Reexamination of the Relationship of Middle Devonian Osteolepids—Fossil Characters and Their Interpretations

MEE-MANN CHANG[1] AND XIAOBO YU[2]

ABSTRACT

Unique features that two recently described Chinese osteolepids (*Thursius wudingensis* and *Kenichthys campbelli*) share with *Youngolepis* and *Powichthys* led to a reexamination of cranial features of Middle Devonian osteolepids. The study reveals uniquely shared features between Middle Devonian osteolepids and porolepiforms in premaxilla, cheek bone complex, sensory pits, pattern of coronoid tooth, and anterior infradentary flange of the lower jaw. Reexamination of features previously used to unite osteolepiforms as a monophyletic group indicates that significant differences between early osteolepids and *Eusthenopteron* were overlooked or misinterpreted in pre- vious work. The study lists 28 features in skull roof, cheek, endocranium, palate, lower jaw and histology in which Middle Devonian osteolepids differ from *Eusthenopteron* and resemble *Youngolepis, Powichthys,* and porolepiforms. We present the result of a cladistic analysis involving 14 taxa and 90 characters. In an alternative phylogenetic scheme, representative Middle Devonian osteolepids (*Thursius, Osteolepis, Gyroptychius, Kenichthys*) shift from the traditional Osteolepiformes-Tetrapoda branch to the Porolepiformes-Dipnoi branch. Major phylogenetic schemes are compared and the effects of preconceived phylogeny on character interpretation and character coding is discussed.

INTRODUCTION

This study examines the monophyly of Osteolepiformes with a special discussion on the phylogenetic position of Middle Devonian osteolepids. The term Osteolepiformes is often used in the approximate sense of Jarvik (1942, 1980) to include Rhizodontidae (containing *Eusthenopteron* and other rhizodontids) and Osteolepididae (containing ear-

[1] Research Associate, Department of Vertebrate Paleontology, American Museum of Natural History; Research Professor, Institute of Vertebrate Paleontology, and Paleoanthropology, Chinese Academy of Sciences, Beijing.
[2] Assistant Professor, Department of Biological Sciences, Kean College of New Jersey.

ly osteolepids from Middle Devonian and osteolepids from later periods). In most recent works on sarcopterygian relationships (Andrews, 1973; Gaffney, 1979; Jarvik, 1980; Long, 1985a; Maisey, 1986; Janvier, 1986; Schultze, 1987, 1991; Panchen and Smithson, 1987; Ahlberg, 1991; Yu, 1990; Chang, 1991b; Cloutier, 1991a, 1991b), Osteolepiformes is generally regarded as a monophyletic group, while paraphyly of the group has been suggested by Janvier (1980), Gardiner (1980), and Rosen et al. (1981).

Although Osteolepiformes includes both Rhizodontidae and Osteolepididae in formal classification, the characters of *Eusthenopteron* are frequently used to represent the condition in Osteolepiformes as a whole. *Eusthenopteron* has been the most thoroughly studied extinct "rhipidistian," particularly because of the detailed and elaborate work of Jarvik (1942, 1954, 1963, 1980). Using *Eusthenopteron* as a general model for Osteolepiformes is justified only if one accepts the monophyly of the group in the first place.

The dichotomous division of "rhipidistian" crossopterygians into osteolepiforms and porolepiforms and the "unity" of osteolepiforms have been questioned by previous workers. Thomson (1964, 1965) and Vorobjeva (1972, 1977) repeatedly pointed out significant differences between *Eusthenopteron* and the early osteolepids (Middle Devonian). Similarities between early osteolepids and porolepiforms were also noticed by Kulcizki (1960), Thomson (1968), and Vorobjeva (1972). However, under the paradigm of rhipidistian dichotomy and the unity of osteolepiforms, differences between *Eusthenopteron* and the early osteolepids tended to be overlooked or explained away as insignificant variations, while similarities between early osteolepids and porolepiforms are regarded as primitive characters common to rhipidistians.

Our attention was initially drawn to the monophyly or non-monophyly of Osteolepiformes by the unusual character combinations revealed by two recently discovered early osteolepids, *Thursius wudingensis* (Fan, 1992) and *Kenichthys campbelli* (Chang and Zhu, 1993), both from the Middle Devonian strata of eastern Yunnan, China. In addition to typical osteolepid charac-

ters, these two new forms share certain unique characters with *Youngolepis* (Chang and Yu, 1981; Chang, 1982; Chang and Smith, 1992) and (to a less extent) *Powichthys* (Jessen, 1975, 1980).

The discovery of *Powichthys, Youngolepis,* and *Diabolepis* (Chang and Yu, 1984) has evoked much debate on their relationships and on the interrelationships of sarcopterygians. Many investigators agree that these forms show transitional features between Porolepiformes and Dipnoi and tend to link the two groups together (Maisey, 1986; Janvier, 1986; Ahlberg, 1991; Yu, 1990; Chang, 1991b; Cloutier, 1991a, 1991b). Different opinions on the positions of *Powichthys* and *Youngolepis* still exist. For instance, Schultze (1987, 1991) and Long (1989) regarded them as primitive rhipidistians, Panchen and Smithson (1987) related *Powichthys* to the Porolepiformes and *Youngolepis* to the group of Osteolepiformes + Tetrapoda, while Bjerring (1989, 1991) regarded *Youngolepis* as osteolepiform.

The similarities of the two Middle Devonian Chinese osteolepids to *Youngolepis* and *Powichthys* prompted us to reexamine the character distributions in other Middle Devonian osteolepids. The results highlight many previously neglected (or ignored) differences between the early osteolepids and *Eusthenopteron*. We present a survey of these characters and discuss the possible phylogenetic implications.

Our analysis focuses on Middle Devonian osteolepids and does not include Upper Devonian and later osteolepids such as *Glyptopomus* and *Megalichthys*. The characters used are chiefly cranial features, because fossils of *Youngolepis, Powichthys, Thursius wudingensis* (Fan, 1992), and *Kenichthys campbelli* (Chang and Zhu, 1993) mainly consist of skull portions; there is little evidence of the endoskeleton of the fins of the Middle Devonian osteolepids (i.e., *Osteolepis, Thursius,* and *Gyroptychius*). We have not incorporated the new Upper Devonian osteolepid material from Australia described by Long (1985a, 1985b, 1988) and Young et al. (1992), because these forms are still under ongoing investigation. Following Young et al. (1992), we use "Osteolepididae" for the
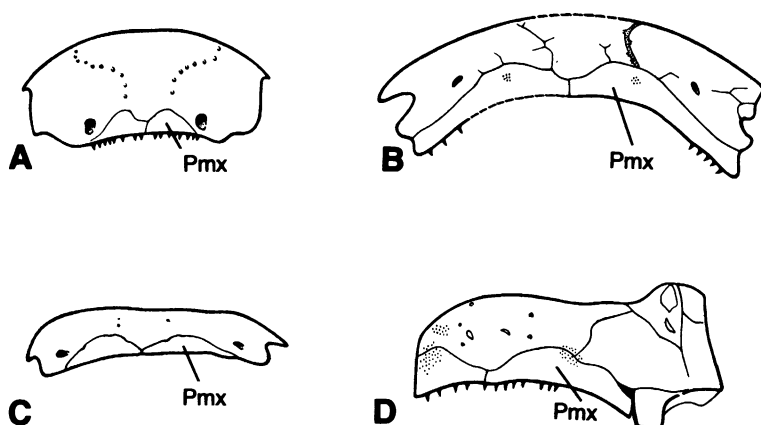
Fig. 1.   Anterior (A, B, C) and anterolateral (D) view of snout showing independent premaxilla. **A.** *Youngolepis,* from Chang, 1991a; **B.** *Powichthys,* from Jessen, 1975; **C.** *Thursius wudingensis,* V9464.1-10 (IVPP); **D.** *Kenichthys campbelli,* from Chang and Zhu, 1993.

formal family name and "osteolepids" as the informal name.

