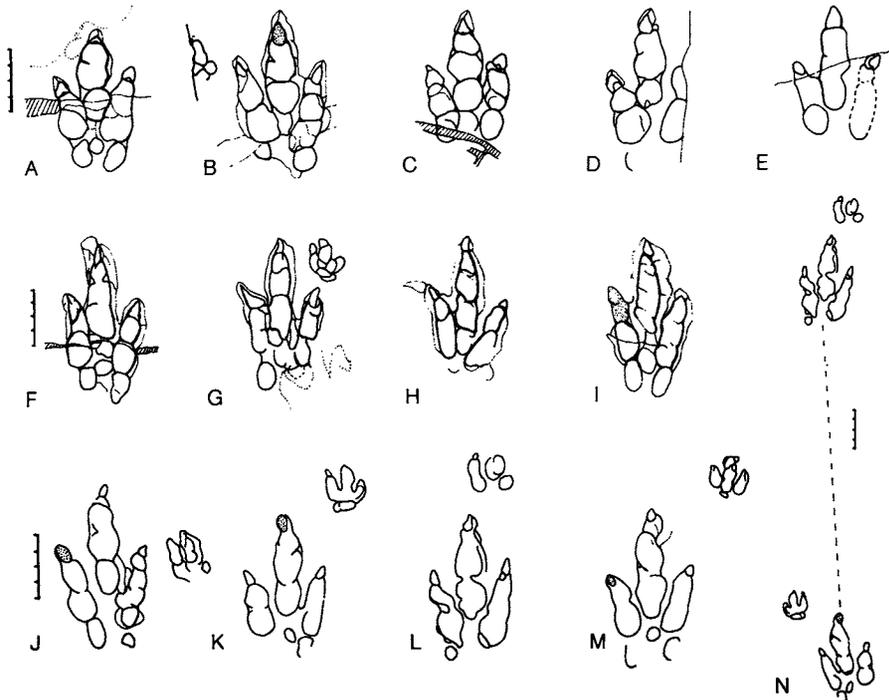
Discussion

An examination of all the specimens in the previous hypodigm and new material from the type locality, in addition to the referred material from the other localities and horizons, allows Baird's (1957) description of this ichnospecies to be enlarged (Figs. 6.4, 6.5, 6.7, 6.8). Most significant is the realization that this ichnospecies represents a habitually quadrupedal form, a condition never seen before in tracks otherwise similar to members of the Ichnofamily Grallatoridae. The block containing the holotype is

unfortunately broken in such a way that it is impossible to tell if there ever was an associated manus impression. The same is true of most of the hypodigm with the exception of MCZ 135 in which a partial manus is present (Fig. 6.4B). The trackways of the smaller individual from the type locality (PU 18581, Fig. 6.4j-n) have clear manus impressions, as do most trackways from other localities. One crucial trackway, of which YPM 9962 is representative, shows that *Atreipus milfordensis* trackways are not consistently quadrupedal (Fig. 6.6o).

Three digits are always present in the manus, and digits II and III of some specimens (such as YPM 9960) have impressions of small claws (Figs. 6.4-6.6). The manual digits represented can be understood only with reference to *Atreipus acadianus*, where they prove to be digits I-IV (see below). The pads of the manus are poorly differentiated even in the clearest of impressions; however, there are often creases at about the midpoints of digits II and III. On many manus impressions, there is also a trans-

Figure 6.4. Type material of *Atreipus milfordensis* (A-E) and *A. sulcatus* (F-I) and new material of *A. milfordensis* from the Smith-Clark Quarry (J-N). A-M all drawn as right pes impressions. A, *Atreipus milfordensis*, type specimen (LC488), a left pes impression slightly distorted by the paratype of *Brachychirotherium parvum* (dotted outline); B, MCZ 135, a right pes and partial manus impression; C, MCZ 229, a left pes impression; D, paratype of *A. milfordensis* (LC 488), a left pes impression; E, plesiotype of *A. milfordensis* (AMNH 1984), a left pes impression; F, type of *Atreipus sulcatus* (MCZ 215), a left pes impression; G, paratype *A. sulcatus* (AMNH 1982), a left manus and pes impression, pes overlapped by another conspecific pes impression (dotted outline); H, paratype *A. sulcatus* (AMNH 1983), a left pes impression; I, paratype *A. sulcatus* (MCZ 216), a left pes impression; J-N, *Atreipus milfordensis* (PU 18581): J-K, left manus and pes impressions; L-M, right manus and pes impressions; N, a trackway composed of successive left (above) and right (below) manus and pes impression sets. Scale is 4 cm.

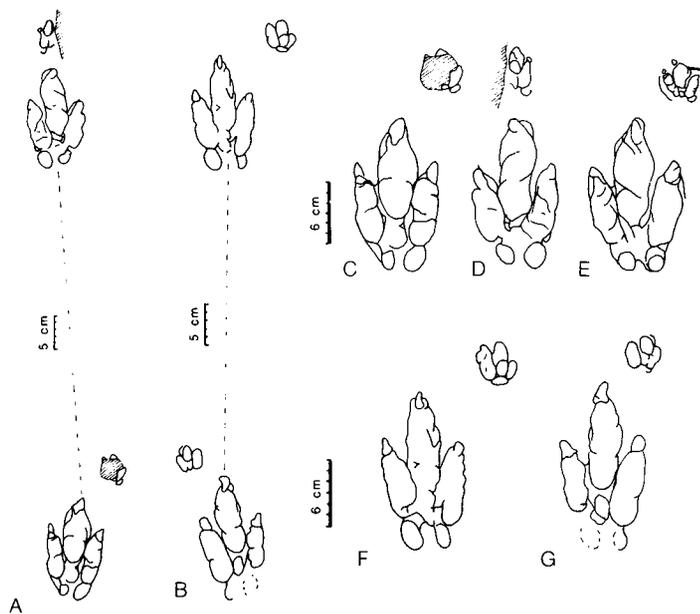


versely elongate pad at the posterior end of digit III, which is usually broader than the adjacent digits. Other creases appear, but these are variable in sequential manus impressions of the same individual and were probably due to interaction of the animal with the substrate. The available trackways show that the manus impressions are usually placed anterior and lateral to the pes impressions, but this pattern is far from consistent [as the Arcola, Pennsylvania trackway shows (Fig. 6.6)].

In the pes, the flexed and hastate claws described by Bock (1952) and Baird (1957) prove discernible only on the deeply impressed type material from Milford, and as a diagnostic feature they are unreliable. As Baird (1957) noted, each proximal pad of the pes is bounded distally by a shallow sulcus rather than a crease, and the more distal pads are more or less confluent. This differs from the situation in the Grallatoridae, in which all of the pads are distinct and separated by creases except those on the distal portion of digit IV. Also, as Baird (1957) noted, in *Atreipus* the metatarsal-phalangeal pads of both digits II and III are often impressed, whereas in grallatorids only that of digit IV is usually present. These last two features are synapomorphies of all three ichnospecies of *Atreipus*.

Composites of the *Atreipus milfordensis* specimens from the major localities are shown in Figure 6.8. There is as much variation in the pedal impressions among specimens of the hypodigm as among any of the specimens from the other localities or their composites. Baird (1957) commented on this variation, noting that in one specimen (MCZ 135), digit IV is relatively shorter than the others and as a consequence digit II projects more anteriorly than IV. In addition, there is also considerable variation in digit divarication. In the smallest specimens from the type locality (PU 18581), the digits do not appear to be as robust as in the hypodigm, but this is almost certainly because their impressions are relatively shallow. Here again, digit II projects further than IV in some specimens, but not others, even in successive tracks of the same individual (Fig. 6.5B and 6.6). The Lyndhurst-Rutherford material shows little variation within the sample, and, despite the individual tracks' greater size, there are no obvious proportional differences between the composite and that of the Milford material (Fig. 6.8). The pads on the pedes, however, are even less well differentiated than in the type material. Pedal impressions from Arcola, Pennsylvania are not as clearly impressed as those from the rest of the Newark Basin material of

Figure 6.5. *Atreipus milfordensis* from the lower middle Passaic Formation of the Lyndhurst-Rutherford area, Bergen County, New Jersey (A, C-E) and the middle Gettysburg Shale of the Trostle Quarry, Adams County, Pennsylvania (B, F, G). C-G drawn as if all were right manus pes sets. A, Trackway (YPM 9960) of successive right and left manus-pes impression sets (drawn reversed). B, Trackway (CM 12081) of successive left and right manus-pes impression sets (drawn reversed). C, Left manus-pes impression set of trackway in (A). D, Right manus-pes impression set of trackway in (A). E, Isolated left manus-pes impression set on same slab as (A). F, left manus-pes impression set from trackway in (B). G, right manus-pes impression set from trackway in (B).



Atreipus. As might be expected in sloppy tracks, the amount of variation between successive tracks is large. The composite (Fig. 6.8), however, still clearly resembles *A. milfordensis*.

Bock's (1952) *Anchisauripus gwyneddensis* appears to be closely comparable to *Atreipus milfordensis*, judging from Bock's plate, and seems especially close to the Trostle Quarry forms described below (Baird, 1957). Unfortunately, careful

searches by each of us and by the museum staff of the Academy of Natural Sciences of Philadelphia failed to locate the type (ANSP 15222). In addition, Bock's plate of the specimen and the negative from which it was printed are cropped too tightly to show whether or not there is an associated manus impression. Our assignment of *A. gwyneddensis* to *Atreipus milfordensis* is thus based solely on our interpretation of Bock's plate of the pes and thus must be

Figure 6.6. *Atreipus milfordensis* from the lower Locketong Formation of Arcola, Pennsylvania. A–N, Successive pes and manus–pes impressions all drawn as if right impressions, from trackway shown in O. A is a right pes impression, B is a left pes impression, etc. O, Trackway showing position of tracks (A–N above). P in O shows trackway of *Rhynchosauroides hyperbates*. J is YPM 9961.

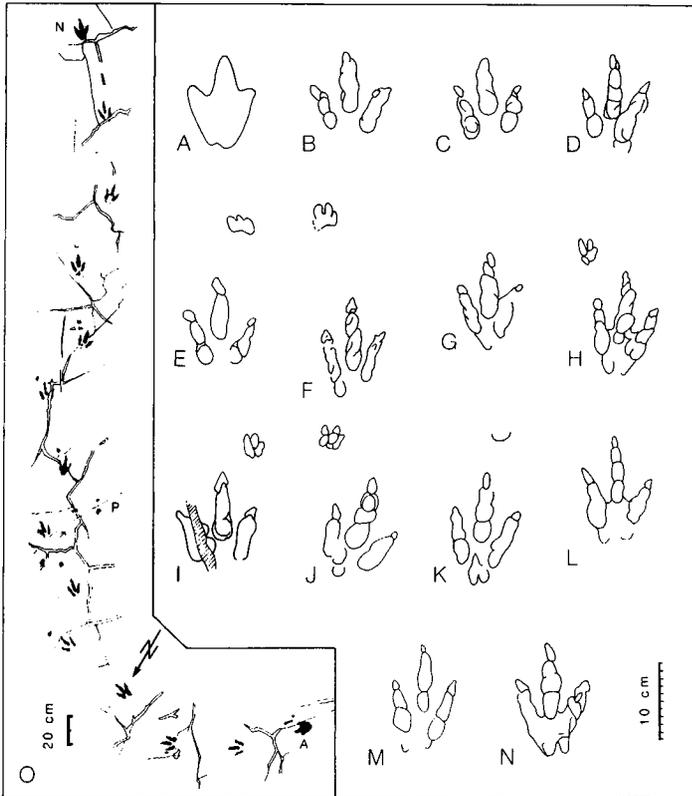
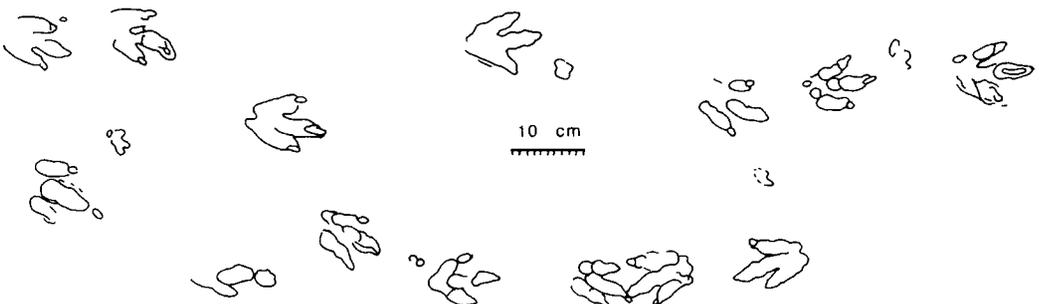


Figure 6.7. Cow Branch *Atreipus milfordensis*. Tracing of a photographed but not collected block from Leaksville Junction, North Carolina–Virginia. Peel of specimen is YPM 9962.



regarded as tentative. Fortunately, *Atreipus milfordensis* has page priority over *A. gwyneddensis*.

