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3 Description and Systematics of Panderichthyid Fishes with Comments on Their Relationship to Tetrapods

Emilia Vorobyeva and Hans-Peter Schultze

The origin of tetrapods has been debated vigorously in phylogenetic discussions. Part of the disagreement stems from the nature of the material that different authors have examined and analyzed. The conclusions of some were derived primarily from analyses of Recent forms (e.g., Szarski, 1962; Parsons and Williams, 1963; Løvtrup, 1977; Medvedeva, 1975; Lebedkina, 1979). Other authors emphasized fossil forms (e.g., Westoll, 1938, 1943; Romer, 1956; Worobjewa, 1975b; Shishkin, 1975; Tatarinov, 1976; Vorobyeva, 1977a), and some, both fossil and Recent forms (e.g., Jarvik, 1942, 1972, 1975; Schmalhausen, 1968; Lombard and Bolt, 1979; Rosen et al., 1981; Bolt and Lombard, 1985; Vorobyeva, 1985; Smirnov and Vorobyeva, 1986). However, the kind of material analyzed is less critical than the phylogenetic approach adopted. Jarvik (1960, 1964), using a "static ancestor-descendent" approach, related tetrapods to rhipidistian crossopterygians (osteolepiforms and porolepiforms, respectively). In contrast, Rosen et al. (1981) based their conclusion that dipnoans are the closest relatives of living tetrapods on a cladistic analysis. These authors maintained (contra Westoll 1938, 1943; Romer, 1956) that one cannot seek the ancestor of tetrapods in a specific osteolepiform rhipidistian. Subsequent studies have demonstrated that cladistic analyses intended to solve the same problem can produce quite different results (cf. Schultze, 1981, 1987; Maisey, 1986; Panchen and Smithson, 1987; Chang, this volume; Schultze, this volume). This variation suggests that the choice of taxa analyzed and the selection and interpretation of

characters are more critical than the phylogenetic philosophy to the analytical results. Nonetheless, there exist various schools of phylogenetic interpretation (Rage and Janvier, 1982; Vorobyeva, 1986) that have had substantial influence on the development of hypotheses explaining the origin of tetrapods.

The Stockholm School (Vorobyeva, 1986) postulated a polyphyletic origin of tetrapods (Jarvik, 1942, 1960, 1964, 1972, 1980, 1986) in which urodeles were derived from porolepiforms ([Urodela + Porolepiformes] = Urodelomorpha of Jarvik), and anurans and all other tetrapods (Eutetrapoda) from the osteolepiforms. The fundamental assumption of this hypothesis is that structural types have remained stable (i.e., not evolved) since the Devonian. Thus, all basic vertebrate morphotypes would have originated more than 400 million years ago in a pre-Devonian adaptive radiation of organisms (Jarvik, 1960, 1964). Particular morphological features of urodeles are attributed to porolepiforms, and those of anurans to osteolepiforms. This line of reasoning involves a retrospective transposition of features of Recent forms into fishes that lived more than 400 million years ago and requires loose interpretations of homology (Rage and Janvier, 1982).

The Stockholm School opposes the monophyletic origin of tetrapods from osteolepiforms as proposed by the Anglo-American School of Westoll and Romer. The monophyletic origin of tetrapods and dipnoans from a common ancestor was proposed by the Transformed Cladist School (Rosen et al., 1981). Transformed cladists base their opposition to the Stockholm and Anglo-American schools of phylogenetic interpretation on Hennig's (1950, 1966) phylogenetic systematics. Nonetheless, transformed cladists, like disciples of the Stockholm School, employ a retrospective approach, because they base their phylogenetic evaluations largely on analysis of features of Recent taxa, but the key taxon in their postulated relationship of dipnoans and tetrapods is a Devonian dipnoan. If the sister-group of Recent tetrapods is the Dipnoi, then the same also must be true of fossil tetrapods. The analysis of Rosen et al. (1981) is restricted to the distribution of patterns without consideration of evolutionary processes; thus, convergences, for example, are ignored (Forey, 1987).

The Soviet School (Vorobyeva, 1986) reinstated use of the triple approach of Haeckel, in which data from comparative anatomy and embryology are combined with paleontology. This method emphasizes careful interpretation of anatomical features and their ontogenetic origin, as well as their occurrence and distribution in the fossil record (Schmalhausen, 1968). Functional, ecological, and physiological attributes are included in the evaluation of characters.

In this chapter, we accept Schmalhausen's (1968) conclusions regard-

ing the origin of tetrapods (cf. Schultze, this volume) as follows. (1) The Tetrapoda is monophyletic (Gaffney, 1979). (2) The Tetrapoda is related closely to osteolepiform rhipidistians and specifically to panderichthyids (Vorobyeva, 1962; Schultze, 1969, 1970; Worobjewa, 1973; Schultze and Arsenault, 1985). Further, we accept Schultze's (1987) classification of osteichthyans. We deal with a restricted number of Rhipidistia, to the exclusion of the Onychodontiformes; thus, the Rhipidistia includes Porolepiformes and Choanata, and the Choanata is composed of Osteolepiformes, Panderichthyida, and Tetrapoda. Within tetrapods, we treat two groups—the Ichthyostegalia and all other tetrapods, the Neotetrapoda (Gaffney, 1979). The position of the Rhizodontida is unresolved within the rhipidistians.

The family Panderichthyidae (Vorobyeva and Lyarskaya, 1968) is composed of two genera, *Panderichthys* Gross 1941 and *Elpistostege* Westoll 1938; a third genus, *Obruchevichthys*, was included provisionally by Vorobyeva (1977a). Because the latter is represented only by fragments of the lower jaw, *Obruchevichthys* is not considered here. Complete skeletons of *Panderichthys* are known (Vorobyeva, 1980); in addition, there are two partial skulls and one postcranial specimen questionably assigned to *Elpistostege* (Schultze and Arsenault, 1985). The first known skull of *Elpistostege* was thought to be that of an amphibian (Westoll, 1938); however, examination of additional specimens revealed it to be a panderichthyid fish (Worobjewa, 1973; Schultze and Arsenault, 1985). Examination of the snout of *Elpistostege* reveals that the skulls of *Elpistostege* and *Panderichthys* are nearly identical (Figs. 1–2).

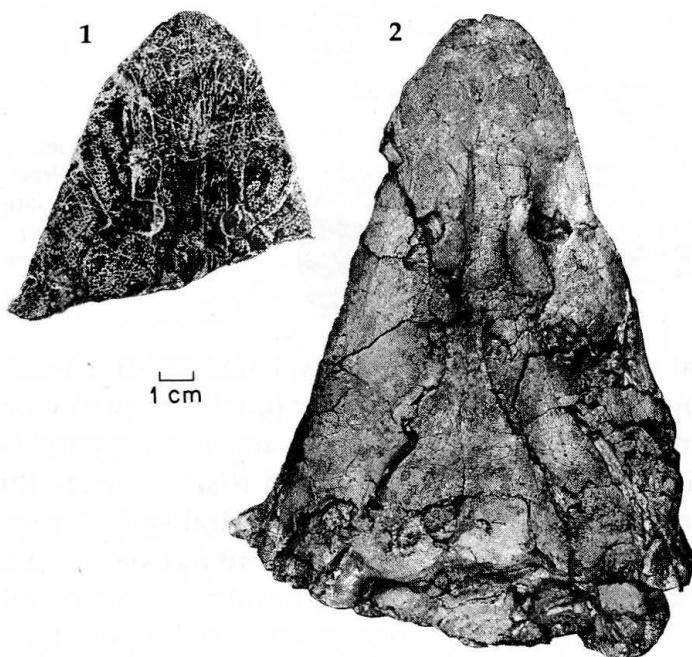
Herein we redescribe *Panderichthys* and compare it with *Elpistostege*. A new order, Panderichthyida, is erected and described. We demonstrate that many features support a sister-group relationship between the Panderichthyida and the Tetrapoda. Further, we suggest that the panderichthyids are related to osteolepiforms and that tetrapod features evolved independently and in parallel within the osteolepiform ancestor of tetrapods as well as in other osteolepiforms.

MATERIALS AND METHODS

The following description of *Panderichthys* is based on three specimens we examined in 1986. Museum acronyms are as follows: MHNM = Musée d'Histoire naturelle de Miguasha, Quebec, Canada; PIN = Paleontological Museum, Academy of Sciences, Moscow, USSR.

P. rhombolepis. PIN 3547/26: head of specimen (Figs. 2, 5, 9, 10, 12, 14–15); PIN 3549/19: shoulder girdle (Figs. 16–17).

P. stolbovi. PIN 54/169: partial snout (Figs. 6–8), previously published



Figs. 1–2. Skull roofs of panderichthyids. (1) *Elpistostege watsoni* Westoll, 1938 (MHNM 538)—Escuminac Formation, Frasnian, Late Devonian, shore of river Ristigouche at Mi-guasha, Province of Quebec, Canada. (2) *Panderichthys rhombolepis* (Gross, 1930) (PIN 3547/26)—Gauja-beds, Frasnian, Late Devonian; Lode, Latvia, USSR.

and figured by Vorobyeva (1960:Figs. 1–3; 1962:Fig. 31A, B, Pl. 19:Figs. 1a–d; 1971:Figs. 1, 2, 6, 8, Pl. 8:Figs. 2a–e; 1977a:Figs. 7B, 8F) and by Vorobyeva and Obruchev (1964:Fig. 32, Pl. 3:Fig. 9).

The snout of *P. stolbovi* had previously been prepared and cut obliquely to the midline. Clay was removed from specimens of *P. rhombolepis* in 1986 in order to reveal the supracoracoid foramen and the glenoid canal in the shoulder girdle and the right jaw articulation, palate, and left nasal capsule.

Photographs were taken with a Nikkormat camera. Enlarged prints served as the basis for the illustrations, although in the course of preparation, each drawing was compared closely with the actual specimen.

SYSTEMATICS OF PANDERICHTHYID FISHES

Redescription of *Panderichthys* Gross 1941

Skull

Snout and skull table. The snout is curved ventrally such that it forms a rostrum with the mouth subterminal. The position of the single pair of external nostrils (Fig. 3) is marginal. Each nostril is surrounded by the

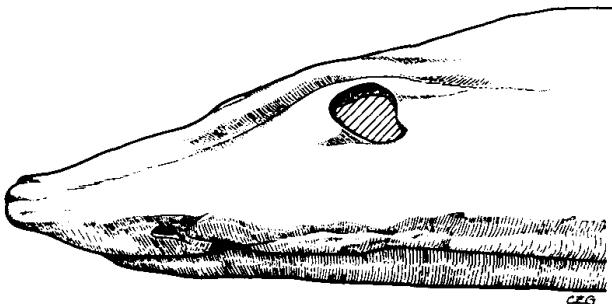


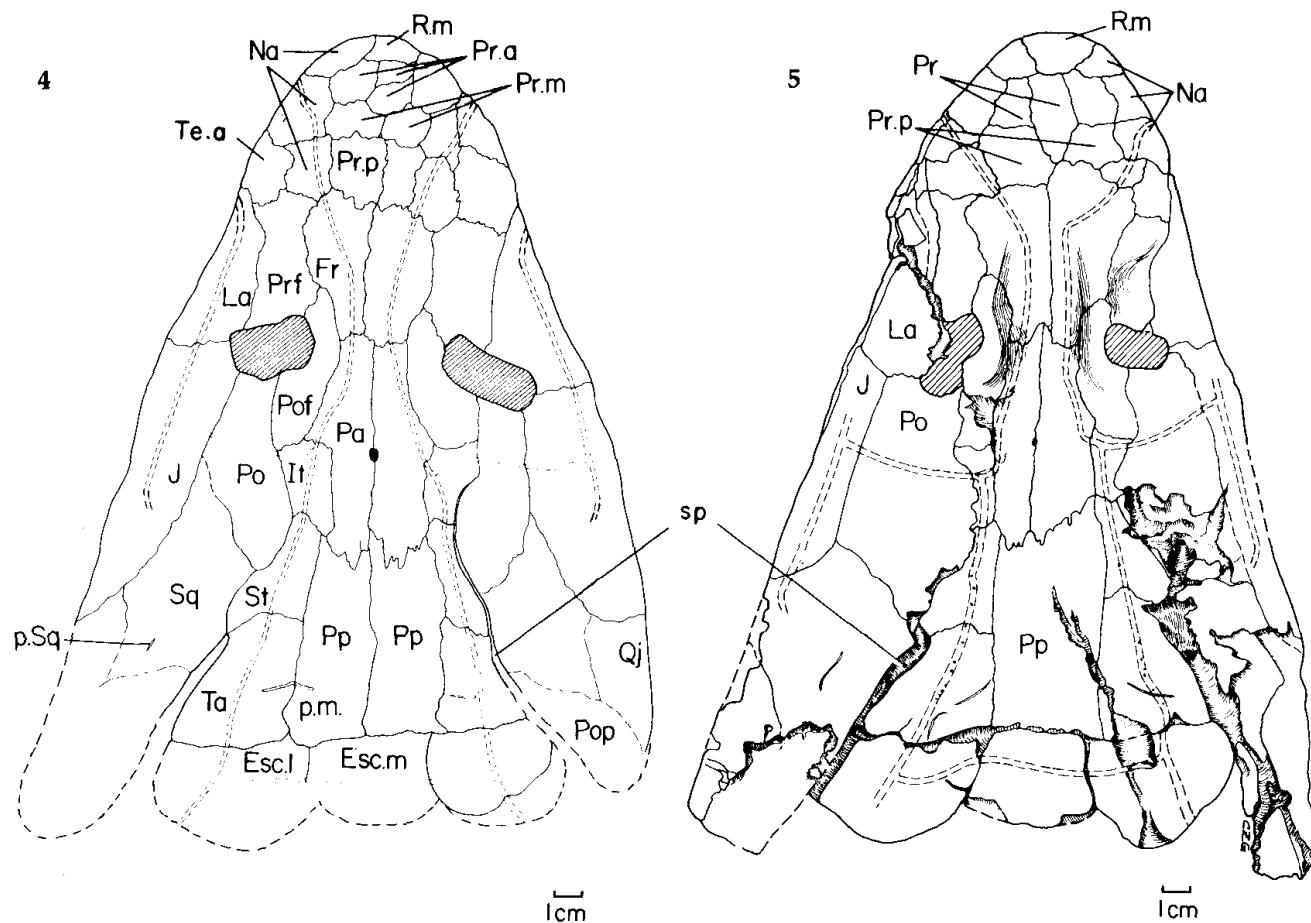
Fig. 3. Lateral view of skull of *Panderichthys rhombolepis* (Gross, 1930) (PIN 3547/18)—Gauja-beds, Frasnian, Late Devonian; Lode, Latvia, USSR. (After Vorobyeva, 1986:Fig. 1.)

anterior tectal dorsally and the narrow lateral rostral ventrally, and is separated from the margin of the upper jaw by a narrow posterior process of the premaxilla (Figs. 6, 12–14). A mosaic of rostral bones covers the snout (Figs. 4–5). A separate median rostral carries the ethmoidal sensory commissure. The nasal and postrostral series are short and do not reach the level of the orbits. A pair of frontals extends anteriorly from the level of the orbits and separates the nasal and postrostral series from the parietals. The narrow anterior portions of the parietals lie between the orbits. The paired postparietals are fused to an unpaired median bone (Fig. 5) or not (Fig. 4).

