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The postcranial skeleton of the family Limnoscelidae and its taxonomic implications for understanding basal amniotes

Natalia Kazimiera Wideman

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THE POSTCRANIAL SKELETON OF THE FAMILY
LIMNOSCELIDAE AND ITS TAXONOMIC
IMPLICATIONS FOR UNDERSTANDING
BASAL AMNIOTES

A Thesis
Presented to the
Faculty of
California State University,
San Bernardino

In Fulfillment
of the Requirements for the Degree
Master of Science
in
Biology

by
Natalia Kazimiera Wideman
September 2002
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Approved by:
Dr. Stuart Sumida, Chair, Biology
Dr. James Ferrari, Biology
Dr. Joan Fryxell, Geology
Dr. Anthony Metcalfe, Biology
ABSTRACT

The Diadectomorpha is a central taxon in understanding the origin and early evolution of amniotes. It is considered a sister taxon to Amniota and is so similar to amniotes that some researchers have placed it within the Amniota itself. This group is composed of three families: the Limnoscelidae, the Tseajaiidae, and the Diadectidae. Being the most basal member of this group, the family Limnoscelidae is especially important in these studies. However, even though it is vital to the studies of early amniote origins and evolution, the postcranial skeleton of Limnoscelis, the most complete member of this family, has never been fully described or illustrated. In this study, the postcranial skeleton of Limnoscelis is fully described. Also, for the first time ever, the full dorsal and partial ventral views of the most complete specimen of Limnoscelis, L. paludis (YPM 811), are illustrated.

The family Limnoscelidae currently consists of four genera with six species. Most of these genera, except Limnoscelis, are based on fragmentary materials. The taxonomic basis and validity of these taxa is reassessed in this study.
Finally, cladistical analyses of the diadectomorphs and primitive amniotes have been conducted using mainly cranial characters. Here, a cladistical analysis is performed using exclusively postcranial characters and the results of this analysis are compared to the hypothesis of relationships based on mainly cranial characters.
I would like to thank Dr. Stuart Sumida, for sharing his knowledge of limnoscelids and for all his support throughout my time at California State University San Bernardino, both with this project and others. Thanks to my thesis committee: Dr. Joan Fryxell, Dr. Anthony Metcalf and Dr. Jim Ferrari; who aided me along the way with their comments and encouragement. I am grateful to the staff of the Raymond M. Alf Museum of Paleontology for all of their support and patience. My sincere appreciation to Dr. David S Berman and Amy Henrici of the Carnegie Museum of Natural History for all of their assistance in studying Limnoscelis, as well as their generous hospitality. Thank you also to the curators who loaned the specimens necessary for this study: Chuck Schaff of the Museum of Comparative Zoology for his above and beyond the call of duty help with seeing and borrowing specimens; Dr. Patricia Holroyd of the University of California Museum of Paleontology; and Robert Smith of the United States National Museum of Natural History.

In the Cal State Vertebrate Paleontology lab, thanks to Gavan Albright and Kim Scott for assistance with
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On the home front, I would like to thank my parents, Dana and Janusz, and my brother, Michael, for their constant support during this project. Thanks also to Sarah and Brian Kennedy for all of their encouragement. And last, but certainly not least, to Brett A. Kennedy, for his patience or impatience with me as necessary, and for his continuous support.

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To Zofia Sczęśniak Antopolska
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CHAPTER ONE

INTRODUCTION

The amphibian - amniote transition was a critical one for vertebrate life on Earth, as it marked the first time animals had the ability to be fully terrestrial. Amphibians are dependent on water for reproduction because of their egg structure; without water they cannot produce viable offspring. Therefore, amphibians must spend at least some of their lives near water or concentrations of moisture. With the introduction of the amniotic egg, tetrapods, for the first time, were not dependent on water to reproduce and could be fully terrestrial. The composition of this egg, which was probably developed over an extended period of time, consists of an embryo with four extraembryonic membranes, which include an amnion, a yolk sac, a chorion and an allantois (Romer, 1957; Lee and Spencer, 1997; Stewart, 1997).

The Late Paleozoic family Limnoscelidae has been a central taxon for understanding the origin and early evolution of amniotes for most of the previous century (e.g. Williston, 1911; Romer, 1966; Berman et al., 1992; Sumida et al., 1992; Sumida, 1997). This may be indicated
by the assignment of the Limnoscelidae and the more inclusive Diadectomorpha in Amphibia, Reptilia, and simply Amniota over the course of the century. However, regardless of the taxonomic/systematic assignment of the Diadectomorpha (and within it Limnoscelidae), they have always been classified very close to the Amphibian-Amniote boundary.

The Late Pennsylvanian and Early Permian (approximately 280 to 300 million years before present) Limnoscelidae are part of the more inclusive tetrapod grouping, the Diadectomorpha, that is generally considered to be the sister group to all Amniota as traditionally defined (Heaton, 1980; Figure 1). The diadectomorphs are so 'amniote-like' that they have at times been hypothesized to be actual amniotes themselves, and the practice is becoming more frequent (e.g. Berman et al., 1992; Lee and Spencer, 1997; Berman, 2000). The Diadectomorpha is composed of three families: Diadectidae, Tseajaiidae, and Limnoscelidae. The latter two families have a strictly North American record, whereas the family Diadectidae is found both in North America and central Europe (Berman
Figure 1. Cladogram of the Relationships of Diadectomorpha and Amniota (based on Sumida et al., 1992).


et al., 1997). Significantly, the limnoscelids have been suggested as basal members of the grouping, making them a reasonable model for the skeletal structure characteristic of extremely primitive amniotes.

Although the Diadectomorpha is generally accepted as a pivotal group in understanding the structure, function, and phylogenetic relationships of basal amniotes, not all of its constituent members have been studied to similar
degrees of detail. Table 1 summarizes the most recent evaluations of the different regions of the skeleton for members of this group.

Clearly, the postcranial skeleton of limnoscelids has never been carefully or completely characterized. Although isolated, species-specific studies do exist (Berman and Sumida, 1990; Sumida, 1997 {in part}), none of the studies address the patterns of postcranial structure throughout the family. This can only be regarded as unfortunate given the importance of the family to our understanding of early amniote interrelationships and function. A complete survey of the postcranial skeleton of the family Limnoscelidae is instrumental in proposing complete hypotheses regarding amniote origins, basal amniote relationships, and primitive amniote locomotor function.

Abbreviations Used in Text:
Comparative Zoology, Harvard University, Cambridge, Massachusetts.

Anatomical Abbreviations Used in the Text: act: acetabulum; cor: coracoid plate; delt: deltoid process; ect: ectepicondyle; ent: entepicondyle; ent for: entepicondylar foramen; f: femur; fi: fibula; gl for: glenoid foramen; h: humerus; icl: interclavicle; mc: medial centralia; ole: olecranon process; p: pisiform; r: radius; rade: radiale; sup: supinator process; t: tibia; u: ulna; ule: ulnare.
Table 1. Recent Studies of the Skeleton of the Families of Late Paleozoic Diadectomorpha.

<table>
<thead>
<tr>
<th>Family</th>
<th>Diadectidae</th>
<th>Tseajaiaidae</th>
<th>Limnoscelidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Skeletal Region</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Skull, Dermal Roof</td>
<td>Berman et al., 1992</td>
<td>Berman et al., 1992</td>
<td>Berman et al., 1992</td>
</tr>
<tr>
<td>Skull, Braincase</td>
<td>Berman et al., 1992</td>
<td>Berman et al., 1992</td>
<td>Berman et al., 1992</td>
</tr>
<tr>
<td>Skull, Palate</td>
<td>Olson, 1947</td>
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<tr>
<td>Lower Jaw</td>
<td>Berman et al., 1999</td>
<td>Moss, 1972</td>
<td>Fracasso, 1983</td>
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<td>Atlas-axis complex</td>
<td>Sumida et al., 1990</td>
<td>Sumida et al., 1990</td>
<td>Sumida et al., 1992</td>
</tr>
<tr>
<td>Vertebral Column</td>
<td>Sumida, 1990</td>
<td>Watliser, 1993a,b</td>
<td>Sumida, 1990</td>
</tr>
<tr>
<td>Appendicular</td>
<td>Sumida, 1997</td>
<td>Watliser, 1993a,b</td>
<td></td>
</tr>
</tbody>
</table>

Note: Clear cells indicate no recent studies. Light grey cells indicate partial studies, dark grey cells indicate complete studies encompassing all available specimens. Citations for respective studies are listed within each cell.
Taxonomic and Literature Review

Williston (1911) was the first to discover and publish information on limnoscelids. He described Limnoscelidae as "a new family of reptiles from the Permian of New Mexico." The basis of this new taxon was the nearly complete, articulated skeleton of *Limnoscelis paludis*. Unfortunately, he illustrated only representative parts of the skeleton instead of the skeleton in whole, and included only a brief description. At the time, Williston classified Limnoscelidae in the Class Reptilia, initiating what was to be a complex history of phylogenetic assignment for *Limnoscelis*.

The following year, Williston (1912) continued his work on *Limnoscelis paludis*, reconstructing it as a slow, crawling reptile with a long body and long tail that hunted slow-moving prey. He suggested that *L. paludis* probably lived a semi-aquatic lifestyle in marshes and hid in the water from its enemies (Williston, 1912).

Romer (1946) redescribed *Limnoscelis*, concluding that it was indeed a reptile, but that its anatomy was so generalized that it could be "regarded as representing the common stem of all lines of reptilian descent."
Later, Romer (1952) described a new limnoscelid, *Limnosceloides dunkardensis*. He described this new genus as a stout, heavy "cotylosaur" indistinguishable from *L. paludis*, except in size, about one half the size of *L. paludis*. Romer also placed this new genus in the Class Reptilia, and in the Order Cotylosauria, which at that time consisted of limnoscelids, as well as romeriid (now known as protoroothyridid) and captorhinid reptiles.

The late 1960s brought a flurry of new limnoscelid descriptions. Lewis and Vaughn (1965) described *Limnoscelops longifemur* as a new genus based on the specimen’s possession of a combination of limnosceloid-like vertebrae and a captorhinid-like femur. Significantly, Lewis and Vaughn classified the Family Limnoscelidae in the Order Cotylosauria and the Suborder Captorhinomorpha, despite the fact that at the time, the suborder Diadectomorpha existed within the Cotylosauria, but only contained the single Family Diadectidae. Limnoscelids were not considered diadectomorphs (in the current sense of the term) at that time.

The following year, Langston (1966) described a new species of *Limnosceloides*, *L. brachyoles* from New Mexico. He found many dissociated elements, all approximately the
same size, and cumulatively assigned them to a single new species. This species was differentiated from *L. dunkardensis* by its more robust and foreshortened femur, which was, as he described it, “clumsily built.” He classified this new species in the same way as Lewis and Vaughn classified *Limnoscelops longifemur*.

In 1967, Carroll described yet another genus of limnoscelid, *Limnostygis relictus*. Carroll considered it the oldest limnoscelid known because it was found in a Middle Pennsylvanian fossil tree stump in a Nova Scotia coal mine. Carroll distinguished this genus based on its size, geological age, and vertebral differences. He described this animal as an early member of the limnoscelid lineage with many primitive features. As this was purported to be such an early member of the limnoscelids, Carroll suggested that it might have been aquatic. However, he also pointed out that most animals found in tree stumps are terrestrial, so there was a possibility *Limnostygis relictus* was terrestrial. He classified this new genus into the Order Cotylosauria, Suborder Captorhinomorpha (Carroll, 1967).

Also in 1967, Baird and Carroll described another limnoscelid – *Romeriscus periallus*. *Romeriscus* was
recovered on Cape Breton Island, Nova Scotia, and is even older than *Limnostygis relictus*; it is Early Pennsylvanian in age. This is a poorly preserved specimen, whose assignment to the Family Limnoscelidae was based on its skull and vertebral structure. However, Laurin and Reisz (1992) reassessed this limnoscelid and concluded that due to the poor preservation, the skeleton could only be classified as *Tetrapoda incertae sedis* and was definitely not a limnoscelid.

Fracasso (1983, 1987) provided very detailed descriptions of the superficial structures of the skull, as well as the braincase, of *Limnoscelis paludis*. He classified the limnoscelids as members of the Order Diadectomorpha in the Class Reptilia, suggesting that diadectomorphs and Seymouria are primitive reptiles related most closely to pelycosaurs (Fracasso 1983, 1987; Berman and Sumida, 1990). The classification of limnoscelids in the Order Diadectomorpha, adopting the strategy of Heaton (1980), was a divergence from previous analyses, which classified limnoscelids as captorhinomorphs.

The most recently described limnoscelid is *Limnoscelis dynatis*, which was found in Late Pennsylvanian sediments of central Colorado (Berman and Sumida, 1990). An almost
complete skeleton of this animal was found and is distinguished from *L. paludis* by a few differences in cranial elements. Berman and Sumida (1990) suggested that *L. paludis* is more derived than *L. dynatis*. Once again, the classification of limnoscelids was changed. Berman and Sumida classified *L. dynatis* in the Order Diadectomorpha; however, they placed it in the Class Amphibia. Significantly, this is the only limnoscelid described under the rigorous rules of phylogenetic systematics, also known as cladistics.