Abbreviations

Institutional

FMNH   Field Museum of Natural History, Chicago
IVPP   Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing

Anatomical

a. i. f.   anterior infradentary flange
l. p.   lateral pavement
n.P.   notch at posteroventral margin of preopercular
p. SQP   external pits on compound bone squamosal + quadratojugal + preopercular
Pmx   premaxilla

MORPHOLOGICAL DATA
CHARACTERS SHARED BY *YOUNGOLEPIS,* *POWICHTHYS,* AND EARLY OSTEOLEPIDS

Our attention turned to the early osteolepids when we first noticed the following five conditions present in both the two new Chinese osteolepids (*Thursius wudingensis* and *Kenichthys campbelli*) and in *Youngolepis* and (to a lesser extent) *Powichthys.*

1. The premaxilla is always independent of the adjacent part of the skull roof, with infraorbital and ethmoid commissural sensory canals running in the suture between premaxilla and adjacent part of skull roof (fig. 1). So far, this condition is observed only in the Chinese Middle Devonian osteolepids and in *Youngolepis* and *Powichthys.* Ahlberg (1991) described a premaxilla free from the median rostral, with a sensory canal running in the suture in *Porolepis.* The infraorbital sensory canal in this specimen follows the lateral and medial parts of the premaxillary suture but traverses the bone at the base of its dorsal process, a condition different from that in *Youngolepis* and *Powichthys* where the premaxilla is completely independent.

2. Squamosal, quadratojugal, and preopercular (recognized by the presence of jugal sensory canal, squamosal and quadratojugal pit-lines, and preoperculo-mandibular sensory canal) are fused into a compound bone (fig. 2A, B, C). This condition is not verifiable in *Powichthys* because there is no preserved material.

3. The surface of the compound bone (squamosal + quadratojugal + preopercular) carries three pits (p.SQP, fig. 2) followed by grooves in *Kenichthys* and *Youngolepis,* with the anterior pit near the area overlapped by the postorbital, the middle pit next to the upper part of preoperculo-mandibular sensory canal, and the posterior pit at the posteroventral corner of the bone. Although not mentioned in the textual description of Fan (1992), a distinct notch at the posteroventral corner of the compound bone of *Thursius wudingensis* shown in his figure 3D looks
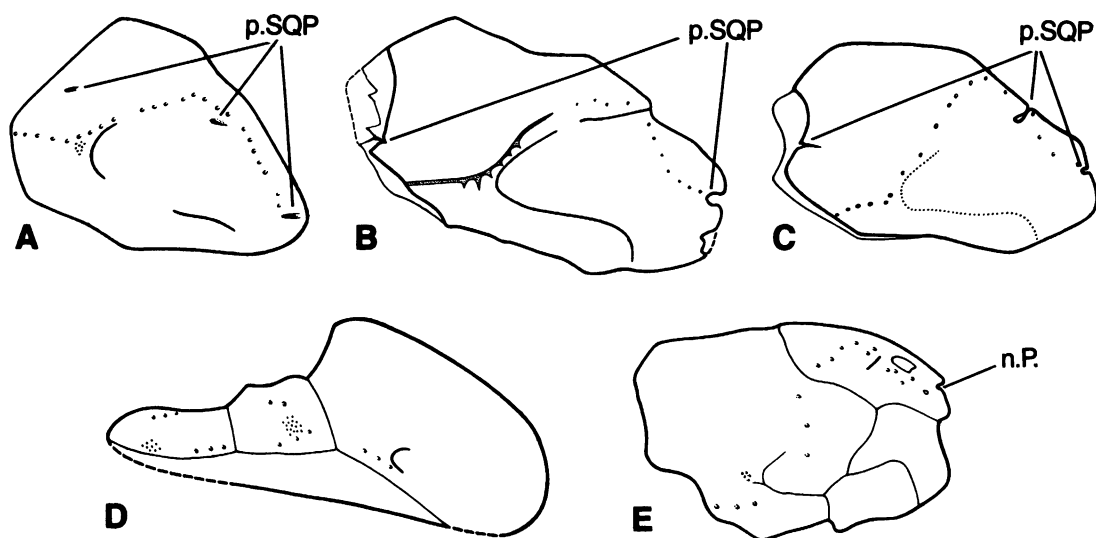
Fig. 2.   Squamosal, quadratojugal, and preopercular as a compound unit (A, B, C, D) and separate plates (E). **A.** *Youngolepis,* from Chang, 1991a; **B.** *Thursius wudingensis,* from Fan, 1992; **C.** *Kenichthys campbelli,* from Chang and Zhu, 1993; **D.** *Thursius pholidotus,* from Jarvik, 1948; **E.** *Gyroptychius,* PF 1327 (FMNH).

very similar to that in *Kenichthys* (Chang and Zhu, 1993: fig. 7F). In addition, a pit at the boundary between the cosmine-covered layer and the area overlapped by the postorbital (Fan, 1992: Pl.II:4) exactly matches the condition in *Kenichthys* (Chang and Zhu, 1993: fig. 7). This condition is not observable in *Powichthys* because there is no preserved material; however, both *Powichthys* and *Youngolepis* possess three similar pits along the lower margin of the lower jaw, raising the possibility of a similar pattern in the cheek bones.

4. The lateral portions of the coronoids are covered with numerous randomly set small teeth (l.p., fig. 3). This condition is observed in all forms except *Thursius wudingensis,* where the lingual side of the lower jaw is not prepared.

5. The ventral margin of the inner side of the lower jaw has an extensive anterior infradentary (splenial) flange (a.i.f., fig. 3). The condition is not observable in *Thursius wudingensis* for the same reason as above.

The abovementioned similarities between the Chinese osteolepids and *Youngolepis* and *Powichthys* prompted us to reexamine corresponding conditions in previously described Middle Devonian osteolepids from

other localities. Of the five conditions present in both the Chinese osteolepids and in *Youngolepis* and *Powichthys,* four conditions also exist to various extents in Middle Devonian osteolepids from other localities, while one condition (independent premaxilla) remains uncertain. The corresponding conditions in Middle Devonian osteolepids from other localities are described below in the same numbered sequence as the five conditions described above.

1. Jarvik (1948: figs. 14, 16A, 17; 1980: fig. 145A) reconstructed a paired naso-rostro-premaxillary in *Osteolepis macrolepidotus* and compared it to the condition in *Eusthenopteron.* The snout region of the *Osteolepis* specimens shown in Jarvik (1948: figs. 15, 38, 54, 78, 79, etc.) is always covered by cosmine, however, and Jarvik himself (1948: 46) remarked that "in no case have traces of sutures been found on the external faces of the lateral and anterior parts of the snout." The specimen (Jarvik, 1948: pl. 7:1) depicted by Jarvik (1948: fig. 14) shows the lateral part of the suture bordering the premaxilla but does not show whether the nasal and median rostral are fused with the bone (see broken lines in Jarvik, 1948: fig. 14). It is therefore still difficult to say wheth-
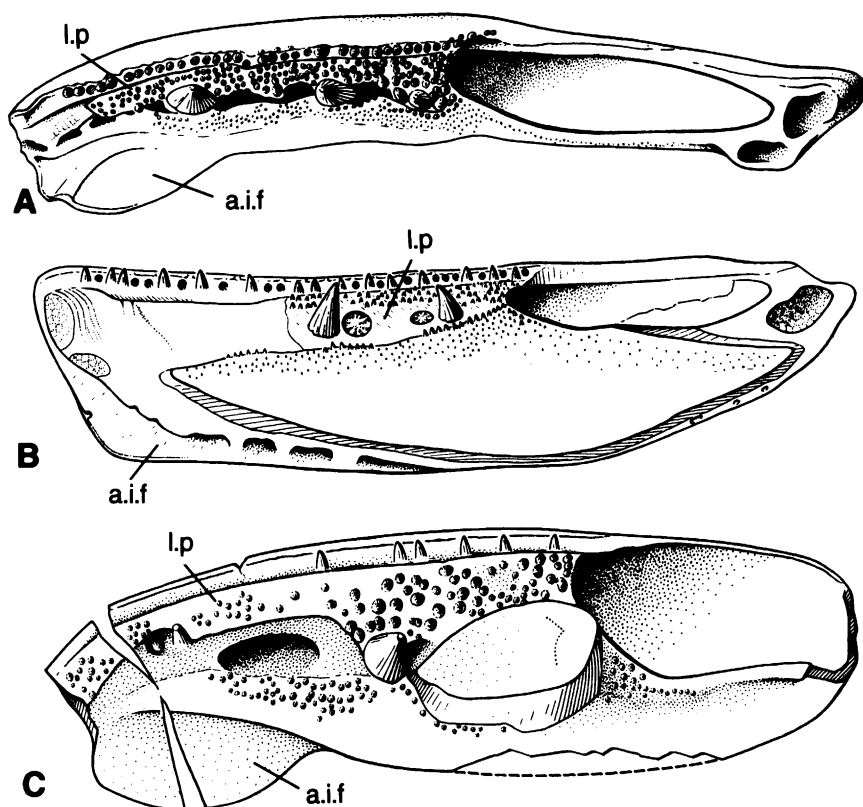
Fig. 3. Lower jaw rami in dorsal (A) and medial (B, C) views. A. *Youngolepis,* from Chang, 1991a; **B.** *Powichthys,* from Jessen, 1980; **C.** *Kenichthys campbelli,* from Chang and Zhu, 1993.

er the premaxilla in osteolepids is fused with the nasal and rostral bones.