The orbits are located high on the flat skull roof (Figs. 4–5). The prefrontal (homologous to the posterior tectal of osteolepiforms) and postfrontal (homologous to supraorbital of osteolepiforms) border the orbit anteriorly and dorsally, respectively. The postfrontal forms a ridge medial to the orbit, the “eyebrow” of Schultze and Arsenault (1985). The bone articulates with the intertemporal posteriorly in *Panderichthys* (Worobjewa, 1973:Fig. 1A), whereas the intertemporal is fused with the postorbital in *Elpistostege*. A small parietal foramen is located posterior to the orbits.

There is no indication of an external intracranial joint between anterior and posterior dermal shields. The supratemporal and tabular lie lateral to the postparietals. The tabular is separated from the cheek region by the long spiracular slit, which extends forward toward the posterolateral corner of the supratemporal. The supratemporal and intertemporal articulate with the postorbital of the cheek region. There is no lateral kinesis between skull roof and cheek region as in osteolepiforms. The extrascapulars are small relative to the length and large size of the skull roof; the lateral extrascapulars overlap the median extrascapular.

A large lacrimal lies between the orbit and the anterior tectal, and it separates the prefrontal (i.e., posterior tectal) from the jugal. The cheek region is composed of a long jugal, a long postorbital that extends to the spiracular slit, a large squamosal, a quadratojugal, and a preopercular. According to Vorobyeva (1969), the squamosal articulates with the maxilla, thereby separating the jugal from the quadratojugal. Although this



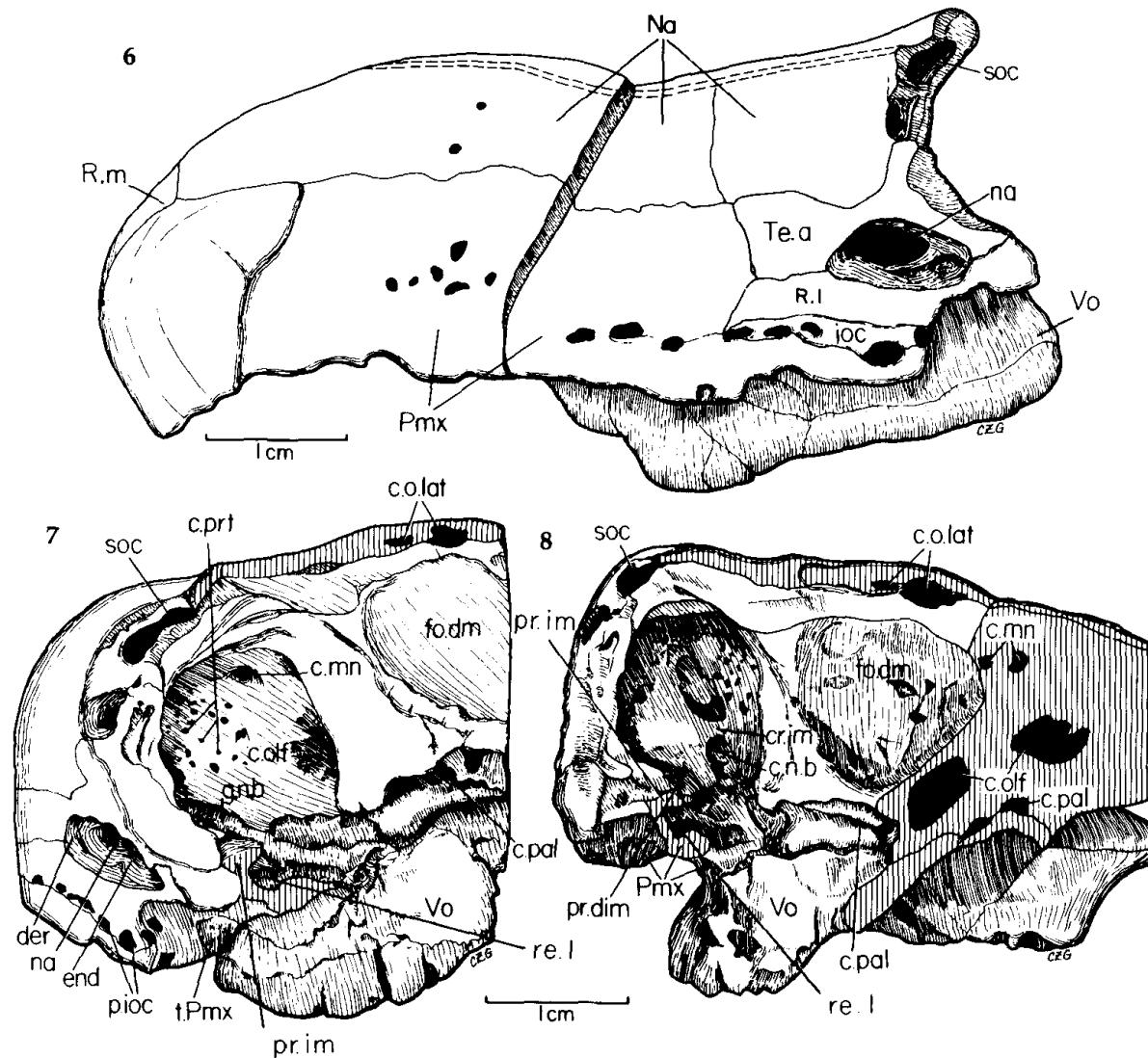
Figs. 4–5. Skull roofs of two specimens of *Panderichthys rhombolepis* (Gross, 1930). (4) PIN 3547/18 with paired postparietals. (5) PIN 3547/26 with unpaired postparietal. Both specimens from Gauja-beds, Frasnian, Late Devonian; Lode, Latvia, USSR. See Appendix I for key to abbreviations.

seems to be true of the left side of specimen PIN 3547/26 (Fig. 5), in some other specimens (e.g., PIN 3547/18; Figs. 4, 37), the jugal articulates with the quadratojugal, thereby separating the squamosal from the maxilla (as in tetrapods). The maxilla is narrow and does not extend as far posteriorly as does the jugal. The quadratojugal is the posterior component of the upper jaw.

Nasal capsule. The elongate, narrow nasal capsule lies adjacent to the lateral ethmoidal wall (Fig. 8). Because the capsule is only one-quarter of the width of the ethmoid, the paired capsules are separated widely (Figs. 7–8). The posterior wall of the nasal capsule is unossified; thus, there is a large ventrolateral opening, and a fenestra endochoanalis cannot be identified. There is only one external narial opening (Vorobyeva, 1986; contra Vorobyeva, 1962 and Worobjewa, 1973); the “posterior external nasal opening” of Worobjewa (1973:Fig. 2A) is a pore of the infraorbital canal. The external nasal opening enters the lower half of the nasal capsule. The internal nasal opening (i.e., choana) extends from the level of the posterior margin of the external nasal opening posteriorly to the level of the dermopalatine fangs (Figs. 9, 14). The length and posterior extent of the exochoanal opening in *P. rhombolepis* (Figs. 13–14) suggest that the nasal capsule extended posteriorly beyond the ethmoid. However, its proximity to the orbit cannot be estimated because the posterior wall of the nasal capsule is not ossified.

The dermintermedial process of the lateral rostral, the anterior tectal process, and the crista intermedia are present in the nasal capsule (Figs. 13–14); a medial recess is absent (Worobjewa, 1973:Fig. 3). The dermintermedial process extends rostrocaudally along the lateral wall of the nasal capsule; together with the anterior tectal process, it divides the lateral nasal capsule into dorsal and ventral chambers. The crista intermedia extends horizontally to unite with the medial wall of the nasal capsule and form a bridge over the nasobasal canal; the lamina inferior cannot be distinguished from the lamina superior. The nasobasal canal and inferior recess are present in the floor of the nasal capsule. The profundus nerve exits the thick medial ethmoidal wall via a single foramen and divides into many small branches within each nasal capsule. The rami exit each nasal capsule through openings in the anteromedial wall. The opening of the olfactory canal lies ventral to the ethmoidal foramen for the profundus nerve.

Palate. The palatal region of the snout has a large anterior palatal pit that accommodates the anterior fangs of the dentary (Figs. 10, 12–13). A premaxillary palatal plate is absent. The vertical tooth-bearing ridge of each vomer articulates with its counterpart medially. An intervomerine



Figs. 6–8. *Panderichthys stolbovi* Vorobyeva, 1960 (PIN 54/169)—Il'menian beds, Frasnian, Late Devonian; Syas River, Stolbov, Leningrad district, USSR. (6) Snout in lateral view. (7–8) Posterior and posteromedial views of nasal capsule. See Appendix I for key to abbreviations.

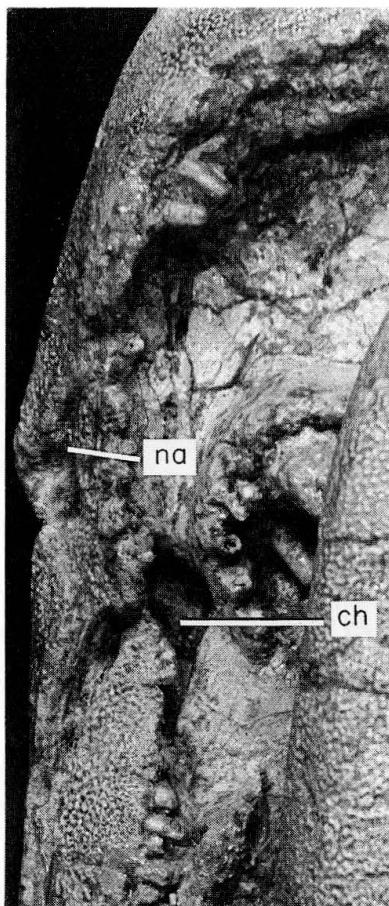
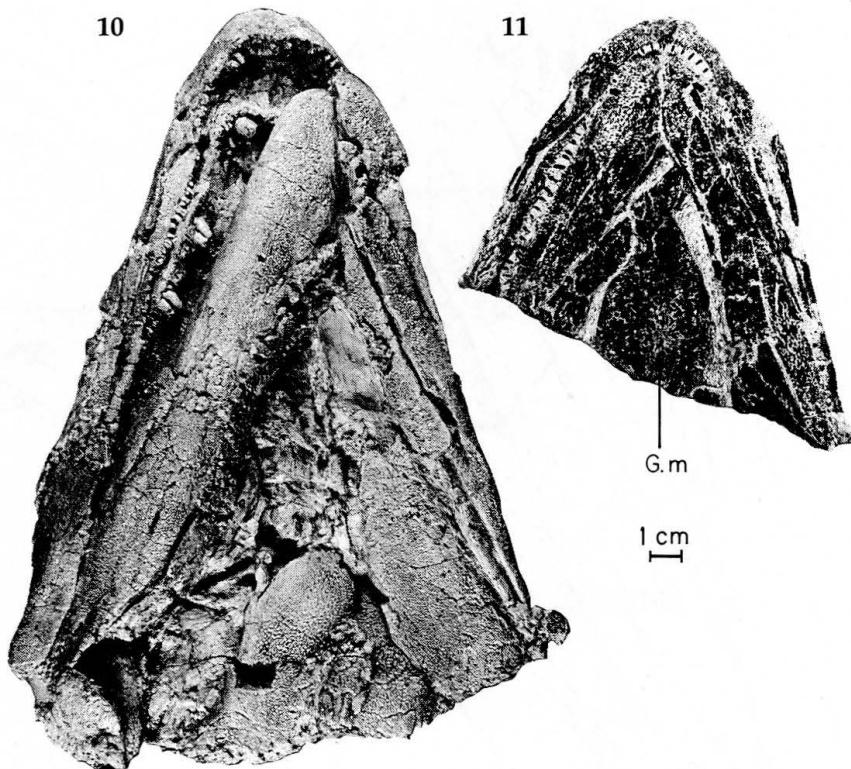


Fig. 9. Choana and external nasal opening in *Panderichthys rhombolepis* (Gross, 1930) (PIN 3547/26)—Gauja-beds, Frasnian, Late Devonian; Lode, Latvia, USSR. Cf. Figure 14. See Appendix I for key to abbreviations.

canal (Worobjewa, 1973:225), which occasionally is paired, traverses the vomerine ridge. A long keyhole-shaped choana is present in the buccal region of the palate; it is bordered by the premaxilla, maxilla, vomer, and dermopalatine (Figs. 9, 14). The wide anterior part of the choana lies between the vomer and premaxilla, whereas the elongate posterior portion lies between the dermopalatine and maxilla. The narrow parasphenoid terminates anteriorly at the level of the dentigerous ridges of the vomers; its anterior portion is flanked by the posterior vomerine processes. The parasphenoid is divided into an expanded dorsal portion and a tooth-bearing plate, which are connected by a narrow septum. The dermopalatines are posterolateral to the vomers, but the marginal tooth row of the dermopalatine is separated from the tooth-bearing ridge of the vomer by a smooth pitlike area (Worobjewa, 1973:227, Pl. 36:Fig. 4; Worobjewa, 1975a:Fig. 2; Rosen et al., 1981:Fig. 16B). The pit lies above the fang borne on the first coronoid of the lower jaw; thus, the fang does not fit into the choana as postulated by Rosen et al. (1981). The dermopalatine fang, in turn, fits into a pit between first and second coronoid of the mandible; thus, when the jaws are occluded, the dermopalatine