**Geological and Geographical Context**

Specimens and taxa assigned to the Limnoscelidae span a temporal range from Middle Pennsylvanian to Early Permian and come from various locations throughout North America. The localities where limnoscelids have been recovered can be found on the map in Figure 2. As the first and most complete taxon described, *Limnoscelis paludis* has always been the standard by which all other limnoscelids are compared. This convention will be followed here. The Late Pennsylvanian/Early Permian *L. paludis* was found in the Cutler Formation of El Cobre Canyon of New Mexico (Figure 3; Williston 1911a,b). This formation is in the vicinity of
Figure 2. Map of North America Showing the Localities Where Limnoscelids Have Been Recovered. 1, Limnoscelis paludis; 2, Limnoscelis dynatis; 3, Limnosceloides dunkardensis; 4, Limnosceloides brachycoles; 5, Limnoscelops longifemur; 6, Limnostygis relictus. Adapted from Schultze and Chorn, 1997.

the Galinas Mountains, east of the Nacimiento Mountains, and reaches as far east as the peak El Cobre north of the Chama River. The deposits in the lower part of the canyon where the specimen was found are much darker than similar deposits of the Cutler Formation in the nearby Rio Puerco Valley and San Diego Canyon, and are overlain by the Triassic Chinle Formation (Eberth and Miall, 1991; Berman, 1993). The matrix containing the fossils is variable, containing red, white and reddish-brown sandstones, and red and black clay (Williston, 1911). The age of the stratigraphic level where these specimens were collected is controversial (Eberth and Miall, 1991; Berman, 1993; Eberth and Berman, 1993). The most recent assignments date the sediments to Missourian (Fracasso, 1980), or Virgilian (Berman et al., 1987, Eberth and Miall, 1991).

The Early Permian (Wolfcampian) *Limnosceloides brachyoles* was also found in the Cutler Formation of New Mexico, in the Camp Quarry locality (UCMP V2814) in Rio Arriba County (Figure 3; Langston, 1966). Significantly, the Cutler Formation is interpreted to span the Pennsylvanian-Permian boundary (Eberth, et al., 1987). The specimen was found in soft, brick red clayey siltstone on
Figure 3. Stratigraphic Section of the Cutler Formation in North-central New Mexico (adapted from Eberth and Miall, 1991) Indicating Sections where the Specimens of *Limnoscelis paludis* and *Limnosceloides brachycoles* were Discovered.


the southeast slope of a small butte about 375 m south of New Mexico State Highway 96 and about 860 m southeast of the Rio Puerco Bridge (Langston, 1966).
The Early Permian *Limnoscelops longifemur* was also found in the Cutler Formation, but in this case in San Miguel County, Colorado (Figure 4; Lewis and Vaughn, 1965). The Cutler Formation in this area crops out in a band from 161 m to 1,207 m wide on both sides of the San Miguel River in two spots, 6.4 km upstream and 6.4 km downstream from the town of Placerville. The base of the Cutler Formation is not exposed in this canyon. The formation is made up of a variety of clastic sedimentary rocks ranging from shale to conglomerate (Lewis and Vaughn, 1965). The rock is mainly dark red, but also contains some gray and greenish-gray rocks. The Upper Triassic Dolores Formation overlies it unconformably (Lewis and Vaughn, 1965).

The Late Pennsylvanian *Limnoscelis dynatis* was discovered in the Sangre de Cristo Formation of central Colorado (Berman and Sumida, 1990). This specimen was recovered from a quarry in a 60 to 90 cm thick black shale deposit near the town of Howard in the Arkansas River valley, Fremont County. The black shale unit lies approximately 442 m above the base of the approximately 2933 m Sangre de Cristo Formation. On the basis of associated fauna, this section was dated as Late
Figure 4. Stratigraphic Section of the Cutler Formation in Central Colorado (adapted from Lewis and Vaughn, 1965) indicating sections where the holotype of Limnoscelops longifemur, Museum of Comparative Zoology 2984, and the paratype, Museum of Comparative Zoology 2979, were recovered.

Pennsylvanian, probably Missourian, in age (Berman and Sumida, 1990).

The Early Permian Limnosceloides dunkardensis was recovered in Jackson County, West Virginia (Romer, 1952). Little locality information is available for this specimen other than that it was collected 8 km southwest of Cottageville, Jackson County, West Virginia. This area lies in the Dunkard group, but the horizon is uncertain (Romer, 1952), though it is probably Early Permian in age.

The oldest purported member of the Limnoscelidae is the Middle Pennsylvanian Limnostygis relictus, found near Florence, Cape Breton County, Nova Scotia (Carroll, 1967). This specimen was recovered from the stump of an upright lycopod in the Morien Group (equivalent to the Westphalian C and D of Europe) of the Dominion Coal Company strip mine number 7, 3.2 km north of Florence. The trees in this region were rooted above the Lloyd Cove (Lower Bonar) coal of the Morien group. Deposition in this area began in late Westphalian B and continued through Westphalian C and D. On the basis of non-marine arthropods, this group was correlated with the Pictou group, which is Westphalian C and D in age (Carroll, 1967).
The Family Limnoscelidae

The Family Limnoscelidae currently consists of six species in four genera:

Tetrapod Suborder Diadectomorpha

Family Limnoscelidae

- *Limnoscelis paludis* (Williston, 1911)
- *Limnoscelis dynatis* (Berman and Sumida, 1990)
- *Limnosceloides brachyoles* (Langston, 1966)
- *Limnosceloides dunkardensis* (Romer, 1952)
- *Limnoscelops longifemur* (Lewis and Vaughn, 1965)
- *Limnostygis relictus* (Carroll, 1967)

These taxa are represented by different amounts of fossil evidence. *Limnoscelis paludis* consists of a complete, articulated skeleton and *Limnoscelis dynatis* consists of a nearly complete, disarticulated skeleton, whereas the rest of the taxa are based on more fragmentary postcranial materials (Table 2).

Study of both the specimens and the literature suggested that the limnoscelid taxa represent an exaggerated estimate of the morphological, and thus taxonomic, diversity of the family. All limnoscelid taxa, except *Limnoscelis*, were in fact determined to be *nomina dubia* (Table 2). The implications of this are two-fold.
Table 2. Specimens of the Late Paleozoic Family Limnoscelidae and Determinations of Their Taxonomic Validity.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Specimen</th>
<th>Material(s)</th>
<th>Determination</th>
</tr>
</thead>
<tbody>
<tr>
<td>Limnoscelis paludis</td>
<td>YPM 811</td>
<td>Complete, articulated skeleton</td>
<td>Valid taxon</td>
</tr>
<tr>
<td>Limnoscelis dynatis</td>
<td>CM 47653</td>
<td>Nearly complete, disarticulated skeleton</td>
<td>Valid taxon</td>
</tr>
<tr>
<td>Limnosceloides brachyloes</td>
<td>UCMP 35767, 40238, 40232</td>
<td>Right femur and isolated vertebrae</td>
<td>Nomen dubium</td>
</tr>
<tr>
<td>Limnosceloides dunkardensis</td>
<td>USNM 12166</td>
<td>Vertebrae, partial pelvis, hind limb</td>
<td>Nomen dubium</td>
</tr>
<tr>
<td>Limnoscelops longifemur</td>
<td>MCZ 2979, 2981</td>
<td>Jaw fragment, partial vertebrae, proximal femur fragment, distal femur fragment, other limb elements</td>
<td>Nomen dubium</td>
</tr>
<tr>
<td>Limnostygis relictus</td>
<td>MCZ 3034</td>
<td>Left maxilla, 8 dorsal vertebrae, cleithrum, scapulocoracoid</td>
<td>Nomen dubium</td>
</tr>
</tbody>
</table>

First, the exclusion of *Limnostygis relictus* from the limnoscelids shortens the temporal range of limnoscelids to Late Pennsylvanian to Early Permian. Second, because all of the other limnoscelids, except *Limnoscelis*, are not distinct enough to warrant generic distinction, the Family Limnoscelidae becomes a monogeneric family. This indicates that the limnoscelids were not as diverse as previously thought and would counter the argument that the limnoscelids underwent a large diversification during Late
Paleozoic time (Romer, 1952; Langston, 1966). This has implications for understanding the postcranial skeleton of a group central to interpreting amniote interrelationships.

Materials and Methods

All available limnoscelids were borrowed from their respective institutions, except for two *Limnoscelis* specimens. Because of their size and uniqueness, the *Limnoscelis* specimens had to remain at the Carnegie Museum of Natural History.

Length, height, and width measurements were made on all skeletal elements available. The processes and depressions that were evident were measured so far as possible at a right angle to one of these axes. Specimens were measured in as many ways as possible as determined by the element and its preservation. For example, the intercondylar distance on the femur of *Limnosceloides brachyoles* can be measured, while that of *Limnoscelops longifemur* cannot because the condyles are missing. Because the *Limnoscelis* specimens could not be borrowed, the author studied the specimens at the Carnegie Museum of Natural History in November 2000. These two specimens were also compared to the other specimens acquired. Along with
measurements, photographs and digital images were taken of specific specimens.

In the postcranial description of the skeleton of *Limnoscelis*, each skeletal element is described in detail. Anatomical descriptions include average size and range of sizes of the bone, descriptions of various surface features, and any differences between the specimens in these anatomical features. Also, full illustrations of the dorsal and ventral views of this holotype of *Limnoscelis paludis* are provided. Illustration of specimens was done in accordance with common paleontological standards: (1) color, as well as black and white, photography; and (2) stippled, black and white pen and ink line drawings with the lighting from the upper left position. This detailed morphological description of the Limnoscelidae now provides the first study to compare all known specimens of limnoscelids in 90 years.

Using these data, along with morphological characters, the taxonomic validity of each of the limnoscelid taxa were examined to determine whether all of the taxa are assignable to Limnoscelidae. The standard of taxonomic description is currently very different and much more rigorous than it was for the description of all known
limnoscelid taxa (with the exception of Limnoscelis dynatis, Berman and Sumida, 1990). Presently, cladistic methodology demands that any valid taxon be diagnosable with one or more apomorphic (unique, derived) characters or, lacking that, a unique combination of primitive and derived characters. Phylogenetic systematics, or "cladistics," states that the interrelationships of taxa must be based not on overall similarity, but on the presence of shared, derived characters. In other words, shared primitive features (symplesiomorphies) may give information about structure, but not about relatedness or phylogenetic position. A clear understanding of cladistic methodology is critical to any study that could be important to understanding the radiation or basal members of an important grouping. As the Limnoscelidae are important in such a way to the understanding of basal Amniota, cladistic methodology was utilized throughout this study. Upon reviewing the anatomy of each limnoscelid taxa, all of the taxa, with the exception of Limnoscelis, were determined to be invalid. Thus, the newer definition of the limnoscelid postcranial skeleton is much more restrictive than previously thought.
Utilizing the description of the postcranial skeleton of the *Limnoscelis*, an assessment of its phylogenetic utility is considered. To construct a phylogenetic tree in which one may have any confidence, one must have at least the same number of informative characters with derived character-states as actual taxa (Stewart, 1993). The best way to produce a valid phylogeny of the Diadectomorpha and its sister taxa would be to combine both the cranial and postcranial characters and use those to generate a cladogram. Unfortunately, this task has been attempted before in a number of doctoral dissertations and other studies, and each of these failed (Fracasso, 1987).

As combining cranial and postcranial characters in a phylogenetic analysis is beyond the perview of this study, the phylogenetic analysis was performed on postcranial characters gathered from literature and from the description of the postcranial anatomy of *Limnoscelis*. The taxa that were analyzed are: three genera from the Diadectomorpha: *Limnoscelis*, *Diadectes* and *Tseajaia*; two primitive amniotes: a basal pelycosaurian synapsid, *Varanops*, and a basal reptile, *Captorhinus*; and an outgroup consisting of a primitive seymouriamorph amphibian, *Seymouria*. First, the informative and non-informative
sites were identified. Eighteen postcranial characters were recognized, with four of these being informative sites. These postcranial characters were assigned character-states tabulated into the standard tabular form for primitive (0) and derived (1,2,3...) character-states. As noted earlier, the number of informative characters necessary to produce a reliable cladogram is any number greater than the number of taxa being studied. However, in this study, the number of informative sites is smaller than the number of taxa. Nonetheless, a maximum parsimony tree was generated using PAUP 4.0 (Swofford, 2002). This tree was then compared to an established cladogram of a recent phylogeny of these groups, based mostly on cranial and atlas-axis characters (Heaton, 1980; Berman et al., 1992; Lombard and Sumida, 1992; Sumida et al., 1992; Sumida, 1997; Lee and Spencer, 1997). Since most of the cladograms published recently agree as to the relationships of the various taxa, an established tree is composed of all of these cladograms. Even though the generated cladogram did not exactly match the established cladogram, their topologies were very similar. The generated cladogram confirms the monophyly of the Diadectomorpha.
All of the postcranial characters used in generating the phylogeny were also mapped onto the established cladogram to determine the place on the phylogeny where they first appeared and where any character-state changes took place. The appearance of these characters and their changes through time do not conflict with the information provided by the established cladogram.
CHAPTER TWO

THE POSTCRANIAL SKELETON

OF LIMNOSCELIS

The description of the postcranial skeleton of Limnoscelis is primarily based on the almost complete articulated holotype of Limnoscelis paludis (YPM 811), along with two fragmentary postcranial skeletons assigned to L. paludis (MCZ 1947 and 1948, formerly YPM 819 and 809, respectively), and disarticulated postcranial materials of L. dynatis (CM 47653). Because of a reliance on YPM 811 in describing the postcranial skeleton, it is important to note that the holotype is partially encased in plaster in the dorso-ventral midsection, making access to some of the dorsal and ventral aspects of the specimen difficult, and sometimes impossible (Figures 5, 6, 7). On the dorsal surface, much of the skeleton is visible, with the exception of most of the ribs, portions of the pectoral and pelvic girdles, and portions of the vertebrae. In ventral view, the cranial section has been prepared, revealing the interclavicle and the ventral surfaces of some of the vertebrae and ribs. Also, a part of the ventral surface of
Figure 5. Dorsal View of Yale Peabody Museum 811, Holotype of *Limnoscelis paludis*.
Figure 6. Yale Peabody Museum 811, Holotype of *Limnoscelis paludis*. Partial Ventral View of Postcranial Skeleton (see text for explanation).