2. In Middle Devonian osteolepids from other localities, the squamosal, quadrato-jugal, and preopercular are often united into one plate and quite frequently the sutures are overgrown by the cosmine layer (fig. 2D) (Jarvik, 1948, 1950; Vorobjeva, 1977). This condition is especially noticeable in *Gyrop-tychius* (Vorobjeva, 1977).

3. Although no pits have been observed on the surface of the squamosal, quadrato-jugal, and preopercular in Middle Devonian osteolepids from other localities, one speci-men of *Gyroptychius* (PF132, FMNH, per-sonal obs. by Chang) shows a distinct notch (n.P, fig. 2E) at the posteroventral corner of the plate, similar to the notch found in the same position in *Thursius wudingensis* (Fan, 1992: fig. 3D) and *Kenichthys* (Chang and Zhu, 1993: fig. 7F).

4. *Gyroptychius* and other Middle Devo-

nian osteolepids show a similar pattern of randomly set small teeth on the lateral por-tions of coronoids. Vorobjeva (1977: 63) spe-cifically pointed out that "in primitive osteo-lepiforms . . . the vertical laminae and lateral processes of coronoids carry several rows of teeth (or bands of shagreen)."

5. An extensive anterior infradentary flange is developed in Middle Devonian os-teolepids (Vorobjeva, 1977).

CHARACTER DIFFERENCES BETWEEN MIDDLE
DEVONIAN OSTEOLEPIDS AND
EUSTHENOPTERON

The above observations led us to conduct a survey of osteolepid characters with special attention to comparisons between Middle Devonian osteolepids and *Eusthenopteron.* The results are presented below and the char-acter conditions are sequentially numbered (1–28). Where applicable, we also make ref-

erence to conditions in *Youngolepis, Powichthys,* and a few other taxa.

SKULL ROOF: With regard to composition and position of the dermal bones, the skull roof is virtually the same in all Middle Devonian osteolepids and in *Youngolepis* and *Powichthys* (Chang, 1982). It resembles *Eusthenopteron* in the type X pattern of the skull table (Andrews, 1973) and in the presence of dermintermedial process under the anterior external nasal opening (condition not known in *Powichthys*). However, a similar X type pattern is also found in Rhizodontiformes [= Rhizodontida sensu Andrews and Westoll, 1970b; and Long, 1989] and Onychodontiformes (Andrews, 1973). Middle Devonian osteolepids (and *Youngolepis* and *Powichthys*) differ from *Eusthenopteron* in:

(1) the presence of an extratemporal (Jarvik, 1948; also present in porolepiforms, rhizodontiforms, and onychdontiforms, Andrews, 1973);

(2) absence of a postspiracular (Jarvik, 1948); and

(3) presence of numerous posterior postrostrals (Jarvik, 1948; Vorobjeva and Obruchev, 1964; Vorobjeva, 1977).

CHEEK: Middle Devonian osteolepids and *Youngolepis* resemble *Eusthenopteron* in the cheek plate being composed of seven bones (assuming the fusion of the squamosal, quadratojugal, and preopercular in the three Chinese forms). However, the condition of the cheek in Middle Devonian osteolepids differs from that in *Eusthenopteron* in the following:

4) postorbital not extending posteriorly to reach spiracular notch (the postorbital in *Youngolepis* extends back to reach the spiracular notch, as in *Eusthenopteron*); and

5) squamosal, quadratojugal, and preopercular forming a tightly united plate with sutures sometimes covered by cosmine.

NEUROCRANIUM: The endocranium of Middle Devonian osteolepids reveals a series of differences from that of *Eusthenopteron,* and the extent of the differences is much more than we expected:

6) The nasal cavities in *Osteolepis* (Thomson, 1965), *Thursius,* and *Gyroptychius* (Vorobjeva, 1977) are short and broad and situated far apart from each other in the very anterolateral part of the ethmoid region, and consequently the prenasal portion of the eth-

moid region is very short. In *Eusthenopteron,* the nasal cavities are large and situated in the posterolateral part of the ethmoid region and the prenasal portion is longer (Jarvik, 1942). The condition in *Youngolepis, Powichthys,* and porolepiforms is similar to that in Middle Devonian osteolepids, while the condition in *Thursius wudingensis* and *Kenichthys* cannot be examined because the endocranial portion is not prepared.

7). As in *Youngolepis, Powichthys,* and porolepiforms, the internasal septum is broad in Middle Devonian osteolepids (Thomson, 1965; Vorobjeva, 1977). It is rather narrow in *Eusthenopteron* (Jarvik, 1942).

8). Since the prenasal region is extremely short in *Thursius,* it cannot possess the type of apical fossa as defined by Jarvik in *Eusthenopteron.* In *Thursius,* the most anterior part of the mouth roof, situated under the internasal portion of the neurocranium and lined mainly with endoskeleton, is partly divided by a median endocranial ridge into two small pits (Vorobjeva, 1977: fig. 3`). The ridge and pits are very similar to the internasal ridge and pits in *Youngolepis* (Chang, 1982: figs. 7A, B, 8); these structures are different from those in *Powichthys* and porolepiforms mainly in their smaller size. Vorobjeva (1977) described the condition in *Gyroptychius* (Vorobjeva, 1977: 137, 140) in these words: "the palatal fossa enters the internasal region" and "the posterior 2/3 of the fossa is divided by an endocranial ridge, broad at its base." The condition is not observable in *Osteolepis* because the corresponding part of the cranium is not preserved (Thomson, 1965).

9). In *Osteolepis,* there are no prominent subdivisions of the nasal cavity (Thomson, 1965: 187). The structure must also be simple in *Thursius* because of a weakly developed dermintermedial process and the absence of the intermedial process (Vorobjeva, 1977). Vorobjeva (1977: 205) attributed the same condition to Middle Devonian osteolepids as a whole. The nasal cavity of *Youngolepis* has no subdivisions except for a recess around the anterior nostril between the processus dermintermedius and the process of the anterior tectal (Chang, 1982). The structure of the nasal cavity is also simpler

in *Powichthys* (Jessen, 1980) and porolepiforms (Jarvik, 1972) than in *Eusthenopteron*.

10). The postnasal wall of *Thursius estonicus* is pierced by a large medial opening for the main branch of N. profundus and several small openings dorsolateral to it for other branches of the nerve (Vorobjeva, 1977: fig. 25^). Similar condition exists in *Powichthys* (Jessen, 1980) and porolepiforms (Jarvik, 1972). However, in *Youngolepis* and *Osteolepis,* the condition resembles that in *Eusthenopteron* and there is only a single opening in the postnasal wall for the N. profundus (Thomson, 1965; Chang, 1982). No information is available on the postnasal wall of *Gyroptychius.*

11). In *Thursius* (Vorobjeva, 1977: fig. 25`), the opening of the canal for the pituitary vein is situated dorsal to the posterior vertical portion of the basipterygoid process. This condition is also found in *Youngolepis, Powichthys,* and porolepiforms (Chang, 1982), while in *Eusthenopteron* the canal for the pituitary vein is situated in front of the process (Jarvik, 1954). Thomson (1965: 189), following Stensiö and Romer, identified a small foramen immediately posterior to the optic nerve foramen as the opening for the pituitary vein in *Osteolepis*; consequently, this opening is situated anterodorsal to the basipterygoid process. In *Gyroptychius,* the canal for the pituitary vein is not described.

12). In *Gyroptychius* (Vorobjeva, 1977: 139), as in *Youngolepis* and probably also in *Powichthys* (compare "c.v.ju", Jessen, 1980: fig. 5 with "c.n.pro", Chang, 1982: 47, fig. 15A), the exit for the profundus branch of the trigeminal complex from the endocranium is situated in the posterodorsal portion of the lateral wall of the ethmosphenoid (Chang, 1982: 47). No such opening was found in the wall of the endocranium in *Eusthenopteron*; Jarvik (1954) suggested that the profundus nerve exited via the gap between the two moieties of the endocranium. Bjerring (1973) suggested a similar position for the exit of the nerve profundus (through the gap) for porolepiforms. No information is available for the condition in *Thursius* and *Osteolepis.*

13). In *Osteolepis,* the crista parotica assumes an oblique orientation (Watson, 1954) and the posterolateral part of the skull roof

formed by the extratemporal lies outside the neurocranium. In *Eusthenopteron,* the crista parotica assumes a longitudinal orientation and the posterolateral corner of the skull roof is supported by the crista itself (Bjerring, 1972).