The composite (Fig. 6.8D) of the Gettysburg Basin (Troastle Quarry) specimens (Fig. 6.5) is closely comparable to the type of *Atreipus milfordensis* and especially to the Lyndhurst–Rutherford material, but here again there are surprising differences in proportions between the left and right pedes of the two successive tracks with respect to the apparent relative projection of digits II and IV. Warner's (1889) undesigned material from near Goldsboro, York County is unfortunately lost, but what can be seen from his figures (especially Plates 9 and 10) is indistinguishable from *A. milfordensis*.

Available material from the Cow Branch Formation (Fig. 6.7) is rather poor and difficult to interpret. The tracks lack the distinguishing features of *A. sulcatus* or *A. acadianus*, and comparison with the composite of all the Cow Branch material suggests that it too belongs in *Atreipus milfordensis*.

Atreipus sulcatus (Baird)

(Fig. 6.3B)

Grallator sulcatus. Baird (1957, pp. 453–61, Fig. 1, Plate 1); full synonymy, and a list of incorrect assignments are given in Baird (1957).

Type. MCZ 215, a left pes impression.

Previous hypodigm. MCZ 215 to 228 inclusive, the type and thirty-six other pes impressions. AMNH 1982 and 1983, six imprints. LC S487, parts of three overlapping pes imprints. All collected by John Eyerman, 1885–7.

Horizon. Early Norian of the Late Triassic, Newark Supergroup, Newark Basin, Passaic Formation, Perkasio Member, Unit O.

Locality. Quarry of the Messrs. Clark about

one-half mile east of the Smith-Clark Quarry, near Milford, Hunterdon County, New Jersey (from Eyerman, 1889, p. 32). Subsequent collecting indicates that the type horizon occurs a little below that of *A. milfordensis* in the same quarry.

Referred Material. Topotypes from Clark Quarry, PU 20743 A-C and a large slab at Upsala College, collected by James Sorensen, 1969; PU 23642, two pedes collected by Olsen and Baird, 1984; from Perkasio Member, Unit O, Passaic Formation.

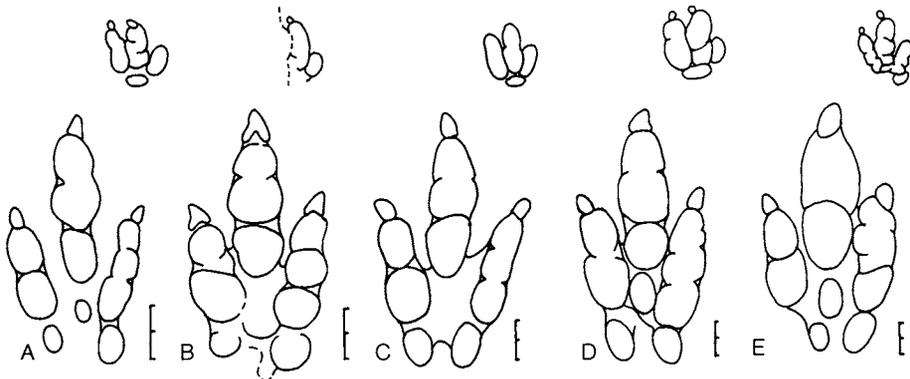
Diagnosis. *Atreipus* distinguished from other ichnospecies by having the impressions of the bases of pes digits II and III closely united, while IV remains separated from III by a deep sulcus that extends back to the metatarsal–phalangeal pad of III.

Discussion

The description of Baird (1957) requires little modification except to add the presence of a manus indistinguishable from that of *A. milfordensis*. A clear manus impression is present on the paratype of *A. sulcatus* (AMNH 1982, Figs. 6.4g and 6.9). Other slabs from the type locality have manual impressions, but none are worth figuring.

New material from the Clark Quarry is evidently from the type horizon; it resembles Eyerman's specimens in all observable features, but includes many associated manus impressions. The quality of most of this material is poor and adds little to our knowledge of pedal morphology of the ichnospecies except to show that it is more similar to *A. milfordensis* than was originally believed. The fact that the *A. sulcatus* impressions were made on softer mud may account for some of the apparent differences. However, on the basis of the available material, the two ichnospecies are morphologically

Figure 6.8. Composites of *Atreipus milfordensis* from each major locality. Tracks arranged in order of increasing size: A, PU 18581, from the Smith–Clark Quarry, Milford, New Jersey. B, Hypodigm of *Atreipus milfordensis* from the Smith–Clark quarry, Milford, New Jersey [modified from Baird (1957)]. C, Lockatong material from Arcola, Pennsylvania. D, CM 12081, from the Troastle Quarry, near Bermudian Springs, Adams County, Pennsylvania. E, YPM 9960, from the Passaic Formation, Lyndhurst–Rutherford area, New Jersey. Scale is 2 cm.



distinct, and *A. sulcatus* cannot be proved to fall within the range of variation of *A. milfordensis*. We, therefore, retain them as separate ichnospecies, while acknowledging the possibility that a larger sample size might show them to be parts of a morphological continuum.

***Atreipus acadianus* nov. (Fig. 6.3C)**

Type. PU 21713B, a slab bearing five manus-pes sets; collected by D. Baird and P. Olsen, 1973.

Hypodigm. PU 21808, 23511, 23512 A-C, 23606, 23607, topotype slabs collected by Princeton parties, 1975, 1976, 1982; PU 23632-23637, collected by P. Olsen, J. Smoot, and M. Anders, 1984.

Locality. Cliffs and beach just south-southeast of Paddy Island, Kings County, Nova Scotia.

Age and Horizon. Late Carnian or early Norian of Late Triassic, Newark Supergroup, Fundy Group, Wolfville Formation, about 8.7 m below the contact with the overlying Blomidon Formation (Baird and Olsen 1983).

Etymology. From Acadia, early name for Nova Scotia.

Diagnosis. *Atreipus* in which digit IV of pes is very small with the center of its most distal phalangeal pad lying opposite the center of first phalangeal pad on digit III, and the manus is consistently tetradactyl.

Discussion

The combination of a small, functionally tridactyl manus and a tridactyl pes of *Grallator*-like form with poorly differentiated distal phalangeal pads marks all of the collected dinosaurian tracks from the upper Wolfville Formation at Paddy Island, Nova Scotia. All of these specimens have a pes with a proportionally long digit III, a robust digit II, an unusually slender digit IV, and less prominent metatarsal-phalangeal pads than other ichnospecies of *Atreipus* (Figs. 6.9 and 6.10). The center of the metatarsal-

phalangeal pad of digit III lies nearly opposite the most anterior part of the first phalangeal pad of digit IV. The center of the most distal pad on digit II lies about opposite the center of the first phalangeal pad on digit III. The center of the first phalangeal pad on digit III is opposite the center of the most distal (pad 4) of digit IV. Finally, digit II projects consistently farther anterior than IV. The last two points reflect how relatively delicate digit IV is. The general proportional resemblance to *A. sulcatus* (Figs. 6.9, 6.10) is especially obvious in the relative length of pedal digit III and the relative projection of digit II. In this new ichnospecies, however, digits II and III remain well separated as in *A. milfordensis*, but digit IV appears closely appressed to III. As in other ichnospecies of *Atreipus*, there is considerable variation, but the Nova Scotian tracks are consistent in the characters cited.

The manus differs from those of other ichnospecies of *Atreipus* in consistently having an impression of an additional digit medial to the three present in the other ichnospecies. This digit has only one pad. We recognize it as digit I and thereby infer that digits I-IV impress in *A. acadianus*. Only digits II, III, and IV impress in the other ichnospecies, and a definite impression of digit V has not been seen in any *Atreipus* specimens.

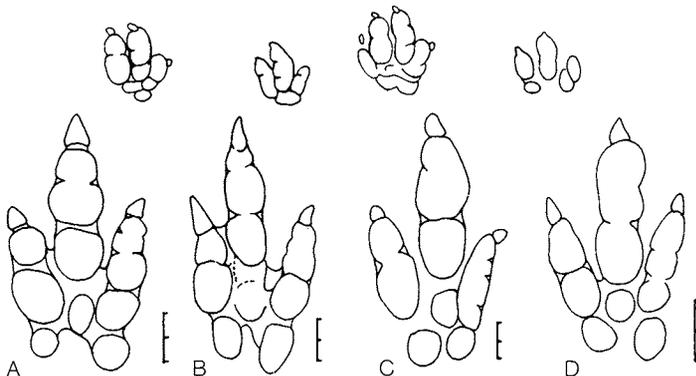
***Atreipus metzneri* (Heller)**

***Coelurosaurichnus metzneri*.** Heller (1952, pp. 135-7; includes his second and third ichnite type), Tafel 9, Figs. 2 and 3.

Type. Specimen in the Geologisches Institut von Erlangen (Heller 1952, Tafel 9, Fig. 2).

Hypodigm. Pes impressions on the type slab of *Chirotherium wondrai* in the Geologisches Institut von Erlangen and in the private collection of Dr. R. Metzner, in Markt Erlbach (Heller 1952, Tafel 9, Figs. 1 and 3). From the same locality and horizon as the type.

Figure 6.9. Composites of, **A**, *Atreipus milfordensis*; **B**, *A. sulcatus*; **C**, *A. acadianus*; and **D**, *A. metzneri*. Scale is 2 cm.



Horizon. Carnian of the Late Triassic, Ansbacher Sandstone of the Germanic Middle Keuper.

Locality. Altselingsbach, Franconia, Federal Republic of Germany.

Discussion

A small footprint faunule from the Ansbacher Sandstone of the Middle Keuper of Germany described by Heller in 1952 contains an almost certain example of *Atreipus* (see also Chapter 15). The assemblage, according to Heller (1952), consists of three kinds of ichnites. The first type is a manus-pes set that he designated *Chirotherium wondrai*. The second type consists of a number of tridactyl pes impressions that Heller named *Coelurosaurichnus metzneri*. The third type consists of a small, three-toed track to which Heller declined to apply a new name. The figured pes impressions [Heller's second type (Heller 1959, Plate 9, Figs. 2 and 3) (composite in Fig. 6.9 in this chapter) suggest a tulip-shaped track reminiscent of the pes of *Atreipus*. Heller's Plate 9, Figure 3 shows one of these pes impressions directly behind his third type of track (Heller's "eine weitere Reptilfaehrtes"), which bears an uncanny resemblance to the manus of *Atreipus* (Chapter 15). No described ichnite pes resembles Heller's third type of track, and we conclude that it is in fact the manus of his second track type, *Coelurosaurichnus metzneri*. Thus, the latter taxon is, pending actual examination of the material, almost certainly referable to *Atreipus*. The figured material bears a definite resemblance to *A. milfor-*

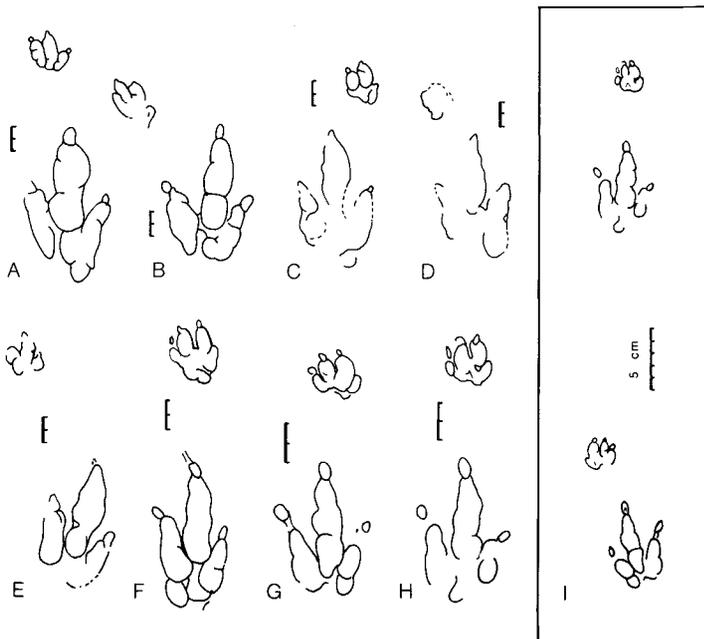
densis (Fig. 6.9), but we feel it is prudent to retain Heller's specific epithet at least until a more detailed comparison can be made.