Note: See figure 7 for Detail of Cranial-most Structures.
Figure 7. Yale Peabody Museum 811, Holotype of Limnoscelis paludis. Oblique Ventral View of Pectoral Girdle and Associated Structures.
the pelvis is visible. Unfortunately, at some point in time, the plaster holding the holotype of *L. paludis* was cracked and this crack was repaired with plaster, blocking some of the ventral surface from view. Furthermore, none of the ventral surfaces of the limb bones are visible in YPM 811.

Axial Skeleton

**Atlas-axis Complex**

The atlas-axis complex of *Limnoscelis paludis* was first described by Williston (1911). However, due to incomplete preparation of the specimen (YPM 811), only the dorsal aspect of this complex was described. Sumida (1990) redescribed the atlas-axis complex in more detail; nonetheless, only the dorsal aspect was described. This complex was finally fully prepared and described in complete detail by Sumida et al. (1992). Sumida et al. (1992) also described the atlas-axis complex of *L. dynatis*, which, due to its fragmentary nature, provided additional insight only into the medial side of the left neural arch.

The complex consists of right and left atlantal neural arches, an atlantal intercentrum, a fused atlantal pleurocentrum and axial intercentrum, and a fused axial
neural arch and pleurocentrum (Figure 8). The elements are preserved in their natural position, except for the proatlases, which are missing (Sumida et al., 1992).

The atlantal intercentrum is blocky wedge with a midventral ridge that is a separate ossified element. A unique feature of the atlantal intercentrum is the two-faceted parapophysis (Sumida et al., 1992). No other Paleozoic tetrapod has divided facets on the parapophyses, making this a distinctive character of limnoscelids. The atlantal intercentrum has two processes on either side of the ventral midline that point anteroventrally. Each of these processes ends in a rounded edge. A ridge connects the ventral, caudal, lateral edge of the intercentrum to these processes. Only a portion of a shaft of what has been identified as the left atlantal rib is preserved. The right atlantal neural arch is complete, whereas the left is missing a portion of its ventral body and its epipophysis is fragmented. The arches are separate, caudodorsally sloping blocks, which are not fused medially, located caudodorsal to the atlantal intercentrum. Epipophyses are present; however, neural spines are not present. The medial surface of the atlantal arch displays
Figure 8. Right Lateral View of the Atlas-axis Complex (a), Left Lateral View (b), Left Lateral Reconstruction (c), Ventral View (d), Ventral Reconstruction (e), of Yale Peabody Museum 811. Adapted from Sumida et al., 1992.

a concave, caudodorsally pointed, thick projection on the caudal side of the body and concentric growth lines on the facet of the medial posterior zygapophysis (Sumida et al., 1992).

Ventral to the atlantal neural spines, the atlantal pleurocentrum is fused to the dorsal aspect of the axial intercentrum forming a single compound element. Thus, exposure of the atlantal pleurocentrum on the ventral side of the column is prevented by the axial intercentrum. The suture between these elements is still present in lateral view as a caudodorsally directed line. The sutural line ends dorsally at the same level as the notochordal canal of the axial vertebra. A possible serial homolog of the ventral processes of the atlantal intercentrum is a small, narrow, cranially pointing process on the right side of the ventral atlantal pleurocentrum. This process is not present on the left side, but it may have broken off, and the assumption that it was originally there is plausible. A cranially directed midventral process is present in the atlantal pleurocentrum continuing the line of the midventral process in the atlantal intercentrum.

The axis is a much more developed, larger and blocky vertebral body than the atlantal segment. The axial neural
arch is not swollen, as other vertebrae are. It has a large dorsal blade-like neural spine, which is narrow cranially, but flares laterally and caudally. It is roughly triangular in cross-section. Three ridges run on the caudal side of the spine, producing two deep sulci. A large circular pit is present directly dorsal to these ridges. The ventral surface of the axis is slightly concave, with the edges of the centrum projecting slightly past the edge of the centrum at the cranial and caudal ends in lateral view. The axis has large transverse processes that extend far beyond the width of the centrum. Cranial zygapophyses are present, but caudal zygapophyses are extremely weathered and thus, difficult to interpret. A short and stout axial rib is present.

**Dorsal Vertebrae and Ribs**

Williston (1911b, 1912) first described the vertebrae of *Limnoscelis paludis* (YPM 811) as being rather uniform, with swollen neural arches and neural spines all of about the same length. Additional descriptions of *L. paludis* and the disarticulated vertebrae of *L. dynatis* (CM 47653; Berman and Sumida, 1990; Sumida, 1990; Sumida et al., 1992) showed that the size and shape of the vertebrae of limnoscelids vary significantly throughout the column.
The one complete specimen of Limnoscelis has twenty-six presacral vertebrae. Immediately caudal to the atlas-axis complex, the third to seventh dorsal vertebrae are located between the scapular blades of the pectoral girdle (Figure 9). The centra are amphicoelous and notochordal. The centra of the most cranial vertebrae are small in diameter and are approximately 25% longer than they are wide (Sumida, 1990). The transverse processes are strongly flared in cranial and caudal views. The planes of the zygapophyses tilt craniomedially at about 30° and about 25° in the caudomedial aspect. The neural spines vary in height, alternating between tall and short spines in a random pattern. The neural spines in the cranial vertebrae are less expanded than in the more caudal vertebrae, but are also longer cranio-caudally. The third and fifth neural spines were substantial with bases about 9 mm in diameter. The ends of these tall spines usually have a ridge running down the midline of the spine on the cranial and caudal surfaces of the spine. On the other hand, the fourth neural spine is narrow, low and ridge-like. Furrows on either side of the neural spine may have facilitated passage of interspinus musculature (Sumida, 1990, 1997). Similar low spines are present in FMNH UR306 on vertebrae...
Figure 9. Vertebrae 3-7 and Associated Ribs of *Limnoscelis paludis*, Yale Peabody Museum 811. Cranial End of Column to Top of Page.

corresponding to the sixth and ninth or seventh and tenth presacral vertebrae. Isolated vertebrae from the cranial section of the column of *Limnoscelis dynatis* confirm this pattern (Figure 10). The neural spine on the sixth vertebra in the holotype is a tall spine, measuring approximately 16.7 mm in height and 11 mm in basal diameter. The seventh and tenth neural spines are also tall. Even though the height alteration pattern does not
Figure 10. Dorsal Vertebrae of *Limnoscelis dynatis*, Carnegie Museum 47653, Demonstrating Variable Neural Spine Height. Tall-spined Vertebra, a; and Low-spined Vertebra, b. Vertebrae are Shown Actual Size.

have a precise pattern and is not identical in all specimens, it is clear that some type of alteration of height and structure does occur in every specimen in the cranial dorsal vertebrae.

Stout, spatulate ribs are visibly associated with dorsal vertebrae three through seven. The ribs on the right side of YPM 811 are positioned at an angle, distally directed in a dorsolateral direction, with some vertebrae abutting the scapula, while the ribs on the left side are
angled ventrally as preserved. The cranial-most ribs are approximately 17 cm long and increase in length caudally through the pectoral girdle. The proximal ends of the ribs have one head, with nearly equal areas for the capitulum and tubercle. Tubercular and capitular facets are visible in craniodorsal and caudoventral views of the rib, respectively. As preserved, all ribs in limnoselids are single-headed. Romer (1946) hypothesized that the proximal ends of the ribs had cartilaginous caps to allow the movement of the vertebral artery between the capitulum and tubercle. The shaft of the ribs is relatively narrow and roughly oval in cross-section. A low, triangular protrusion is visible on the caudoventral margin of the shaft just distal to its narrowest point. The distal ends are very thin dorsoventrally and spatulate in shape.

The vertebrae located more caudally in the dorsal series vary from the vertebrae of the pectoral girdle. The centra are significantly longer than they are wide and they have beveled anterior and posterior edges ventrally. A midventral depression is formed by the edges of these anterior and posterior ridges by the middle of the column. The zygapophyseal planes of the mid-dorsal vertebrae tilt medially about 15 degrees, but are no longer tilted
posteriorly. The neural spines of the #12,#14,#16, #17 and #19 vertebrae are tall-spined, in a manner similar to those described from the more cranial vertebrae, whereas vertebrae 13 and 15 have no neural spine at all. The spine of vertebra 18 is also tall; however, it is much narrower than in the more cranial vertebrae, only about 5 mm in width. Clearly, the pattern of neural spine height alteration continues in the mid-dorsal vertebrae. Isolated dorsal vertebrae from Limnoscelis dynatis demonstrate that both the high and low-spined morphology was present in this species as well. Although the elements are disarticulated, they are clearly associated (Berman and Sumida, 1990). Thus, the phenomenon of neural spine variability is found throughout the genus.

Most of the ribs in this section are not visible in dorsal view in Limnoscelis paludis; only the left rib of vertebra 10, and partial right ribs of vertebrae 10, 11, 12 and 13 are visible. They are much narrower and longer than the pectoral ribs and are sharply recurved. In cross-section, the size and shape of the rib shaft remain constant throughout the rib’s length. In ventral view, the ribs of vertebrae 9-16 are visible. These ribs extend in natural position from the vertebrae to about their
midpoint. At the midpoint, the ribs collapse on themselves ventrally and their distal ends point caudomedially. The ribs are slender in ventral view, with their ends slightly dilated distally. A much shorter rib (5.5 cm) is present close to the ventral surface of vertebra 17. This rib overlies another deeper rib mostly hidden by matrix. This short rib is visible in lateral view and has a broadened proximal end with a long narrow body. The disarticulated dorsal ribs of *L. dynatis* indicate that the ribs have a single articular facet with distinct areas for the capitulum and tubercle. The capitular area occupies more of the articular facet and is subrectangular, long and narrow, whereas the tubercular area is short, wide and almost oval. While the craniodorsal surface of the head is slightly convex, the caudoventral surface is marked by a fairly deep basin.

The most caudal dorsal vertebrae exhibit ongoing changes in the structure of the centra, pedicels, zygapophyses, transverse processes and neural spines. The centra continue to be longer than they are wide. The posterior zygapophyses maintain an inward tilt of 15 to 20 degrees and the anterior zygapophyses are not canted. This lack of serial congruence suggests that the zygapophyseal
surfaces must have had some degree of cartilagenous capping. The transverse processes and neural arch pedicels are proportionately shorter than those in the cranial portion of the column. Vertebrae 17 to 26 all have tall neural spines, except the 22nd, which seems to have had a low spine. Even though the spine is not preserved, a long, slender break mark remains. The median ventral cranial and caudal lips of the neural spines are not easily viewed in the holotype; however, disarticulated elements of *Limnoscelis dynatis* demonstrate them clearly. In some of the vertebrae, coarse projections extend from the later surface of the ventral portion of the neural spine. The tip of the last neural spine is strongly bifid in structure. All presacral vertebrae up to vertebra 23 have been described as having accompanying ribs (Williston, 1912). However, only the left rib of vertebra 18 is present in the holotype and the ribs of CM 47653 are disarticulated and therefore, cannot be assigned to a particular vertebra. The 18th left rib of *L. paludis* is shaped similarly to the preceding ribs but about 50% shorter and less recurved.
Sacral Vertebrae and Ribs

Differing interpretations of the sacral region of *Limnoscelis paludis* have been presented (Williston, 1911a,b, 1912) described a single sacral vertebra in the holotype with a following large caudal vertebra, whereas Romer (1946) suggested that *Limnoscelis* was a transitional model between "...a one-ribbed and two-ribbed condition." Sumida (1990) described two sacral vertebrae and ribs. Upon examination of YPM 811, the only limnoscelid with an intact pelvic girdle, it is evident that *Limnoscelis* most likely had two sacral vertebrae. Although the neural spines have been broken off and the ventral aspect is not visible, the first sacral vertebra is obvious and well-developed. It is a large, robust vertebra, approximately 5.3 cm wide, with swollen neural arches and widely spaced anterior zygapophyses. The ribs of the first sacral vertebra are similarly robust, extending laterally for a short distance and then turning caudally for a length of 2.6 cm. Their distal ends are wide and point ventrally, where they contact the ilium almost vertically. The second vertebra is much smaller than the first and has relatively much narrower neural arches and more closely spaced anterior zygapophyses. The neural spines are also missing
on this vertebra. Confusion over the presence of one or two sacral vertebrae is understandable given the morphology of the associated ribs. Only the distal fragment of the right rib of the second sacral vertebra is present. It is broken off proximally, yielding a short and robust rib, approximately 1.8 cm in length, which touches the ilium. This rib is not as robust as those of the first sacral vertebra. Even though this rib does not directly contact the second sacral vertebra, it is clear from its size and placement that it articulated with the second sacral vertebra. An insipient potential third sacral rib is present on the vertebra caudal to the second sacral vertebra. The left rib of associated with this vertebra extends directly laterally and nearly contacts the ilium. If this rib did contact the ilium, it would have required a ligamentous connection. Since this is impossible to verify without additional specimens of Limnoscelis, this vertebra is considered the first caudal vertebra.

**Caudal Vertebrae and Ribs**

Approximately 60 caudal vertebrae are found in the complete holotype of *Limnoscelis paludis*. The first few caudal vertebrae resemble the second sacral vertebra. Caudal centra are significantly longer than they are wide,
but decrease in length caudally through the column. Intercentra are present between the ventral surfaces of the vertebrae (Sumida et al., 1992). The neural arches are not swollen and the transverse processes point precisely laterally. The neural spines of the caudal vertebrae are tall and blade-like at the cranial end of the series and decrease in height quickly caudally. No alteration of spine height is present. Chevrons are described as being attached beginning at the third caudal vertebra and ribs pointing sharply caudomedially are attached to the first 10 or 11 caudals (Williston, 1911a,b, 1912; Sumida, 1990). However, the chevrons are not visible in the holotype due to its encasement in plaster. Only the first two left caudal ribs are visible in the holotype. They extend directly laterally and have rounded distal ends.