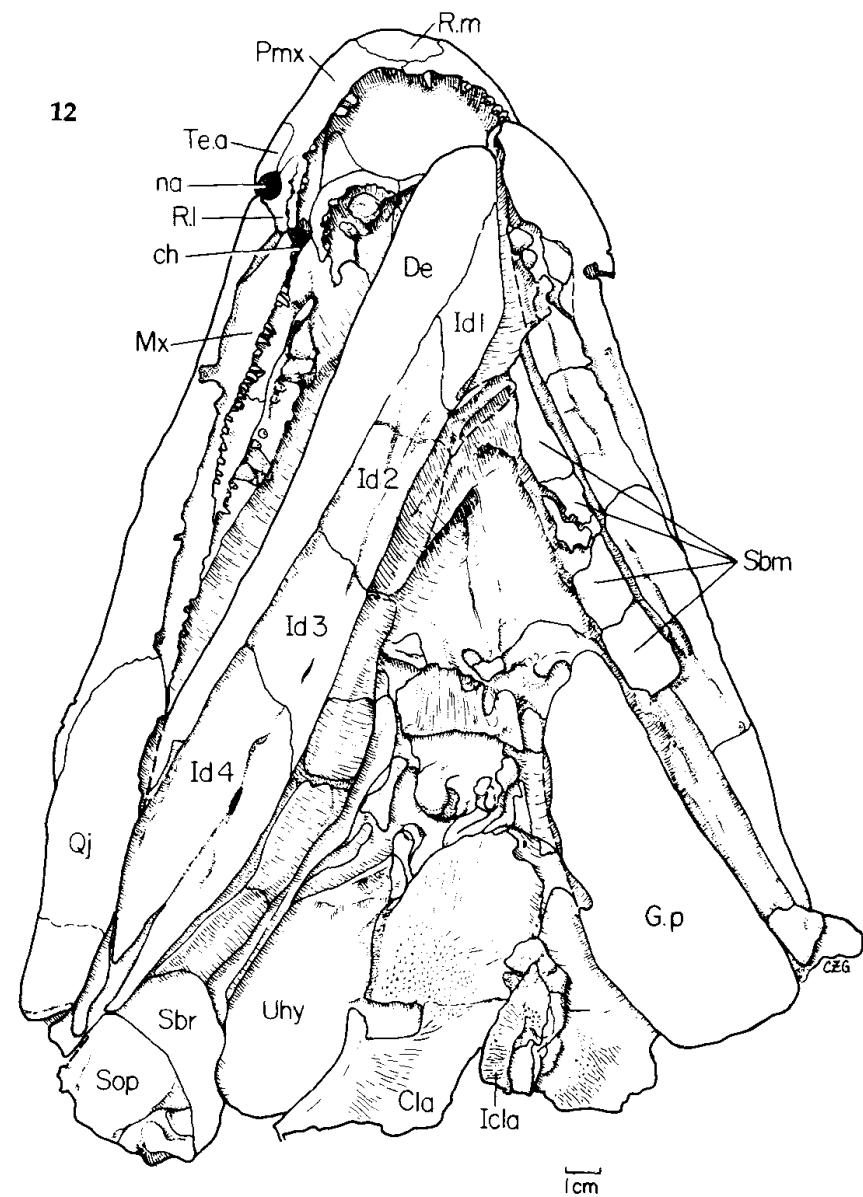


Figs. 10–11. Ventral views of heads of panderichthyids. (10) *Panderichthys rhombolepis* (Gross, 1930) (PIN 3547/26)—Gauja-beds, Frasnian, Late Devonian; Lode, Latvia, USSR. Cf. Figure 12. (11) *Elpistostege watsoni* Westoll, 1938 (MHNM 538)—Escuminac Formation, Frasnian, Late Devonian; shore of river Ristigouche at Miguasha, Province of Quebec, Canada. See Appendix I for key to abbreviations.

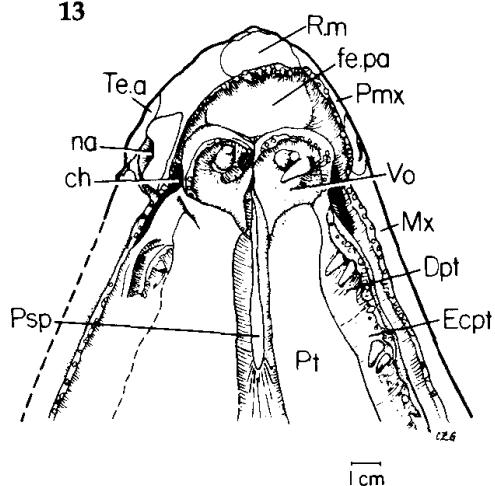
fang would lie posterolateral to the fangs of the first coronoid. The third and fourth fangs of the ectopterygoid are accommodated by the second and third coronoid pits, respectively. The uninterrupted marginal tooth row extends from the dermopalatine to the ectopterygoid. An interpterygoid vacuity is absent owing to the presence of an entopterygoid between the dermopalatine, ectopterygoid, and parasphenoid.

Suspensorium. Medially, the palatoquadrate articulates synchondrotically with the ethmoidal region. A trigeminal notch and otic process may be present but were not observed. The posterior end of the right palatoquadrate was prepared on specimen PIN 3547/26 (Fig. 15). The double-headed quadrate articulates with the saddle-shaped glenoid surface of the articular. An elongate, flat hyomandibular lies in a depression on the dorsomedial side of the palatoquadrate. The size of the hyomandibular is moderate, it is straight rather than arched and lacks a foramen. The rough, unfinished anterior end of the bone indicates coverage by cartilage. A short stylohyal, which terminates far anteriorly to the jaw

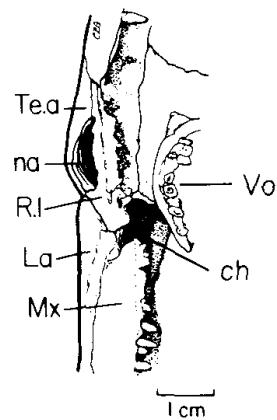
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13



14



Figs. 12–14. Skull of *Panderichthys rhombolepis* (Gross, 1930) from Gauja-beds, Frasnian, Late Devonian; Lode, Latvia, USSR. (12) Ventral view of PIN 3547/26. Cf. Figure 7. (13) Anterior palate of PIN 3547/18. (14) Choana and external nasal opening of PIN 3547/26. Cf. Figure 7. See Appendix I for key to abbreviations.

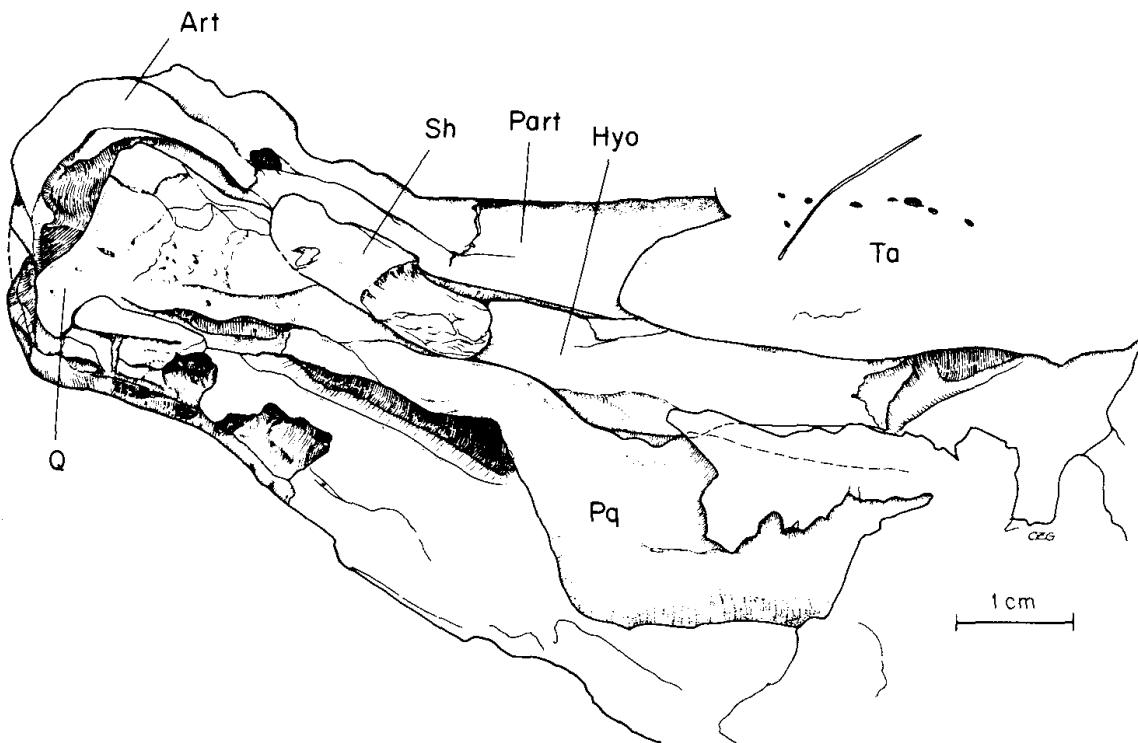


Fig. 15. Palatoquadrate, hyomandibula, stylohyal, and jaw articulation in oblique dorsal view of right side of skull of *Panderichthys rhombolepis* (Gross, 1930) (PIN 3547/26)—Gauja-beds, Frasnian, Late Devonian; Lode, Latvia, USSR. See Appendix I for key to abbreviations.

articulation, lies posteriorly adjacent to the hyomandibular. The stylohyal is thin anteriorly and thick posteriorly.

Lower jaw. The lower jaw (Figs. 10, 12) is typical of rhipidistians in being composed of a tooth-bearing dentary, four infradentaries, a prearticular on the lingual side, and three coronoids and an adsymphysial plate dorsally. The mandibular canal opens on the lateral surface through a single row of pores (Gross, 1941:Fig. 19B). The dentary bears small teeth, but a single fang lies close to the symphysis (Gross, 1941:Fig. 19A). The prearticular extends to the symphysis, where it is overlain by the adsymphysial plate (Vorobyeva, 1962:Fig. 50, Pl. 18:Fig. 3B). The adsymphysial plate bears small teeth or fangs. There are three well-developed coronoid pits—one anterior to the first coronoid, a second between Coronoids 1 and 2, and the third between Coronoids 2 and 3; these pits accommodate the fangs of the vomer, dermopalatine, and ectopterygoid, respectively.

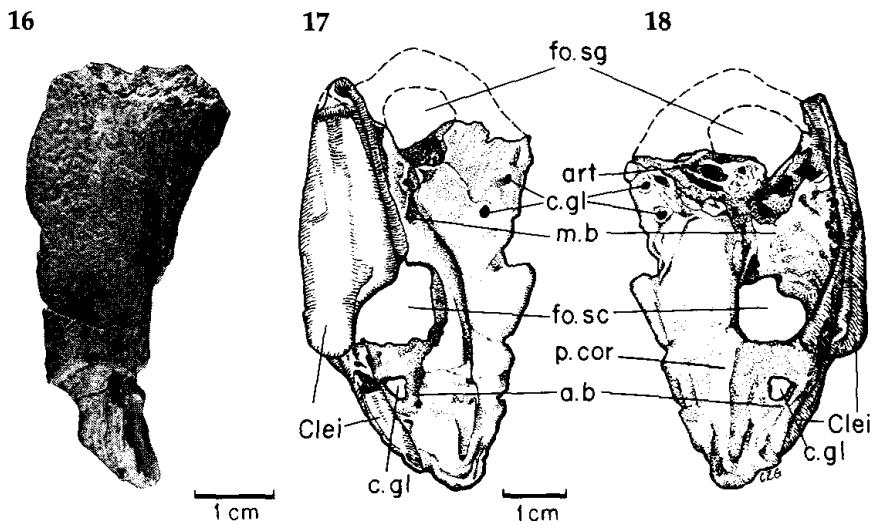
Dentition. The teeth have polyplodont structure with little or no attachment bone between the folds (Fig. 22; Schultze, 1969; Vorobyeva, 1977b).

Opercular Series

The opercular series is composed of extrascapulars, an opercular, subopercular, submandibulobranchiostegal, a long submandibular series of seven plates, and gulars (Vorobyeva, 1980:Fig. 2), as in osteolepiforms. The median gular is exceptionally large, and the lateral gulars shorter and wider than those in osteolepiforms. The median gular extends 40% the length of the lower jaw and comprises over 60% of the length of the principal gulars. The principal gulars of either side may articulate with one another for a short distance, or may be separated completely by the clavicles.

Postcranial Skeleton

Dermal shoulder girdle. The dermal shoulder girdle has a relatively narrow outer exposure; it is connected to the skull roof via the anocleithrum, supracleithrum, and posttemporal. The posttemporal articulates with the lateral and median extrascapulars. The abutment of the anocleithrum against the cleithrum is marked by a ridge that extends along the inner side of the anocleithrum. The ventral portion of the cleithrum is a short, anteroventrally directed ridged process that is overlapped by the clavicle (Fig. 16). Anterodorsally, the ascending process of the clavicle is overlapped by a rectangular part of the cleithrum. The dorsal ascending process of the clavicle fits into a groove between the cleithrum and scapulocoracoid. The clavicle has a broad ventral extension, and the



Figs. 16–18. Shoulder girdle of *Panderichthys rhombolepis* (Gross, 1930) (PIN 3547/19)—Gauja-beds, Frasnian, Late Devonian; Lode, Latvia, USSR. (16) Cleithrum in anterolateral view. (17) Anterodorsal view. (18) Posteroventral view. See Appendix I for key to abbreviations.

paired clavicles have an extensive medial articulation. The small inter-clavicle lies posteromedian to the anterior articulation of the clavicles (Figs. 10, 12). The clavicles extend between, and are overlapped anteriorly by, the principal gulars.