Middle Devonian osteolepids differ from *Eusthenopteron* in the following cranial structures related to the articulation of palatoquadrate:

14). The lateral ethmoidal articulation for the palatoquadrate observed in *Eusthenopteron* (art$_1$l, Jarvik, 1942: fig. 48) is absent in Middle Devonian osteolepids (Vorobjeva, 1977: 123) and in *Youngolepis* and *Powichthys.* According to Jarvik (1972: 70), the ethmoidal articulation of porolepiforms corresponds to the anteromedial ethmoidal connection in *Eusthenopteron* but not to the posterolateral connection.

15). Thomson's description (1965: 183) and the illustration in his figure 1 indicate that *Osteolepis* possesses a fossa autopalatina. A similar structure is also described in *Thursius* and *Gyroptychius* (Vorobjeva, 1977: 127, 139, fig. 25`). *Gyroptychius* also possesses a well-defined area for the apical process of palatoquadrate. A fossa autopalatina is usually present in porolepiforms, *Powichthys* (Jessen, 1980), and *Youngolepis* (Chang, 1982) and a well-defined area for the apical process is also present in *Powichthys* and *Youngolepis.* In *Eusthenopteron,* there are no fossa autopalatina but there is a well-defined area for the apical process of palatoquadrate.

16). In *Thursius* (Vorobjeva, 1977: fig. 25B), the basipterygoid process is situated low and is comparatively detached from the endocranium. In *Gyroptychius* (Jarvik, 1980: fig. 147A; Vorobjeva, 1977: pl. III:1a), the ventral horizontal portion of the basipterygoid process is expanded laterally. In *Osteolepis,* as described by Thomson (1965: 184), the process is "prominent, arc-shaped, the ventral portion of which extends forwards to merge with the ventral margin of the endocranium." In fact, a broad ventral portion of the basipterygoid process is correlated with the presence of the fossa autopalatina (Chang, 1995). In *Eusthenopteron,* the basipterygoid process is situated high up in the lateral wall of the endocranium.

17). In *Thursius* and *Gyroptychius* (Vorobjeva, 1977), the suprapterygoid process is absent or underdeveloped. Similarly, *Osteolepis* (Thomson, 1965: 184) lacks a "specialized region for the reception of an antotic process of the palatoquadrate." The suprapterygoid process is also absent in *Youngolepis* and *Powichthys*. In forms where the suprapterygoid process is absent or underdeveloped, the ascending process of palatoquadrate is assumed to be in ligamentous connection with the endocranium (Jarvik, 1972; Vorobjeva, 1977). The suprapterygoid process is present in *Eusthenopteron*. The development of the suprapterygoid process varies in different porolepiforms. In some forms, the condition resembles that in *Eusthenopteron*. In some other forms, as revealed by the sectioned specimen of *Glyptolepis groenlandica* (Jarvik, 1972: figs. 20, 21A, 24E), both the suprapterygoid process and the ascending process have a complete periosteal lining and consequently Jarvik suggested that the ascending process of palatoquadrate in this form is connected to the endocranium by ligament.

PALATE: 18). In Middle Devonian osteolepids, the anterior portion of the palatoquadrate occupies a more or less horizontal position (Vorobjeva, 1977: fig. 13"`, ´, ˜, ¯ ") and the skull is usually compressed dorsoventrally (i.e., the platybasic skull type according to Stensiö, 1963). The comparatively deep fossa autopalatina, the expanded horizontal portion of the basipterygoid process, and the absence or weak development of the suprapterygoid process are apparently correlated to the horizontal position of the palatoquadrate. In *Eusthenopteron*, where the palatoquadrate occupies a comparatively vertical position (Vorobjeva, 1977: fig. 13"`^, ˜ "; Jarvik, 1980: figs. 84, 108) and the head is laterally compressed (i.e., the tropibasic skull type, Stensiö, 1963), the structures on the endocranium related to the palatoquadrate articulation are correspondingly different. In porolepiforms, the position of the anterior portion of the palatoquadrate is horizontal (Jarvik, 1972: fig. 16). Judging by the presence of the fossa autopalatina, the laterally stretched horizontal portion of the basipterygoid process, and the absence of the suprapterygoid process, the position of the

anterior portion of the palatoquadrate in *Youngolepis* and *Powichthys* might also be horizontal.

19). In *Thursius*, the vomers have no posterior process and are widely separated from each other (Vorobjeva, 1977: fig. 25B). In *Gyroptychius* (Ibid: fig. 29A), the vomer carries a weakly developed posterior process and is posteriorly separated by a gap; however, the vomers still meet at the anterior end. The condition in *Osteolepis* is unknown. In *Youngolepis, Powichthys,* and porolepiforms, the vomers are far apart. In *Eusthenopteron*, the vomers meet at the midline and carry long posterior processes.

20). The vertical tooth-bearing lamina of the vomer is low in *Thursius, Gyroptychius* (Vorobjeva, 1977), *Youngolepis* (Chang, 1982), and porolepiforms (Jarvik, 1972) while it is high in *Eusthenopteron* (Jarvik, 1942).

21). No intervomerine canal can be formed in *Thursius, Youngolepis, Powichthys,* and all porolepiforms because the vomers do not meet at the midline. The intervomerine canal is also absent in *Gyroptychius pauli* (Vorobjeva, 1977: 140). An intervomerine canal is described in *Eusthenopteron* (Jarvik, 1942).

22). In *Thursius estonicus* and *Gyroptychius pauli*, the parasphenoid does not extend forward to the ventral side of the ethmoidal region and it widens posteriorly and partially attaches to the basipterygoid process (Vorobjeva, 1977: 127, 140). Similarly, the parasphenoid does not extend to the ethmoid region in porolepiforms and *Powichthys* while in *Youngolepis*, as in *Eusthenopteron*, the parasphenoid extends to the ethmoid region.

LOWER JAW: 23). The lateral portions of the coronoids are covered with a shagreen of small teeth in Middle Devonian osteolepids (Vorobjeva, 1977: 63) and in *Youngolepis* and *Powichthys* (Jessen, 1980; Chang, 1991a). In *Eusthenopteron*, as well as in porolepiforms, there is only a single row of pointed, small teeth along the lateral margin of the coronoids.

24). In Middle Devonian osteolepids, the adsymphysial plate is covered with a shagreen of small teeth and extends back to adjoin the anterior process of the first coronoid

which is also covered with shagreen (Jessen, 1966: fig. 5B; Vorobjeva, 1977: 130). In *Eusthenopteron,* the adsymphysial plate is small and separated from the first coronoid (Jarvik, 1980: fig. 125B). In *Youngolepis* and *Powichthys,* as in porolepiforms, the most anterior part of the dentary margin lacks teeth. No adsymphysial plate with tooth whorl (which is present in porolepiforms) has been observed in situ in *Youngolepis* and *Powichthys,* although a toothwhorl-like structure has been observed in the primordial canal of a broken lower jaw ramus (IVPP V11277).

25). In early osteolepids, the transverse section of the lower jaw ramus is "horizontally oval or wider than deep" (Vorobjeva, 1977: 123), with the outer surface facing ventrolaterally and the tooth-bearing lingual side facing dorsomedially, just as in the case of porolepiforms (Jarvik, 1972: fig. 16), *Youngolepis,* and *Powichthys.* In *Eusthenopteron,* the transverse section of the lower jaw is deeper than wide (Jarvik, 1980: fig. 84) with the outer surface facing laterally.

26). A broad anterior infradentary flange is present in Middle Devonian osteolepids as well as in *Youngolepis, Powichthys,* and porolepiforms. It is absent in other osteolepiforms according to Vorobjeva (1977). Well-developed infradentary flange was also illustrated by Gross (1941) in *Glyptolepis* and *Holoptychius* but it also exists in *Platycephalichthys* (Vorobjeva, 1962), which is a rhizodontid (sensu Jarvik).

HISTOLOGY: 27). Cosmine is present in Middle Devonian osteolepids, *Youngolepis, Powichthys,* and early porolepiforms but is absent in *Eusthenopteron.* It is also present in some of the later osteolepids such as *Megalichthys* and *Gogonasus* (Jarvik, 1966; Long, 1985b).

28). The scales of Middle Devonian osteolepids are rhombic but cycloid in *Eusthenopteron. Youngolepis, Powichthys,* and early porolepiforms also have rhombic scales.