Appendicular Skeleton

Pectoral Girdle

The components of the pectoral girdle have only been completely preserved in YPM 811. However, CM 47653 provides important information that compliments the plaster-encased elements not visible in the holotype. CM
47653 has a partial pectoral girdle preserved, including the right clavicle and both scapulocoracoids.

The limnoscelid pectoral girdle consists of a single interclavicle, paired cleithra, clavicles, and scapulocoracoids (Figure 14a). The interclavicle is known only from *Limnoscelis paludis*, and has recently been prepared out of the plaster to allow its viewing on the ventral side of the block. The articulation of the interclavicle with the clavicles hides the cranial portion of the diamond-shaped head of the cranial part of the interclavicle. What is visible is composed of a large, robust head with a long posterior process. The visible portion of the head is slightly convex in caudo-ventral view, and is in the shape of a small arc (Figure 7). The shaft is dilated cranially where it contacts the head and slightly waisted caudally continuing to a rounded end.

The cleithra of limnoscelids are small, vestigial splints of bone (Williston, 1911a,b). The clavicles are larger bones located ventral to the cleithra. They are partially visible in YPM 811 and a disarticulated right clavicle is preserved from CM 47653. The clavicles consist of a dorsal stem and ventral plate that meet at an angle of approximately 110°, forming a half-sling like shape. Most
of the dorsal stem is occupied on its lateral margin by the
caudolaterally projecting lamina that served as an
articulation for the cranial margin of the scapulocoracoid.
In the area connecting the lateral flange with the dorsal
stem itself is a vertical groove that most likely served as
the articulation for the ventral part of the cleithrum.
The ventral plate turns sharply dorsally to form a high
ridge, which is reduced as it joins the dorsal stem. This
plate is subdivided into two similarly sized cranial and
caudal sections by a deep groove on the medial margin.
The ventral plate is bowed ventrally and is slightly
sculptured with dense, transverse striae (Berman and
Sumida, 1990). In the fully articulated YPM 811, the
cranial suture between the two clavicles is not apparent.

Characterization of the positioning of the components
of the scapulocoracoid in limnoscelids is problematic
because the scapulocoracoid is not fully visible in the
only articulated specimen, YPM 811. Also, the pectoral
girdle is partially crushed in this specimen, making the
relative position of the scapula and coracoid even more
difficult. The scapulocoracoid is a large bone caudal to
the cleithrum and clavicle and dorsal to the interclavicle.
It is partially visible in Limnoscelis paludis, and both
scapulocoracoids of *L. dynatis* are preserved, with the ventral portion of the left element in the latter being obscured by the left maxilla. The scapulocoracoid is composed of dorsal scapular and more ventral coracoid regions. No suture is visible between these parts. The scapular blade is short dorsoventrally, but expanded in its dorsal region craniocaudally. Whereas the dorsal margin is thin, slightly convex and smooth in *L. dynatis*, the dorsal margin of the scapula in *L. paludis* is thicker and relatively more convex. The anterior border is almost vertically straight, while the posterior border is curved caudally in the more dorsal, expanded portion of the blade. Williston (1911a) and Romer (1946) both suggested that the dorsal portion of the scapular blade had a cartilaginous suprascapula attached in *L. paludis*. If there was a cartilaginous suprascapulate element, the base of attachment for this element would have been thick in *L. paludis* but would probably have been too thin for an extensive suprascapula in *L. dynatis* (Berman and Sumida, 1990). The scapulocoracoid is preserved in a single plane in *L. dynatis*, and Berman and Sumida (1990) suggested that the coracoid plate had a significant ventromedial curvature. Unfortunately, the coracoid plate is not
completely visible in *L. paludis*. Hence, the degree of the ventromedial curvature of the coracoid plate cannot be confirmed. A triangular, supraglenoid buttress faces caudolaterally and is well developed in the scapula. A vertically expanded supraglenoid foramen is found near its dorsal apex. The existence of a suture between the anterior and posterior coracoids in *L. paludis* was described by Williston (1911a), but this suture’s existence cannot be confirmed in YPM 811, as the coracoids are no longer fully visible, and the suture is not present in *L. dynatis*. However, an angular notch at approximately the same level as the coracoid suture in *L. dynatis* may indicate the connection of these two elements. The coracoid plate is smooth and thin mediolaterally at its cranoventral segment, where it would have been covered by the clavicle and interclavicle. The glenoid fossa is clearly visible extending from the supportive elements of the supraglenoid buttress and laterally flared thickened portion of bone cranially to the caudal end of the dorsal margin of the coracoid plate. This fossa is screw-shaped and faces slightly ventrally and caudolaterally at its cranial end and dorsally at its posterior end. The glenoid fossa is supported by the supraglenoid buttress dorsally.
and a flange of thickened bone craniolaterally. A coracoid foramen probably lies directly cranial to this flange in a deep fossa that undercuts the cranial portion of the glenoid fossa (Berman and Sumida, 1990).

Part of the dorsal scapular blade is visible in YPM 811, as well as ventral parts of the right and left coracoid plates. On the left side, the coracoid is crushed and the glenoid fossa is present as a flat plateau. A small open hole, which may be the glenoid foramen, also known as the coracoid foramen, extends dorsally from a small depression in the coracoid. The coracoid extends posteriorly past the end of the posterior process of the interclavicle, where it was cracked and repaired with plaster in the holotype. This repair resulted in the displacement of the caudal end of the coracoid and also a slight medial shift of the coracoid as evidenced by the offset of a fracture on the medial side of the element. On the right side, the coracoid is slightly better preserved and the small depression seen on the left side is filled in with plaster. The glenoid foramen is crushed closed and the glenoid fossa is present. The foramen and fossa are located on the caudal end of the coracoid, directly lateral to the caudal process of the interclavicle. Despite these
preservational distortions, there appear to be no significant differences between the pectoral girdle in YPM 811 and the more easily visible example in *Limnoscelis dynatis*.

**Forelimb**

Elements of both forelimbs are present in *Limnoscelis paludis*, but their view in YPM 811 is partially obscured by plaster, especially on the ventral surface. However, due to postmortem cranio-caudal crushing, the ventral surface of the left humerus of YPM 811 is partially visible (Figure 11). The elements of the forelimbs are also preserved in *L. dynatis*, although not fully in some cases (Berman and Sumida, 1990).

The humerus of limnoscelids is a compact, extremely stout bone, approximately 13.2 cm in length in *Limnoscelis paludis* and 11.0 cm long in *L. dynatis*, which resembles two tetrahedra set one on top of the other at approximately a 90° offset. It has a large, broad, quadrangular entepicondyle that is convex in caudal outline. The ectepicondyle is robust, extends significantly in the cranial direction, and has a concave cranial outline. A large entepicondylar foramen is present in CM 47653, but appears to have been crushed closed in YPM 811. Stout
Figure 11. Dorsal View of Left Forelimb of Yale Peabody Museum 811, Holotype of Limnoscelis paludis.
is more craniocaudally flared than the proximal end and has parallel striae on its dorsal surface. The flat distal articular surface is narrower dorsoventrally, but wider mediolaterally.

The ulna is longer, approximately 84% of humeral length in *Limnoscelis paludis* and 80% in *L. dynatis*, and more heavily built than the radius. A narrow shaft is deeply concave in the radial direction. This shaft connects a proximal end that is flared cranially on the cranial surface and medially on the caudal margin, and a distal end that is flared slightly more cranially than caudally. The dorsal surface is slightly convex. Due to postmortem crushing of *L. dynatis*, the ventral surface is not complete enough for confident description. The olecranon process is only slightly developed and lacks muscle scars. However, a rugose ossification is present, which Berman and Sumida (1990) suggest most likely indicates the area of attachment for the triceps muscle mass. A narrow band of unfinished bone covers the sigmoid notch and extends over the apex of the olecranon. The sigmoid notch is wider dorsoventrally on its medial margin, where it points slightly dorsally. A long, narrow ridge runs the length of the ventral surface. This is the point
of origin for the flexor musculature of the manus (Berman and Sumida, 1990). The distal articular surface is clearly divided into three facets for articulation with the metacarpals. The slightly laterally facing facets articulate with the ulnare and pisiform, while the slightly medially facing surface articulates with the intermedium. Interestingly, Williston (1911a) described the ventral surface of the radius and ulna as more flattened than the convex dorsal surface. This may indicate slight postmortem compression on the ventral surface of the holotype. The ulna and radius have been reconstructed in figure 14e.

The manus was only preserved in Limnoscelis paludis. In YPM 811, the right manus has three proximal carpal bones visible, while the left manus has four. Williston (1911a,b) described the right manus as also having four proximal carpals, but that is not the case currently. The four carpal bones are from lateral to medial: the pisiform, ulnare, intermedium and radiale. The pisiform is a semi-oval bone, tapered slightly on its lateral margin, articulating with the ulna on its proximal margin and the ulnare on its medial edge. The ulnare is the largest of the carpal bones, almost circular in shape with a ridge running from the lateral margin approximately three-fourths
of the width of the bone, where it splits into a small proximo-distal ridge. A small fossa is visible on either side of the medially running ridge. It articulates with the ulna proximally and intermedium medially but does not seem to have clearly defined facets for articulations with any other carpal elements (Williston, 1911a,b). The intermedium is a smaller, dorsoventrally thickened bone with two distinct ridges running proximo-distally on its lateral and medial sides in the left manus, but is a much flatter bone in the right manus. A fossa is situated between these two ridges in the intermedium of the left manus. In the right manus, the intermedium can be seen to articulate with the ulna, ulnare and the radius, while in the left manus, the intermedium has shifted slightly medially, giving the misleading impression of articulating only with the ulnare and radius. The radiale is the smallest of the four proximal carpals, almost oval in shape, flat on its dorsal surface with a straight and flat radial border. It touches the intermedium, but does not have a large articular surface for it. Williston (1911a,b) described the ventral surface of these proximal carpal bones as flattened.
Three distal carpal elements were preserved in YPM 811. Originally, Williston (1911a,b) described three distal carpals in each manus; however, only one is currently visible in the right and three in the left. The distal carpals are all smaller than the proximal carpals and are all roughly circular in shape. Williston’s (1911a,b) illustration of the right manus shows these elements as one directly proximal to digit III, one directly proximal to that carpal and distal to the intermedium, and one proximal to digit IV. However, the one carpal currently present in the right manus in located directly proximal to digit III, while the carpals present in the left manus are located proximal to digit V, proximal to and directly in between digits III and IV, and proximal to digit II. If the carpal proximal to digit II is preserved in approximately correct position, then it may tentatively be identified as the medial centralia. The positional information for the other two carpals of the left manus is not sufficient for a confident identification. This indicates that the one remaining carpal in the right manus is most likely correctly positioned, while the three distal carpals in the left manus may have shifted from their natural positions. These
distal carpals most likely represent the centrale and the third and fourth distal carpals (Williston, 1911a,b). The digits were differentially preserved in the right and left manus in YPM 811. Williston (1911a) described digits II, III, and IV as being preserved completely, except for the distal phalanges, or ungual phalanges, of digits II and IV. The ungual phalange of digit I is also described as missing, as well as the phalanges of digit V not being correctly articulated to the metacarpal. However, those digits were preserved in the right manus, allowing for a reconstruction of both hands (Williston, 1911a). The phalangeal formula for limnoscelids appears to be 2-3-4-5-3. The most proximal phalanges are usually the longest and the phalanges reduce in length distally. The overall shape of the manus is rather broad with the ungual phalanges shaped like small hooves, with a thin rounded distal edge, which may have had a keratinous covering in life (Williston, 1911a).

Pelvic Girdle

The pelvic girdle has been at least partially preserved in Limnoscelis paludis, L. dynatis, and Limnosceloides dunkardensis. The pelvis of L. dunkardensis is incomplete, while the pelves of Limnoscelis are
complete. The right pelvis of CM 47653 is complete, but fractured, so its sutures are not evident. However, Berman and Sumida (1990) used the sutures from the left pubis and ischium to reconstruct the sutures of the right pelvis. In YPM 811, the complete pelvis is preserved in articulation; however, due to its curation in plaster only a portion of the dorsal and ventral surfaces are visible. Thus the description below is, necessarily, based on a combination of observations of both L. paludis and L. dynatis. The pelvic girdle is reconstructed in figure 14b.

The pelvis is composed of the ilium dorsally, the pubis ventrally and cranially, and the ilium ventrally and caudally. The ilium is concave in cranial outline and extends slightly dorsally from its pubic border and then turns caudally, extending as a caudally directed iliac process. The end of the caudal process of the ilium is far shorter than the caudal extension of the ischium. Romer (1946) suggested that this caudal extension of the ilium was tipped with cartilage and served as an attachment point for caudal tendons and ligaments. No anterior expansion is seen on the ilium. The ilium is proportionally short and wide. On the caudal process, a significant lateral shelf extends across the dorsal half of the iliac blade, also
called the external iliac shelf (Romer, 1946). This shelf is a characteristic unique to diadectomorphs (Berman and Sumida, 1990). A lateral iliac ridge and depression are present in Seymouria and the pelycosaurian-grade synapsid Ophiacodon (Berman and Sumida, 1990; Romer and Price, 1940). However, the lateral iliac shelf is developed to a much greater degree in Limnoscelis and in all other diadectomorphs for which data on the ilium are available.