Endoskeletal shoulder girdle. The endoskeletal shoulder girdle (Figs. 17–18) is formed by a massive scapulocoracoid. The three scapulocoracoid buttresses (i.e., anterior, middle, and posterior) converge to form a single extensive articulation with the cleithrum. The extensive coracoid plate is perforated by a large supracoracoid foramen. Because the posterior buttress is not preserved, the posterior margin of the supraglenoid foramen was reconstructed. The supraglenoid and supracoracoid foramina do not extend to the cleithrum as they do in *Eusthenopteron* (Jarvik, 1980:Figs. 100, 165A). Instead, cartilage bone separates them from the inner side of the cleithrum as in *Ichthyostega* (Jarvik 1980:Fig. 165B). Two small canals perforate the scapulocoracoid medial to the glenoid fossa; the latter is preserved only partially in the specimen illustrated. Anterior to the supracoracoid foramen lies another smaller foramen. The head of the humerus fits into a shallow groove, the glenoid fossa, on the scapulocoracoid. The exact shape of the glenoid fossa cannot be determined because its borders are not preserved.

Fins. Pectoral and pelvic fins are located in an extreme ventral position (Fig. 19). The pelvic fins are much smaller than the pectoral fins and lie posterior, close to the caudal fin. The endoskeleton of the pectoral fin is of the uniserial archipterygial type (Worobjewa, 1975a:Fig. 3A). The long (about half the length of the pectoral endoskeleton) humerus has a well-developed deltoid crest, but no entepicondylar (postaxial) process. The

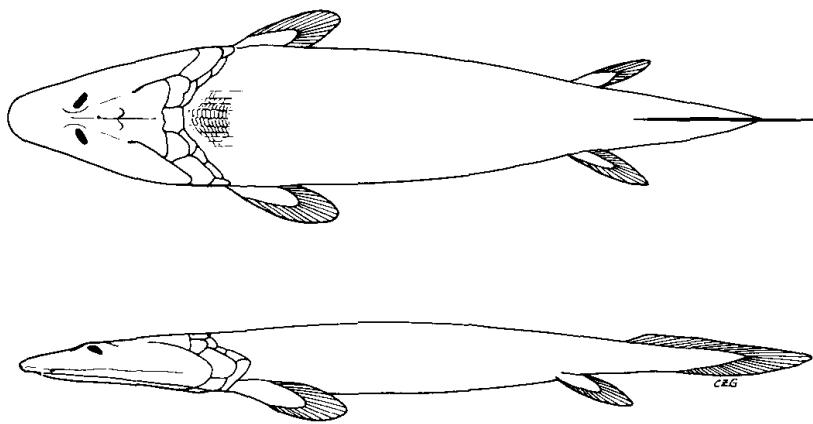


Fig. 19. Reconstruction of *Panderichthys rhombolepis* (Gross, 1930) in dorsal and lateral views.

radius and ulna articulate with the distal end of the humerus. The radius is as long as the humerus and has a well-developed external ridge on its ventral side. The ulna is three-quarters to one-half the length of the humerus. Two bones, the intermedium and ulnar plate, articulate with the distal end of the ulna. The intermedium lies between the radius and ulnar plate. The latter is large and includes the distal fin elements (i.e., ulnare and carps). The bases of articulated and distally branched lepidotrichia overlie the distal portion of the radius, intermedium, and ulnar plate. Anal and dorsal fins are absent; a fin fold surrounds the tail to form a diphycercal tail. The lepidotrichia of all fins are articulated distally and branched.

Axial skeleton. The vertebrae (Fig. 20) are composed of broad intercentra and neural arches that are attached to the dorsal border of the intercentra; pleurocentra are absent. A median groove for the dorsal aorta and a lateral branch for the intermetameric artery are visible on the ventral side of each intercentrum (Vorobyeva and Tsessarskii, 1986:Fig. 3B). The neural arches do not meet dorsally, and the neural spines are paired (Vorobyeva and Tsessarskii, 1986:Fig. 3E). A large broad rib attaches to both the intercentrum and neural arch (Vorobyeva and Tsessarskii, 1986); the abdominal ribs are short (i.e., equal in length to the neural arch and spine).

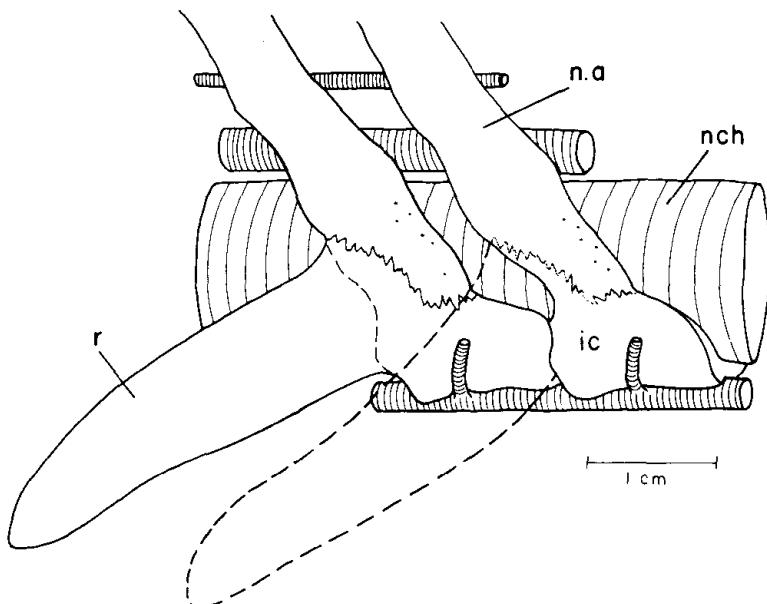


Fig. 20. Lateral view of vertebrae of *Panderichthys rhombolepis* (Gross, 1930) (PIN 3547/19)—Gauja-beds, Frasnian, Late Devonian; Lode, Latvia, USSR. See Appendix I for key to abbreviations. (After Vorobyeva and Tsessarskii, 1986:Fig. 3D.)

Scales. The rhombic scales lack a cosmine cover and are unexpectedly small relative to the large size of the organism. Their bony surface is tuberculate and ridged like the skull bones (Vorobyeva, 1962:Figs. 29A–D, Pls. 21–23). The superficial sculpturing of the scales is comparable to the ornamentation of the bones of labyrinthodonts.

Comparison of *Panderichthys* and *Elpistostege*

Similarities

Elpistostege resembles *Panderichthys* in features of the parietal shield (Worobjewa, 1973) and snout (Schultze and Arsenault, 1985). The snout of *Elpistostege watsoni* is similar in shape and size to that of *Panderichthys rhombolepis* (Figs. 1–2); in both species, the snout is prominent and the mouth subterminal (Figs. 10–11). The orbits are located high on the skull roof. The presence of “eyebrows” medial to the orbits results in a depression in the skull roof in which the suture between frontals and parietals and the parietal opening are located. Because the external nasal opening is located ventrally close to the margin of upper jaw, it is not visible in dorsal aspect. Most snout bones are arranged in pairs (paired postrostrals and nasals); exceptions include the unpaired median rostral and, when present, the unpaired median postrostral (Fig. 5). The pair of frontals is flanked by prefrontals and lies anterior to the postfrontals, which form the “eyebrows” along the dorsomedial margin of the orbits. The lower jaw is shallow in both taxa and bears a wide medial portion flanked by a narrow series of submandibulars. Both genera possess a large median gular (cf. Fig. 11, *E. watsoni* with *P. rhombolepis*, Vorobyeva, 1980:Fig. 2) and labyrinthodont-like bony ornamentation on the skull and scales. The ornamentation in *P. rhombolepis* is tuberculate, whereas that of *P. bystrowi* (Vorobyeva, 1962) is composed of a network of ridges similar to that of labyrinthodonts. These genera are alike and differ from all others known in possessing neural arches and intercentra that surround the notochord ventrally. Pleurocentra have not been discovered.

Differences

There are distinct differences between *Elpistostege* and *Panderichthys* (Schultze and Arsenault, 1985). The orbits are round in *Elpistostege* and elongated in *Panderichthys*, and the posterior margin of the skull roof is invaginated in *Elpistostege* and straight in *Panderichthys*. The genera differ in the shapes of numerous elements of the skull roof and in at least one proportion of the skull roof. The frontals are 29% of skull-roof length in *Elpistostege*; the posterior margin of the frontal lies just anterior to the level of the orbits, and the posterior part of the bone is half the width of

the anterior part. In contrast, in *Panderichthys* the frontals are 20% of the skull-roof length; the bones that extend between the orbits diminish in width more gradually. The prefrontal is larger and much narrower in *Elpistostege* (width about 20% of length) than in *Panderichthys* (width 40–50% of length). The lacrimal of *Elpistostege* is unusually long; it forms an anterolateral flange above the contact between premaxilla and maxilla posterior to the nasal opening. Such a flange is absent in *Panderichthys*. The lacrimal reaches the postorbital in some specimens of both genera (cf. Schultze and Arsenault, 1985:Fig. 5A, *Elpistostege*, with Fig. 5, *Panderichthys*, in this chapter), and excludes the jugal from the margin of the orbit. These differences are correlated with the longer snout of *Elpistostege*; the ratio of the distance between the anterior border of the orbit and the tip of the snout to the distance between the posterior border of the orbit and the posterior margin of the parietal is twice as great in *Elpistostege* (3.5 vs. 1.8 in *Panderichthys*). In *Panderichthys*, the postorbital part of the posterior shield is longer than in *Elpistostege*; thus, the parietals and postorbitals are longer, and the postorbital portion of the postfrontal is longer and broader. The shapes of the parietals also differ. The width of the parietal is more or less uniform in *Panderichthys*. However, in *Elpistostege*, the anterior interorbital portion of the parietal is narrow; postorbitally, there is a narrow lateral expansion, and posteriorly the bone is broad. A separate intertemporal is absent through loss or fusion with the postorbital in *Elpistostege*.

Taxonomic Conclusions

On the basis of the material described herein, we deem panderichthyids to be sufficiently distinct from both osteolepiforms and tetrapods (cf. discussion of relationships, below) to justify the erection of a new order¹ to accommodate them.

Panderichthyida nov. ord.

Diagnosis. Choanate fishes that possess the following characters, some of which are shared with primitive tetrapods, and some of which are reversals (i.e., also occur in Porolepiformes). Skull roof flat; orbits dorsal, closely placed; external nasal opening ventral, close to the margin of the upper jaw. Nasal capsules relatively small and widely separated. Paired frontals sutured closely with parietals between the orbits; external intracranial joint not developed; extratemporal absent. The spiracular slit extending posteriorly to form squamosal embayment (= “otic notch”). Jugal meeting quadratojugal to separate squamosal from maxilla. Laby-

¹The ordinal name may be preoccupied by *Panderichthyida* Vorobyeva, 1989. This name appeared in an article (in Russian) titled “Panderichthyida—New Order of Paleozoic Cross-ptyctyngian Fishes (Rhipidistia),” Dokl. Akad. Nauk SSSR 306, no. 1 (1989): 188–189.

rinthodont plicidentine. No median fins except caudal fin fold, which may include the second dorsal fin. Paired appendages developed as fins with uniserial internal skeleton. Body covered with rhombic bony scales.

The following features are synapomorphies of the order: (1) Median rostral separated from premaxilla; (2) paired posterior postrostrals; (3) large median gular (occupying 40% of the length of lower jaw); (4) lateral recess in nasal capsule; and (5) subterminal mouth (= prominent snout).

Content. The order contains a single family, Panderichthyidae Vorobyeva 1968, comprising three genera and five species.

1. *Panderichthys* Gross 1941: *P. rhombolepis* (Gross 1930); *P. bystrowi* Gross 1941; *P. stolbovi* Vorobyeva 1960
2. *Elpistostege* Westoll 1938: *E. watsoni* Westoll 1938
3. ?*Obruchevichthys* Vorobyeva 1977: ?*O. gracilis* Vorobyeva 1977

Remarks. Vorobyeva (in Vorobyeva and Lyarskaya, 1968) erected the family Panderichthyidae for the genus *Panderichthys*. She considered the Panderichthyidae to be one of the families of the Osteolepiformes (Worobjewa, 1975b) not closely related to tetrapods, whereas Schultze (1969, 1970, 1987), Worobjewa (1973), and Schultze and Arsenault (1985) placed *Panderichthys* or the Panderichthyidae as the closest relatives of the tetrapods. Long (1985) also removed the panderichthyids from the osteolepiforms.

Some of the features of the Panderichthyida may have resulted from preservation of juvenile structures. Thus, relative to a juvenile osteolepiform (Schultze, 1984), the short postorbital region, marginal position of the naris, narrow interorbital region, and presence of unossified postnasal wall and floor in the nasal capsule are indicative of fetalization. On the other hand, *Panderichthys* has an elongated cheek region as in osteolepiforms. The lengthening of the preorbital region is also the result of late ontogenetic development (also shown for temnospondyls by Shishkin, 1973:165), and not preservation of juvenile structures.

DISCUSSION OF RELATIONSHIPS OF PANDERICHTHYIDA

Panderichthyida and Osteolepiformes

Long (1985) proposed four advanced characters to unite the Osteolepiformes (i.e., the Osteolepididae and Eusthenopteridae): (1) unique cheek complex with enlarged lacrimal, and postorbital and jugal of equal size; (2) barlike preopercular in steeply inclined position at posterior margin of

cheek; (3) well-developed dermal anocleithrum; and (4) large basal scutes on paired and unpaired fins. He excluded the Rhizodontida (which he placed closer to the porolepiforms) from the Osteolepiformes and admitted that the panderichthyids did not fit his definition of osteolepiforms.