Comparison of *Atreipus* with other dinosaurian ichnites

The combination of a manus impression with a tridactyl pes of the *Grallator* type is almost unknown in the ichnological literature. The Early Jurassic Connecticut Valley forms *Ammopus*, *Corvipes*, *Plectropterna*, *Xiphopeza*, *Arachnichnus*, *Orthodactylus*, *Sauropus barrattii*, and *Tarsodactylus caudatus* (see Lull 1953) show various combinations of tridactyl to tetradactyl pes impressions with tridactyl to pentadactyl manus impressions. All but the last two ichnotaxa were made in very muddy substrate. The tracks show little constancy of digit number or footprint form even in their types and, therefore, should be regarded as indeterminate. *Sauropus barrattii* and *Tarsodactylus caudatus*, however, are figured by Lull with a *Grallator*-like pes in association with a five-toed manus, and they, therefore, need to be considered in relation to *Atreipus*.

Sauropus barrattii as figured by Lull (1953) is comparable to *Atreipus* in having a pes virtually indistinguishable from that of *Grallator* (*Anchisauripus*). It is combined with a manus that in this case bears five toes. Lull (1953) placed *Sauropus* in the ichnofamily Anomoepodidae because of the manus and because of the supposed sitting posture in which "heel" imprints occur. Restudy of the original spec-

Figure 6.10. Holotype (A) and hypodigm (B-H) of *A. acadianus*. A-H all drawn as right manus and pes. A-E, PU 21713B; F, PU 23636; G-I, PU 23635.



imens, however, reveals that *Sauropus barrattii* is an unnatural composite of two ichnotaxa that has perpetuated factual and nomenclatural misinterpretations for nearly 120 years. The *Sauropus* of Lull's rendering has been often reprinted and used as the basis of additional inferences about trackmakers, posture, and behavior. It has also formed the basis of an ichnofamily, the Sauropodidae (Haubold 1969). In Appendix 1, we review the confused history of *Sauropus*, declare it indeterminate, and conclude that it requires no additional attention.

Lull's (1904, 1915, 1953) figures of *Tarsodactylus caudatus* Hitchcock (1858) indicate a walking trackway of small, somewhat *Grallator*-like pedal impressions associated with five-toed, outwardly rotated manual imprints. On reexamination, the type (AC 42/5), from the Turners Falls Sandstone of Turners Falls, Massachusetts, appears to be a rare quadrupedally walking example of *Anomoepus*. (The manus impressions of *Anomoepus* are usually impressed only in sitting position.) We believe that the resemblance between *Anomoepus* and *Atreipus* may indicate phylogenetic relationship, as we discuss in the section on osteological correlations.

As we know of no other forms that resemble *Atreipus* in having a three- or four-toed manus associated with a *Grallator*-like pes, additional ichnological comparisons seem unwarranted.

Biostratigraphy of *Atreipus*

The isolated basin sections of the Newark Supergroup can be broadly divided into the lower and upper Newark Supergroup (Froelich and Olsen 1984). The upper Newark Supergroup is characterized by extrusive basalt formations at its base and is Early Jurassic in age, while the lower Newark Supergroup completely lacks extrusive igneous rocks and is Late Triassic or older in age (Cornet 1977a; Cornet and Olsen 1985; Froelich and Olsen 1984).

Atreipus is widely distributed in the lower Newark Supergroup. Details of the stratigraphy of each of the basins in which *Atreipus* occurs, along with details of the stratigraphy of each locality and lists of associated biota are given in Appendix 2. Only the outlines of the distribution will be given here.

Newark Basin

Together, the Stockton, Lockatong, and Passaic formations make up the lower Newark Supergroup in the Newark Basin. There are seven younger formations making up the upper Newark Supergroup (Fig. 6.11). Thus far, although *Atreipus* has been found only in the Lockatong and Passaic formations, the range of the ichnogenus comprises more than 30 percent of the cumulative thickness of the basin section. Within the Lockatong and Passaic formations,

definite *Atreipus* specimens have been found at five horizons spread through about 1,700 m from the Weehawken Member of the Lockatong Formation to the Mettlars Brook Member of the Passaic Formation (Fig. 6.11). Another locality that produces pes impressions of the *Atreipus* type, but as yet has yielded no manus impressions, is from about 700 m higher (Ukrainian Member of the Passaic Formation), bringing the total range of *Atreipus* in the basin to 2,400 m. This is the greatest stratigraphic thickness over which *Atreipus* is known in the Newark Supergroup.

Gettysburg Basin

The Gettysburg Basin section is similar to that of the Newark Basin. There, *Atreipus* has been found at two horizons about 2,400 m apart, both within the lower Gettysburg Formation (Appendix 2), which is laterally equivalent and connected to the Passaic Formation of the Newark Basin. The Gettysburg Formation rests below the Aspers Basalt, the basal portion of the upper Newark within the basin.

Dan River Basin

Unlike the Newark, Gettysburg, and Fundy basins, the Dan River Basin contains no extrusive basalt flows and consists entirely of lower Newark Supergroup. Only one locality has produced *Atreipus* in the basin, and it is within the upper member of the Cow Branch Formation. The Cow Branch Formation is lithologically very similar and apparently the same age as the Lockatong Formation of the Newark Basin.

Fundy Basin

Atreipus is known from one locality in this basin as well. In this case, the horizon is within the uppermost Wolfville Formation about 360 m below the North Mountain basalt, the basal formation of the upper Newark Supergroup in the Fundy Basin. This horizon seems to correlate with the Lockatong or lower Passaic of the Newark Basin.

Stratigraphic relationship of *Atreipus* assemblages

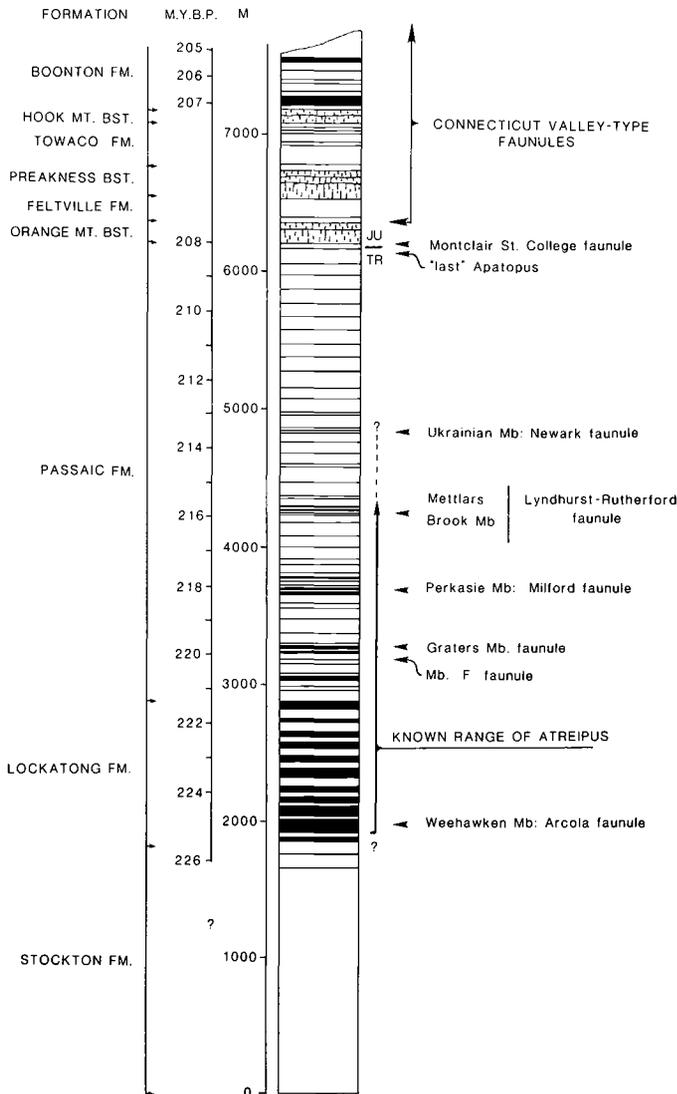
Atreipus and its associated ichnites make up a consistent assemblage, usually dominated by *Atreipus*, small *Grallator* spp. and *Rhynchosauroides* spp., but also including *Apatopus* and *Brachychirotherium* spp. Only in the Newark and Fundy basins can the stratigraphic relationship between *Atreipus* faunules (which are the oldest footprint assemblages in those basins) and subsequent ichnite faunules be demonstrated.

In the Newark Basin, the stratigraphically highest occurrence of the *Atreipus* assemblage ap-

pears to be a trackway of *Apatopus* (PU 21235) in the Passaic Formation at a level about 10 m below the Orange Mountain Basalt at Llewellyn Park, West Orange, New Jersey. In the uppermost meter of the same formation, however, there appears a distinctly different ichnofauna that heralds a change to the classic, dinosaur-dominated ichnofaunas of the Connecticut Valley. This intermediate fauna was recovered by Chris Laskowich during excavation for the Montclair State College parking lot in Little Falls, Passaic County, New Jersey. As a carryover from the earlier, typically Triassic ichnofaunas, it

includes *Rhynchosauroides brunswickii* (PU 22005, 22006, 22204, 22214); this genus is rare in the higher (postextrusive) beds of the Newark Basin and is unknown in the Connecticut Valley. On the other hand, the small crocodyloid ichnogenus *Batrachopus* makes its earliest known appearance at Little Falls, New Jersey in the form of abundant and well-preserved trackways of *Batrachopus* cf. *B. deweyi* (PU 21902, 21933, 22001, 22004–22007, 22205, 22213–22214), the common species in the Connecticut Valley. Theropod-type tracks include the large *Grallator* (*Anchisauripus*) *minusculus* (PU 21900, 21901), the

Figure 6.11. Stratigraphy of the Newark Basin showing the positions of the major footprint faunules discussed in the text and the known ranges of *Atreipus* and the Connecticut Valley-type faunules. Black horizontal bars and lines indicate gray and black clusters of Van Houten cycles, with the most obvious spacing being the 100 m (400,000 year) compound cycle. The gross aspects of the time scale are derived from the DNAG scale (Palmer 1983), but the fine calibration is based on the inferred durations of Van Houten cycles from Olsen (1984a, b). Members from Olsen (1984a).



medium-sized *G. (A.) sillimani* (PU 21900, 21903, 21904, 21933, 22003, 22202, 22210, 22313, 22366), and *Grallator* sp. (PU 21903, 22201, 22313, 22366). (Duplicated numbers indicate slabs bearing several species.) The Little Falls faunule is decidedly different from any older Newark Basin assemblage and is the only preextrusive assemblage from the Newark Supergroup that bears a definite Connecticut Valley aspect.

The sedimentary sequence – Feltville, Towaco, and Boonton formations – that overlies and is interbedded with the Newark Basin extrusives of the upper Newark Supergroup of the Newark Basin has yielded many footprint faunules at different horizons. These faunules are very similar and as a whole are indistinguishable from the Connecticut Valley assemblage described by Hitchcock (1858, 1865), Lull (1904, 1915, 1953), and Olsen (1980a). The characteristic ichnogenus *Anomoepus* makes its first appearance in the Feltville Formation (PU 18565), and in this and higher formations is accompanied by *Grallator (Eubrontes)* spp., *G. (Anchisauripus)* spp., *G. (Grallator)* spp., and *Batrachopus* spp. The Towaco Formation has also yielded examples of cf. *Rhynchosauroides* sp. and *Ameghinichnus* sp. Citations of specimens and a complete faunal list are given in Olsen (1980b,c).