In these 28 conditions, Middle Devonian osteolepids differ from *Eusthenopteron* while resembling *Youngolepis, Powichthys,* and some porolepiforms in many cases. In contrast to Jarvik's statement that "it is hardly possible to find a single character distinguishing the Osteolepidae from the Rhizo-

dontidae" (Jarvik, 1966: 42), Middle Devonian osteolepids do differ from *Eusthenopteron* (included in Rhizodontidae sensu Jarvik). Even though Jarvik (1980) later recognized some of the differences, they were not properly reflected in the coding of osteolepiform characters in general.

DISCUSSION
PREVIOUS CODING OF OSTEOLEPIFORM CHARACTERS

Ideas on the unity of Osteolepididae and Rhizodontidae may have influenced the process of character coding in previous works. Although many authors were more or less aware of the differences between *Eusthenopteron* and Middle Devonian osteolepids, the significance of such differences tends to be diminished by assuming a transition from primitive conditions in Middle Devonian osteolepids to advanced conditions in *Eusthenopteron.* In addition, because of the different amount of available information, the better known conditions in *Eusthenopteron* are frequently used to represent the condition for Osteolepiformes as a whole. The few examples below may help to illustrate this point.

Although Jarvik (1980) pointed out conspicuous differences between osteolepids and rhizodontids (sensu Jarvik, including *Eusthenopteron*), he cited many characters shared among osteolepiforms that differ in porolepiforms and other fishes. We briefly summarize and comment on some of the characters cited by Jarvik (1980) as common to osteolepids and rhizodontids here:

1). Number and position of dermal bones of skull and shoulder girdle, including the overlapping relationship of dermal bones and the course and position of sensory canals and pit-lines. [Comment: This might include the type X skull table; premaxilla incorporating components of nasal and median rostral (Jarvik, 1948); postorbital junction of supraorbital and infraorbital sensory canals; seven bones in cheek region, etc. Middle Devonian osteolepids also differ markedly from *Eusthenopteron* in many respects, such as presence of numerous posterior postrostrals, presence of extratemporal, absence of postspiracular, and postorbital not reaching spiracular notch in osteolepids. Additionally, it is uncertain

whether the premaxilla incorporates nasal and rostral elements as Jarvik suggested.]

2). Processus dermintermedius provided by lateral rostral and tectal process, indicating subdivision of anterior part of nasal cavity. [Comment: See previous section (condition 9 on p. 6) for distribution of processus dermintermedius and subdivision of nasal cavity.]

3). Anterodorsal medially curved process of maxilla. [Comment: This condition is also present in *Youngolepis*.]

4). Apical fossa in anterior part of palate. [Comment: See previous section (condition 7) for different conditions in early osteolepids.]

5). Intervomerine canal. [Comment: See previous section (condition 19) for different conditions in early osteolepids.]

6). Palatine canal between vomer and lower face of ethmoid region of endocranium, anteriorly dividing into three branches. [Comment: This condition is not seen in *Thursius* and *Gyroptychius*.]

7). Parasphenoid pierced by a single buccohypophysial canal and having a pair of pockets for insertion of subcranial muscle. [Comment: A single buccohypophysial canal is present in most fishes, and the depression for insertion of subcranial muscle on posterior part of parasphenoid is also seen in porolepiforms.]

8). Endocranium. [Comment: See previous section for different conditions in the ethmoidal region, articulation with the palatoquadrate, and position of some openings for nerves and blood vessels.]

9). Palatoquadrate. [Comment: See previous section (condition 18) and more detailed discussion in Vorobjeva, 1977: 48–54).]

10). Hyomandibula. [Comment: In *Thursius estonicus* (Vorobjeva, 1977: 129, fig. 14ˇ , E), the shape of the hyomandibula differs considerably from that of *Eusthenopteron*.]

11). Endoskeleton of pectoral fin. [Comment: The endoskeletal supports of the pectoral fin are unknown in *Osteolepis, Thursius,* and *Gyroptychius* (Andrews and Westoll, 1970b: 410)].

A similar tendency to infer osteolepiform characters from conditions in *Eusthenopteron* is seen in other works. For instance, Ahl-

berg's (1991: table 1) list of characters of Osteolepiformes has been influenced by the *Eusthenopteron* model. Brief comments on a few characters in Ahlberg's list follow.

1.) Ahlberg's characters of paired fins and most characters of median fins (characters 4–13, 16–18) are based on *Eusthenopteron* and partly on the Carboniferous osteolepid *Megalichthys*. There is no information on the paired fins of Middle Devonian osteolepids except for the obtuse outline of the fins that also occurs in Rhizodontiformes (sensu Andrews and Westoll, 1970b, not including *Eusthenopteron*) and Onychodontiformes (sensu Andrews, 1973). Practically the only thing we know about the median fins in Middle Devonian osteolepids is the anal fin support of *Osteolepis* and here the condition is different from that of *Eusthenopteron, Tristichopterus,* and *Rhizodopsis* (Andrews and Westoll, 1970b; fig. 4). As described by Andrews, the anal fin support of *Osteolepis* is a broad plate with no rodlike proximal portion, which articulates with the distal ends of two hemal spines that fit into the stepped proximal margin. Its distal end seems to carry articular facets for four distal radials. Andrews (ibid: fig. 23) actually mentioned the "most embarrassing resemblance" between the anal fin support in *Osteolepis* and that in the porolepiform *Glyptolepis*. However, Ahlberg's characters on median fins (16–18) do not reflect the inconsistency noted above. Instead, Ahlberg's character 17 (related to the anal fin support) is given as "2nd dorsal fin more radials than anal fin" while nothing is known about the second dorsal fin support in early osteolepids. Actually, even the condition of median fin radials in *Megalichthys* is not known.

2). Ahlberg's character 45 (the presence of choana in all osteolepiforms) reflects a reasonable assumption widely accepted by many other authors, but our examination of available information on the related snout structures in Middle Devonian osteolepids calls for caution in this interpretation. In the only specimen of *Osteolepis* with prepared endocranial structures, the ventral surface of the braincase in the nasal region is not preserved (Thomson, 1965). In *Thursius,* although Vorobjeva (1977: fig. 25B) indicated the presence of a choanal notch, the condi-

tion of the anterior part of the palate is very much like that in porolepiforms (Vorobjeva, 1972; Chang, 1991b). In *Gyroptychius pauli,* Vorobjeva's (1977: fig. 29A) reconstruction of the palate looks very similar to that of *Eusthenopteron* (Jarvik, 1972). However, Jarvik's figure of *Gyroptychius milleri* (Jarvik, 1980: fig. 147A, same as fig. 62B in Jarvik, 1942) shows a condition different from that in *Eusthenopteron.* Actually, the bending of the snout, the position of the incurrent nostrils, and the position of the fenestra ventrolateralis (designated by Jarvik as fenestra endochoanalis) make *Gyroptychius milleri* resemble *Youngolepis* in these respects. In *Youngolepis,* there are two external nostrils and no choana (Chang, 1982). Consequently, we believe that there is not enough information to say anything definite about the choanal situation in early osteolepids. Similarly, it is too early to reach the conclusion that early osteolepids have only a single external nostril instead of two (Ahlberg's character 44).

3). Ahlberg's other lower jaw and snout characters similarly neglect variations or exceptions found in early osteolepids. For instance, as noticed in the previous section, marginal tooth pavement on the lingual side of lower jaw (character 35) is present in *Youngolepis, Thursius wudingensis, Kenichthys campbelli* (Chang, 1991a; Fan, 1992; Chang and Zhu, 1993), *Powichthys* (Jessen, 1980), *Thursius,* and *Gyroptychius* (Vorobjeva, 1977). The internasal pits (character 39) are also present in all these forms. Anteriorly divergent vomers (character 40) are seen in *Thursius* (Vorobjeva, 1977). The dermintermedial process is weakly developed and the intermedial process (character 46) is absent in *Thursius* (Vorobjeva, 1977). *Thursius estonicus* (Vorobjeva, 1977) also possesses a large medial profundus canal and a few smaller dorsal and lateral canals for the dorsolateral branches of that nerve in the postnasal wall (character 47). The exit of the profundus nerve from the endocranium is situated in the posterodorsal corner of the lateral wall of the ethmosphenoid (character 54) in *Gyroptychius* (Vorobjeva, 1977).

The above examples illustrate how character interpretation and character coding can be influenced by existing ideas on the phylogeny of the group(s).