Nevertheless, panderichthyids share many features with osteolepiforms. Among these are the shape and composition of the lower jaw, wide separation of nasal capsules, the shapes and relationship of the opercular and subopercular, the composition of the exoskeletal shoulder girdle, and possession of rhombic scales, polyplacodont teeth, and numerous bones on the snout; however, all these features are primitive for rhipidistians. In addition, the following features characterize the Choanata (i.e., Osteolepiformes + Panderichthyida + Tetrapoda): possession of one external nasal opening, choana, adsymphysial tooth plate, undivided palatal recess, connection between vomers and long parasphenoid, lateral rostral ventral to nasal opening, large lacrimal, high number of narrow submandibulars, median gular, ball-and-socket articulation of pectoral appendage, and dorsal position of ribs. The adsymphysial tooth plate, submandibular, and median gular are lost in tetrapods. The presence of a submandibulobranchiostegal, a median gular, and the overlap of the lateral over the median extrascapular are features shared by Osteolepiformes and Panderichthyida.

The rhombic scale with a broad-based peg of panderichthyids is a primitive sarcopterygian feature (Schultze, 1977; Vorobyeva, 1977a). However, the loss of cosmine and presence of bony ornamentation are advanced features that occur in many lineages of sarcopterygians (Schultze, 1977). The bony ornamentation (especially that of the skull bones of *Panderichthys stolbovi* and *P. bystrowi*, Vorobyeva, 1962) is similar to that of labyrinthodonts.

The lower jaw of panderichthyids is a conservative structure that preserves primitive features. The broad and comparatively low anterior end of the jaw, the presence of three coronoids separated by well-developed pits for the upper fangs, a Meckelian bone extending to the symphysis (Gross, 1941:Figs. 17–19), and long prearticulars are characters also found in osteolepiforms and porolepiforms. Panderichthyids have an adsymphysial tooth plate, as do osteolepiforms; porolepiforms have a parasympathetic tooth spiral in a similar position which is distinct in structure and position from the adsymphysial plate of panderichthyids and osteolepiforms. In *P. rhombolepis*, the adsymphysial plate bears a shagreen of small teeth, as in osteolepiforms, whereas it is developed into a coronoid-like plate with fangs in *P. bystrowi* (Vorobyeva, 1962) and *Obruchevichthys gracilis* (Vorobyeva, 1977a:Figs. 15D, 46A).

Possession of polyplacodont teeth (Fig. 21) often is cited as a synapomorphy of the Choanata (Schultze, 1969, 1970; Vorobyeva, 1977b),

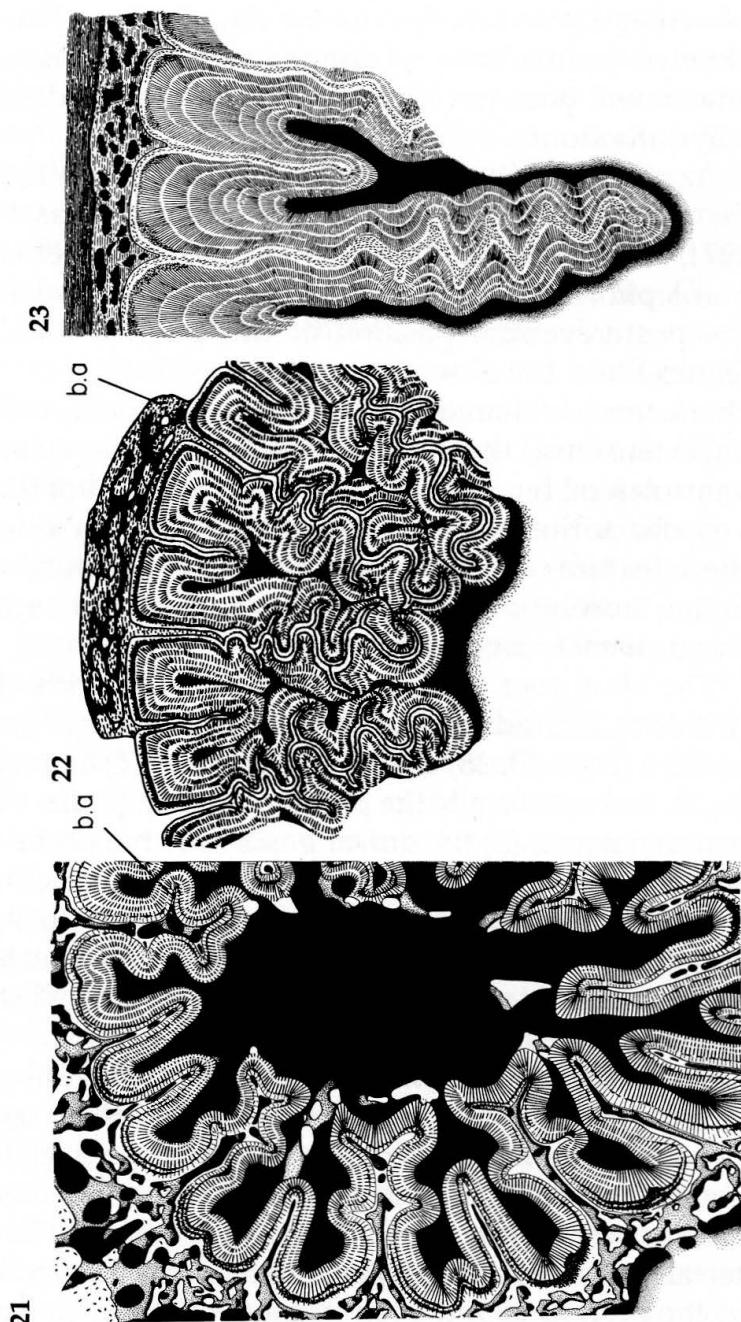
but Jessen (1980) described the same tooth structure in *Powichthys*, a primitive member of Porolepiformes or a primitive rhipidistian (Youngolepiformes, Gardiner, 1984). Therefore, the structure must be interpreted as a primitive feature for rhipidistians. The teeth of *Panderichthys* closely resemble those of primitive tetrapods (Figs. 22–26) in that bone of attachment does not reach far into the folded dentine and the teeth are labyrinthodont.

Another primitive feature of panderichthyids is the wide separation of the relatively small and poorly differentiated nasal capsules (Vorobyeva, 1971; Worobjewa, 1973). In this respect, panderichthyids are similar to porolepiforms. The structure of the nasal capsules may be explained by the posteroventral position of the external nasal opening (a derived feature) and the absence or weak ossification of the nasal walls—both characters are shared with tetrapods. In their possession of a rostrocaudal extension of the dermintermedial process, an ororostral groove, large ventrolateral fenestra, and posterior position of the opening for the nervus olfactorius, panderichthyids differ from osteolepiforms. Some of these features are similar to those in porolepiforms; panderichthyids are either more primitive than osteolepiforms or secondarily simplified in these characteristics.

The skull roof and cheek of panderichthyids (Figs. 31, 37) combine primitive and advanced features. The changes from the osteolepiform pattern (Figs. 30, 38) can be explained by (1) elongation of the preorbital, jugal, and specifically the prenasal region, (2) the marginal position of the external nares, (3) the dorsal position of the orbits, and (4) shortening of the posterior shield. The lengthening of the lacrimal and prefrontal (= posterior tectal of osteolepiforms) is related to the lengthening of the snout; the reduction of the external portion of the lateral rostral is related to the marginal position of the external nares. Posterior extension of the jugal separates the squamosal from the maxilla.

The presence of numerous rostral, postrostral, and nasal elements is primitive, although the number of elements is reduced compared with those osteolepiforms and porolepiforms in which the bone mosaic of the snout is visible. The presence of a pair of frontals in panderichthyids changes the whole appearance of the region. The rhipidistian posterior tectal and supraorbital(s) are altered to approach the shape and position of the prefrontal and postfrontal of tetrapods, respectively.

The position of the parietal foramen posterior to the level of the orbits and the shortening of the posterior shield occur in some osteolepiforms also. The ratio of the anterior to posterior shield lengths is about 2:1 in *Eusthenopteron* (Jarvik, 1948:Fig. 16B), *Platycephalichthys*, and *Jarvikina* (Vorobyeva 1977a:Fig. 42), whereas the posterior shield is nearly equal in length to the anterior shield in primitive osteolepiforms (Jarvik, 1948:Ta-

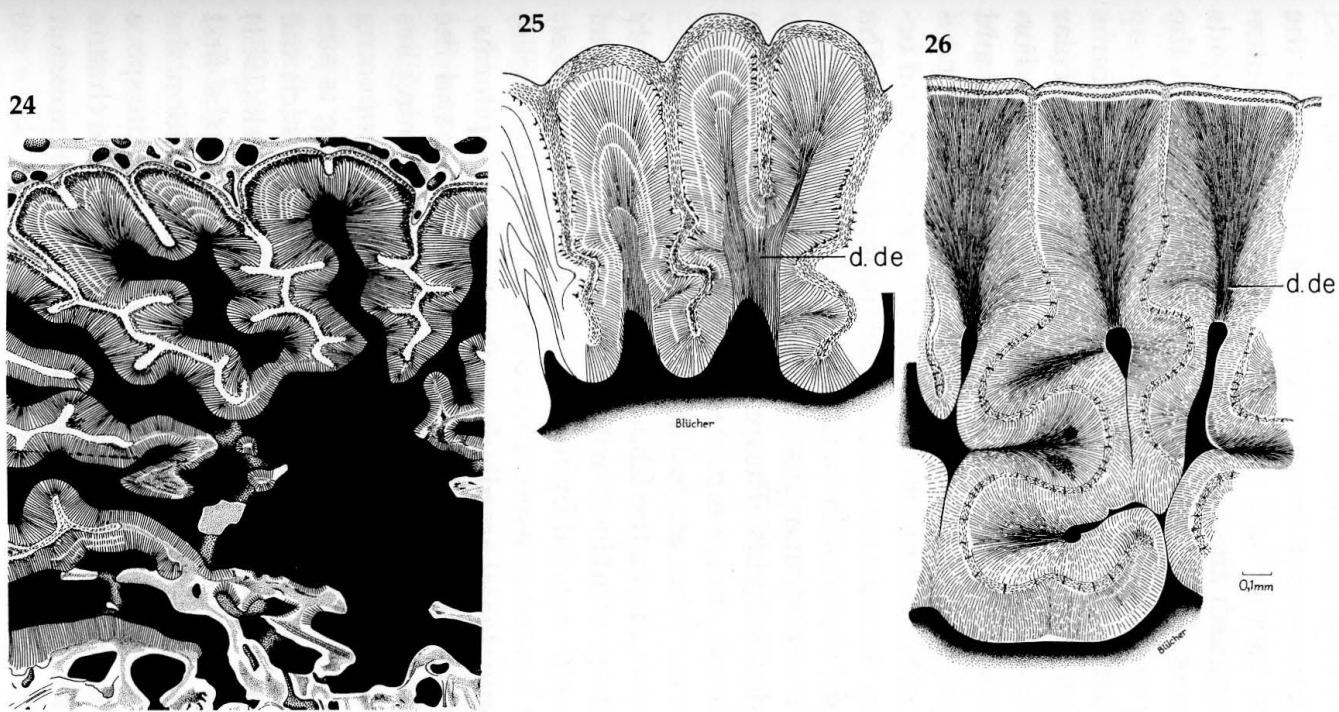


bles 3, 5, 7, 9). Nevertheless, panderichthyids with a ratio between 2.7:1 to 2.9:1 are similar to Ichthyostegalia (3:1 to 4.5:1, Säve-Söderbergh, 1932:Figs. 2, 15) and loxommatid tetrapods (3.1:1, *Colosteus*, Hook, 1983:Fig. 1; 4.2:1, *Greererpeton*, Smithson, 1982:Fig. 7). The loss of the extratemporal and postspiracular and the absence of an external intracranial joint clearly distinguish the posterior skull of panderichthyids from that of osteolepiforms. A unique feature of panderichthyids is the deep spiracular slit.

The opercular series of *Panderichthys* is similar to that of osteolepiforms (Figs. 37–38). The topographic and size relationships of the opercular and subopercular are characteristic of osteichthyan fishes, whereas Porolepiformes are specialized in the high dorsal position of opercular and subopercular. Branchiostegals are missing in osteolepiforms and panderichthyids; instead, a submandibulobranchiostegal is present and occupies the space between the opercular and submandibular series. The presence of the submandibulobranchiostegal and the overlap of the lateral extrascapulars over the median extrascapular are features shared by osteolepiforms and panderichthyids. They could be interpreted as synapomorphies of both groups, but we prefer to interpret them as synapomorphies for all Choanata that are lost secondarily in tetrapods.

An important feature that unites the Choanata is the presence of only one external nasal opening combined with the presence of a palatal opening (choana) that is surrounded by the premaxilla, maxilla, vomer, and dermopalatine, and located between the outer (maxilla, premaxilla) and inner (vomer, palatine) dental arcade. In contrast to osteolepiforms, in panderichthyids the palatal choanal opening is elongated and the nariochoanal lamina is narrow because the external nasal opening lies near it. There can be no doubt about the homology of this opening between both groups and tetrapods. In tetrapods, the opening is surrounded by the same bones, except in ichthyostegids, in which the premaxilla is excluded from the margin of the choana. Rosen et al. (1981) argued that this opening in panderichthyids is a pit to accept the first coronoid fang of the lower jaw. However, in its natural position the coronoid fang of the lower jaw of specimen PIN 3547/19 fits into the space between the fangs of the vomer and dermopalatine medial to the choana where the lateral toothed ridge is interrupted and a shallow depression formed (cf. pit in Fig. 14 of Rosen et al. 1981).

In the palatal region, the lack of dermal covering of the large anterior palatal recess is a primitive feature of Choanata. A median endocranial ridge separates the posterior part of the palatal recess in *Panderichthys stolbovi* (Worobjewa, 1975b:Fig. 2E; Vorobyeva, 1977a:Fig. 3E); this may be comparable to the division of the palatal recess in primitive osteolepiforms and porolepiforms (Worobjewa, 1975b). Such a structure is absent



Figs. 21–26. Plicidentine in Choanata. (21) Polyplacodont plicidentine in osteolepiform *Eusthenopteron foordi* (after Schultze, 1969:Fig. 10). (22–26) Labyrinthodont plicidentine: (22) Panderichthyid *Panderichthys rhombolepis* (after Pander, 1860:Pl. G, Fig. 7); (23) Temnospondyl *Loxomma allmanni* (after Schultze, 1969:Fig. 15A); (24) Ichthyostega sp., cross section at base of tooth (after Schultze, 1969: Fig. 14); (25) *Ichthyostega* sp., higher cross section with “dark dentine” (after Schultze, 1969:Fig. 13); (26) Anthracosaur *Eogyrinus attheyi* with “dark dentine” (after Schultze, 1969:Fig. 15B). See Appendix I for key to abbreviations.

in *P. rhombolepis* (Figs. 12, 13). Behind the palatal recess, the vomerine tooth ridges of each side meet one another. This feature must be interpreted as a parallel development in advanced osteolepiforms (Worobjewa, 1975b), as also may be the case for the lateral and posterior processes of the vomer.