In the Fundy Basin of Nova Scotia, we have discovered several footprint faunules that are younger than the *Atreipus* assemblage (Baird 1984). A small faunule comprising *Grallator (Grallator)* spp., *G. (Anchisauripus)* spp., and *Rhynchosauroides* sp. occurs in the Blomidon Formation (which overlies the Wolfville Formation) on the north shore of St. Marys Bay, Digby County, Nova Scotia, about 250 m below the North Mountain Basalt. This horizon, therefore, falls roughly 110 m above the level of the *Atreipus* faunule. In the Fundy Basin, the upper Newark consists of the North Mountain Basalt and the overlying Scots Bay Formation and McCoy Brook formations. In the type Scots Bay Formation, theropod-type tracks occur on the top surface of an eolian brown sandstone that overlies the fish-bearing lake beds: *Grallator (Eubrontes) giganteus*, *Grallator (Anchisauripus) sillimani*, and *G. (A.) cf. tuberosus*. These have been photographed but not collected. On the north shore of the Minas Basin at Five Islands Provincial Park (Colchester County), and at Blue Sac and McKay Head (Cumberland County), the lower McCoy Brook Formation has yielded tracks of *Anomoepus* spp., *Grallator (Eubrontes)* spp., *G. (Anchisauripus)* spp., *Batrachopus* spp., and *Otozoum moodii*. Specific localities and specimen citations for these localities are given in Olsen (1981). The Scots Bay and McCoy Brook formations are lateral equivalents, and their footprint faunules are indistinguishable from

those of the Connecticut Valley and those of the post-Passaic sediments of the Newark Basin.

To find footprint faunules older and different from those containing *Atreipus*, we must go to the Sanford Subbasin of the Deep River Basin in North Carolina, where the Pekin Formation of the Chatham Group has produced a small but significant ichnofauna. This Pekin assemblage can be placed in stratigraphic perspective, vis-à-vis the *Atreipus* faunules of the Dan River Group, Gettysburg Basin, Newark Basin, and Fundy Group, by correlative means independent of footprints.

Only one locality in the Pekin Formation has produced a reasonable ichnofaunule: the Pomona Pipe Products clay pit near Gulf, North Carolina. So far the identifiable forms include relatively short-toed, tridactyl, presumably dinosaurian footprints; very large- to medium-sized bipedal tracks resembling *Brachychirotherium* sp.; and *Apatopus* sp. Apart from *Apatopus* there are no forms in common with the *Atreipus* and younger assemblages. Associated skeletal remains include the dicynodont *Placerias*, the phytosaur *Rutiodon*, the aetosaur *Typothorax*, and large carnosaur-like teeth that presumably represent a rauisuchid pseudosuchian (Baird and Patterson 1967). This assemblage lies roughly 300 m below the base of the Cumnock Formation and is Middle Carnian on the basis of associated mega- and microfossil florules (Hope and Patterson, 1969; Cornet 1977a). The overlying Cumnock Formation has produced a microflorule that correlates with the basal New Oxford Formation of the Gettysburg Basin and the lower member of the Cow Branch Formation of the Dan River Group (Cornet 1977a; Robbins 1982; Cornet and Olsen 1985). The middle New Oxford Formation contains mega- and microfloras correlating with the Lockatong Formation and the upper member of the Cow Branch Formation (Cornet 1977a, b; Robbins 1982). These floral correlations are completely supported by correlation by vertebrate skeletal evidence (Olsen et al. 1982). The Lockatong, in turn, correlates with the middle Wolfville of the Fundy Group on the basis of skeletal remains (Olsen 1981; Olsen et al. 1982; Baird and Olsen 1983). These correlations show that the Pekin faunule is significantly older than those containing *Atreipus*.

The palynology and skeletal remains of the *Atreipus*-bearing beds in the Newark and Gettysburg basins allow the younger ichnofaunules to be correlated. Microflorules from the Heidlersburg Member of the Gettysburg Shale of the Gettysburg Basin (which overlies the *Atreipus* faunules) are Norian in age and correlate with the Perkasio Member of the Newark Basin (Cornet 1977a). Pollen and spore assemblages from near the Mettlars Brook Member in the Newark Basin indicate a middle Norian age, and

those from the Ukrainian Member indicate an early late Norian (early Rhaetian of older works). Likewise, in the Fundy Basin, the Wolfville *Atreipus* faunule lies some 360 m below a latest Norian or earliest Jurassic florule (Olsen 1981) and, therefore, is of late Carnian or Norian age.

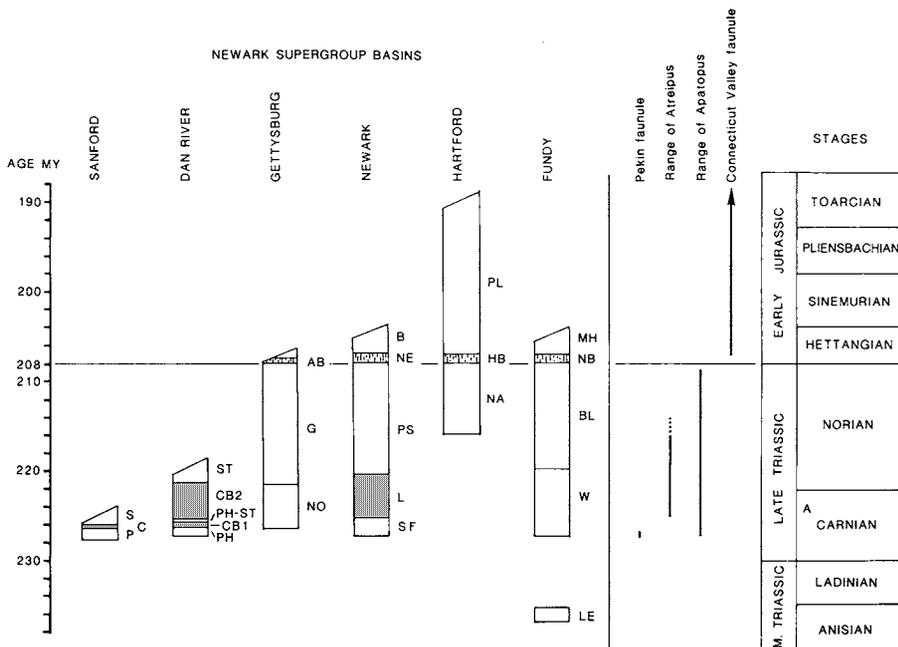
To summarize for the entire Newark Supergroup, the oldest *Atreipus* occurs in the Lockatong Formation and upper member of the Cow Branch Formation of late Carnian age and the youngest occurs near the Mettlars Brook Member of the Passaic Formation of middle Norian age or possibly in the overlying Ukrainian Member, embracing a stratigraphic thickness of about 2,400 m. At an approximate sedimentation rate of 400,000 years per 100 m, calibrated both by varves in the characteristic and permeating lacustrine rhythmic sedimentary sequences called Van Houten cycles (a detailed description of which is given in Appendix 2) and by published radiometric scales (Olsen 1984a,b), this

works out to roughly 9,600,000 years (or possibly 12,400,000 years if the Ukrainian Member is included) for the known temporal range of *Atreipus*. This is roughly three-quarters of the estimated duration of the Late Triassic.

Atreipus (Coelurosaurichnus) metnerzi comes from the Ansbacher Sandstone of the German Middle Keuper. This unit lies between the Schilfsandstein and the Blasensandstein, both thought to be of late Carnian age (Laemmlen 1956; Gall, Durand, and Muller 1977: but see Chapters 24 and 25). We can, therefore, conclude that both in Europe and in eastern North America, the known range of *Atreipus*, is late Carnian to at least middle Norian (Fig. 6.12).

It is worth noting that the manus impressions of *Atreipus* were overlooked for nearly a century: they were either not recognized or thought to be tracks of another animal. It is possible, therefore, that a number of *Grallator*-like tracks in the litera-

Figure 6.12. Correlation of Sanford, Dan River, Gettysburg, Newark, Hartford, Fundy basins of the Newark Supergroup with the European standard stages, the radiometric scale, and ranges of the Pekin and Connecticut Valley faunules, *Atreipus*, and *Apatopus*. Position of the German *Atreipus metzneri* shown by "A" in the standard stages column. Abbreviations for formations of the Newark basins as follows: AB, Aspers Basalt; B, Boonton Formation; BL, Blomidon Formation; C, Cumnock Formation; CB1, lower member of Cow Branch Formation; CB2, upper member of Cow Branch Formation; G, Gettysburg Shale; HB, Hartford Basin extrusive zone (Talcott Basalt, Shuttle Meadow Formation, Holyoke Basalt, East Berlin Formation, Hampden Basalt); L, Lockatong Formation; LE, Lower Economy beds of Wolfville Formation; MH, McCoy Brook and Scots Bay Formations; NA, New Haven Arkose; NB, North Mountain Basalt; NE, Newark Basin extrusive zone (Orange Mountain Basalt, Feltville Formation, Preakness Basalt, Towaco Formation, Hook Mountain Basalt); NO, New Oxford Formation; P, Pekin Formation; PH, Pine Hall Formation; PH-ST, Pine Hall plus Stoneville Formations; PL, Portland Formation; PS, Passaic Formation; S, Sanford Formation; SF, Stockton Formation; ST, Stoneville Formation; W, Wolfville Formation.



ture may be *Atreipus* with manus impressions that have gone unnoticed. All such Late Triassic material should accordingly be reexamined.

Osteological correlations

Attempts to assign a footprint to a trackmaker should consist of a search for derived and primitive features, just as the placement of a biological taxon within a phylogenetic classification does. These features of the footprint should reflect the osteology of the maker. Only two classes of trackmaker characters are important: first, those that are primitive (plesiomorphic) for a group and that serve *only* to bar membership in the groups possessing derived states of that character and, second, those that are shared with and derived for a group (synapomorphic) and hence uniquely identify membership in a group. Thus, merely showing that an osteological reconstruction from a footprint is identical to the feet of small theropod dinosaurs does not mean that the track might not have been made by a primitive bird, because many of the typical "avian" characters are primitive for theropod dinosaurs *including* birds (Gauthier 1984; Gauthier and Padian, 1985). However, such an osteological reconstruction does indicate that the trackmaker was a dinosaur (including birds) because such structure was attained *uniquely* by that group. Thus, assignment of an ichnotaxon to a particular biological group demands some a priori knowledge of the phylogenetic relationships of the groups under consideration. It is not enough to show that a track and a known skeleton are similar.

The foregoing consideration becomes a special problem with *Atreipus* because its combination of features is unknown in osteological taxa. As we show below, it apparently represents a new kind of dinosaur, at this stage known only by its feet.

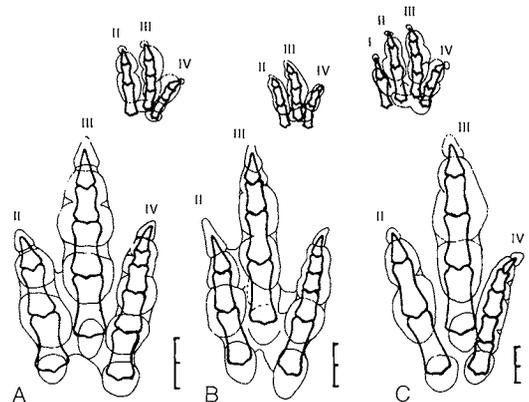
According to the rules of osteological reconstruction worked out by Heilmann (1926), Peabody (1948), and Baird (1957), joints between bones in the pes are reconstructed in the center of the pads as they are in cursorial birds (Heilmann 1926; Peabody, 1948; Baird 1957) and in crocodiles (Chapter 20) and large lizards (Padian and Olsen 1984). In many ways, the pes imprints of *Atreipus* and *Gralalior* spp. could be attributed to small theropod dinosaurs. It comes as a great surprise, therefore, that *Atreipus* proves to have a manus completely incompatible with those of any known theropod. The *Atreipus* manus imprint shows three to four short digits with only tiny claw imprints, if there are claw imprints at all. All known theropods (except post-*Archaeopteryx* birds) have large trenchant claws on the manus. In addition, the manus of theropods is thought to be a grasping hand, not a walking hand; but *Atreipus* has a theropod-like pes in combination

with a short-clawed, functionally tridactyl manus that was habitually used in locomotion.