The pubis extends cranially past the cranial margin of the ilium and has a large cranial process, which has a rounded convex cranial outline in YPM 811. This is unlike the ilium, which has a much more quadrangular shape and only a slightly concave cranial outline in CM 47653. A craniocaudally directed obturator foramen is present on the craniocaudal margin of the acetabulum in the pubis in CM 47653. It is partially crushed, yet visible in the right pubis of YPM 811. The puboischiadic plate in CM 47653 is nearly quadrangular in outline. Although no puboischiadic suture is evident, a notch is present on the ventral margin of this plate in the acetabulum that indicates the point of fusion of these two elements (Berman and Sumida, 1990). On its caudal margin, the pubis ends in a nearly straight dorsoventral line at its suture with the ischium.
Williston (1911a,b) described the pelvis of YPM 811 as having a large ventral midline keel formed by a ventral deepening of the pubic and ischiadic symphyses. As preserved, the medial surface of the ilium is convex and is touched by the two sacral ribs on each side.

The ischium is only visible in CM 47653, but that of *Limnoscelis paludis* has been described in detail by Williston (1911a,b) and Romer (1946). The ischium has a large caudal extension and is slightly concave in caudal outline.

The acetabulum is large and oval with its long axis directed craniocaudally; its articular surface is oriented almost directly laterally. It is partially visible in the right pelvis of YPM 811 and fully visible in the right pelvis of CM 47653. The acetabulum is supported dorsally by a small ventrolaterally expanded buttress in the ilium and a larger dorsolaterally expanded buttress on the puboischiadic plate. The cranioventral margin of the acetabulum extends cranially in a narrow channel that reaches the cranial border of the pubis in CM 47653 and has been described as reaching cranially, but not to the pubic margin in YPM 811 (Romer, 1946). This channel is bordered by lip-like flanges on its dorsal and ventral margins. The
flange on the dorsal margin of the channel is more
developed than that on the ventral side and is also more
rugose (Berman and Sumida, 1990). The function of this
channel is unclear.

Hindlimb

Elements of the hindlimb are present in most
Limnoscelis specimens and consist of the femur, tibia,
fibula and pes (Figures 12, 13). However, as with the
manus, the pes is not preserved completely in any single
specimen.

The femur of Limnoscelis is a very robust bone with
large, expanded ends connected by a relatively short,
narrow shaft, approximately 12.4 cm in length on average in
L. paludis and 11.1 cm in length in L. dynatis. It is
visible in dorsal view in YPM 811 and in both dorsal and
ventral views in CM 47653. Prior to its encasement in
plaster, Williston (1911a,b, 1912) described and
illustrated the ventral view of the holotypic left femur.
These observations are incorporated here to provide a more
complete description. The proximal head is angled caudally
with an almost straight cranial border and a gently concave
caudal border. The dorsal surface of the proximal head is
concave and smooth, except for a significantly rugose area
on its posterior border where the puboischiocomorals
internus and ischiotrochantericus muscles probably inserted
(Berman and Sumida, 1990). The proximal articular surface
is slightly convex dorsally and slightly concave ventrally.
Whereas the proximal end of the femur is a single head, the
distal end of the femur is split into two distinct condyles
that articulate with the tibia and fibula. The distal
condyles of the femur are bulbous in shape and expanded
dorsoventrally more than the proximal head. The cranial
border of the femur points is for the most part straight,
although it angles slightly cranially towards its distal
end. The caudal border of the distal end resembles that of
the proximal end in that it expands caudally to accommodate
the articular surfaces. The distal articular surface of
the caudal condyle is visible in YPM 811 and is shaped like
a parallelogram with the dorsal edge slightly longer than
the ventral margin. A small intercondylar fossa is present
in the distal end between the two condyles. The surface of
the distal end of the femur is smooth and convex, and the
caudal condyle is slightly longer than the cranial condyle.
The cranioproximal portion of the internal trochanter is
visible in dorsal view in YPM 811 and CM 47653. Ventrally,
the femur is characterized by a large, well-developed
Figure 12. Dorsal Aspect of the Femur, Tibia and Fibula of Yale Peabody Museum 811, Holotype of *Limnoscelis paludis.*
Figure 13. Dorsal Aspect of the Right Pes of *Limnoscelis paludis*, Museum of Comparative Zoology 1948.

adductor ridge, which extends from the craniodistal section of the intertrochanteric fossa diagonally to the caudal condyle. The ventral proximal end is rounded in shape, sloping distally to a greater degree on the caudal margin. A deep, oval intertrochanteric fossa is present, which covers approximately 40% of the proximal end of the femur of *Limnoscelis dynatis* (Berman and Sumida, 1990). This fossa angles craniodistally and ends in the region of the
fourth trochanter. The fourth trochanter is only partially preserved in CM 47653 but can be seen to be elevated and wide with a rugose texture on its dorsal and ventral surfaces. The fourth trochanter is located distally approximately 40% of the length of the cranial portion of the femur. An interior trochanter is not preserved in CM 47653. The well-developed adductor ridge continues diagonally across the femur and ends on the caudal condyle at approximately the same level as the ventral margin of the cranial condyle, where the caudal and cranial condyles meet. The adductor ridge forms the caudal border of the deep popliteal fossa. No shelf is visible on the proximal surface of the popliteal fossa, as has been suggested for the femur assigned to *Limnosceloides brachycoles* by Langston (1966). When viewed on end, the distal end of the femur has a sigmoid-shaped articular surface. Williston’s (1912) illustration of the ventral surface of the femur of *L. paludis* is similar to this description, except that the internal trochanter is present and located caudodistally to the fourth trochanter and the adductor ridge appears to extend to the ventral margin of the caudal condyle. Sumida (1997) also reconstructed the ventral aspect of the femur.
of *Limnoscelis*, and it is very similar to Williston's description (Figure 14d).

The tibia is a robust bone with flared proximal and distal ends. The right tibia is preserved completely in CM 47653 and both tibiae are present in YPM 811, although only their dorsal surfaces are visible. It is on average 80% of the length of the femur in *Limnoscelis dynatis* and 88% of the femoral length in *L. dynatis*. The tibia of CM 47653 is rather narrow dorsoventrally, while the tibia of YPM 811 is relatively thicker dorsoventrally, especially at its proximal end. This may be due to postmortem dorsoventral compression of CM 47653. The tibia is craniocaudally broad, with an almost straight cranial margin and a distinctly concave caudal margin, due primarily to extensive flaring of the caudoproximal end caudally. However, a somewhat lesser degree of flaring of the caudodistal end caudally also contributes to this distinctly concave caudal margin. The proximal articular surface is sigmoid in shape with the cranial end pointing ventrally. The cnemial crest expresses itself as a large cranial ridge originating on the dorsal proximal head and terminating proximally in a small knob. Caudal to the crest is a broad, shallow concavity. The element narrows
substantially to produce a well-defined shaft and then expands craniocaudally again, although not as drastically as the proximal head. The distal head has a smooth surface and a rounded convex distal margin. The ventral articular surface bows dorsally, resulting in the tibia being slightly shorter in ventral view. The ventral surface has a moderately high ridge running almost the entire midline length. A very low rugosity is present approximately midway along the ridge that indicates where the tibialis posterior muscle originated (Berman and Sumida, 1990).

The fibula is shorter than the tibia, being on average 77% of the length of the femur in Limnoscelis paludis and approximately 80% of the femoral length in L. dynatis. Like the tibia, it is visible in dorsal view in YPM 811 and in dorsal and ventral views in CM 47653. It is an element with a slightly flared proximal end, a proportionally longer shaft and a more flared distal end. The cranial outline is more convex, whereas the caudal outline is almost straight. The articular surface of the proximal head is rugose, with a slightly convex dorsal margin and the caudal margin greatly expanded. The dorsal surface of the proximal head is flat, and it is much thicker dorsoventrally than the distal head. The dorsal surface of
the distal head is slightly concave and has very fine parallel striae. The distal articular surface is very thin dorsoventrally and longer craniocaudally than the proximal surface. It bows slightly ventrally and widens slightly cranially. The ventral surface of the proximal head is slightly concave and, due to the dorsoventral thickening of its caudal section, faces craniocaudally. In this concave surface, a small, rounded, thin flange projects cranially approximately 5.3 mm distal to the proximal articular surface. The ventral surface of the distal head is slightly convex and bears very fine parallel striae, as does the dorsal surface. A small, very fine ridge is present on the ventral surface running the midline length of the entire bone. Based on the descriptions of the tibiae and fibulae of *L. paludis* and *L. dynatis*, Sumida (1997) reconstructed the tibia and fibula of *Limnoscelis*.

The pes is partially present in three of the four *Limnoscelis paludis* specimens. No elements of the pes are present in CM 47653. Williston (1911a,b) described the hindfoot of YPM 811 as having only part of the left pes preserved. In MCZ 1948 (formerly YPM 809) the feet are much better preserved with four tarsals and partial digits present (calcaneum with either 3rd and 4th distal tarsal,
or centrale and a distal tarsal, probably the former). The foot of FMNH UC 650 is best preserved with the same four tarsals present, but all in one foot. Williston (1911a,b) described the bones of the hind foot of YPM 811 as weathered and mostly disarticulated. However, this cannot be confirmed as the hind foot bones of YPM 811 have been reconstructed with plaster, and it is impossible to determine which bones are the original elements Williston described without preparation of the specimen. In the left hind foot of MCZ 1948, Williston (1911a,b) identified the tarsals as the fibulare and the fused tibiale and intermedium. He also recovered some disarticulated phalanges. He described and illustrated the fibulare as an almost circular, thin element with its tibial side thicker dorsoventrally than its fibular side, and the tibiale/intermedium as cuboidal, with articular surfaces for the fibula and tibia, and a slight notch between those two surfaces. However, he admitted the possibility that the tibiale was cartilaginous and the two tarsals preserved are the fibulare and intermedium. Romer (1946) agreed with the view in his redescription of *Limnoscelis*. In the right foot of MCZ 1948, Williston (1911a,b) described the phalanges of digit I, three phalanges of digit II, four
phalanges of digit III, five phalanges of digit IV, and four phalanges of digit V. The phalanges were found in two separated blocks whose surfaces had been damaged during excavation, thus distorting the articular surfaces of the phalanges, making their correspondance difficult to verify. However, Williston (1911a,b) joined them together based on their similar morphologies, apparently seamless anatomical association, and similar matrix. The phalanges of the hind foot are similar to those of the manus, except that they are slightly broader. The phalanges are longer proximally and then shorten distally. The ungual phalanges are hoof-like. If the interpretation of the phalangeal elements as discussed above is accepted, then the phalangeal formula for the hind foot is 2-3-4-5-4 (Figure 13). Romer (1946) described the intermedium as having a convex rolling surface on its tibial surface, which likely supported the tibia. He also suggested that the incomplete preservation of the carpus and tarsus is due to imperfect ossification of the elements. Berman and Henrici (in press) have reported such a condition in a new diadectid and suggest it as a mechanism to allow appropriate cranial orientation of the manus and pes during locomotion. While such an interpretation might be applicable in the case of
Limnoscelis, a cautious approach warrants awaiting the discovery of additional or more complete specimens. Williston based further description of the hind foot of *L. paludis* on FMNH UC 650. This specimen has since been identified as "Diadectoides," a taxon that Olson (1947) synonymized with *Diadectes.*

Following page:

Figure 14. Reconstructions of Various Elements of *Limnoscelis*. Left Lateral Aspect of Pectoral Girdle, a; Left Lateral View of Pelvic Girdle, b; Distal Ventral Aspect of Left Humerus, c; Ventral View of Left Femur, d; Dorsal Aspect of Right Radius and Ulna, e; Dorsal Aspect of Left Tibia and Fibula, f. All Scalebars Equal 1 cm.

Adapted from Sumida, 1997.
CHAPTER THREE
REASSESSMENT OF THE TAXONOMIC
VALIDITY OF OTHER
LIMNOSCELID GENERA

The best known member of Limnoscelidae is *Limnoscelis*,
for which two species are currently recognized, *L. paludis*
(Williston, 1911a) and *L. dynatis* (Berman and Sumida,
1990). In the 1960s, there was a small flurry of
descriptions in which additional taxa were assigned to the
family. Laurin and Reisz (1992) removed "Romeriscus" from
the family, but a number of other taxa based on fragmentary
and almost exclusively postcranial materials remain in
addition to the genus *Limnoscelis*. Currently the family
Limnoscelidae includes four genera: *Limnoscelis* (Williston,
1911a; Berman and Sumida, 1990), *Limnosceloides* (Romer,
1952; Langston, 1966), *Limnoscelops* (Lewis and Vaughn,
1965), and *Limnostygis* (Carroll, 1967).

Of these genera, all except *Limnoscelis* are described
on the basis of fragmentary postcranial materials. Here,
*Limnosceloides dunkardensis*, *Limnosceloides brachycoles*,
*Limnoscelops longifemur* and *Limnostygis relictus* are
compared to the postcranial skeleton of Limnoscelis, and their taxonomic validity is re-evaluated.

Limnosceloides

Systematic Paleontology
Tetrapoda incertae sedis
Limnosceloides dunkardensis, Romer, 1952
nomen dubium

Holotype - United States Natural History Museum, USNM 12166. Partially weathered lumbar, sacral and caudal vertebrae, pelvic fragments, right crushed femur, right tibia, and phalanges.

Geological Age and Distribution - Dunkard group of unclear horizon, Early Permian; eight km southwest of Cottageville, Jackson County, West Virginia, USA.

Discussion - Even though various elements were found, the only element complete enough for a thorough description was the right femur. Romer (1952) erected a new genus, Limnosceloides, based on the morphology of this femur (Figure 15).

Romer (1952) described the femur of Limnosceloides dunkardensis as varying from the femur of Limnoscelis in two ways: 1) the "antero-proximal trochanteric crest is not extended anteriorly," and 2) the distal part of the ventral ridge (or the adductor ridge) is a distinct low crest
Figure 15. Right Femur of *Limnosceloides dunkardensis*, United States National Museum 12166, in Ventral View.