The presence of only one medial ethmoidal articulation of the palatoquadrate may be a primitive feature of Choanata. However, the palatoquadrate is immobile and synchondrotically united to the ethmoid, as in advanced Late Devonian osteolepiforms such as *Eusthenopteron*, *Jarvikina*, and *Platycephalichthys* (Vorobyeva, 1977a). The articulation is ligamentous in earlier osteolepiforms (e.g., *Thursius estonicus*, *Osteolepis macrolepidota*, *Megapomus markovskyi*) or movable in other osteolepiforms (e.g., *Megalichthys nitidus*, *Megistolepis klementzi*, *Gyroptychius pauli*).

The Choanata have a different form of articulation between scapulocoracoid and first, proximal pectoral endoskeletal element (i.e., humerus) than do other fishes (Schultze, 1987). The humerus forms the ball that resides in the socket of the scapulocoracoid. In other features of the postcranial skeleton, panderichthyids are distinct from osteolepiforms. They lack median fins except the caudal fin fold. The pelvic fins are located far posteriorly—at about the level of the anal fin in osteolepiforms. Basal scutes, a typical feature of osteolepiforms, are absent at the base of the paired fins. The fusion of the distal elements in the endoskeleton of the pectoral fin (Worobjewa, 1975a) may be another feature distinguishing panderichthyids from osteolepiforms.

The composition of the vertebrae varies tremendously from Porolepiformes to tetrapods and within each group (Andrews and Westoll, 1970; Vorobyeva and Tsessarskii, 1986). Only three elements take part in the formation of these vertebrae—the basiventral (= intercentrum), basidorsal (= neural arch), and interdorsal (= pleurocentrum) arcocentrum. Primitively, the pleurocentrum is small, but it is enlarged in some osteolepiforms and tetrapods (gastrocentrous vertebrae). *Panderichthys* and *Elpistostege*, like *Crassigyrinus*, lack pleurocentra (Fig. 20). The notochord is unconstricted in these forms, even though the intercentrum, neural arch, and rib fuse to form one unit in *Panderichthys*. The weak ossification of the vertebrae in *Crassigyrinus* was considered to be a degeneration by Panchen (1985), but it is comparable to that in Panderichthyida. Taking the weak vertebrae of panderichthyids and the small pleurocentrum in some osteolepiforms into account, one can argue that rhachitomous vertebrae developed independently in osteolepiforms and tetrapods, owing to the plasticity of their morphogenesis (Vorobyeva and Tsessarskii, 1986).

In conclusion, comparison of the distribution of characters in Panderichthyida and Osteolepiformes shows that the characters common to

both groups are either primitive features or features of the larger unit, Choanata (Fig. 39). Of the four synapomorphies for Osteolepiformes (Long, 1985), only the barlike preopercular and large basal scute seem to remain. Postorbital and jugal bones of nearly equal size occur in *Porolepis* (similar to the osteolepiform *Beelarongia*, Long, 1987) and may be present in some panderichthyids, but most panderichthyids tend toward enlargement of the jugal, as do tetrapods. There is a morphocline of increasing size of the lacrimal; thus, the lacrimal is relatively larger in panderichthyids, Ichthyostegalia, and primitive tetrapods than in osteolepiforms. The preopercular lies at the posterior margin of the cheek in panderichthyids and ichthyostegids; however, in the latter (except *Acanthostega*) it has an oblique orientation. The external exposure of the anocleithrum may be similar in panderichthyids and osteolepiforms. Three other features (the submandibulobranchiostegal, the presence of a median gular, and the overlap of lateral over median extrascapular) are common to panderichthyids, osteolepiforms, and rhizodonts, whereas in porolepiforms, actinistians, and dipnoans the median extrascapula overlaps the lateral one. These must be interpreted as synapomorphies for the Choanata to be consistent with the large number of features that are common to panderichthyids and tetrapods (see below). Unfortunately, they cannot be examined in tetrapods because they are lost.

Panderichthyida and Rhizodontida

Our knowledge of the Rhizodontida is limited and based mainly on publications by Andrews (1972, 1973, 1985). The pattern of the posterior skull roof (separate supratemporal), the overlap of the lateral extrascapulars over the median one, the presence of a median gular, and the uniserial archipterygium are features that rhizodontids share with osteolepiforms and panderichthyids. The articulation between humerus and scapulocoracoid is another choanate character that unites rhizodontids with choanates; the rounded head of the humerus lies in a glenoid fossa (Andrews and Westoll, 1970) in contrast to the situation in porolepiforms and other sarcopterygians (Schultze, 1987), in which the humerus rotates around a rounded head of the scapulocoracoid.

Although the polyplacodont structure of the teeth is well developed in rhizodontids, osteolepiforms, panderichthyids, and tetrapods, this feature must be considered to be primitive because it also occurs in youngolepiforms. The "dark dentine" utilized by Panchen (1985) to characterize Anthracosauroidea occurs in rhizodontids (Schultze, 1969:Pl. 12, Fig. 3). Rhizodonts are more similar to panderichthyids than to osteolepiforms in possessing small pelvic fins and a symmetrical caudal fin. At present, we know of no features that would ally the rhizodontids more closely to one of these groups than the other; nonetheless, the aforementioned features

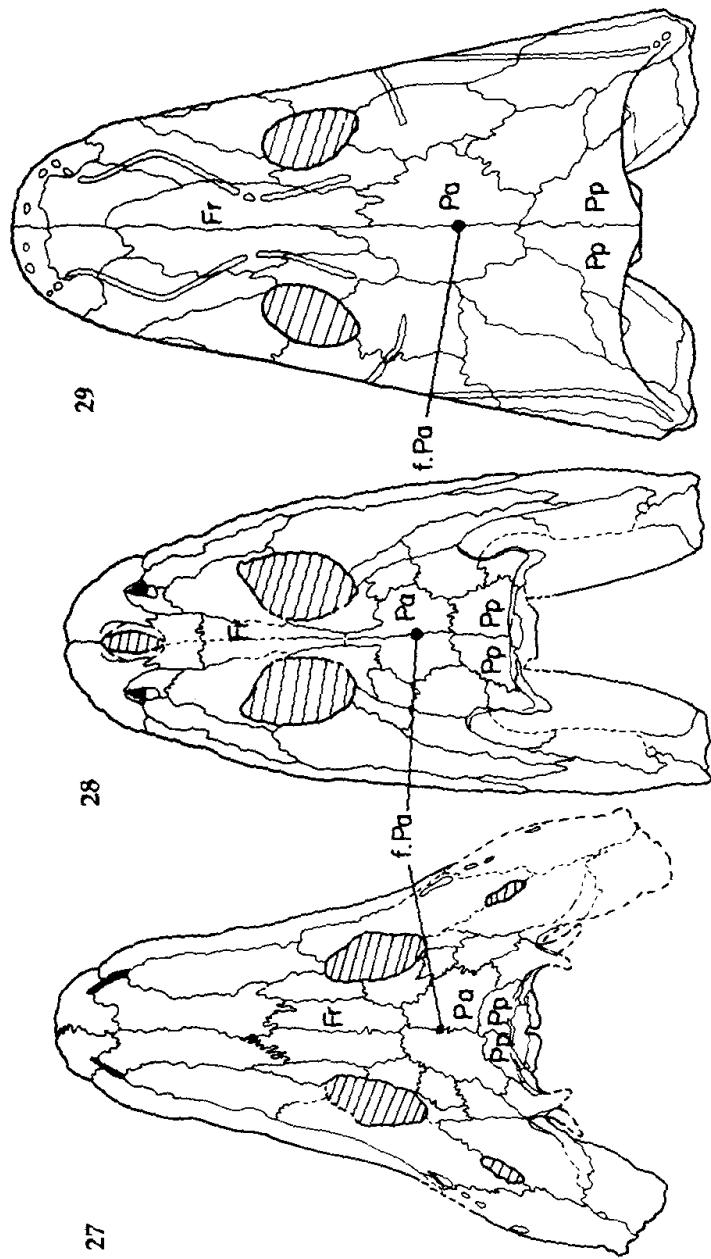
would place them within the Choanata (Fig. 39). However, the presence of two external nares (as reconstructed by Andrews [1985]) is a primitive feature for rhipidistians and argues against such placement. If the Rhizodontida possesses two external nares, its phylogenetic position would lie between the Porolepiformes and Choanata. The characters they share with the Choanata would no longer be unique to the Choanata.

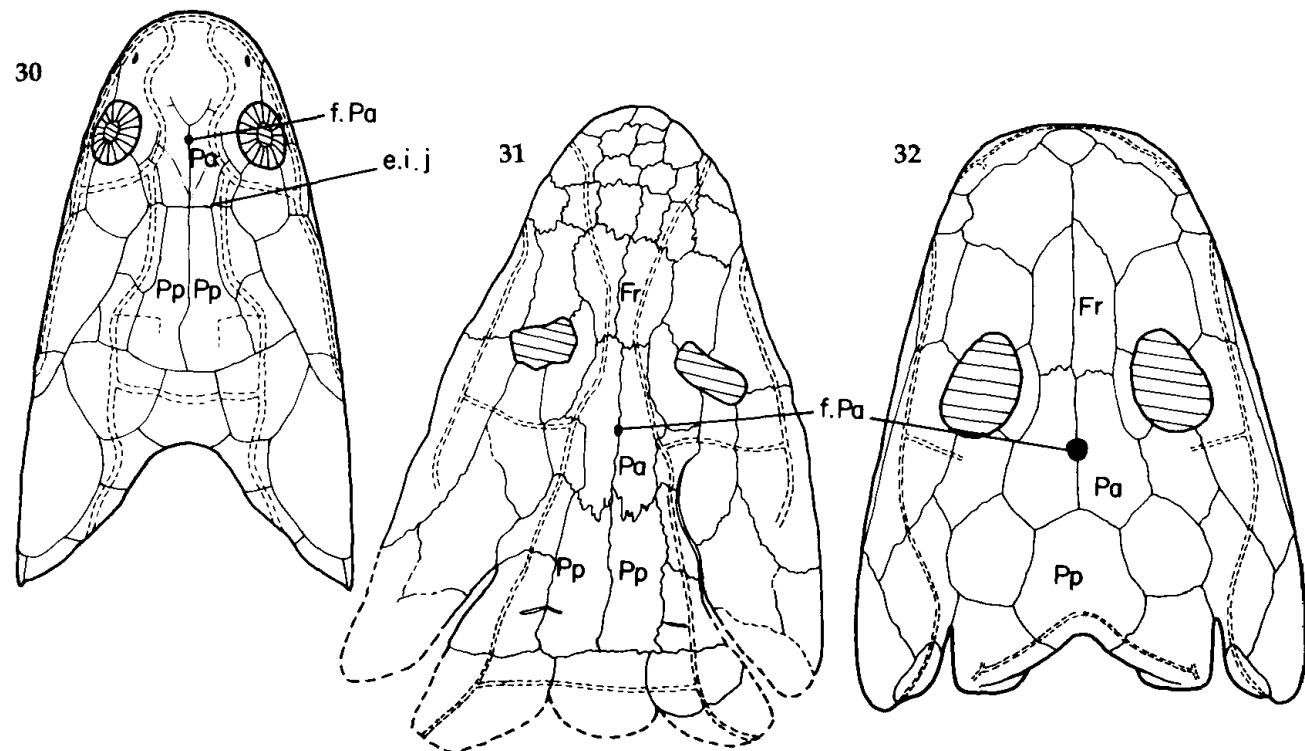
Panderichthyida and Tetrapoda

The earliest tetrapods are known from the Late Devonian. Whole skeletons of *Ichthyostega* have been described from the Late Devonian of Greenland (Säve-Söderbergh, 1932; Jarvik, 1952, 1980), whereas the second genus, *Acanthostega*, of the Ichthyostegalia is known only from the skull (Jarvik, 1952) and a little postcranial material (Clack, 1988). Recently, the fragmentary remains of a third Late Devonian genus, *Tulerpeton*, were described from central Russia (Lebedev, 1984, 1985). Monographic descriptions of early members of various new tetrapod groups are available: Temnospondyli—*Greererpeton* (Smithson, 1982); *Colosteus* (Hook, 1983); Batrachosauria—*Eoherpeton* (Smithson, 1985); *Proterogyrinus* (Holmes, 1984); *Anthracosaurus* (Panchen, 1977; Clack, 1987). *Crassigyrinus*, the amphibian recently described by Panchen (1985), deserves special consideration because some of the features that Panchen used to distinguish the genus from anthracosaurs also occur in panderichthyids (Schultze and Arsenault, 1985).

All early tetrapods except *Tulerpeton* (which possesses an ano- and supracleithrum) lack an opercular apparatus—i.e., the connection of the shoulder girdle with the skull roof—and fins. Each possesses typical tetrapod features such as dactylic extremities and a pelvic girdle fixed to the vertebral column (see Gaffney, 1979, for monophyly of Tetrapoda). In addition, they share the features listed below with panderichthyids (Fig. 39).