The osteological reconstruction of the pes of the North American species of *Atreipus* poses no problems (Fig. 6.13). Obviously, the pedal skeleton was functionally tridactyl, a unique feature of dinosaurs (and their immediate relative *Lagosuchus*). The dinosaurs are divided into ornithischians and saurischians. The proportions of the pes correspond to those of theropods that have a comparatively long digit III; ornithischian pedes tend to have a relatively shorter digit III. It is not known, however, whether theropod-like proportions are primitive for dinosaurs in general or derived for theropods. Therefore, we cannot conclude that the pedal structure excludes ornithischians.

The manus of *Atreipus* is clearly highly derived with respect to the primitive condition in archosaurs (Peabody 1948; Krebs 1976). In the primitive archosaur manus, digits I, II, and III are more robust than IV and V, but all five toes are functional. Less derived archosaur footprints, such as *Chirotherium*, show a five-toed imprint (Peabody 1948). Digit III (or more rarely IV) tends to be the longest, and digit I or V the shortest. The manus of *Atreipus* retains some of this primitive pattern, but is clearly not functionally pentadactyl, and there is a clear shift of emphasis to digits II, III, and IV rather than I, II, and III. In order of increasing length, the digits are I, IV, II, III, with no impression of V. The weakly differentiated pads and very short toes suggest strong digitigrady. The tiny claws of the manus suggest the presence of small, pointed unguals. The manus of saurischians was not primitively tridactyl, although digits I, II, and III were already dominant (as in ornithosuchians and crocodiles). In later theropods, however, there is a continued reduction of the number of digits to three (and two in tyrannosaurs). All

Figure 6.13. Osteological reconstructions of *Atreipus*: A, *Atreipus milfordensis*; B, *Atreipus sulcatus*; C, *Atreipus acadianus*. Scale is 2 cm.



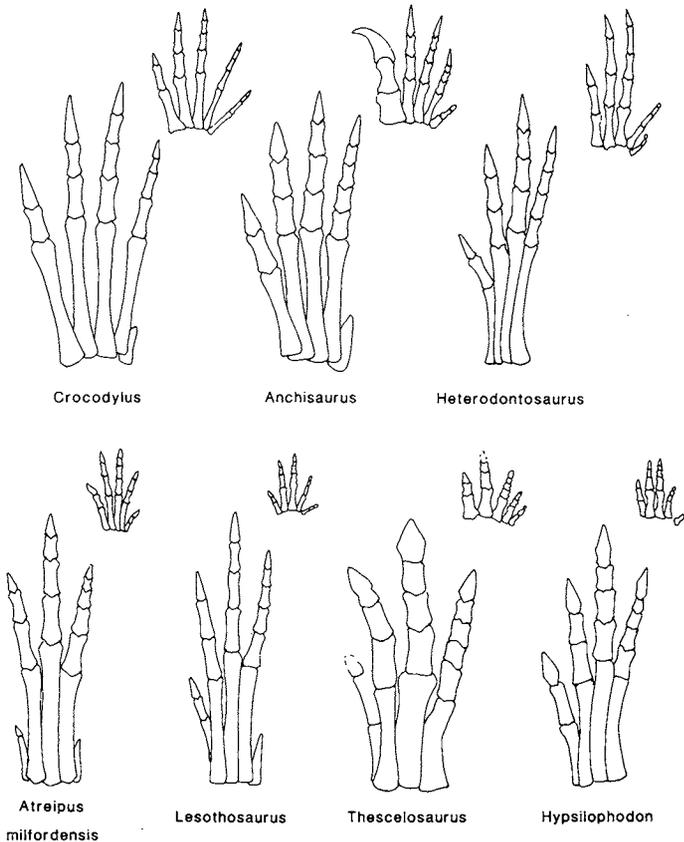
saurischians retain large claws on the dominant manual digits, and all but some carnosaur retain a large manus, however.

Ornithischians also had a tendency toward functional tridactyly and reduction of trenchant claws in the manus; however, this tendency took at least two different directions. *Heterodontosaurus*, from the Early Jurassic of southern Africa, has a manus that is very similar proportionally to those of some prosauropods and theropods (Bakker and Galton 1974), with large trenchant claws on the non-reduced digits I, II, and III. According to Bakker and Galton (1974), this resemblance is a synapomorphy uniting ornithischians and saurischians, and hence such a manus is primitive for dinosaurs in general. This hypothesis has been severely criticized by a number of authors (Thulborn 1975; Walker 1977), although Gauthier (1984) and other workers accept it.

In contrast, the manus of a number of ornithischians, such as *Leptoceratops*, *Tenontosaurus*, and *Thescelosaurus* (Brown and Schlaikjer 1942; Galton 1974a) are similar in proportions to the manus in nondinosaurian archosaurs, such as *Euparkeria* (except for the dinosaurian reduction in phalangeal formula of digit IV and V). This resemblance could be interpreted as a shared primitive condition between ornithischians and their nondinosaurian ancestors. A manus with elongated digits I, II, and III with trenchant claws would thus be a synapomorphy of saurischians, and the proportions and massive claws of *Heterodontosaurus* would be convergent. *Atreipus* would thus share the condition of small nontrenchant unguals with predinosaurian archosaurs and ornithischians primitively.

On the other hand, if the prosauropod-heterodontosaur-like manus is primitive for dinosaurs, the manus of *Atreipus* would be derived for

Figure 6.14. Comparison of dorsal views of manus and pedes of various archosaur taxa: *Crocodylus* (adapted from Romer 1956); the prosauropod *Anchisaurus* (adapted from Galton 1976); the heterodontosaurid ornithischian *Heterodontosaurus tuckii* (adapted from Santa Luca 1980); reconstruction of *Atreipus milfordensis* from Figure 6.13, with the addition of hypothetical digits I and IV of the manus (the former based on *A. acadianus*) and digits I and V of the pes; the fabrosaurid ornithischian *Lesothosaurus* (loosely adapted from Thulborn 1972) with the manus reconstruction from illustrations of the actual material restored to the pattern seen in the ichnogenus *Anomoepus* in Figure 6.15; the ornithopod ornithischian *Thescelosaurus* (adapted from Galton 1974a; Romer 1956); and the ornithopod ornithischian *Hypsilophodon foxii* (adapted from Galton 1974b).



either group unless it is not a dinosaur. Reduced unguis could be a synapomorphy uniting nonheterodontosaurid ornithischians, including *Atreipus*.

The configuration of the manus in the other early ornithischians adds some weight to the first hypothesis. Unfortunately, the earliest (Carnian) forms, including *Pisanosaurus* (Bonaparte 1976) and new forms from the Newark Supergroup of Nova Scotia and North Carolina (Galton 1983) and the Dockum Group of Texas (S. Chatterjee pers. comm.), are fragmentary, without a well-preserved manus or pes. The next oldest ornithischians, including *Scutelosaurus* (from the Early Jurassic of the Glen Canyon Group of Arizona) and *Lesothosaurus* (from the Early Jurassic Upper Stormberg Group of southern Africa), are represented by much more complete material, although neither has a complete manus. Thulborn (1972) reconstructed the manus of the latter genus to fit the pattern seen in the Cretaceous ornithischian *Hypsilophodon* (Galton 1974b). The manus of *Scutelosaurus* is even less complete than that of *Lesothosaurus*, although Colbert (1981) reconstructed it after the pattern seen in *Lesothosaurus* and *Hypsilophodon*. *Scutelosaurus* provides no additional information except that it does have small pointed unguis.

A different reconstruction of *Lesothosaurus* and *Scutelosaurus* is possible if a different phylogenetic model is used. The very reduced digit V of

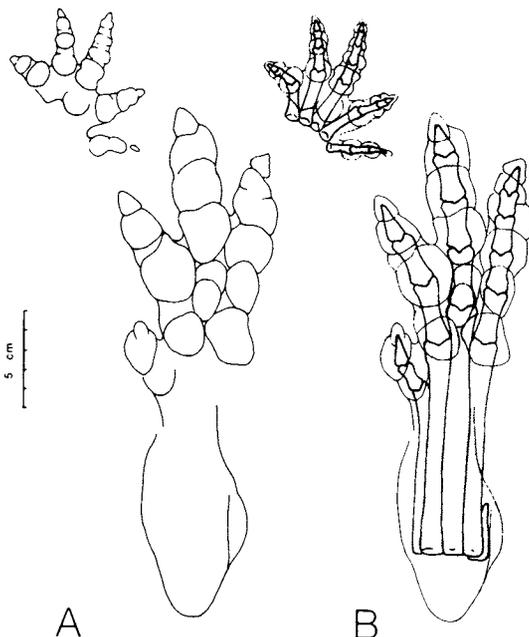
Hypsilophodon is surely a derived feature because a more complete digit V is seen in ceratopsians, ankylosaurs, stegosaurs, *Camptosaurus*, *Tenontosaurus*, *Thescelosaurus*, and other ornithischians and is almost certainly primitive for the group (e.g., *Heterodontosaurus*). It seems more prudent to reconstruct the manus of *Lesothosaurus* and *Scutelosaurus* according to the primitive rather than a derived pattern. If the manus of *Lesothosaurus* is restored after these latter forms, particularly *Thescelosaurus* (see Galton 1974a), it resembles the reconstructed manus of the common Early Jurassic ichnite *Anomoepus* (Figs. 6.14 and 6.15). The manus of *Anomoepus* also closely resembles that of the chirotheres (including *Brachychirotherium*) and crocodiles (including *Batrachopus* and *Otozoum*), except for the presence of the dinosaurian specialization of a reduced number of pads on digits IV and V. In addition, the reconstructed pes of *Anomoepus* bears a very strong resemblance to the pes of all the well-preserved early ornithischians.

Nothing in the manus of the early ornithischians suggests the pronounced tridactyl digitigrady of *Atreipus*. The Early Jurassic *Anomoepus* makes a much better trackway for Early Jurassic gracile ornithischians than does the Late Triassic *Atreipus*. Nonetheless, the differences between the manus of *Atreipus* and *Anomoepus* is basically one of degree, not of kind, with the basic difference being that digitigrady is more pronounced in *Atreipus*.

Digitigrady of the manus is well developed in some later Mesozoic ornithischians, such as iguanodontids and hadrosaurs, but digit I is very reduced in these forms. The manus of *Atreipus* could, however, be regarded as an early expression of that trend. Interestingly, digit I of the pes, which does not impress in *Atreipus*, is lost in these same later Mesozoic groups.

In summary, *Atreipus* is a dinosaur (or very close to being a dinosaur) because of the birdlike, tridactyl pes. However, according to which hypothesis of dinosaur monophyly is followed (Fig. 6.16), *Atreipus* could be either an ornithischian with a more derived condition than *Heterodontosaurus* or a dinosaur less derived than saurischians. In the latter case, it could be either an ornithischian or a very plesiomorphic dinosaurian belonging neither to ornithischians nor saurischians. In any case, the manus of *Atreipus* finds a close dinosaurian counterpart in the ornithischians. However, there are no really close skeletal correlatives now known, and our best guess is that *Atreipus* may have been made by a very early ornithischian with marked quadrupedal, cursorial adaptations, in which a somewhat hadrosaur-like manus was combined with a coelurosaur-like pes that had a short digit I. We have thus reconstructed the maker of *Atreipus* as a gracile ornithischian dinosaur (Fig. 6.17).

Figure 6.15. *Anomoepus*: A, composite manus-pes set of *Anomoepus crassus*, left side of standard sitting trackway [based principally on RU main display slab (figured in Olsen 1980a)]; B, osteological reconstruction of A.



If this reconstruction is accepted, *Atreipus* and *Anomoepus* reflect the presence of two temporally distinct ornithischian taxa in Newarkian time. *Atreipus*, the Triassic form, has certain derived features, while *Anomoepus*, the Jurassic form, has no apparently derived features (within ornithischians). Both ichnogenera are characteristic of their times, whatever the zoological affinities of their makers.