PHYLOGENETIC IMPLICATIONS OF DIFFERENCES BETWEEN EARLY OSTEOLEPIDS AND *EUSTHENOPTERON*

Thomson (1964, 1965, 1968) paid considerable attention to the differences between the two subgroups of Osteolepiformes, stating that "the Osteolepididae differ from the Rhizodontidae as greatly as they differ from the Porolepidae and Holoptychidae combined" (1964: 353). According to Thomson, these differences had led Berg (1955) to divide the Rhipidistia into three main groups of equal rank—the Porolepiformes, the Osteolepiformes, and the Rhizodontiformes (sensu Berg, including *Eusthenopteron*) although the interrelationships between the three groups remained unresolved. Vorobjeva (1972, 1977) noticed the similarities between the early osteolepiforms and porolepiforms. Vorobjeva's "early osteolepiforms" referred to Middle Devonian osteolepids, i.e., the osteolepid taxa discussed in the present paper; she did not include Upper Devonian and later osteolepids. Vorobjeva believed that Jarvik (1942, 1972) may have overemphasized the differences between Osteolepiformes and Porolepiformes. These observations by Thomson and Vorobjeva were made at a time when the major attention focused on controversies surrounding the homogeneity of "Rhipidistia" and the monophyletic or diphyletic origin of tetrapods. It is now worthwhile to incorporate their earlier observations into an updated data set for cladistic analysis.

Our survey on Middle Devonian osteolepids generated a data set where the character state differences between Middle Devonian osteolepids and *Eusthenopteron* are coded as objectively as possible. The data set (table 1) incorporates 14 taxa and 90 characters. The 14 taxa include Actinopterygii, Actinistia, Porolepiformes, *Powichthys, Youngolepis, Diabolepis,* Dipnoi, *Osteolepis, Thursius, Gyroptychius, Kenichthys, Eusthenopteron, Panderichthys,* and Tetrapoda. The four Middle Devonian osteolepids (*Osteolepis, Thursius, Gyroptychius,* and *Kenichthys*) are treated as separate OTUs (Operating Taxonomic Units). The Upper Devonian and later osteo-

TABLE 1

Data Matrix

See appendix 1 for character list and coding conventions for different character states (0, 1, 2). "?" represents unknown condition.

TAXA	0000000001111111111222222222233333333333344444444444555555555556666666666677777777777788888888889 1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
ACTINOPTERYGII	00000000001000000000?0000000000010000?0000000000000?0??00000000100000100100000?0000000000?0000
ACTINISTIA	10000010010101001211?000001000000100100000011110?01?0000000010000000020000?00011010107000
POROLEPIFORMES	1000011011011011200010100010100101011011101110200010101101000001010011110011101110011100
POWICHTHYS	0011001100101000?7?01001010101110011010110110?7107?7777?1??10100001?00171?00017777777111010
YOUNGOLEPIS	0011107?01101000?21110010101001100110101110011011111010110000001110010?700171077077111010
DIABOLEPIS	0011011?01101010?7110000110100171017?171117777777777100000010117?017011107101107777777111011
DIPNOI	01??011100101010121000001101001?7777770117701012?07?07000010111177017011107101011000110??1
OSTEOLEPIS	0??71001000010111001001000170?01717?7101?7017101101007?7777?0000007000077701000011101010
THURSIUS	0??71001000010111001001000171701017?101710171011?1001011010000010000?1001101000?1717?1010
GYROPTYCHIUS	0???100100000101110010010001?77000171017701710110007?10000001010000001000?100110100071717?1010
KENICHTHYS	0?11100?0000010177001001000?777777777777777777701111707777777000100000100177707777171771010
EUSTHENOPTERON	0100100000000101110070100001100010010100011101001000110101000000000010000010000110?1010
PANDERICHTHYS	0100100100000011100700000011?777777777?07771770100111011110070000000001001700101077107107 0
TETRAPODA	01001000100000107007000000110077777771007701101001110110010010000000001700017107107101010

lepids (e.g., *Megalichthys, Gogonasus*) are not included because new *Gognasus* material from Australia is still under investigation (Campbell and Long, personal commun.). The study on *Gognasus* and the most recently published works on other Upper Devonian osteolepids from Australia and Kazakhstan (Fox et al., 1995; Lebedev, 1995) will provide valuable information for future study. The Rhizodontiformes (sensu Andrews and Westoll, 1970b, not including *Eusthenopteron*) and Onychodontiformes are not included for lack of detailed information.

Most features in the data set are from the dermal skull and endocranium. A few features from the postcranial skeleton are included if information is available for most taxa. Endoskeletal characters of the fins are excluded because of insufficient information in early osteolepids and many other taxa. The range of selected characters is mainly based on the work of Ahlberg (1991), Forey et al. (1991), Vorobjeva and Schultze (1991), and Schultze (1994), with deletions, modifications, and reinterpretations based on our own observations. The characters of the early osteolepids are mainly from Jarvik (1948), Thomson (1965), Vorobjeva (1977), Fan (1992), and Chang and Zhu (1993).

In coding the character states in our data set, we tended to be conservative in inferring unknown conditions because we wanted to avoid extrapolations based on better known taxa or expected "character correlations."

For instance, the states of the choana (our character 29) and external nostrils (our character 2) in early osteolepids are coded as "?" (unknown) even though most other authors have coded choana as "present" and external nostrils as "one pair". As explained earlier, the ethmoidal region of the cranium has been prepared and thoroughly examined in only a few specimens of early osteolepids and the exact condition of these characters is unknown.

Although cosmine (our character 85) was usually coded as "present" in Osteolepiformes (with assumed later loss in *Eusthenopteron*), we code this character as "absent" in *Eusthenopteron* and "present" in the four early osteolepids. We give a unified "cosmine present" coding for Porolepiformes and Dipnoi even though we are aware that early porolepiforms and dipnoans possess cosmine and later members of these two groups lack it. This is mainly because the focus of our study is on the relationships of Middle Devonian osteolepids and not interrelationships of the various porolepiforms or dipnoans. For Actinistia, we follow Cloutier (1994) and code the character as "cosmine absent", although the presence of cosmine was once suggested for *Miguashaia* by Cloutier in his earlier works (1991a, 1991b).

The data set was analyzed by using Swofford's (1993) Phylogenetic Analysis Using Parsimony (PAUP version 3.1.1) for Macintosh computers (courtesy of Dr. M. McKen-
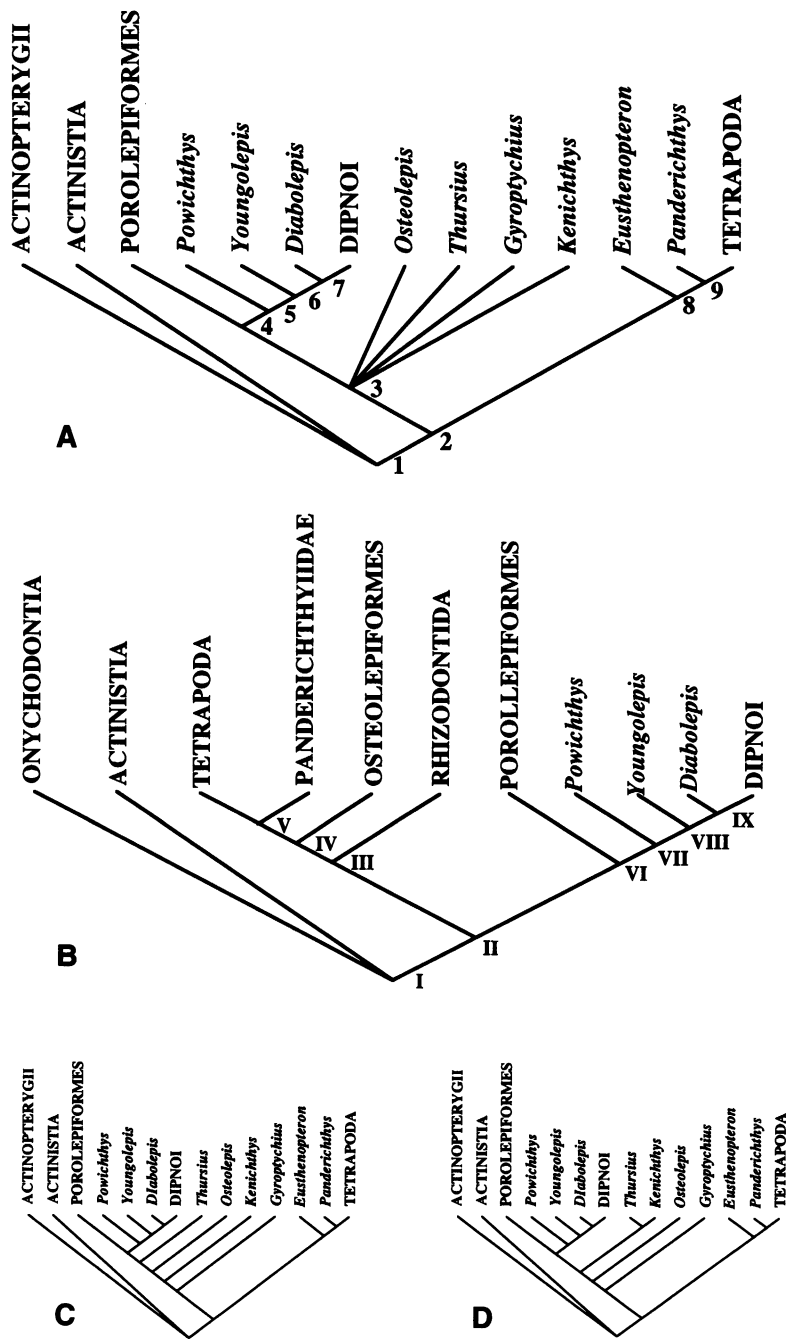
Fig. 4. Comparison of consensus tree (**A**) from current study with (**B**) from Ahlberg, 1991 showing different positions for early osteolepids. **C** and **D** illustrate two of the seven retained trees of the current study. See text for discussion on characters used to support each node. (B redrawn from Ahlberg, 1991).