1. The skull roof is flat (Figs. 33–34, 36–37) relative to that of the typical fish and osteolepiform skull (Fig. 38).
2. The dorsally placed orbits are narrowly separated (Figs. 27–29, 31–32); the orbits are lateral in osteolepiforms.
3. The external naris (Figs. 33–34, 36–37) is located near the margin of the upper jaw (Panchen, 1967). Thus, the external naris and choana are close to each other, and both are visible in ventral view.
4. The presence of paired frontals is unique to panderichthyids and tetrapods (Figs. 27–29, 31–32). There are only two bones lateral to the frontals—the prefrontal and postfrontal; these are named the posterior tectal and supraorbital, respectively, in osteolepiforms.
5. The external intracranial joint is absent (Figs. 27–29, 31–32). Little is





Figs. 27–32. The skull roofs of Choanata. (27) Anthracosauridae: *Anthracosaurus russelli* (after Panchen, 1977:Fig. 4). (28) *Crassigyrinus scoticus* (after Panchen, 1985:Fig. 7). (29) Temnospondyli: *Greererpeton burkemorani* (after Smithson, 1982:Fig. 7). (30) Osteolepiformes: *Osteolepis macrolepidotus* (after Jarvik, 1948:Fig. 32B). (31) Panderichthyida: *Panderichthys rhombolepis*; compare with Figure 8. (32) Ichthyostegalia: *Ichthyostega* sp. (after Jarvik, 1952:Fig. 35B). See Appendix I for key to abbreviations.

known about the endocranial intracranial joint in these groups. Neotetrapods lack the joint, but vestiges of it may be represented in embryonic stages (Roček, 1986; Schultze, 1987). Jarvik (1980) argued that *Ichthyostega* possessed an endocranial intracranial joint. The condition of this character is unknown in panderichthyids.

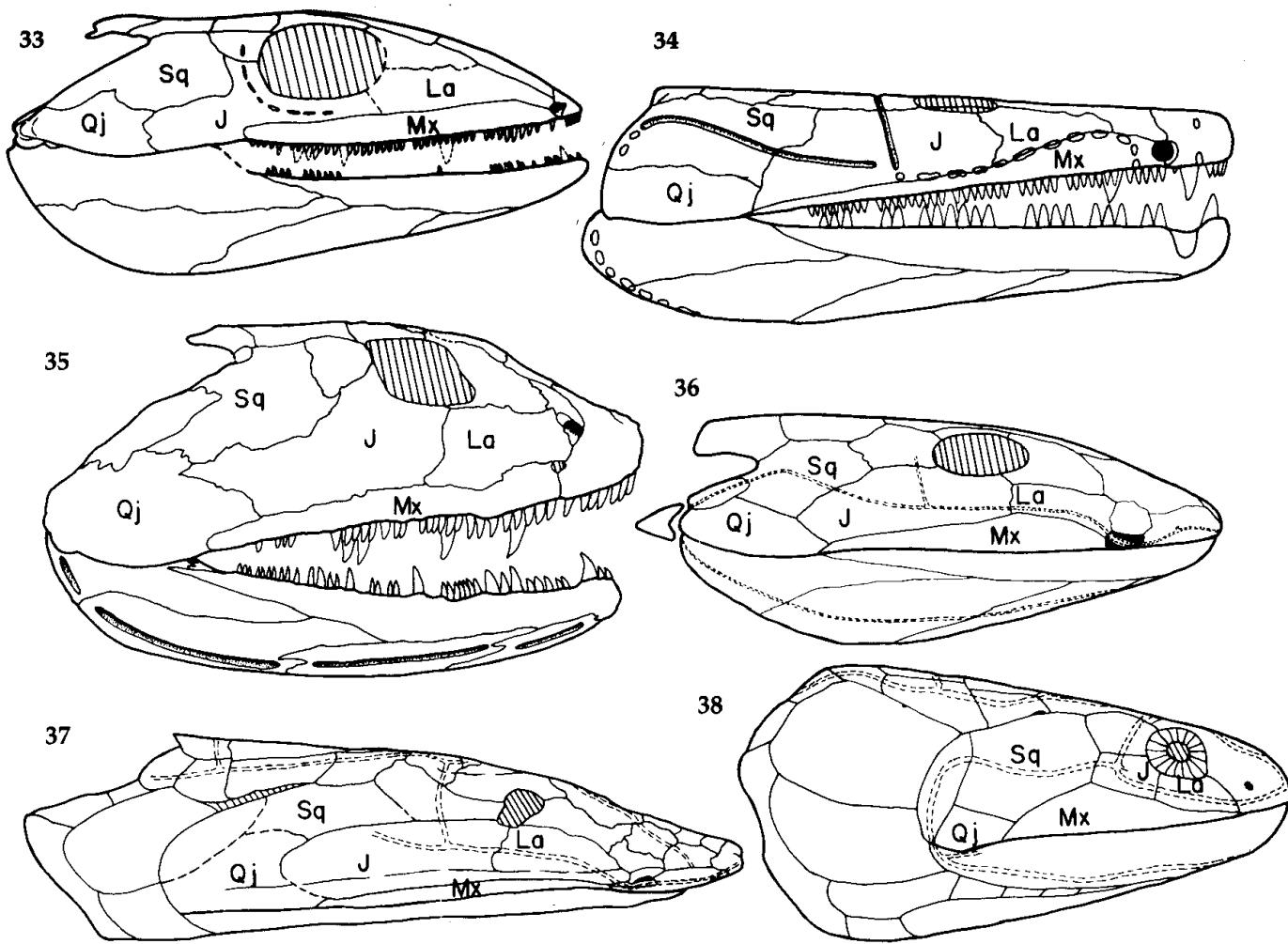
6. The postparietal shield is short in panderichthyids but longer than that of tetrapods (Figs. 27–29, 31–32). The parietal has a more posterior position in panderichthyids than it does in osteolepiforms; the bone extends between the orbits, but its main portion lies posterior the orbits, as it does in early tetrapods. The parietal foramen lies posterior to the level of the orbits. The Ichthyostegalia (Fig. 32) often are characterized as having an unpaired postparietal (Gaffney, 1979); however, in *Acanthostega* the postparietals are paired. In *Panderichthys*, pairing of the postparietal (Fig. 5) is individually variable.

7. The Tetrapoda (Figs. 33–36) is distinct from the Osteolepiformes (Fig. 38) in the composition of the cheek region; the jugal and quadratojugal articulate, thereby separating the squamosal from the maxilla (Panchen, 1985). In *Panderichthys*, the relationship between these bones varies. Whereas *Elpistostege* has the osteolepiform condition, one specimen of *Panderichthys rhombolepis* (Figs. 4, 37) has the tetrapod condition. In another specimen of *P. rhombolepis* (PIN 3547/26), the squamosal reaches the maxilla on the left side but not the right. This feature unites panderichthyids and tetrapods, and is not exclusive to tetrapods (contra Panchen and Smithson, 1987).

8. The teeth of panderichthyids and early tetrapods have an advanced polyplodont structure (Figs. 22–26). The bone of attachment extends only a short distance into the folds of dentine, and the central axes of the folds undulate. The labyrinthodont structure of the teeth of *Panderichthys* and *Ichthyostega* is nearly indistinguishable (Schultze, 1969, 1970). The dentine folds of these genera retain side branches—a feature of polyplodont teeth (Fig. 21) that is absent in advanced labyrinthodont teeth.

9. Panderichthyids lack median fins (Fig. 19) except for a caudal fin fold like that of *Ichthyostega*. The dorsal portion of this fin fold extends farther forward than the ventral portion, and it is possible that the second dorsal fin is incorporated into the caudal fin fold, an interpretation suggested for *Ichthyostega* by Jarvik (1980).

10. Attachment of ribs to the neural arch and intercentrum occurs in panderichthyids and the Ichthyostegalia. The small pleurocentrum of Ichthyostegalia is unknown in panderichthyids. The composition of the vertebrae of some osteolepiforms (i.e., *Osteolepis*, Andrews and Westoll, 1970; Andrews, 1977) more closely resembles that of certain neotetrapods than that of panderichthyids and ichthyostegids. In our opinion, this resemblance represents parallel evolution (Vorobyeva and Tsessarskii, 1986). Support for such an interpretation comes from *Crassigyrinus*,



Figs. 33–38. Lateral views of the heads of Choanata. (33) Anthracosauridae: *Proterogyrinus scheelii* (after Holmes, 1984: Figs. 3a, 15a). (34) Temnospondyli: *Greererpeton burkemorani* (after Smithson, 1982: Fig. 9). (35) *Crassigyrinus scoticus* (after Panchen, 1985: Fig. 9). (36) Ichthyostegalia: *Ichthyostega* sp. (after Jarvik, 1952: Fig. 35A). (37) Panderichthyida: *Panderichthys rhombolepis*. (38) Osteolepiformes: *Osteolepis macrolepidotus* (after Jarvik, 1948: Fig. 32A). See Appendix I for key to abbreviations.

which possesses vertebrae similar to those of panderichthyids; thus, an intercentrum and neural arch are present, but the pleurocentrum is absent.

Crassigyrinus (Figs. 28, 35) is an unusual form that possesses a combination of tetrapod, panderichthyid, and osteolepiform features. Panchen (1985) placed *Crassigyrinus* within anthracosauroids on the basis of five shared features. The first, the presence of a consolidated braincase, seems to be a synapomorphy for all Neotetrapoda. The second feature is the presence of characteristic dermal ornament. The third, possession of a tabular horn, "may not seem a very compelling character. . . . Taken in combination with the next character [absence of posttemporal fossae] . . . the whole is quite unique" (Panchen, 1985:552). The fifth character, "dark dentine," is a primitive feature that occurs in *Ichthyostega* (Fig. 25; cf. Schultze, 1969:Pl. 13, Fig. 2b) and in the rhizodont *Strepsodus* (Schultze, 1969:Pl. 12, Fig. 3). The "dark dentine" results from the rapid retreat of peripheral odontoblasts toward the pulp cavity. This phenomenon is observed only in thin sections made at the proper level. Thus, Figure 3 of Plate 7 (Schultze, 1969) shows indications of "dark dentine" in *Panderichthys* that could be well developed at a slightly higher level. In any case, "dark dentine" is not a feature uniting anthracosauroids.

Two of the four autapomorphies of *Crassigyrinus* are features shared with panderichthyids—i.e., the presence of constricted parietals and frontals in the interorbital region, and a deep cheek below the orbit. There are many other characters that contraindicate the placement of *Crassigyrinus* within Neotetrapoda—e.g., the presence of preopercular, an undivided open palatal recess, anterior projection of notochord into basioccipital, the position of external nasal opening, and the distribution of foramina on the humerus. The grooves described by Panchen (1973) on the jugal are exaggerated (deep and narrow) components of the ornament. The lateral-line canal is limited to a superficial groove on the lower jaw. There are characters that Panchen (1985) interpreted as being degenerate—e.g., the lack of occipital condyle, the presence of weak vertebrae composed only of an intercentrum and neural arch, and ribs not clearly bicipital. Some characters, such as the wide separation of the external naris from the margin of upper jaw (reversal for *Crassigyrinus*) and the lack of reduction of the pars facialis of the lateral rostral, are primitive among tetrapods.

The composition of the lower jaw is stable in rhipidistians and lower tetrapods, consisting of four infradentaries and three coronoids. Coronoids are lost within tetrapods. Primitively, coronoids bear fangs that are bordered laterally by a row of small teeth. This arrangement changes in tetrapods; fangs are absent, and only a lateral row of small teeth is present. *Crassigyrinus* has a shagreen of small teeth on the coronoids

comparable to that of anthracosauroids; the larger teeth are similar to the fangs in osteolepiforms and panderichthyids. The fangs of the upper jaw fit into large coronoid pits between the coronoids in rhipidistians. These pits and the dermopalatine and ectopterygoid fangs are absent in tetrapods. Like other early tetrapods, *Crassigyrinus* possesses fangs in the upper jaw on the dermopalatine and ectopterygoid; like osteolepiforms, it has small teeth on the pterygoid. To accommodate the tips of the palatal fangs in the lower jaw, *Crassigyrinus* has a row of pits lateral to the coronoids on the medial side of the dentary. Thus, a primitive upper jaw structure is combined with specialization of the lower jaw of *Crassigyrinus*.

It seems that the presence of so many primitive characters in *Crassigyrinus*, combined with the lack of many tetrapod synapomorphies, would place *Crassigyrinus* close to the base of tetrapod phylogeny, perhaps even below Ichthyostegalia. *Crassigyrinus* lacks four of the seven cited synapomorphies for Neotetrapoda in our cladogram (Fig. 39); the remaining three are not known or uncertain in *Crassigyrinus*. The genus resembles *Ichthyostega* in having a preopercular, a palatal recess not covered by bone, and a notochord entering the braincase; all these are primitive features. In addition, *Crassigyrinus* lacks some tetrapod synapomorphies involving the pelvic region and external nasal opening. The presence of only 11 of the 14 synapomorphies of tetrapoda would place *Crassigyrinus* below the branching between Ichthyostegalia and Neotetrapoda. Panchen (1985) dismissed some of Gaffney's (1979) tetrapod characters; in so doing he was able to support Watson's (1929) proposal that *Crassigyrinus* is an anthracosauroid.

A flat skull roof uniting panderichthyids and tetrapods is correlated with the dorsal position of the orbits. Lengthening of the preorbital region is correlated with the formation of frontals. The shortening of the postorbital region in connection with a lengthening of the preorbital region may require loss of the dermal intracranial joint. In addition, some of the features indicate correlation with environmental factors. Some Recent actinopterygians that leave the water in the intertidal zone possess dorsally placed eyes for subareal observation. The "eyebrows" in panderichthyids are indicative of an elevated position of the eyes in the dorsally placed orbits. The ventral position of the external nostrils also could be related to an amphibious life style.