Appendix 1: the problem of *Sauropus barrattii*

In 1837, Edward Hitchcock gave the name *Sauroidichnites barrattii* to a natural cast of a manus on a paving stone from Middletown, Connecticut, presumably from the Portland Formation. This specimen (AC 20/4) is illustrated by Olsen and Padian (Chapter 20). On the same surface are one fairly clear small pes impression and two small, poor tracks of the *Grallator* type, as well as at least one *Batrachopus* trackway. There is no obvious relation between the relatively large manus on the slab and the relatively small pedes. In 1841, Hitchcock redescribed and refigured the same manus. He renamed it *Sauropus barrattii* in 1845, referred it to *Anomoepus* in 1848, and renamed it *Chimaera barrattii* in 1858. His son, Charles H. Hitchcock, for good measure, renamed it *Chimaerichnus barrattii* in 1871.

Meanwhile, in 1843 Edward Hitchcock had given the name *Ornithichnites lyellii* to an isolated medium-sized track of what we would call *Grallator* from the Turners Falls Sandstone of Turners Falls, Massachusetts (AC 31/85). In succession, he renamed the same track *Fulicopus lyellianus* (1845), then *Aethyopus lyellianus* (1848), and

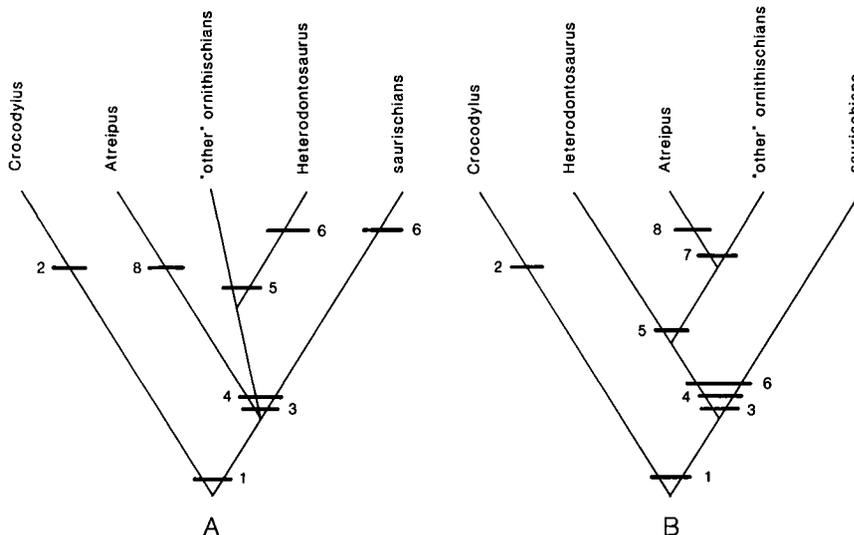
finally he referred the species to *Amblonyx* in 1858. In 1858, E. Hitchcock also referred trackways of a grallatorid on a large slab (AC 1/1) from the Turners Falls Sandstone at Gill, Massachusetts to *Amblonyx lyellianus*. Both specimens were designated as types of *Amblonyx lyellianus* by E. Hitchcock in 1865.

Edward Hitchcock (1858) referred one other trackway on AC 1/1 to the genus *Anomoepus*, giving it and another specimen (AC 1/7) the new specific name *A. major*. Hitchcock thought that this trackway was made by an animal sitting down, in the standard sitting pose of *Anomoepus*, because he thought he could see two parallel manus-pes sets and two "heel" impressions posterior to the pedal impressions, as well as a more posterior central "ischial" impression. Let us now trace how this interpretation evolved.

In Plate VIII of Hitchcock (1858), a line drawing, the left pes is drawn entirely with dashes except for two small circular depressions. Both manus impressions were drawn with solid lines and clearly resemble Hitchcock's 1837 rendering of the manus of *Sauropus barrattii*. On the excellent lithograph in the same volume (E. Hitchcock 1858, Plate XXXVIII) only two irregular impressions are shown where Hitchcock had drawn the manus imprints, and only two small depressions show in the line drawing for the left pes.

In 1904, Lull traced the left half of Hitchcock's line drawing of AC 1/1, but turned the dashed lines into solid lines, labeling the illustration *Fulicopus lyellianus*. He also provided a reconstruction showing an ornithopod-like dinosaur in sitting position and listed the type specimens of *F. lyellianus* as AC 1/1 and 31/85 (only the latter, of course, is the true type). At the same time, Lull correctly noted

Figure 6.16. Alternate cladograms of the relationships of *Atreipus* to other dinosaur groups and crocodiles, mostly based on characters of the manus. Characters as follows: 1, "archosaurian" nonpedal characters (from Thulborn 1975; Walker 1977); 2, reduction in number of phalanges in digit IV of the manus (may be synapomorphy of crocodiles plus dinosaurs and may be related to character 4); 3, tridactyl dinosaurian pes; 4, reduction of number of phalanges in manual digits IV and V; 5, "ornithischian" nonpedal characters (from Thulborn 1975; Walker 1977); 6, enlargement of digits I, II, and III of manus; 7, reduction in length of digits I, II, and III of manus; and 8, great reduction of digit I of pes.



that the left pes of the specimen referred to *Ambloonyx lyellianus* on AC 1/1 and the left pes of the trackway of *Anomoepus major* on the same slab both had a unique deformity or injury and, therefore, must have been made by the same individual. In 1915, Lull synonymized *Sauropus barrattii* with *Anomoepus major* and *Ambloonyx lyellianus*, the first having priority, and listed the types as AC 1/1 and AC 1/7 with AC 31/85 being dropped from mention. Lull (1953) retraced all of Hitchcock's (1858) line drawing of *Anomoepus major*, again filling in the dotted lines, and repeated his previous opinion (Lull 1915) on the synonymy of *Sauropus* and the supposed type specimens; he also provided a new reconstruction of the trackmaker.

This convoluted situation requires rectification. First, only the Middletown slab (AC 31/81) can be the holotype of *S. barrattii*, because it was the only specimen figured in 1836 when the genus was named. In regard to this specimen, C. H. Hitchcock (1858, p. 55) stated, "This is the true type of the genus and species *Chimaera* [*Sauropus*] . . ." Thus, the type of *Sauropus barrattii* is an isolated manus (as it can hardly belong with any of the several gallatorid tracks on the same slab), and, because it is so

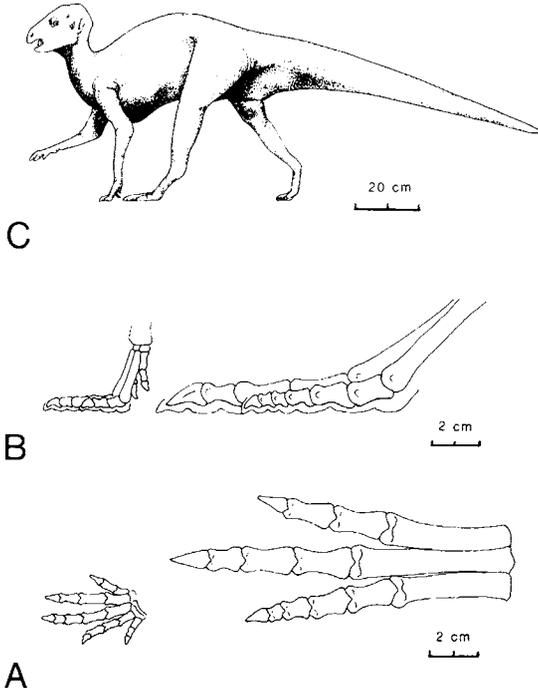
worn as to be indeterminate, we regard the genus and species as *nomina vana*.

Second, the often-figured specimen AC 1/1, which is both a syntype of *Anomoepus major* and incorrectly listed as a type of *Ambloonyx lyellianus*, shows no indication whatsoever of manus impressions except for a single irregular mark in the position of the left manus in Hitchcock's line drawing of *A. major*. There are several similar impressions over the surface in other locations. What Hitchcock (1858) figured as the left "heel" of *A. major* proves to be a complete left pes, and the supposed left pes belonging to the same "heel" consists, as shown in Hitchcock's lithograph, of two small impressions that are like dozens of others dotting the slab. The "ischial" impression is very faint and seems to bear no connection to what is clearly a perfectly normal walking trackway, apparently made by the same individual that made the adjacent "*Ambloonyx*" trackway. These are clearly two excellent trackways of the *Gallator* (*Anchisauripus*) *tuberosus* type and have nothing to do with *Anomoepus*.

Third, the other syntype of *Anomoepus major* (AC 1/7) is a poor but typical *Anomoepus* sitting trackway with a genuine "ischial" impression. With the removal of AC 1/1, AC 1/7 becomes the lectotype of *A. major* by elimination.

Fourth, all the other specimens cited as examples of *Sauropus* (E. Hitchcock, 1858) prove to be either very sloppy and indeterminate tracks (13/2, 13/14) or good specimens of *Anomoepus* (37/9). Therefore, we can conclude that the concept of *Sauropus barrattii* as envisioned by Lull (1904, 1915, 1953) and shown in his figures has no basis in the morphology of any actual footprints. *Sauropus* and its type species, *S. barrattii*, are therefore *nomina vana* based on indeterminate material.

Figure 6.17. Reconstruction of *Atreipus*: A, ventral view of right restored manus-pes set of *A. milfordensis* with hypothetical metapodials and digits I and V in foreshortened perspective (digit I based on *A. acadianus* and digit V is hypothetical); B, lateral view of left manus and pes; C, hypothetical flesh reconstruction of *A. milfordensis* based on a gracile relatively unspecialized ornithischian and proportioned after the Arcola, Pennsylvania trackways of *A. milfordensis* (Figure 6.5).



Appendix 2: geological occurrences and associated fossils Newark Basin

Material referred to *Atreipus* has been found at five localities in the Passaic Formation and two localities in the Lockatong Formation. These localities represent six separate main horizons within the Newark Basin spanning roughly 2,400 m of the Newark Basin section. We begin by discussing the general stratigraphic framework of the Lockatong and Passaic and follow this with descriptions of each Newark Basin locality, its stratigraphic position, and the associated faunal and floral remains.

Stratigraphy of the Lockatong and Passaic formations

As currently understood (Van Houten 1969; Olsen 1980a,b) the Newark Basin is divided into ten formations (Fig. 6.2A) that are in ascending order: the Stockton Formation, Lockatong Formation, Passaic Formation and its lateral equivalent the Hammer Creek Conglomerate, Orange Mountain Basalt, Feltville Formation, Preakness Basalt, Towaco Formation, Hook Mountain Basalt, and Boonton Formation. Only the Lockatong and Passaic formations need be considered here.

The Lockatong and Passaic formations together make up a natural lithologic facies package united by a common theme of repetitive and permeating transgressive-

regressive lacustrine cycles (Van Houten 1964, 1969, 1980; Olsen 1980a,b, 1984a,b). The fundamental sedimentary cycle consists of:

1. A lower thin (<1 m), shallow water, transgressive gray siltstone or fine sandstone (division 1) overlain by
2. A 0.5–2-m deeper water (high stand), gray to black, often laminated siltstone (division 2), which grades up into
3. A shallow water, regressive, thicker (1–4 m) gray or red siltstone and sandstone (division 3).

These are called Van Houten cycles (Olsen 1985) after their discoverer, and have a mean thickness of 4–6 m throughout much of the Newark Basin. Very similar cycles characterize most of the finer-grained sediments of the Newark Supergroup.

These transgressive–regressive cycles make up larger compound cycles that are mainly expressed as ordered sequences of Van Houten cycles. They differ principally in the degree to which their division 2 approaches an organic-rich, microlaminated siltstone – the deepest water lithology. Two orders of compound cycles are obvious: a cycle 25 m thick and one 100 m thick. The 25-m cycles consist of four to five Van Houten cycles in which division 2 is better developed in the lower cycles. There is a strong tendency for the upper Van Houten cycles in these sequences to be mostly red. The 100-m cycles consist, in turn, of about four of the 25-m cycles. Division 2 of the contained Van Houten cycles is best developed in the lower 25-m cycles, and the upper 25-m cycles tend to be red. The main difference between the Lockatong and Passaic formations is that most of the 100-m cycles of the Passaic tend to be red, and these red intervals have less well-developed Van Houten cycles. The boundary between the Lockatong and Passaic is operationally defined as where red beds become dominant over gray.