na). The analysis generated seven shortest trees, each 157 steps in length, with an overall consistency index of 0.592. Figure 4A shows the strict consensus tree and 4C and 4D illustrate two of the seven retained trees. All of the retained trees show two major groupings, with (Tetrapoda + *Panderichthys*) + *Eusthenopteron* on the one hand and {[(Dipnoi + *Diabolepis*) + *Youngolepis*] + *Powichthys*} + Porolepiformes on the other. These two groupings have appeared together in a series of recent works (Maisey, 1986; Janvier, 1986; Ahlberg, 1989, 1991; Yu, 1990; Cloutier, 1991a, 1991b). The first grouping appeared alone in Schultze (1987), Panchen and Smithson (1987) and Young et al. (1992), while the second appeared alone in Chang (1991a, 1991b).

The main difference between our trees and the results of previous workers is in the position of the four osteolepid genera: they all shifted from the Osteolepiformes-Tetrapoda branch to the Porolepiformes-Dipnoi branch (see node 3, fig. 4A). The difference is partly the result of our revised character codings for these four genera (as explained above) and partly because these four genera are treated as four separate OTUs rather than being lumped together as members of Osteolepiformes. The differences between our seven shortest trees mainly involve the exact positions of the four early osteolepids relative to each other on the Porolepiformes-Dipnoi branch. This is understandable partly because the four Middle Devonian osteolepids are not equally informative for all characters and partly because some characters present a mosaic pattern of distribution among these four osteolepids. Actinopterygii, Actinistia, and other sarcopterygian groups appear as an unresolved trichotomy on all seven trees.

Among the recently published phylogenetic schemes, we chose Ahlberg (1991; see fig. 4B of this paper) for a detailed comparison with our strict consensus tree (fig. 4A). Many of the characters (with the exception of characters related to fin structures excluded from our data set) supporting his node VI (Porolepiformes-Dipnoi) also support the node denoting the same grouping in our cladogram (node 18), while the rest of Ahlberg's characters at node VI move down to node 19 (grouping of [Porolepiformes-Dip-

noi] + early osteolepids) in our consensus tree. The shift of these characters is caused by their presence in some of the early osteolepids. For instance, the anterior part of the infraorbital sensory canal and the ethmoidal commissure also follow the premaxillary suture (Ahlberg's character 31; our character 4) in *Kenichthys* and *Thursius wudingensis*, although this condition is coded as "?" (unknown) for *Thursius* in our data set. The presence of the internasal pits (our character 57, same below), the anteriorly divergent vomers (54), and the large medial profundus canal in the postnasal wall (30) are also true for *Thursius* and the presence of the internasal pits (57) is true for *Gyroptychius*.

Other significant characters supporting node 19 (grouping of [Porolepiformes-Dipnoi] + early osteolepids) are: postrostral mosaic (8; the distribution of this character depends on its exact definition, cf. Ahlberg, 1991), fossa autopalatina (35), laterally expanded basipterygoid process (38), broad internasal septum (40), exit of pituitary vein above dorsal, vertical portion of basipterygoid process (42), broad anterior infradentary flange (72; this character may have broader distribution because it is also present in *Platycephalichthys*, a genus not included in the present analysis), transverse section of lower jaw wider than deep (76), and cosmine (85; see above for explanation).

Characters supporting Ahlberg's node III (Rhizodontiformes-Tetrapoda) are all related to the structures of paired fins, which are not included in the present analysis. However, among the characters supporting his node IV (Osteolepiformes-Tetrapoda), only one (single external nostril) is left in our cladogram to support the same grouping (node 8). Of the other two characters at Ahlberg's node IV, one (biserial pectoral fin) is not included in our analysis and the other (dermintermedial and tectal processes) has a wider distribution than the groups at Ahlberg's node IV. Our node 8 is supported by a few other characters: choana (29 from our character list, same below—the choana is coded as present in Porolepiformes in Ahlberg's data set but we believe that Porolepiformes does not have the choana); lateral ethmoidal articulation for palatoquadrate (34); subdivision of nasal cavity (39); and high vertical tooth-bearing

lamina of vomer (55). In Ahlberg's clado-gram there are two characters (Ahlberg's characters 21, 34) supporting the close rela-tionship between Dipnoi and *Diabolepis,* i.e., "B"-bone and tooth plate. In our trees, this grouping (node 7) is supported by a few more characters: lower border of anterior ex-ternal nostril not formed by lateral rostral (6, our character list, same below; it is formed by premaxilla in *Diabolepis* while no lower dermal bone border is found in Dipnoi); Westoll-lines (25); dorsal palatal process of palatoquadrate (61); marginal teeth reduced (64); labial pit (68, defined as pit on antero-lateral side of lower jaw surrounded by den-tary and anterior infradentaries, bottom lined by Meckelian bone—Chang, 1995; Forey et al. [1991] and Schultze [1994] coded this condition as present also in the Actinistia, but it does not seem to be surrounded and lined by the same structures—and syndentine (90, Smith and Chang, 1990).

ALTERNATIVE INTERPRETATIONS AND
CONCLUSION

Our study demonstrates the need for ad-ditional examination of the phylogenetic im-plications of the character differences in ear-ly osteolepids and *Eusthenopteron.* Even though our cladistic analysis suggests a close relationship between early osteolepids and Porolepiforms plus Dipnoi, other interpreta-tions are possible.

1. Most of the differences between early osteolepids and *Eusthenopteron* may be functionally related to the position of the pal-atoquadrate, its mode of articulation to the endocranium, and the platybasic or tropibasic type braincase. Characters related to palato-quadrate include: absence of lateral ethmoid-al articulation of palatoquadrate, presence of fossa autopalatina, laterally expanded basip-terygoid process, absent or weakly devel-oped suprapterygoid process, and horizontal position of anterior portion of palatoquad-rate. Other characters in early osteolepids re-lated to the comparatively flat platybasic skull type include: broad internasal septum and presence of paired internasal pit, anteri-orly divergent vomers and low vertical tooth-bearing lamina, broad anterior infradentary flange and wider than deep transverse section

of lower jaw ramus, and postrostral mosaic in anterior part of skull roof. Thus, the phy-logenetic significance of these differences may (or may not) be compromised by such functional correlations. How to treat func-tionally related characters presents a hard choice for systematists who still believe in organisms as functionally integrated entities rather than as random collections of numer-ically coded character states.

2. While early osteolepids differ from *Eusthenopteron* in many characters, some of these character states are also shared between early osteolepids on the one hand and Upper Devonian and later osteolepids (such as *Lat-vius, Glyptopomus, Gogonasus, Megalich-thys, Ectosteorhachis,* and a few new forms under study) on the other hand. Here we will briefly point out a few characters showing such "mosaic" distribution. The extratem-poral is present in the forms mentioned above. Cosmine is present in all forms except for *Glyptopomus* and the lateral pavement of lower jaw is shown in *Gogonasus* from the Upper Devonian of Australia (Long, 1988: fig. 10) and a new osteolepid from Kazakh-stan (Ahlberg et al., 1993, fig. 16). On the other hand, some character states coded as present in *Eusthenopteron* but not in early osteolepids do exist in some Upper Devonian and later osteolepids in which the endocra-nium is well known [e.g., in *Ectosteorhachis* (Romer, 1937), *Megalichthys* (Jarvik, 1966; Fox et al., 1995), *Gogonasus* (Long, 1988), and *Medoevia* (Lebedev, 1995)]. All these forms probably possess a single pair of ex-ternal nostrils and possibly a choana, and the vomers meet at the midline.