Figure 16. Right Femur of *Limnoscelis dynatis*, Carnegie Museum 47653, in Ventral View, for Comparison. Adapted From Illustration of a Left Femur from Berman and Sumida, 1990.

“running diagonally distally to the outer ventral margin of the posterior (caudal) condyle.” Dorso-ventral postmortem crushing has taken place and Romer acknowledged that the trochanteric crest itself is actually missing. Nonetheless, he described the trochanteric crest in *Limnoscelis* as flaring widely and suggested that it did not flare as widely in *Limnosceloides*. Since Romer’s (1952) study, Berman and Sumida (1990) described another species of *Limnoscelis*, *L. dynatis*, allowing an assessment of the degree of variation present within the genus itself. In their description of this more complete material of *L. dynatis*, Berman and Sumida (1990) did not discuss the trochanteric crest, but subsequent study of this specimen (CM 47653) suggests that it is not clear that *L. dynatis* even had a trochanteric crest that flared widely anteriorly. Comparison of the femora of *Limnoscelis dynatis* and *Limnosceloides dunkardensis* does not demonstrate any significant difference between the bases of the trochanteric crests (Figures 15, 16). As Williston’s (1911a) description was not complete and because permission was not given to further prepare the mounted skeleton of YPM 811, a comparison could not be made to the femur of the holotype, *Limnoscelis paludis* (YPM 811).
Romer (1952) characterized the low crest of the ventral adductor ridge in *L. dunkardensis* as "running diagonally distally to the outer ventral margin of the posterior (caudal) condyle." Due to dorso-ventral postmortem crushing, the adductor ridge is low and not very prominent, but it clearly extends to the ventral margin of the caudal condyle. According to Berman and Sumida (1990), the adductor ridge of *Limnoscelis* "terminates distally at a level along the ventral margin of the distal articular surface where the anterior and posterior condyles join."

Even though the adductor ridges vary slightly in their termination points, possibly due to the incomplete preservation of the *L. dynatis* adductor ridge, this character is not adequate to warrant generic distinction. Rather, it more likely reflects expected degrees of variation within a genus (Sumida, 1997).

It is also important to note that the two features utilized by Romer (1952) to distinguish between *Limnosceloides* and *Limnoscelis* do not meet the current strict requirements for taxonomic distinction. As cladistic methodology was not widely accepted until the late 1960’s, it is not surprising that Romer used the features he did to distinguish between these two genera.
Taken together, these two features do not provide either a clearly distinguishable autapomorphic feature for *L. dunkardensis* or a unique combination of primitive and derived features necessary for taxonomic distinction. It is therefore assigned to Tetrapoda.

**Systematic Paleontology**

*Diadectomorpha incertae sedis*

*Limnosceloides brachycoles*, Langston, 1966

*nomen dubium*

**Holotype** - University of California Museum of Paleontology, UCMP 35767. A complete, well-preserved right femur.

**Geological Age and Distribution** - Cutler Formation, UCMP locality V2814, Early Permian; southeast slope of small butte 375 meters south of New Mexico State Highway 96, and about 860 meters southeast of the Rio Puerco bridge at Arroyo del Agua, Section 8, Township 22 North, Range 3 East, Rio Arriba County, New Mexico, USA.

**Discussion** - Based on Romer's 1952 description of *Limnosceloides dunkardensis*, Langston (1966) tentatively assigned a femur and referred materials (UCMP 40238, 40237, 40232, 40235, 40236, 40234; complete dorsal vertebra, partial dorsal vertebrae, first sacral vertebra and its detached rib, partially preserved fibula, ulna and proximal
end of a tibia, respectively) to *Limnosceloides*. He erected a new species, *L. brachycoles*, based on three morphological features of the femur: 1) it is approximately the same size as the femur of *L. dunkardensis*, 2) the orientation of the ventral adductor ridge is the same as in *L. dunkardensis* (i.e., it terminates on the ventral margin of the caudal condyle), and 3) the presence of a "shelf-like proximal edge of the popliteal depression" is the same as in *L. dunkardensis*. He based the specific distinction on the robustness of the femur and the "waist-like construction of the femoral shaft" as compared to that of *L. dunkardensis*.

The femur of *L. brachycoles* (Figure 17) is approximately 9.4 cm long, whereas the femur of *L. dunkardensis* is approximately 10.0 cm long. However, due to proximo-distal postmortem crushing, the femur of *L. brachycoles* was telescoped at least once. If it had not been crushed, it would probably have been approximately 10.0 cm or more in length.

Langston (1966) described the adductor ridge of *L. brachycoles* as continuing "onto the posteroventral part of the posterior (caudal) condyle" and stated that it is the same in orientation as that of *L. dunkardensis*. This
Figure 17. Right Femur of *Limnosceloides brachycoles*, University of California Museum of Paleontology 35767, in Ventral View.

description suggests that the adductor ridge of *L. brachycoles* should continue caudo-distally to the end of the caudal condyle. However, upon re-examination of the specimen, UCMP 35767, the adductor ridge, which is divided into two ridges separated by a narrow sulcus, continues into the caudal condyle but terminates 1.3 cm proximal to
the caudal condyle. While perhaps different from Romer’s original *L. dunkardensis* material, there is sufficient variation among diadectomorphs (Sumida, 1997) to cast doubt on its taxonomic validity.

The presence of a proximal shelf-like edge on the popliteal depression is similar in both *Limnosceloides* species. This shelf does not seem to be present in *Limnoscelis*. Berman and Sumida (1990) described *Limnoscelis dynatis* as having a popliteal fossa, but no proximal popliteal shelf. A proximal popliteal shelf is also not present in Williston’s (1911a) illustration of *L. paludis* (YPM 811). However, in the presence or absence of the popliteal shelf in *Limnosceloides* and *Limnoscelis*, generic and specific distinctions cannot be made based on these two characters alone. Furthermore, the degree of disturbance to the popliteal shelf by postmortem crushing cannot be determined.

In their study of *Limnoscelis dynatis*, Berman and Sumida (1990) indicated that characters of the postcranial skeleton were not adequate to separate it from *L. paludis* and that the specific distinction relied on cranial characters. Consequently, generic distinction requires the
characters to be found in a specimen complete enough to assess both cranial and postcranial features.

Sumida (1997) distinguished *Diadectes* and *Limnoscelis* as having a very large internal trochanter on the femur, as opposed to the rest of early amniotes, which at most had a distinct, but relatively smaller, internal trochanter. The femur originally used by Langston (1966) to erect *Limnosceloides brachycoles* is here assigned to the Group Diadectomorpha based on the presence of a very large internal trochanter.

*Limnoscelops*

Significantly, much of the rationale for the taxonomic distinction of *Limnoscelops* was based on its comparison to *Limnosceloides*. This study has demonstrated that materials assigned to *Limnosceloides* may be considered to be diadectomorph but that no greater resolution is possible. Thus, comparison of any element of *Limnoscelops* to *Limnosceloides* cannot be considered adequate for assignment to *Limnoscelidae*, let alone generic distinction. For the rest of this study, any comparisons Lewis and Vaughn (1965) made to *Limnosceloides* will be considered as comparisons to a more generalized diadectomorph.
Systematic Paleontology
Diadectomorpha incertae sedis
Limnoscelops longifemur, Lewis and Vaughn, 1965
nomen dubium

Holotype - Museum of Comparative Zoology, Harvard University, MCZ 2984. Small jaw fragment, the tips of two teeth, seven incomplete vertebrae, a partial inominate, proximal and distal parts of a left femur, proximal ulna fragment and other fragments.

Referred Specimen - Museum of Comparative Zoology, MCZ 2979. Four articulated dorsal vertebrae, partially encased in matrix.

Geological Age and Distribution - Cutler Formation, Early Permian. Holotype is from locality 10, approximately 152 to 158 meters below the top of the Cutler Formation, 129° and 2.22 km southeast of Placerville, Colorado. Referred specimen is from locality 4, approximately 24-27 meters below the top of the Cutler Formation, 72° and 772 meters east of Placerville, Colorado, and approximately 1.9 km from locality 10.

Discussion - A small amount of cranial material was proposed by Lewis and Vaughn (1965) to be assignable to Limnoscelops, but they deemed the small jaw fragment and the two partial teeth uninformative. Lewis and Vaughn
suggested that a new genus, *Limnoscelops*, was warranted, based mainly on the morphology of the vertebrae and the pelvic girdle. The femur will also be discussed here as it is the element for which the species is named, as well as being an element used to distinguish other genera assigned to *Limnoscelidae* (Romer, 1952; Langston, 1966).

Lewis and Vaughn (1965) described the vertebrae of *Limnoscelops* as very similar to *Limnoscelis paludis* and *Limnosceloides dunkardensis*. However, the comparison of vertebrae or any other elements of *Limnoscelops* to *Limnosceloides* no longer supports assignment to *Limnoscelidae*, as materials previously assigned to *Limnosceloides* can only be identified as diadectomorph. As *Limnosceloides* is no longer a valid means of comparison, the potential limnoscelid nature of the vertebrae of *Limnoscelops* is considered by comparison to those of *Limnoscelis*. The vertebrae have a circular notochordal centrum, with an hour-glass shaped canal (Fig. 18). They are similar in proportions to *Limnoscelis* in that the width of the centrum is significantly greater than the cranio-caudal length. In *Limnoscelops*, the ratio of width to length of the centrum is approximately 1.5, whereas in
Figure 18. Dorsal Vertebra of *Limnoscelops longifemur* (Museum of Comparative Zoology 2984) in Cranial, a, and Caudal, b, View.

*Limnoscelis*, a corresponding vertebra has a ratio of 1.4. However, the similarities in the size and shape of the vertebrae are not unique to limnoscelids alone. Other diadectomorphs, such as *Diadectes* and *Tseajaia*, have similar vertebral proportions (Moss, 1972; Heaton, 1980; Sumida, 1990; Walliser, 1998a,b). Therefore, the size and shape of the vertebrae are not adequate to distinguish a discrete limnoscelid or diadectomorph taxon.
Lewis and Vaughn (1965) also designated these vertebrae as limnoscelid due to the broad, wedge-shaped process that projects ventrally on the dorsal surface of the caudal side of the neural arch. This process is found in *Limnoscelis* and in "Limnosceloides," but can also be found in *Seymouria* (Sumida, 1990). Thus, this character is not enough for distinguishing the vertebrae specifically as limnoscelid, and it may be that the feature is more broadly applicable to higher terrestrial tetrapods of the time (Sumida, 1990).

Along with the seven incomplete vertebrae of the holotypic specimen, Lewis and Vaughn (1965) referred a series of four articulated vertebrae, MCZ 2979, found in geographic proximity to the holotype to *Limnoscelops longifemur*. They described these vertebrae as having the same proportions as the holotypic vertebrae, with the centrum width exceeding the length, and widely separated zygapophyses with nearly horizontal articular surfaces. These features are common to a wide array of Late Paleozoic tetrapods (Heaton, 1980; Sumida, 1990, 1997). Lewis and Vaughn (1965) suggested the vertebrae are from a more caudal position than those of the holotype due to the dimples found at the junction of the centrum and the neural arch.
arch. This reasoning was based on the vertebrae of "Limnosceloides dunkardensis" (USNM 12166), in which the dimples at the centrum-neural arch junction become deeper the more caudal the vertebra. However, a few problems exist with this interpretation and the assignment of these vertebrae to Limnoscelops longifemur. First, it is very difficult to determine the region from which the four vertebrae originally came because the ontogenetic stage and regional variability of the vertebral column of the referred specimen is unknown. Second, upon re-examination of the referred specimen, only one dimple can be found. Finally, because materials assigned to "Limnosceloides" no longer support a valid taxon, the comparison of these vertebrae to those of "Limnosceloides dunkardensis" reduces the resolution of Lewis and Vaughn's (1965) original description.

The pelvic girdle of Limnoscelops is very poorly preserved. Lewis and Vaughn (1965) described the three component elements preserved and features of each. They described the ilium as not having a horizontal iliac shelf, which is a character of all diadectomorphs. The pubis is described as having a very thick symphysis and an "...almost vertical, captorhinomorph-like face of the
conjoined internal ridges of the pubes." However, upon re-examination of MCZ 2984, due to poor preservation it is very difficult to determine the dorsal and ventral surfaces and the characters Lewis and Vaughn (1965) described are not distinguishable.