Van Houten cycles and the compound cycles they make up apparently can be traced over very large areas. In the Passaic, the 100-m cycles comprise relatively easily mapped units because of the alternation of thick gray and red units. McLaughlin (1941, 1946, 1948) has traced all of the 100-m cycles of the lower 1,000 m of the Passaic Formation throughout the Hunterdon Plateau Fault Block and has designated the gray portions of the 100-m cycles as individual informal members of the Passaic. These members have since been recognized in the adjacent fault blocks and provide a relatively precise stratigraphy for much of the Newark Basin. A similar framework of members has been proposed for the Lockatong (Olsen 1984a,b).

Some Van Houten cycles have varved beds in division 2. Varve counts from these beds can be used to calibrate the duration of the cycles. Using this method Van Houten (1964, 1969, 1980) and Olsen (1984a,b) estimated the duration of Van Houten cycles at about 21,000–23,000 years and the duration of the compound cycles at 100,000 years for the 25-m cycles and 400,000 years for the 100-m cycles. Fourier analysis of long sections in the Lockatong, comparison of the number of cycles in the Lockatong plus Passaic Formation, and published radiometric scales confirm these estimates of the cycles' duration (Olsen 1984a, b).

Van Houten cycles have a paleontological as well as lithological expression. Fossil fish and crustaceans gen-

erally occur in division 2 and reptile footprints in divisions 1 and 3. In those Van Houten cycles with an especially poorly developed division 2, however, reptile footprints can occur in the deepest water portions of the unit. At most localities, *Atreipus* occurs in division 1 or the lower parts of division 3 of Van Houten cycles. These facts allow the bulk of Lockatong and Passaic footprint faunules to be placed in stratigraphic and temporal position with unusual precision.

Atreipus localities and associated biota in the Newark Basin of Newark, New Jersey

Within the city of Newark, a footprint faunule in which *Atreipus* is questionably present was collected in 1971 by Neal K. Resch. It occurs in the Ukrainian Member of Olsen (1984a), which is the Easton Avenue member and Second Precinct Station member of Cornet (1977a) of the Passaic Formation, about 700 m above the Mettlars Brook Member (Fig. 6.11) and 1,000 m below the Orange Mountain Basalt. This poorly preserved faunule, part of which was mentioned by Olsen (1980b, p. 30), is dominated by small grallatorids of uncertain affinities (PU 21516) but also contains single footprints comparable to *Grallator* (*Anchisauripus*) *sillimani* (Hitchcock) (PU 21518) and a *Grallator* of the "A. *tuberosus* group" (PU 21516). Pes imprints of the *Atreipus* type (PU 21517) are present, but in each of the three cases the slab terminates immediately anterior to the pes, so that the presence or absence of a manus cannot be determined. Associated quadrupeds include the ubiquitous *Rhynchosauroides brunswickii* (PU 21520), several sizes of *Brachychirotherium* cf. *B. eyermani* (Baird) (PU 23645–23647), and obscure tracks of *Apatopus* sp. (PU 23643–23644).

The associated biota includes conchostracans and a palynoflorule dominated by *Corollina meyeriana*, the oldest such florule in the Newark Basin. This florule can be dated as probably late middle Norian (late Norian of Cornet and Traverse (1975, pp. 27–8), who recognized the Rhaetian as a separate stage). The lateral equivalent of this member at Ukrainian Village, Mercer County, New Jersey has produced well-preserved *Semionotus* sp. and an identical florule. In the same area, red siltstones within 100 m below this member have produced a single, small *Brachychirotherium* sp. (PU 23423).

Lyndhurst–Rutherford area, New Jersey

A diverse collection of footprints was made at a lower Passaic locality during the late 1960s by Mr. Larry Black. Unfortunately, the exact locality was not recorded at the time of collection, and the area has changed so much in the following twenty years that the original site cannot be located. Apparently, the locality was on the east side of the ridge that underlies the towns of Lyndhurst and Rutherford, Bergen County, New Jersey, which places it roughly 1,400 m above the local base of the Lockatong [if the thickness of the Palisades Sill (300 m) is subtracted] and 1,700 m below the Orange Mountain Basalt. The local lithology consists of beds of platy red siltstone and fine sandstone separated by more massive red siltstones and sandstones. At about this level, in the New Brunswick area, 48 km to the southwest, is the Mettlars Brook Member of the Passaic Formation (Olsen 1984a) (Fig. 6.11).

Associated ichnites include *Grallator* (*Grallator*)

spp., *Grallator* (*Anchisauripus*) spp., *Coelurosaurichnus* sp. (*sensu stricto*, characterized by a long digit IV), *Brachychirotherium parvum*, *B. eyermani*, *Apatopus* sp., and *Rhynchosauroides brunswickii*.

Perkasie Member, Milford Area, New Jersey

The Perkasie Member (Drake, McLaughlin, and Davis 1961) of the Passaic Formation consists of two sequential 25-m compound cycles, each consisting of two well-developed Van Houten cycles and one red and purple, weakly developed Van Houten cycle. McLaughlin named the lower 25-m cycle N and the upper one O. All of the *Atreipus* from the Milford area comes from division 3 of the second gray and black Van Houten cycle of unit O of the Perkasie Member (Fig. 6.11), and all of those specimens apparently come from the Clark Quarry, not the two supposedly different localities mentioned by Baird (1957).

The Perkasie Member occurs in the highest exposed beds of the Passaic along the Delaware River. Once thought to be the youngest strata in the Newark Basin (Fig. 6.2A), it is now clear that this interval actually lies in the lower Passaic Formation, roughly 2,800 m below the top of the formation. All the overlying strata have been eroded in the Milford area. Correlation of the Milford area with the Sourland Mountain Fault Block and the Newark Basin area (Olsen 1984a) places the Perkasie roughly 800 m below the Mettlers Brook member.

The gray footprint bearing horizons in unit O of the Perkasie that produce the type material of *A. milfordensis* and *A. sulcatus* have also produced the types of *Brachychirotherium parvum* (C. H. Hitchcock 1889), *B. eyermani* (Baird 1957), *Apatopus lineatus* (Bock 1952) and *Rhynchosauroides hyperbates* (Baird 1957), as well as examples of *Grallator* (*Anchisauripus*) *parallelus* (E. Hitchcock), *Rhynchosauroides* cf. *R. brunswickii* (Ryan and Willard 1947) (Baird 1957), *Coelurosaurichnus* sp. (same ichnospecies as the Mettlers Brook Member) (PU 23651), and an uncertain small tridactyl form (Baird 1957). Gray sandstones of undetermined position within unit N have produced an important megafossil plant assemblage (Newberry 1888; Bock 1969) including *Glyptolepis platysperma* and *G. keuperiana* (Cornet 1977a), *G. delawarensis* (Bock 1969) (which may be equivalent to one of the preceding species), *Pagiophyllum* spp., and (?) *Cheirolepis munsteri*, *Clathropteris* sp., and *Equisetites* spp. In addition, conchostracans have been found in division 2 of the upper cycle of unit O.

The purplish and red footprint-bearing units overlying the Perkasie have produced, in addition to *A. milfordensis*, the type of *Chirotherium lulli* Bock 1952, cf. *Coelurosaurichnus* sp. [still *sensu stricto* but a different ichnospecies than the two previous occurrences (Baird 1954)], and numerous tracks of a small *Grallator* (PU 19910) associated with *C. lulli*. Gray and red claystones form division 2 of a Van Houten cycle about 50 m above the base of unit O of the Perkasie in the same area (Fig. 6.11). These contain *Semionotus* sp., the conchostracans *Cyzicus* sp. and cf. *Ellipsograptus*, and nondarwinulid ostracodes. Outcrops of these same two units along Route 519 are Cornet's (1977a) localities M-4 and M-3. These, along with a gray unit about 100 m above the Perkasie (Cornet's locality PF-3) contain a pollen and spore assemblage belonging to Cor-

net's (1977a) and Cornet and Olsen's (1985) lower Passaic-Hiedlersburg Palynoflora. The age of this assemblage is Early Norian (Cornet 1977a; Cornet and Olsen 1985).

Graters Member, Frenchtown, New Jersey

Footprints are common in the red and gray platy siltstones that comprise McLaughlin's (1941, 1946, 1948) Graters Member along Nishisackawick and Little Nishisackawick Creek, east of Frenchtown, New Jersey. This set of two 25-m cycles lies about 400 m below the Perkasie Member. The single *Atreipus* pes from this locality was collected from gray siltstones underlying division 2 of the upper cycle of member H of the Graters Member in Little Nishisackawick Creek adjacent to the boro boundary of Frenchtown, Hunterdon County, New Jersey. Associated ichnotaxa include *Gwyneddichnium minor* and *Rhynchosauroides brunswickii*. Cornet (1977a) has described a palynomorph florule from the underlying cycle of H exposed along Nishisackawick Creek. This assemblage belongs in the transitional zone between the New Oxford-Lockatong Palynoflora and the lower Passaic-Heildersburg Palynoflora and thus appears to be latest Carnian or earliest Norian (Cornet 1977a; Cornet and Olsen 1985).

A probable occurrence of *Atreipus* is mentioned by Lyman (1902) from Fisher's Quarry on the south side of Lodel Creek about 1.6 km northwest of Graterford (Grater's Ford), Pennsylvania. The quarry exposes beds that appear to be just above the Graters Member of the Passaic Formation. Lyman describes several dinosaur footprints with small manus impressions; unfortunately, their present whereabouts are uncertain.

Member F, Frenchtown, New Jersey

Atreipus occurs in abundance in red and purple siltstones about 1.5 m below McLaughlin's (1941, 1948) member F. This horizon is about 75 m below the Graters Member (Fig. 6.11) and is part of a pair of 25-m cycles, which, like the Perkasie and Graters Members, have been traced over a large part of the Newark Basin. In the area north of Frenchtown, along Nishisackawick Creek, Member E becomes wholly red and difficult to separate from the rest of the Passaic. Member F, however, still retains a thin gray-green and purple unit, above which are flaggy red and purple siltstones with abundant reptile footprints. In addition to *Atreipus*, this horizon has produced *Brachychirotherium eyermani* (PU 23639, 23641).

Gwynedd (North Wales), Pennsylvania

The slab containing the lost type of Bock's (1952) *Anchisauripus gwyneddensis* was collected in rubble excavated from the deep railroad cut at Gwynedd, Montgomery County, Pennsylvania (Fig. 6.2A). The precise bed that was the source of this specimen is unknown. Footprints occur at a number of levels within the cut, a detailed section of which is given in Olsen (1984a). The exposed interval represents the lower, but not lowest Lockatong [Gwynedd I and II members of Olsen (1984a, b)], which occurs about 1,000 m below members E and F (Fig. 6.11).

Fossils are abundant in the forty or so Van Houten cycles exposed in the Gwynedd cut, and the types of a large number of Newark vertebrate taxa come from this site. These include the types of *Anchisauripus gwyneddensis*, *Gwyneddichnium elongatum* Bock 1952 (= cf. *Rhyncho-*

sauroides sp.), and *G. minor* Bock 1952 (a minute chirotheriid), as well as the osseous taxa *Rhabdopelix longispinis* Cope (1869–70) [now lost specimens possibly consisting of a composite of the tanystropheid *Tanytrachelos* Olsen (1979) and possibly the flying lizard *Icarosaurus* Colbert (1966)]; *Gwyneddosaurus erici* Bock (1945) (another composite, this of a coelacanth and possibly *Tanytrachelos*); *Lysorocephalus euri* Huene and Bock (1954) [thought to be an amphibian but really a skull roof of *Turseedus* (Baird 1965)] *Gwyneddichthys major*, *G. gwyneddensis*, and *G. minor* Bock (1959) (the last three may all belong in *Turseedus*); *Cionichthys* (*Redfieldius*) *obrai* (Bock 1959), (?) *Semionotus howelli* Bock (1959), *Diplurus* (*Osteopleurus*) *newarki* (Bryant 1934), *Diplurus* (*Pariostegus* = *Rhabdolepis*) *gwyneddensis*, and *D. striata* Bock (1959); and *Carinacanthus jepseni* Bryant (1934). Phytosaur teeth, *Synorichthys* sp., conchostracans, ostracodes, and coprolites have also been found. Bock (1946) has described a supposed phyllocarid crustacean from this locality, but the specimen has proved to be the anal plate and associated scales of a fish.