In conclusion, the number of common features shared by tetrapods and panderichthyids is surprisingly large (Fig. 39) and includes four features that Gaffney (1979) used to justify the monophyly of tetrapods. Anterior and posterior shields of the skull roof are sutured (part of Character 1 of Gaffney, 1979; the situation in the endocranum is unknown). There is a clear tendency in tetrapods toward the shortening of the otico-occipital region (Character 2 of Gaffney, 1979); although pan-

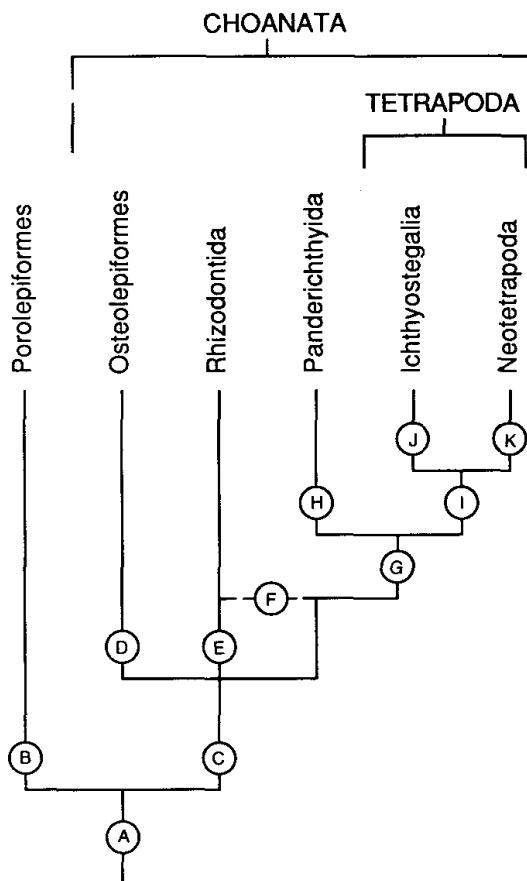


Fig. 39. Interrelationships of rhipidistian crossopterygians. See Appendix II for explanation of distribution of characters across Nodes A–K.

derichthyids have not attained the same degree of shortening found in tetrapods, the difference is only gradational. There is some ambiguity about the "otic notch" (Character 3 of Gaffney, 1979). Gaffney (1979) defined the "otic notch" as "a V-shaped cleft formed at the posterior margin of the skull between the tabular and squamosal" (= squamosal embayment of Godfrey et al., 1987), whereas Panchen (1985) associated the term with a restored tympanum. The opening of the spiracular cavity in rhipidistians has the same position as the squamosal embayment in labyrinthodonts (Shishkin, 1973:188; Smirnov and Vorobyeva, 1986). The spiracular canal opens lateral to the anterior part of the tabular and posterolateral to the supratemporal in osteolepiforms (Jarvik, 1980:Figs. 122, 144A) and in panderichthyids (Figs. 2, 4–5). In osteolepiforms, the posterior continuation is covered, whereas it is open in panderichthyids and tetrapods. The squamosal embayment has the same relative position in *Crassigyrinus* and neotetrapods (Figs. 27–28), whereas it is shortened in ichthyostegids (Fig. 32). *Greererpeton* (Fig. 29) and *Colosteus* (Hook, 1983:Fig. 1A) lack a squamosal embayment. The latter forms and the ichthyostegids have no lateral kinetism between the skull roof and cheek region, as is found in osteolepiforms (Vorobyeva, 1977a) and anthracosaurs (Holmes, 1984). There is also no movement possible among the

supratemporal, intertemporal, and cheek in panderichthyids. It is difficult for Panchen (1985:514) to establish the presence of lateral kinetism in *Crassigyrinus* because the skull material is either incomplete or badly crushed. *Crassigyrinus* differs in the arrangement of the bones in the posterior skull roof from anthracosauroids in that it shows the primitive osteolepiform arrangement—i.e., tabular and supratemporal lateral to postparietal, and no contact between the tabular and the parietal.

Ossified ribs (Character 11 of Gaffney, 1979) also occur in panderichthyids. They are large relative to those of osteolepiforms, but not compared with tetrapods. Finally, the status of Gaffney's Character 8 (pectoral skeleton free from skull) is uncertain because Lebedev (1984:1471) described an anocleithrum and supracleithrum in a Late Devonian tetrapod, *Tulerpeton*.

The characters common to panderichthyids and tetrapods, and the close resemblance of *Crassigyrinus* to panderichthyids clearly indicate a close sister-group relationship between panderichthyids and tetrapods.

CONCLUSIONS

Panderichthys and *Elpistostege* are the two best known members of the Panderichthyida. Although they are similar in shape and proportions of the skull roof, there are clear differences (the shape of cranial elements—orbit, prefrontal, lacrimal, and parietal; presence vs. absence of an intertemporal; the posterior margin of the skull roof) that justify the separation of the two genera. The large median gular and the subterminal mouth are the most readily recognizable synapomorphies of panderichthyids.

The panderichthyids show a combination of porolepiform, osteolepiform, and tetrapod features that we could interpret as a case of mosaic development ("Watson's rule," de Beer, 1954). This means that panderichthyids retain primitive characters in common with porolepiforms and osteolepiforms—i.e., they are rhipidistians or choanates, respectively—and they share other advanced characters with tetrapods, which makes them the sister-group of the latter. Three characters (the presence of submandibulobranchiostegal, a large median gular, and an overlap of lateral over median extrascapular) could be used to unite panderichthyids with osteolepiforms. These bones are lost in tetrapods, so it is not possible to demonstrate that these features are part of the character set of the Choanata. Nevertheless, the numerous characters common to panderichthyids and tetrapods make it more parsimonious to support such an interpretation.

Although many characters unite panderichthyids and tetrapods (Fig. 39), features such as extrascapulars, opercular series with gular plates

and submandibulars, and paired fins allow us to recognize the panderichthyids as fishes. However, ichthyostegids possess so-called fish features such as fin rays (lepidotrichia) and fin-ray supports in the caudal fin, and preopercular, subopercular, dermal scales, and lateral-line canals inside the bones. *Tulerpeton*, a tetrapod from the Late Devonian of the USSR, possesses still more of these features (e.g., anocleithrum and supracleithrum); therefore, it is possible that the connection between skull roof and shoulder girdle still exists or that the gap between skull and girdle is narrow. Like *Tulerpeton*, another tetrapod, *Crassigyrinus*, is placed within the anthracosauroids (Panchen, 1985), although it shares many features that are primitive for tetrapods with panderichthyids. It even retains osteolepiform features (e.g., the nature of the external nares and the shape of humerus). It seems more reasonable to place *Crassigyrinus* at the base of the tetrapods immediately above or below the ichthyostegid level because it has not acquired all tetrapod synapomorphies. The similarities between *Crassigyrinus* and panderichthyids are another strong indication that the panderichthyids are related closely to tetrapods.

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APPENDIX I. Anatomical Abbreviations Used in the Figures

a.b = anterior buttress; Art = articular; art = articular (glenoid) fossa

b.a = bone of attachment

c.gl = glenoid canal; ch = choana; Cla = clavicle; Clei = cleithrum; c.mn = canal for ramus medialis of nervus profundus; c.n.b = nasobasal canal; c.o.lat =

canal for ramus lateralis of nervus ophthalmicus; c.olf = canal for nervus olfactorius; c.pal = canal for palatine branch of nervus facialis; c.prt = canals for twigs of medial terminal branch of nervus profundus; cr.im = crista intermedia

d.de = "dark dentine"; De = dentary; der = dermal process of anterior tectal; Dpt = dermopalatine

Ecpt = ectopterygoid; e.i.j = external intracranial joint; end = endochondral bone; Esc.l, m = lateral, median extrascapula

fe.pa = palatal recess; fo.dm = dorsomedial depression in posterior face of postnasal wall; fo.sc = supracoracoid foramen; fo.sg = supraglenoid foramen; f. Pa = parietal foramen; Fr = frontal

G.m = median gular; g.n.b = nasobasal groove; G.p = principal gular

Hyo = hyomandibular

ic = intercentrum; icla = interclavicle; Id 1,2,3,4 = infradentary 1,2,3,4; ioc = infraorbital canal; It = intertemporal

J = jugal

La = lacrimal

m.b = middle buttress; Mx = maxilla

Na = nasal; na = external nasal opening; n.a = neural arch; nch = notochord

Pa = parietal; Part = prearticular; p.cor = coracoid plate; p.ioc = pores of the infraorbital canal; p.m. = middle pitline; Pmx = premaxilla; Po = postorbital; Pof = postfrontal; Pop = preopercular; Pp = postparietal; Pq = palatoquadrate; Pr = postrostral; Pr.a, m, p = anterior, median, posterior postrostral; pr.dim = dermintermedial process of lateral rostral; Prf = prefrontal; pr.im = intermedial process; Psp = parasphenoid; p.Sq = pitline of squamosal; Pt = pterygoid (endopterygoid)

Q = quadrate portion of the palatoquadrate; Qj = quadratojugal

r = rib; R.l, m = lateral, medial rostral; re.l = recessus lateralis

Sbm = submandibular; Sbr = preoperculosubmandibular; Sh = stylohyal; soc = supraorbital canal; Sop = subopercular; sp = spiracular slit; Sq = squamosal; St = supratemporal

Ta = tabular; Te.a = anterior tectal; t.Pmx = cross section of premaxillary teeth

Uhy = urohyal

Vo = vomer

APPENDIX II. Distribution of Character-States in Rhipidistian Crossopterygians (Fig. 39)

Node A: Rhipidistia excluding onychodonts (see Schultze, 1987). (1) Extratemporal lateral to tabular; (2) many narrow submandibular bones; (3) fenestra ventrolateralis, covered by vomer in porolepiforms; (4) four infradentaries; (5) three coronoids; (6) plicidentine, simply folded, polyplocodont being primitive; (7) supraorbital canal joining cephalic division of main lateral line.

Node B: Porolepiformes. (8) Intertemporal fused with parietal; (9) supratemporal

fused with postparietal; (10) nariodal bone between anterior and posterior external nasal opening; (11) two or three squamosals versus only one; (12) prespiracular bone in upper cheek region; (13) preoperculosubmandibular, an additional bone at posterior margin of the cheek region; (14) high, dorsally placed opercular; (15) short anterior margin of opercular; (16) dorsolaterally placed "triangular" subopercular; (17) parietal foramen closed; (18) dendrodont tooth structure (Youngolepiformes, which have polyplodont teeth, not included here); (19) teeth of dentary not reaching symphysis; (20) parasymphysial tooth spiral on symphysis; (21) olfactory bulbs ventral to cerebral hemisphere; (22) paired bucohypophysial canal.

Node C: Choanata. (23) One external nasal opening; (24) choana between premaxilla, maxilla, vomer, and dermopalatine; (25) median rostral fused with premaxilla; (26) few unpaired or paired postrostrals; (27) lateral extracapulars overlapping median extrascapular; (28) lateral rostral ventral to external naris; (29) large lacrimal; (30) narrow preopercular bone at posterior margin of cheek; (31) submandibulobranchiostegal present, but no branchiostegals; (32) seven submandibulars; (33) median gular always present; (34) superior, inferior, and often median recess present in nasal capsule; (35) crista intermedia present; (36) nasobasal canal present; (37) palatal recess unpaired and without bone cover; (38) posterior process on vomer in most osteolepiforms; (39) long parasphenoid extending below otico-occipital region; (40) ossified dorsal ribs; (41) two-headed articulation of ribs; (42) uniserial archipterygium in pectoral fin; (43) tetrapod articulation between humerus and scapulocoracoid.

Node D: Osteolepiformes. (44) Steeply inclined preopercular at posterior margin of cheek region; (45) basal scutes on all fins; (46) large, ornamented anocleithrum.

Node E: Trichotomy of Rhizodontida, Osteolepiformes, and other Choanata. (47) Lateral extrascapulars overlapping median extrascapula; (48) median gular present; (49) uniserial archipterygium in pectoral fin.

Node F: Rhizodontida above Osteolepiformes. (50) Lateral line diverting from tabular and supratemporal into elongated postparietal; (51) reversed overlap between cleithrum and clavicle.

Node G: Panderichthyida and Tetrapoda. (52) Flat skull roof; (53) closely placed of orbits; (54) marginal position of external naris; (55) paired frontals in front of parietals and orbits; (56) external intracranial joint lost (intimate suturing between anterior and posterior portion of skull roof); (57) parietals extending anteriorly between orbits, but main portion with parietal opening behind orbits; (58) extra-temporal absent; (59) long spiracular fenestra extended posteriorly to form squamosal embayment; (60) jugal meeting quadratojugal (squamosal separated from maxilla; not in all panderichthyid specimens, as far as known); (61) obliquely placed preopercular at posterior margin of cheek; (62) lateral wall and posterior floor of nasal capsule not ossified; (63) nasal capsule extending posteriorly beyond ethmoid region; (64) labyrinthodont plicidentine; (65) large dorsal ribs directed ventrally; (66) no median fins (except caudal fin fold).

Node H: Panderichthyida. (67) Median rostral separated from premaxilla (reversal; also in Porolepiformes); (68) paired posterior postrostrals; (69) large median gular; (70) lateral recess in nasal capsule (reversal; also in Porolepiformes); (71) subterminal mouth.

Node I: Tetrapoda (cf. Gaffney, 1979). (72) One pair of nasals meeting in midline; (73) posterior postrostrals lost; (74) lateral rostral transformed to septomaxilla

(not in *Crassigyrinus*); (75) extrascapulars lost; (76) opercular and submandibulo-branchiostegal lost; (77) submandibulars lost; (78) gulars lost; (79) otico-occipital region of skull longitudinally compacted; (80) stapes; (81) fenestra ovalis; (82) presence of phalanges in fore and hind limbs combined with ankle and wrist joints; (83) pectoral girdle free from skull roof (opercular, supracleithrum and anocleithrum, posttemporal lost, except *Tulerpeton*); (84) iliac blade of pelvis attached to vertebral column (except in *Crassigyrinus*); (85) well-developed ischiac ramus of pelvis (except in *Crassigyrinus*, where the ischium is dermal [!] after Panchen, 1985).

Node J: Ichthyostegalia. (86) Premaxilla excluded from margin of choana (paralleled by some neotetrapods); (87) intertemporal fused with supratemporal; (88) short parasphenoid between and behind pterygoids; (89) adsympophysial plate incorporated into coronoid series as anterior coronoids (after Jarvik, 1980).

Node K: Neotetrapoda. (90) Preopercular lost (except in *Crassigyrinus*) and subopercular lost; (91) palatal recess covered by bone or divided by bony bridge (not in *Crassigyrinus*); (92) anterior coronoid (possibly including adsympophysial plate) lost; (93) ethmosphenoid and otico-occipital portions of braincase fused in adults; (94) notochord excluded from braincase in adults (except *Crassigyrinus*); (95) lateral-line system absent or in grooves; (96) median bony fin supports and lepidotrichia lost.

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