We realize that the distribution of some of the characters in our data set may change when existing and forthcoming information on later osteolepids is incorporated into the analysis. Over the past several decades, opin-ions on sarcopterygian phylogeny have been changing rapidly. Traditionally, the Sarcop-terygii incorporates Crossopterygii and Dip-noi. Crossopterygii includes Actinistia and Rhipidistia which, in turn, consists of Osteo-lepiformes and Porolepiformes. Following the discovery of *Powichthys* from the Ca-nadian Arctic and *Youngolepis* and *Diabo-lepis* from southwestern China, an alternative scheme showing a close relationship between

Porolepiformes and Dipnoi was suggested by Maisey (1986) and others. The new character combinations found in *Powichthys, Youngolepis,* and *Diabolepis* provided essential information which helps to change the existing hypothesis of sarcopterygian phylogeny (Donoghue et al., 1989), i.e., linking Porolepiformes with Dipnoi rather than with Osteolepiformes. A recent case provides an interesting example of how exclusion or inclusion of certain taxa can influence the resulting trees. Schultze (1994) and Cloutier (in press) used the same sets of characters for cladistic analysis of sarcopterygian fishes. Cloutier included the taxa *Powichthys* and *Youngolepis* and produced a cladogram with the Porolepiformes-Dipnoi grouping. Schultze (1994) did not include *Powichthys* and *Youngolepis* and produced a cladogram without the Porolepiformes-Dipnoi grouping, much like the earlier cladogram in Schultze, 1987 (fig. 12).

The fact that early osteolepids switch back and forth between the traditional Osteolepiformes-Tetrapoda branch and the Porolepiformes-Dipnoi branch may relate to the lack of sufficient characters or to differences in interpreting and coding observed characters. In our opinion, this may also relate to the possibility that osteolepids represent stem groups—i.e., osteolepids may turn out to be stem-group rhipidistians. Janvier (personal commun.) also alluded to this possibility and we hope that this paper will generate new discussions on the assumed monophyly of osteolepiforms. We are anxiously waiting to see how future work will change our views on the phylogenetic position of early osteolepids.

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APPENDIX 1
CHARACTER LIST

Skull roof

1. skull table: (0) type X, (1) type Y
2. external nostrils: (0) two pairs, (1) one pair
3. premaxilla canal-bearing: (0) yes, (1) no
4. infraorbital sensory canal following premaxillary suture: (0) no, (1) yes
5. processus dermintermedius + tectal process: (0) absent, (1) present
6. lower border of anterior external nostril: (0) formed by lateral rostral, (1) not formed by premaxilla or no dermal lower border
7. bones carrying supraorbital sensory canal: (0) few, (1) many
8. postrostral mosaic: (0) absent, (1) present
9. frontals: (0) absent, (1) present
10. pineal opening: (0) present, (1) closed
11. pineal organ: (0) surrounded by parietals, (1) not surrounded by parietals
12. position of anterior pit-line: (0) on parietal, (1) on postparietal
13. parietal-supraorbital contact: (0) present, (1) absent
14. dermal portion of intracranial joint: (0) absent, (1) present
15. "B"-bone: (0) absent, (1) present
16. postorbital junction between supraorbital and infraorbital sensory canals: (0) absent, (1) present
17. median extrascapular: (0) absent, (1) present
18. extrascapular overlap: (0) no, (1) medial, (2) lateral
19. interruption of infraorbital sensory canal at anterior nasal opening: (0) no, (1) yes
20. postotic sensory canal: (0) enclosed in bone, (1) along roof margin
21. groups of small pores: (0) absent or extremely rare, (1) numerous
22. prespiracular: (0) absent, (1) present
23. postspiracular: (0) absent, (1) present
24. extratemporal: (0) absent, (1) present
25. Westoll-lines: (0) absent, (1) present
26. posterior elements of nasal series and anterior elements of supratemporal series: (0) do not lie side by side, (1) lie side by side

Neurocranium

27. rostral organ: (0) absent, (1) present
28. fenestra ventrolateralis: (0) absent, (1) present

29. choana: (0) absent, (1) present
30. large medial opening and several small dorsolateral openings for profundus nerve and its branches in postnasal wall: (0) no, (1) yes
31. rostral tubuli: (0) absent, (1) present
32. processus descendens: (0) absent, (1) present
33. well-defined articular area for apical process of palatoquadrate: (0) absent, (1) present
34. lateral ethmoidal articulation of palatoquadrate: (0) absent, (1) present
35. fossa autopalatina: (0) absent, (1) present
36. exit for N. profundus: (0) within gap, (1) within ethmosphenoid
37. position of $V_{2,3}$ (0) within joint, (1) within otoccipital
38. basipterygoid process: (0) narrow or small, (1) laterally expanded
39. subdivision of nasal cavity: (0) no prominent subdivision, (1) subdivided into superior, inferior, and median recesses
40. internasal septum: (0) broad, (1) narrow
41. tectum orbitalis: (0) narrow, (1) extensive
42. position of exit of pituitary vein: (0) in front of basipterygoid process, (1) dorsal to vertical portion of basipterygoid process
43. suprapterygoid process: (0) absent or weakly developed, (1) present
44. endocranial portion of intracranial joint: (0) absent, (1) present
45. supraotic cavity: (0) absent, (1) present
46. hyomandibular: (0) with one proximal articular head, (1) with two heads

Cheek

47. maxilla: (0) absent, (1) present
48. cheek bones: (0) less than seven, (1) seven, (2) more than seven
49. squamosal, quadratojugal, and preopercular: (0) not fused, (1) fused or sutures sometimes covered by cosmine
50. pits on cheek bones: (0) absent, (1) present
51. postorbital: (0) restricted to anterior cranial division, (1) spanning anterior and posterior cranial divisions
52. jugal: (0) equal in size to lachrymal, (1) larger than lachrymal
53. preopercular canal: (0) complete, (1) reduced to horizontal pit-line

Palate

54. vomers: (0) meeting at midline, (1) divergent anteriorly
55. vertical tooth-bearing lamina of vomer: (0) low, (1) high
56. vomerine tusks: (0) absent, (1) present
57. internasal pit: (0) single, (1) paired

58. intervomerine canal: (0) absent, (1) present
59. anterior extension of parasphenoid: (0) reaches ethmoidal region, (1) does not reach ethmoid region
60. position of anterior portion of palatoquadrate: (0) horizontal, (1) vertical
61. dorsal palatal process of palatoquadrate: (0) absent, (1) present
62. pterygoids: (0) not meeting at midline, (1) meeting at midline
63. tooth plate: (0) absent, (1) present
64. marginal teeth: (0) not reduced, (1) reduced

Lower jaw

65. teeth of dentary: (0) reaching symphysis, (1) not reaching symphysis
66. lateral tooth pavement: (0) absent, (1) present
67. parasymphysial tooth whirl: (0) absent, (1) present
68. labial pit: (0) absent, (1) present
69. number of coronoids: (0) 3, (1) 4, (2) 5
70. infradentary foramina: (0) absent, (1) present
71. Meckelian bone: (0) not exposed in front of coronoids, (1) exposed
72. anterior infradentary flange: (0) narrow or absent, (1) broad
73. prolingual field covered with denticles: (0) no, (1) yes
74. enlarged tusks in anterior expanded lamina of dentary: (0) absent, (1) present
75. adsymphysial plate: (0) separated from coronoid 1, (1) continuous with anterior branch of coronoid 1
76. transverse section of lower jaw ramus: (0) deeper than wide, 1) wider than deep

Operculogular series

77. preoperculosubmandibular: (0) absent, (1) present
78. submandibulars: (0) absent, (1) present
79. median gular: (0) present, (1) absent

Postcranial skeleton

80. anocleithrum: (0) exposed, (1) subdermal
81. shape of pectoral fin: (0) not elongated, (1) elongated
82. scapulocoracoid: (0) perforate (tripartite), (1) imperforate
83. basal scutes: (0) absent, (1) present
84. supraneural spines: (0) present, (1) absent

Histology

85. cosmine: (0) absent, (1) present
86. mesh canals: (0) with horizontal partition, (1) without horizontal partition
87. plicidentine: (0) absent, (1) present
88. dendrodont plicidentine: (0) absent, (1) present
89. polyplocodont plicidentine: (0) absent, (1) present
90. syndentine: (0) absent, (1) present