Scraps of plants are not uncommon, but tend to be poorly preserved. An unfortunately large number of taxa have been founded on mostly indeterminate remains from Gwynedd by Bock (1969), including the types of *Brachyphyllum conites*, *Thujatostrobos triassicus*, *Gloeotrichata formosa*, *Stolophorites lineatus*, *Cycadenia elongata*, *Cycadospadix gwyneddensis*, *Zamiostrobus minor*, *Z. minor*, *Z. rhomboides*, *Carpolithus carposerratus*, *C. amygdalus*, *Albertia gwyneddensis*, *Araucarites cylindroides*, and *Pagiophyllum crassifolium*. Most of these are conifer shoots, cone scales, or invertebrate ichnofossils. One of Bock's (1961) forms, *Diplopororundus rugosus* from Gwynedd, is definitely the arthropodan ichnite *Scoyenia*; namely, Waner's (1889) *Ramulus rugosus*, was based on *Scoyenia* from his *Atreipus* locality. Bryant (1934) cites "*Podozamites*" and Bock (1952) also lists *Pterophyllum powelli* (? = *Zamites powelli*) without locality, and "*Neocalamites* from Gwynedd."

Pollen and spores also occur within portions of Van Houten cycles at Gwynedd. The palynomorph assemblage is dominated by *Patinosporites densus* and nonstriate bisaccates and belongs to Cornet's (1977a,b) New Oxford–Lokatong palynoflora (Cornet and Olsen, 1985). According to Cornet (1977a) and Olsen and Cornet (in press), this assemblage is of late Carnian age.

Arcola, Pennsylvania

A long series of road cuts (now covered) for the Schuylkill Expressway near the towns of Arcola and Oaks, Montgomery County, Pennsylvania exposed roughly 200 m of lower Lokatong Formation [Weehawken and Hoboken Members of Olsen (1984a, b)]. About 100 m of this section were repeated by faults within the outcrops. At the northernmost cut, an enormous (900 m²) area of a single footprint-bearing bed was exposed during construction. This unit was the source for the *Atreipus* trackway shown in Figure 6.6. It lies roughly 100 or 200 m below the Gwynedd horizon and 1,100 m below members E–F of the Passaic Formation.

The exposed sections showed a long sequence of unusually fossiliferous Van Houten cycles. Footprints occur at several intervals in these sections. The main footprint-

bearing layer occurs in red siltstones of a division 1 of a Van Houten cycle near the top of the section, with only a green division 2. Very abundant *Rhynchosauroides* cf. *R. brunswickii* and rare, poor dinosaur tracks (? *Atreipus*?) occur in the lower parts of this division. At the main track locality, about 7 cm below the top of division 1, is a very laterally persistent parting surface, traceable over the entire exposure, which is so unusual that it deserves special description. The bed forming the track-bearing surface is about 1 to 2 cm thick. It is finely laminated at the base and ripple laminated at the top; the ripple troughs are filled with fine siltstone so that the upper surface shows no ripples. There are no internal parting planes, but there are small calcareous nodules within the oscillation–ripple bedded portion of the bed. This unit is broken by narrow but deep (+ 30 cm) mud cracks propagated down through at least the overlying 5 cm of division 1. The track-bearing surface is covered by irregular patches of very fine, short (1–4 mm) wavy lines, which we suggest could be the impression of a filamentous algal scum. Large (4–20 cm) cylindrical siltstone tubes puncture the surface at irregular intervals. Because these tubes branch downward in the underlying units, we assume that they represent small trees. Detailed impressions of conifer fronds (cf. *Pagiophyllum simpsoni*) drape around a number of these tubes where they intersect the main footprint surface, proving that the trees lived at the time the footprints were made. Conifer shoots occur sporadically over the rest of the surface. We infer that the trees puncturing the footprint surface produced the foliage present on the surface, although this cannot be proved.

The most common ichnite on the main surface appears to be *Rhynchosauroides hyperbates* Baird (1957), originally known from the Perkasio Member of the Passaic Formation. Many of the individual manus–pes sets have scaly plantar surfaces completely preserved in exquisite detail. Sinuous trackways of this form crisscross the surface, and some trackways come full circle. Because all the material is almost precisely the same size, it is possible that all of these trackways were made by the same individual wandering (stalking?) back and forth. Some of the trackways have belly impressions where the trackmaker seems to have rested; others show a transition from walking to swimming, strongly suggesting that the footprint surface was under a few centimeters of water at the time of impression.

Only two trackways belonging to other ichnotaxa crossed the exposed part of the surface. One faint trackway appears to be referable to *Brachychirotherium eyermanni* (YPM 9963), known elsewhere from the Perkasio Member and Stockton Formation of the Newark Basin and the Gettysburg Formation of the Gettysburg Basin. The other trackway was, of course, the *Atreipus milfordensis* of Figure 6.6. The most western tracks of this series are much deeper and sloppier than the more eastern ones, so that the track surface was not of uniform competence. No other dinosaurian tracks could be found on this surface.

No fossils were found in the green claystone of division 2 of this cycle, but small, poor *Rhynchosauroides* occur sporadically in division 3. Other cycles exposed in these cuts contained abundant fragmentary to complete fish [*Diplurus* (*Osteopleurus*) *newarki*, *Diplurus* (*Pariostegus*) sp., *Turseedus*, *Synorichthys*, and *Semionotus* spp.], as well

as conchostracans, ostracodes, phytosaur teeth and bones, and the burrow *Scoyenia*. Nearby, the old Reading Railroad cut between Arcola and Oaks exposes the same cycles with the same fossils, including abundant *Rhynchosauroides* cf. *brunswickii* from division 1 of the same cycle that produced the *Atreipus* and other ichnites at the road cut. This exposure is Bock's (1959) "Yerkes" locality.

The context of the main track-bearing surface within the cyclic section suggests that the reptiles walked in very shallow water upon a drowned soil that still supported living trees. This surface was already draped with several centimeters of lacustrine mud deposited by a recent transgression of what was shortly to become a perennial lake.

Gettysburg Basin

Newark strata of the Gettysburg Basin of Pennsylvania and Maryland are divided into three formations, which are (from the bottom up): the Gettysburg Formation, made up of mainly red clastics; the New Oxford Formation, consisting of gray and red sandstones and siltstones; and the Hammer Creek Conglomerate, composed principally of red conglomerate (Glaeser, 1963). Near the top of the Gettysburg Formation are the Aspers Basalt and thin, overlying, red and gray clastics, and in the upper middle of the Gettysburg is the gray, black, and red Heidlersburg Member (Stose 1932; Stose and Jonas 1939). The Gettysburg Formation is the fine lateral equivalent of the Hammer Creek Conglomerate, and the latter is the coarse equivalent of the Passaic Formation; together they make up a single cohesive lithosome. Likewise, the New Oxford Formation is laterally continuous with the Stockton and Lockatong formations of the Newark Basin, and these make up another major lithosome.

Atreipus occurs at two localities in the Gettysburg Basin. Both are in the Gettysburg Formation between the Heidlersburg Member and the New Oxford Formation. Wanner's (1889) material was collected from a small quarry opened in a hillside about 1.6 km (1 mi) south of Goldsboro, York County, Pennsylvania. This locality is a calculated 4,120 m above the base of the New Oxford Formation and 2,850 m below the Heidlersburg Member of the Gettysburg Formation. Based solely on Wanner's illustrations, associated fossils include *?Apatopus* sp., the same small short-toed form that occurs at Milford (Baird 1957), *?Rhynchosauroides* sp., and the arthropod burrow *Scoyenia* (Wanner's *Ramulus rugosus*).

The Trostle Quarry ichnofauna was collected by Elmer R. Haile, Jr. in 1937 from the quarry located on Bermudian Creek, 4.8 km (3 mi) east of York Springs near Bermudian Springs (Pondtown), Adams County, Pennsylvania. The horizon is roughly 6,000 m above the base of the New Oxford Formation, within 450 m of the base of the Heidlersburg Member of the Gettysburg shale, and about 3,900 m below the base of the Jurassic Aspers Basalt. Other ichnotaxa from this locality include *Brachychirotherium eyermani*, an odd pentadactyl stubby-toed form suggestive of a dicynodont foot (Stose and Jonas 1939, Plate 22 lower right; Baird 1957), *Rhynchosauroides brunswickii*, and *Scoyenia*.

Dan River Basin

Four formations comprise the Dan River Group in the contiguous Dan River and Danville basins of Virginia

and North Carolina: the Pine Hall and Dry Fork formations, of gray and buff sandstone and red siltstone; the Cow Branch Formation, made up of gray and black siltstones and sandstones; and the Stoneville Formation of red siltstone and conglomerate (Meyertons 1963; Thayer 1970). The Pine Hall and Stoneville formations are the basal units and complexly interfinger with the other three formations in all directions.

The Cow Branch Formation *Atreipus* was found in the Solite Company Quarry in Leakville Junction, Virginia–North Carolina. The Solite Quarry exposes more than 300 m of the upper member of the Cow Branch Formation (Olsen et al. 1978). The footprint-bearing block was not found in place, but does come from the currently active part of the quarry, which limits its origin to the middle 150 m of the section measured by Olsen et al. (1978) and Olsen (1979, 1984a). Like the Lockatong, the Cow Branch Formation consists of transgressive–regressive Van Houten cycles (Olsen 1984a), but at this point the exact cycle from which the *Atreipus* originated would be very difficult to determine.

A large and varied faunal and floral assemblage has been found in the Cow Branch Formation in the Solite Quarry. Ichnites from this locality include *Atreipus* sp. and *Grallator* (*Grallator*) spp. (Olsen et al. 1978). Vertebrate skeletal taxa found in association include *Rutiodon* sp., the type of *Tanytrachelos ahynis*, *Turseodus* spp., *Cionichthys* sp., *Synorichthys* sp., *Semionotus* sp., *Diplurus* (*Pariostegus*) sp., and a new fish, possibly a pholidophorid. Conchostracans, ostracodes, a large new crustacean, and diverse insects are abundant. Nineteen nominal megafloreal taxa and a small palynoflora have also been recovered (Robbins 1982). The diverse faunule and megaflorelule have been reviewed in detail by Olsen et al. (1978).

Fundy Basin

Klein (1962) and Keppie et al. (1979) divide the Nova Scotian portion of the Fundy Group into five formations, which are from the bottom up: the Wolfville Formation (0–400 m), of coarse red and brown clastics; the Blomidon Formation (10–350 m), of red siltstone and sandstone; the North Mountain Basalt (250 m); and the Scots Bay Formation (0–20 m) of gray and white limestone chert and brown sandstone, which is laterally equivalent to the McCoy Brook Formation (+ 300 m) of red clastics.

We have recovered slabs of footprints from just below the contact between the Wolfville and Blomidon formations along the cliffs and on the beach just southeast of Paddy Island, Kings County, Nova Scotia (Fig. 6.10). The footprint-bearing unit appears to be a single bed of brown sandstone overlying a thin red siltstone in the uppermost Wolfville 8.5 m below what is locally the basal, horizontally bedded sandstones of the Blomidon Formation. The footprint level is 18.6 m below the lowest red mudstone of the Blomidon in the same section. This works out to about 360 m below the North Mountain Basalt. Abundant *Rhynchosauroides* occur on the same slabs as the *Atreipus*, and two trackways of *Brachychirotherium parvum* have also been found. In addition, a procolophonid skull with partial skeleton (apparently *Hypsognathus* sp.) have been found about 6.8 m below the track-bearing horizon. This faunule will be the subject of a more detailed future paper.

Abbreviations of cited repositories

AC, Pratt Museum of Geology, Amherst College, Amherst, Massachusetts
 AMNH, American Museum of Natural History, New York, New York
 ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania
 CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
 LC, Geology Department of Lafayette College, Easton, Pennsylvania
 MCZ, Museum of Comparative Zoology of Harvard University, Cambridge, Massachusetts
 PU, Museum of Natural History, Princeton University, Princeton, New Jersey, collection now housed at Yale University
 RU, Rutgers University, Geological Museum, New Brunswick, New Jersey
 YPM, Peabody Museum of Natural History of Yale University, New Haven, Connecticut

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