Along with the characters of the pelvic girdle, Lewis and Vaughn (1965) gave a thorough description of the femur of Limnoscelops longifemur, the element for which the species was named (Figure 19). The femur is represented by left proximal and distal fragments, the former measuring 6.1 cm in length and the latter measuring 4.9 cm in length. The femur was described as similar to that of the large captorhinid reptile Labidosaurus, and it was restored with an approximate length of at least 13.0 cm, but with a much more slender shaft than Labidosaurus. The assumption that the femur had a more slender shaft was based partly on the comparison of the pelves and femora of Limnoscelops and "Limnosceloides dunkardensis." When compared, the pelves of these animals are similar in size, while the femur of "L. dunkardensis" is shorter than that of Limnoscelops. This variation in size of the femora as compared to the pelves suggested to Lewis and Vaughn (1965) that the latter had a similarly sized body but longer limbs. However, as
Figure 19. Ventral Views of the Proximal, a, and Distal, b, Fragments of the Left Femur of *Limnoscellops longifemur* (Museum of Comparative Zoology 2984).

previously discussed, the comparison to "*Limnosceloides*" is no longer a valid means of generic distinction; therefore, this feature is not diagnostic of a distinct genus of limnoscelid. Upon reexamination, it is evident that accurate reconstruction of the MCZ 2984 femur is very difficult due to poor preservation of the broken ends of the fragments. However, even though the length may not necessarily be a distinguishing characteristic of the femur, the position of the trochanteric crest is unique. The trochanteric crest in MCZ 2984 is set off from the head
of the femur by a notch, and the trochanteric crest makes an almost 90° angle with the head. It is difficult to confirm whether this differs from Limnoscelis due to the preservation of L. dynatis and the inaccessibility of the ventral side of the femur of L. paludis. The trochanteric crest was not preserved in L. dynatis and the ventral surface of the holotype of L. paludis, YPM 811, is not visible at this time, and permission was not given to prepare it, so this characteristic in Limnoscelops longifemur cannot be compared to that of L. paludis. Thus, Williston's (1912) illustration of the ventral surface of the left femur of L. paludis must serve as a point of comparison. Williston (1912) illustrated the trochanteric crest as flaring slightly cranioventrally away from the femur at a lesser angle compared to that in Limnoscelops. The differing orientations of the crests could be a distinguishing character, but here it is tentatively suggested that this feature is indicative of the differing fidelity of preservation. The proximal fragment of this femur is most likely very well preserved and thus has the crest oriented in the 90° position, in contrast to L. paludis. The preservation of L. paludis may well reflect some degree of distortion of the ventral side of the
specimen suffering dorso-ventral compression during preservation. The suboptimal preservation of this region of *L. paludis* might explain Williston's (1911a) observation of the flattened ventral sides of many of the limb bones in *L. paludis*.

Collectively, the morphology of the vertebrae, the pelvic girdle and the femur do not provide enough unique characters or character combinations upon which to base a generic distinction. The only unique character in *Limnoscelops* is the perpendicular orientation of the trochanteric crest, and this feature may be an artifact of differential preservation. However, even if this character is valid, it alone probably does not warrant generic distinction in the absence of cranial materials. As previously mentioned, Berman and Sumida (1990) pointed out that the postcranial skeletons in *Limnoscelis paludis* and *L. dynatis* were not adequate for distinguishing the two species, and that specific distinction was dependent on cranial characteristics. Given that cranial characters were necessary to warrant specific distinction in a nearly complete skeleton, it seems unlikely that a single postcranial feature is adequate to warrant generic distinction for *Limnoscelops*. Due to the presence of a
very large internal trochanter on the femur, a character that is only found in Diadectes and Limnoscelis, (Sumida, 1997), MCZ 2984 and MCZ 2979 are assigned to the order Diadectomorpha but at no greater degree of resolution. This, in combination with the lack of diagnostic features in the vertebral column, renders Limnoscelops as a nomen dubium.

Limnostygis

Systematic Paleontology
Amniota? incertae sedis
Limnostygis relictus, Carroll, 1967
nomen dubium

Holotype - Museum of Comparative Zoology, Harvard University, MCZ 3034. Partial left maxilla, eight dorsal vertebrae, right cleithrum, right scapulocoracoid. Also, an undescribed element assigned to the holotype.

Geological Age and Distribution - Morien Group, Middle Pennsylvanian. Holotype is from the Florence locality, from lycopod tree stump #3 of the Dominion Coal Company, strip mine No. 7, 3.21 km north of Florence, Cape Breton County, Nova Scotia, Canada.

Discussion - Carroll (1967) based Limnostygis on the morphology of all elements of the holotype - a partial left
maxilla, eight dorsal vertebrae, right cleithrum and scapulocoracoid. However, the structure of the element described as the cleithrum and the structure of the vertebrae were of particular importance in his description.

The partial left maxilla of *Limnostygis relictus* is exposed on the medial side (Figure 20). It currently contains nine teeth, as opposed to Carroll's (1967) description, which lists fourteen teeth. Upon re-examining the specimen (MCZ 3034), it is apparent that parts of both the rostral and caudal ends of this maxilla that were present when Carroll described the genus are currently missing. What remains of the maxilla is approximately 2.3 cm in length and the teeth increase in length from rostral to caudal, reaching a maximum length of 6.2 mm in the fourth tooth of the series. This tooth is most likely a caniniform as tooth length decreases progressively in the caudal direction of this tooth. The teeth are small, narrow, conical pegs with longitudinal ridges indicating slight labyrinthine infolding. A shelf extends medially from the ventral edge of the element above the tooth row. Carroll (1967) assigned this partial maxilla to *Limnostygis* based on its resemblance to the maxilla of *Limnoscelis*. 

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Figure 20. Medial View of Partial Left Maxilla of *Limnostygis relictus*, Museum of Comparative Zoology 3034.

Since Carroll's description of *Limnostygis*, a new *Limnoscelis* specimen was described — *L. dynatis* (Berman and Sumida, 1990), providing additional comparative material for the maxilla of *Limnostygis*. No medial view of a limnoscelid maxilla was published until Berman and Sumida (1990) illustrated it for *L. dynatis*. Thus, it is presumed that Carroll (1967) based his estimate of the similarity *Limnostygis'* medial maxilla to that of *Limnoscelis* on the overall outline of the element and the teeth. The maxilla of *Limnoscelis* is much larger than that of *Limnostygis* (Williston, 1911a,b, 1912; Romer, 1946; Berman and Sumida, 1990) and has a shelf supporting the tooth row and the
dentition; this shelf is not seen in *Limnostygis* (Berman and Sumida, 1990). However, the dentition of *Limnoscelis* and *Limnostygis* is comparable, though that of *Limnoscelis* is somewhat more robust. Although the partial maxilla of MCZ 3034 is similar in this respect to that in *Limnoscelis*, it also bears a strong resemblance to the maxilla of certain pelycosaurian-grade synapsids (Reisz, 1986). Pelycosaur maxillae have a medial shelf very similar to that of *Limnostygis relictus*, and their maxillary dentition is also similar in outline. More importantly, the maxilla of MCZ 3034 is approximately the same size as that of some pelycosaur maxillae found in other stumps at this same locality, as well as other localities of the same age (Reisz, 1972). On the other hand, no other limnoscelids have been recovered from these Middle Pennsylvanian sites. Thus, two possibilities arise. First, as the maxilla does not have any unique characters or character combinations that would allow assignment into Limnoscelidae, it is not confidently assignable to this family and does not warrant generic distinction. Second, because the maxilla is not necessarily limnoscelid and is morphologically similar to a pelycosaurian maxilla, many of which have been found in
great abundance in Middle Pennsylvanian localities, especially this one, it may be most parsimonious to say that this maxilla is assignable to a pelycosaur. Regardless of which possibility is considered, the characters of this maxilla are not enough to suggest the presence of a limnoscelid at this locality.

Carroll (1967) also based his description of *Limnostygis* on the morphology of the dorsal vertebrae (Figure 21). The vertebrae are preserved randomly, and thus their relative position in the vertebral column cannot be determined. However, because they are all similar in size and proportion to one another, Carroll (1967) suggested that it was reasonable to conclude they were from the same region of the axial column. The vertebrae are preserved as eight elements in four different pieces. One section contains two well preserved articulated vertebrae, another contains two vertebrae compressed together by postmortem crushing, a third section contains one vertebra partly crushed dorso-ventrally, and the last section contains what are probably three poorly preserved vertebrae compressed together by postmortem crushing. Together, these four sections provide cranial and caudal views of the vertebrae. The vertebrae are relatively small, measuring
Figure 21. Dorsal Vertebrae of *Limnostygis relictus* (Museum of Comparative Zoology 3034) in Cranial, a, and Caudal, b, View.

approximately 7.0 mm in centrum length and having a maximum width at the posterior zygapophyses of 12.6 mm. The neural arches are significantly swollen and the zygapophyses extend well beyond the centra.

Carroll (1967) distinguished the vertebrae of *Limnostygis* from Permian limnoscelids by their differing proportions. He compared the proportions of the vertebrae of *Limnostygis relictus* to those of the other limnoscelids described at that time: the Late Pennsylvanian complete articulated skeleton of *Limnoscelis paludis* (YPM 811), *Limnosceloides dunkardensis* (USNM 12166), *Limnosceloides*
brachycoles (UCMP 35767, 40238, 40232), and Limnoscelops longifemur (MCZ 2979, 2981). The materials assigned to Limnosceloides and Limnoscelops longifemur have been declared nomina dubia and interpreted as diadectomorphs with no further resolution. As comparison to “Limnosceloides” and “Limnoscelops” is no longer useful, the vertebrae of Limnostygis must be compared to those of Limnoscelis paludis and L. dynatis. The width of the vertebral centra of Limnoscelis exceeds their length (Williston, 1911a; Berman and Sumida, 1990). On the other hand, the width and length of the vertebrae of L. relictus are nearly equivalent. Carroll (1967) also distinguished Limnostygis relictus vertebrae from other limnoscelids based on the differences in the proportions of their neural arches, and there are clear differences in these proportions relative to Limnoscelis. The width of the neural arch in Limnoscelis paludis is greater than twice the width of the centrum. On the other hand, the difference between the width of the neural arch and centrum in L. relictus is not as dramatic. In L. relictus, the width of the neural arch ranges from 12 to 14 mm, whereas the width of the centra is 6.8 mm.
Carroll (1967) suggested that both the differences in the proportions of the centra and of the neural arch between *Limnostygis relictus* and *Limnoscelis paludis* are to be expected because *L. relictus* is an early member of the limnoscelid lineage and therefore much more primitive than later limnoscelids. This hypothesis was based on the prevailing notion at the time that the neural arches of primitive reptiles could be modeled on those of protothyridid reptiles (Carroll, 1969, 1970), a group with relatively concave neural arches as opposed to the convex condition seen in limnoscelids and various primitive amniotes. However, Sumida (1990) and Sumida and Modesto (2001) have demonstrated that expanded, or "swollen," neural arches are in fact the basal condition for Diadectomorpha and Amniota and that the narrower neural arch of protothyridids is actually a more derived condition. Thus, comparison of the vertebrae assigned to *Limnostygis* to those of *Limnoscelis* demonstrates that the vertebrae are not attributable to limnoscelids, partially based on the characters Carroll (1967) attributes to their primitiveness.
The vertebral column of *L. relictus* is approximately the same length and width. This is a character not present in limnoscelids, but it is present in captorhinid reptiles (Sumida, 1990; Figure 22). Moreover, the transverse processes of the vertebrae of MCZ 3034 extend to the centrum, unlike the transverse processes of comparably proportioned vertebrae of *L. paludis*, which are independent of the centrum. On the other hand, the transverse processes of the vertebrae of captorhinid reptiles do
extend to the centra, in a manner similar to the condition in *L. relictus* (Sumida, 1990). These characters suggest that the vertebrae are potentially assignable to captorhinid reptiles. If this is the case, then MCZ 3034 represents the earliest record of captorhinid reptiles. The presence of captorhinids at this time resolves the previous perceived temporal paradox of the more derived protorothyridids that have been found earlier in the fossil record and the more primitive, yet seemingly more recent, based on their fossil record, captorhinid reptiles (Sumida and Modesto, 2001).

A partial pectoral girdle is also present in materials assigned to *Limnostygis relictus*. Carroll (1967) described the two elements present as the right cleithrum and scapulocoracoid (Figure 23A). The scapulocoracoid described by Carroll was well-preserved with only the anteroventral part of the scapula and the corresponding portion of the anterior coracoid missing (right of Figure 23A). However, upon reexamination of MCZ 3034 it is apparent that either part of the scapulocoracoid is missing or that the element is not as well-preserved as initially described. A thin layer of bone is present on the surface of the rock which corresponds in shape to the
Figure 23. Right "Cleithrum" and Outline View of Scapulocoracoid of Limnostygis relictus (Museum of Comparative Zoology 3034) in Lateral View, a; Right Clavicle of Ophiacodon retroversus for Comparison, b, Adapted from Illustration of Left Clavicle from Romer and Price, 1940.


scapulocoracoid illustrated by Carroll (1967); however, the cracks described as bounding the posterior coracoid, the scapula, and anterior coracoid cannot be currently seen due to the surface being covered by a specimen number and Type specimen designation. The outline of this element resembles the scapulocoracoid of Limnoscelis paludis,
Limnoscelis dynatis, Seymouria, and pelycosaurs (Williston, 1911a; Romer and Price, 1940; Reisz, 1986; Berman and Sumida, 1990; Sumida, 1997). Therefore, the morphology of the scapulocoracoid alone cannot distinguish L. relictus as a limnoscelid.

The other element of the pectoral girdle is described as the cleithrum (Carroll, 1967). The element is a large bone, approximately 3.3 cm in length, with a long stem ending in an expanded blade with sculpturing present on the blade (left of Figure 23A). On the other end of the stem is a small ridge separated from the rest of the bone by anterior and posterior grooves. The stem ends in a blunt, broken off, curved surface. Carroll (1967) interpreted this element as the cleithrum, similar to the cleithrum of Diadectes, and suggested that the cleithrum in Limnoscelis paludis had been incorrectly described by Williston (1911a) as a small sliver of bone. Instead, Carroll (1967) suggested that the bone described as the clavicle in L. paludis is actually the ventral part of the cleithrum and that the element described as the cleithrum is actually the dorsal portion of the cleithrum that connects to the clavicle. He identified the clavicles as two corresponding bones that lie caudal to the coracoids in Limnoscelis.
Williston described these bones as the hyoids (1911a) and fourth ribs (1912), and Romer (1946) redescribed them as pectoral girdle ribs and then as ceratobranchials (Romer, 1956). However, the element Carroll (1967) identified as an unusual cleithrum with dorsal sculpturing is more likely a clavicle, most likely of an ophiacodontid pelycosaur. This interpretation is reinforced by the presence of sculpturing on what is here interpreted as the ventral surface of the element. This suggestion is much more conservative, and conforms to the pattern common to many Late Paleozoic tetrapods (Sumida, 1997). The element displays sculpturing on what is identified as the ventral blade of the clavicle, which is common in ophiacodontid pelycosaur clavicles (Romer and Price, 1940; Reisz, 1986), as well as a variety of other Late Paleozoic tetrapods, including Limnoscelis (Sumida, 1989). However, this is most likely not a Limnoscelis clavicle due to its smaller size and its age. Also, the clavicle has a narrower dorsal portion and a mediolaterally thinner and anteriorly expanded ventral blade. It would not be surprising to find ophiacodontid pelycosaur remains in this tree stump as Reisz (1972) has identified partial specimens of
ophiacodontid pelycosaurs in another tree stump from the same locality.

In addition to the elements described by Carroll (1967), another element was recovered from tree stump #3 and assigned to MCZ 3034 (Figure 24A). This element appears to be a partial pelvis of an ophiacodontid pelycosaur (Figure 24B). It contains all three component elements, with the ischium and pubis only partially preserved and exposed on the lateral side only. The iliac blade is dorsally elongate and pointed caudally, ending dorsally at a broken margin with a prominent ridge running from the caudal margin of iliac blade and rising slightly in height as it approaches the acetabular area. The dorsal margin of the iliac blade is characterized by a notch formed by an extension of the dorsal iliac blade cranially. This extension is not completely preserved, but the outline of the cranial portion of the blade can be seen to be convex, except for the notch, whereas the outline of the caudal edge is concave. In medial aspect, the iliac blade has a ridge running dorso-ventrally from the notch to the matrix that covers the rest of the medial surface of the pelvis. The iliac blade connects ventrally with the partially preserved ischium and pubis. These two bones are
Figure 24. Undescribed Element of *Limnostygis relictus* (Museum of Comparative Zoology 3034) in Lateral View, a; Right Pelvis of *Ophiacodon retroversus* in Lateral View for Comparison, b, Adapted from Illustration of Left Pelvis from Romer and Price, 1940.


poorly preserved and do not display any distinguishing features. The pubis has a convex cranial outline and a thick, rounded caudal extension on its caudal surface. A small, shallow pit is present on the pubis, close to the ilio-pubic suture. The ischium has a small ridge running close to the ilio-ischial suture. The ischium has a mostly convex outline on its caudal margin and is not fully preserved at the cranial margin. In contrast to the pelvis
of *Limnoscelis* and other diadectomorphs, this pelvis does not have the external iliac shelf. It also has a taller iliac blade as compared to the low and almost horizontal iliac blade of *Limnoscelis* (Williston, 1912; Berman and Sumida, 1990).

These data can be interpreted in two ways: (1) the tree stump contained remains of a variety of different animals; or (2) the tree stump contained skeletons of a partial ophiacodontid pelycosaur (pelvis, clavicle, scapulocoracoid) and captorhinid (vertebrae) and possible amniote (maxilla). The first, more conservative of the two approaches is to assign the pelvis and clavicle to an ophiacodontid pelycosaur, the scapulocoracoid to either the Amniota, as traditionally defined (Heaton, 1980), or to Diadectomorpha or Seymouria, the jaw to Amniota as traditionally defined, and the vertebrae to a captorhinid reptile. This approach suggests that the tree stump may have contained various different animals. However, if the latter approach is taken, only two known animals would be present: an ophiacodontid pelycosaur and a captorhinid. In either instance, the temporal range of the captorhinids is extended and that of limnoscelids is restricted.
Cladistic Analysis

Cladistic analyses have been performed numerous times on the Group Diadectomorpha and its closest relatives to determine their relationships to each other and their relationship to Amniota (e.g., Heaton, 1980; Berman et al., 1992; Sumida et al., 1992; Lee and Spencer, 1997; Laurin and Reisz, 1997;). All of these studies, except for that of Sumida et al. (1992), utilized cranial characters exclusively. The results of these studies have been similar, confirming the monophyly of the Diadectomorpha and its status as the sister taxon to the Amniota. A cladogram based on these studies, from here on referred to as the established cladogram, can be seen in Figure 25.

With characterization of the postcranial skeleton of limnoscelids added to data from other diadectomorphs (Table 1 and references therein), the currently accepted hypothesis of relationships (Figure 25) can be tested. Postcranial characters were gathered from this study of Limnoscelis, as well as through a thorough literature review. Some characters gathered from the literature were included in the study, such as atlas-axis complex characters (Sumida et al., 1992), whereas others were not. For example, Romer (1946) suggested that the offset
Figure 25. Established Cladogram of Diadectomorph and Amniote Interrelationships Based on Cranial Characters. Note: See text for pertinent references.

position of digit V on the manus may have been a limnoscelid character. However, the position of digit V relies on unaltered, articulated preservation of a specimen. As this type of preservation is rare, this character was not included in the study.
The taxa used in this analysis consist of the best known representatives of the three families of Diadectomorpha: Limnoscelis, Tseajaia, and Diadectes; and two primitive amniotes: the pelycosaurian-grade synapsid family Varanopseidae and the primitive reptile Captorhinus. The seymouriamorph amphibian Seymouria was used as an outgroup. Each of the taxa is represented by a well-known genus with the exception of the primitive pelycosaurian family Varanopseidae. Although Varanopseidae is not the most primitive pelycosaurian family known, it does preserve the most complete postcranial data set available for a basal synapsid.

Eighteen postcranial characters were identified (Table 3), and their character-states determined (Table 4). However, only two of these characters (characters 1, 13) were informative characters - characters where at least two character-states were shared by at least two taxa (Stewart, 1993).
Table 3. Characters and Character-states of the Postcranial Skeleton of Selected Late Paleozoic Tetrapods.

Note: The primitive or ancestral state is indicated as 0 and 1 indicates the derived state. Citations indicate studies identifying and/or using these characters in a phylogenetic analysis. The character numbers and character-states listed correspond to those listed in Table 4.

Character 1. Horizontal iliac shelf (Berman and Sumida, 1990; this study)

0. Absent

1. Present

Character 2. Variability of neural spine height and general construction (Sumida, 1997; this study)

0. Present, yet irregular in pattern

1. Present in regular pattern

2. Absent

Character 3. Length of tibia relative to the femur (Sumida, 1997; this study)

0. Tibial length is less than 50% of femur length

1. Tibial length is greater than or equal to 50% of femur length
Character 4. Pisiform bone in manus (Sumida, 1997; this study)

0. Absent
1. Present

Character 5. Differentiated atlas-axis complex (Sumida and Lombard, 1991; Sumida et al., 1992)

0. Absent
1. Present

Character 6. Axial neural spine (Sumida and Lombard, 1991; Sumida et al., 1992)

0. Paired halves
1. Fused along dorsal midline

Character 7. Structure of axial pleurocentrum (Sumida and Lombard, 1991; Sumida et al., 1992)

0. Composed of paired elements
1. Single element that reaches ventral midline

Character 8. Relationship of atlantal and axial intercentra to atlantal pleurocentrum (Reisz, 1980; Sumida et al., 1992)

0. Atlantal pleurocentrum separates atlantal and axial intercentra to reach ventral midline of column
1. Atlantal and axial intercentra articulate to exclude atlantal pleurocentrum from ventral midline of column
Character 9. Processes of atlantal neural spines (Sumida and Lombard, 1991; Sumida et al., 1992)

0. Large, posterodorsally directed processes
1. Small epipophyses

Character 10. Atlantal pleurocentrum (Sumida and Lombard, 1991; Sumida et al., 1992)

0. Composed of paired elements
1. Single ossified element in mature individuals

Character 11. Fusion of axial neural arch and pleurocentrum (Gauthier et al., 1998)

0. Not fused
1. Fused

Character 12. Relationship ofatlantal pleurocentrum to axial intercentrum (Reisz, 1980; Sumida et al., 1992)

0. Atlantal pleurocentrum contacts or is narrowly separated from anterior surface of axial intercentrum
1. Atlantal pleurocentrum articulates with, or is fused to, dorsal surface of axial intercentrum

Character 13. Anteriorly directed, midventral process of axial intercentrum (Sumida and Lombard, 1991; Sumida et al., 1992)

0. Absent
1. Present

Character 14. Facets of atlantal parapophysis (Sumida et al., 1992)

0. Single
1. Paired

Character 15. Ventral processes of atlantal intercentrum (Sumida et al., 1992)

0. Absent
1. Present

Character 16. Shape of interclavicle (White, 1939; this study)

0. Slightly waisted with a rounded end
1. Tapered caudally with a pointed end

Character 17. Manus phalangeal formula (Williston, 1911a,b; this study)

0. 2-3-4-4-3
1. 2-3-4-5-3

Character 18. Pes phalangeal formula (Williston, 1911a, b; this study)

0. 2-3-4-5-3
1. 2-3-4-5-4
Table 4. Distribution of Character-states of Taxa Used in Phylogenetic Analysis.

Note: Description of characters and their states are given in Table 3. Question marks represent missing data.

| characters | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|
| Seymouria  | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Limnoscelis| 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| Tseajaia   | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | ? | 1 | 1 | ? |
| Diadectes  | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | ? | 1 | ? | 1 | ? |
| Varanopseidae | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | ? | 1 | 1 | 1 | 1 |
| Captorhinus| 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |

A maximum parsimony tree using an exhaustive search was generated with these characters using PAUP 4.0 (Swofford, 2002). A maximum parsimony tree represents the least number of steps necessary to group the taxa using the designated characters, and an exhaustive search examines every tree generated to determine whether it is the most parsimonious. Missing data were entered in as dashes (−). Seymouria was designated as the outgroup. The end result is a tree with the smallest number of steps possible from the input data. Two equivalent maximum parsimony trees.
were produced. These trees were checked for robustness using the branch and bound bootstrap test at 1,000 repetitions. The branch and bound bootstrap consensus tree, which is equivalent in topology to the two maximum parsimony trees generated, can be found in Figure 26. A description of pairwise differences between taxa can be seen in Table 5.

Even though only two informative characters were available, the maximum parsimony tree verifies the monophyly of the Group Diadectomorpha with a high bootstrap value of 88. This tree also groups Varanopseidae and Captorhinus as a monophyletic group, consistent with their position within Amniota as traditionally defined. In the analysis based on postcranial features exclusively, both the Diadectomorpha and Amniota are grouped as polytomies and their relationships are not resolved any further. Recall that the number of characters necessary to produce a reliable cladogram is any number greater than the number of taxa. As only two informative characters were available compared to six taxa, the incongruence of this tree with the established cladogram is not unexpected.
Figure 26. Bootstrap Consensus Tree Based on Postcranial Characters.
Table 5. Pairwise Differences Between Taxa in Cladistic Analysis.

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>-</td>
<td>0.556</td>
<td>0.412</td>
<td>0.438</td>
<td>0.412</td>
<td>0.444</td>
</tr>
<tr>
<td>2</td>
<td>10</td>
<td>-</td>
<td>0.118</td>
<td>0.125</td>
<td>0.294</td>
<td>0.333</td>
</tr>
<tr>
<td>3</td>
<td>7</td>
<td>2</td>
<td>-</td>
<td>0.000</td>
<td>0.188</td>
<td>0.235</td>
</tr>
<tr>
<td>4</td>
<td>7</td>
<td>2</td>
<td>0</td>
<td>-</td>
<td>0.188</td>
<td>0.188</td>
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<td>7</td>
<td>5</td>
<td>3</td>
<td>3</td>
<td>-</td>
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</tr>
<tr>
<td>6</td>
<td>8</td>
<td>6</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>-</td>
</tr>
</tbody>
</table>

Note: Mean character differences, adjusted for missing data, are above the diagonal and total character differences are below the diagonal.

The postcranial characters used in this analysis were also mapped onto the established cladogram to determine whether there were any discrepancies between the origin and change of these postcranial characters and those of cranial characters represented by the established cladogram (Figure 27). Most of the characters do not show any discrepancies; however, a few characters are missing and therefore cannot confirm the relationships definitely.

The two cladograms, one based on postcranial characters, and the other based primarily on cranial
characters are almost identical in topology. The one difference is the unresolved polytomies of the diadectomorphs and amniotes. Nonetheless, the monophyly of the diadectomorphs and amniotes are confirmed in the postcranial cladogram. Taking into account that only two informative characters were available from the postcranial skeletons of six taxa, the resulting cladogram is unexpectedly similar to the established cladogram.
Figure 27. Postcranial Characters Mapped onto Established Cladogram Based on Mainly Cranial Characters. Informative Characters are Shown in Bold. Characters that have Constant States Through All Taxa are not Included.
Conclusions

Prior to this study, the Family Limnoscelidae consisted of six species within four genera: Limnoscelis paludis, Limnoscelis dynatis, Limnosceloides dunkardensis, Limnosceloides brachycoles, Limnoscelops longifemur, and Limnostygis relictus. These limnoscelids were found throughout North America, extending as far west as Colorado and New Mexico, and as far east as Nova Scotia, with a temporal range spanning from the Middle Pennsylvanian to the Early Permian. Concomitant with this presumed geographic and temporal range, Romer (1946) hypothesized that the limnoscelids underwent a large radiation in the Late Pennsylvanian, not recorded in the fossil record, yielding the Early Permian Limnosceloides and Limnoscelops longifemur.

With the results of this study, the properties of the Limnoscelidae change drastically. With the declaration of all of the "limnoscelids" except Limnoscelis as nomina dubia, the family becomes a monogeneric family consisting of two species, L. paludis and L. dynatis. The temporal range of the family is reduced to Late Pennsylvanian-Early Permian, and the geographic and geologic range is drastically reduced to the Sangre de Cristo Formation of
Colorado and the Cutler Formation of New Mexico. With only two species of *Limnoscelis* valid, the Early Permian radiation of limnoscelids is no longer tenable.
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