THE PANDERICHTHYID FISH *ELPISTOSTEGE*: A CLOSE RELATIVE OF TETRAPODS?

by H.-P. SCHULTZE *and* M. ARSENAULT

ABSTRACT. The anterior skull roof and a possible postcranial skeleton of *Elpistostege watsoni* Westoll 1938 are described from the Escuminac Formation, upper Devonian, of Miguasha, Quebec, Canada. In agreement with Worobjewa (1973), *Elpistostege* is placed within the osteolepiform family Panderichthyidae. Within the osteolepiforms, the Panderichthyidae are the group closest to early tetrapods. Their skull roof pattern readily permits the transfer of tetrapod terminology to the skull roof of other osteolepiforms (contrary to Borgen 1983).

DURING the summer of 1937, T. S. Westoll acquired a skull roof from a local collector, supposedly Mr. E. Plourde of Miguasha, Province of Quebec. The incomplete dermal skull roof was published one year later without diagnosis as a 'stegocephalian' amphibian (Westoll 1938). No additional specimens were discovered over the next thirty years.

With the establishment of the Musée d'Histoire Naturelle de Miguasha in 1978, a new period of collecting and research began at the famous upper Devonian locality of Miguasha. During inventory of the collection of the late Allan Parent of Miguasha, an interesting unprepared specimen that had been collected by Parent in 1970 was discovered. Preparation by O. Bonner, Museum of Natural History, Lawrence, Kansas, revealed a skull of amphibian appearance, but with submandibular bones and a gular plate between the lower jaws, a condition found only in fish. The specimen was acquired in 1983 by the Government of the Province of Quebec for the Musée d'Histoire Naturelle de Miguasha.

The staff of the Musée d'Histoire Naturelle de Miguasha sought to collect additional material from the horizon in which the skull was thought to have been found. Their efforts were rewarded by recovery of a partial postcranial skeleton of probable panderichthyid affinities. The horizon where this skeleton was found is 87–88 m above the basal beds of the Fleurant Formation, upper Devonian. This unit is formed by pyrite-rich grey-green shales lying one to two metres below the thick sandstone-channel complex within the Escuminac Formation (Hesse and Sawh 1982). The horizon also contains *Eusthenopteron foordi*, *Scaumenacia curta* and *Bothriolepis canadensis*. That the Parent specimen (MHNM 538) may have come from this horizon is indicated by its preservation, the surrounding shales, and the pyrite content.

Depositional environment of the Escuminac Formation is considered by most authors to be freshwater/lacustrine in origin based on its tectonic position and on its fauna (Dineley and Williams 1968; Carroll *et al.* 1972; Thomson 1980; Hesse and Sawh 1982). The sedimentological features are compared by Dineley and Williams (1968, p. 252) with those of marine upper Devonian rocks of south-central New York State. The fauna, however, could be interpreted as marine, too, because most of the fishes occurring in the Escuminac Formation are found in other Devonian localities together with marine invertebrates (see Schultze in Carroll *et al.* 1972). That is the case for forms with wide distribution in the Devonian such as *Cheirolepis* (scales in marine deposits, see e.g. Gross 1973), *Eusthenopteron* (in the Baltic and Russia, Jarvik 1937; Vorobyeva 1977), *Bothriolepis* (Young 1974, 1981), and *Plourdosteus* (Obrutschew 1933; Obrucheva 1962). We tentatively interpret the depositional environment of the Escuminac Formation as coastal marine, based on the fauna present within the formation (see Schultze in Carroll *et al.* 1972).

[Palaeontology, Vol. 28, Part 2, 1985, pp. 293–309]

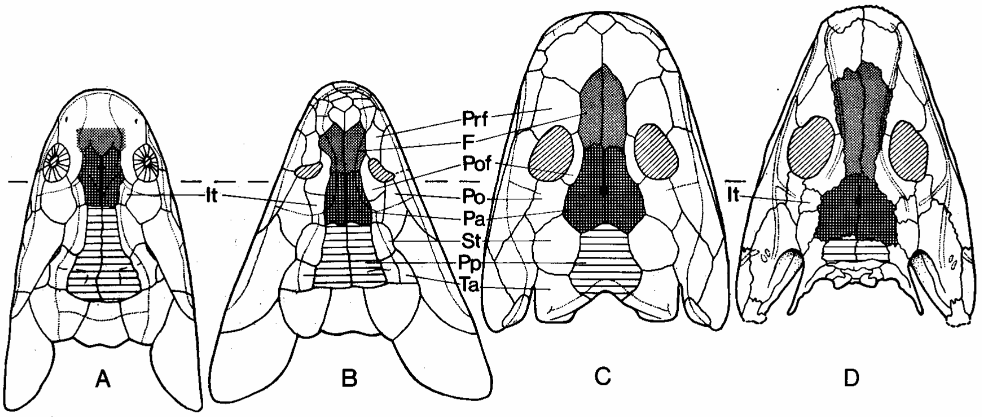
TERMINOLOGY OF SKULL ROOFING BONES

We use Westoll's (1938) terminology of skull roofing bones for osteolepiforms, contrary to the traditional terminology favoured by Jarvik (1967). Borgen (1983, Fig. 1) summarized the opposing views on the terminology of skull roofing bones. Contrary to Jarvik (1967), he accepted the traditional ('orthodox') terminology of these bones for reptilomorphs and labyrinthodonts except *Ichthyostega*. However, he followed Jarvik (1967) by insisting on the traditional terminology for these bones in *Eusthenopteron*. He could accept these contrasting traditional terminologies only:

1. by denying correlation in position between dermal bones and endocranial structures (contrary to Jarvik 1967), and between parietal foramen and parietal (as in Jarvik 1967).

2. by moving the extrascapulars of osteolepiforms onto the otico-occipital region of tetrapods. That results in a change in the correlation between frontal and parietal with underlying structures during the transition from osteolepiforms to tetrapods.

We agree with Borgen (1983, p. 744) that 'the basic criterion for homology is that of evolutionary continuity' (see similar statement in Gregory 1933, p. 92). Similarities are used to recognize homologies, and these similarities should be sought by comparison of closely related forms. Thus, by accepting a close relationship between osteolepiform rhipidistians and tetrapods (Jarvik 1967, 1972, 1980; Schultze 1970, 1977, 1981; Vorobyeva 1977*a*, 1977*b*; Borgen 1983; contrary to Rosen *et al.* 1981), we prefer to compare early tetrapods with osteolepiforms, and specifically with osteolepiforms which are probably most closely related to early tetrapods (text-fig. 1).



TEXT-FIG. 1. Terminology of skull roofing bones. Skull roof of A, *Osteolepis macrolepidotus* (after Jarvik 1972, fig. 61C), B, *Panderichthys rhombolepis* (after Vorobyeva 1977*b*, fig. 2B), C, *Ichthyostega* sp. (after Jarvik 1952, fig. 35B), and D, *Paleoherpeton decorum* (after Panchen 1970, fig. 1*a*).

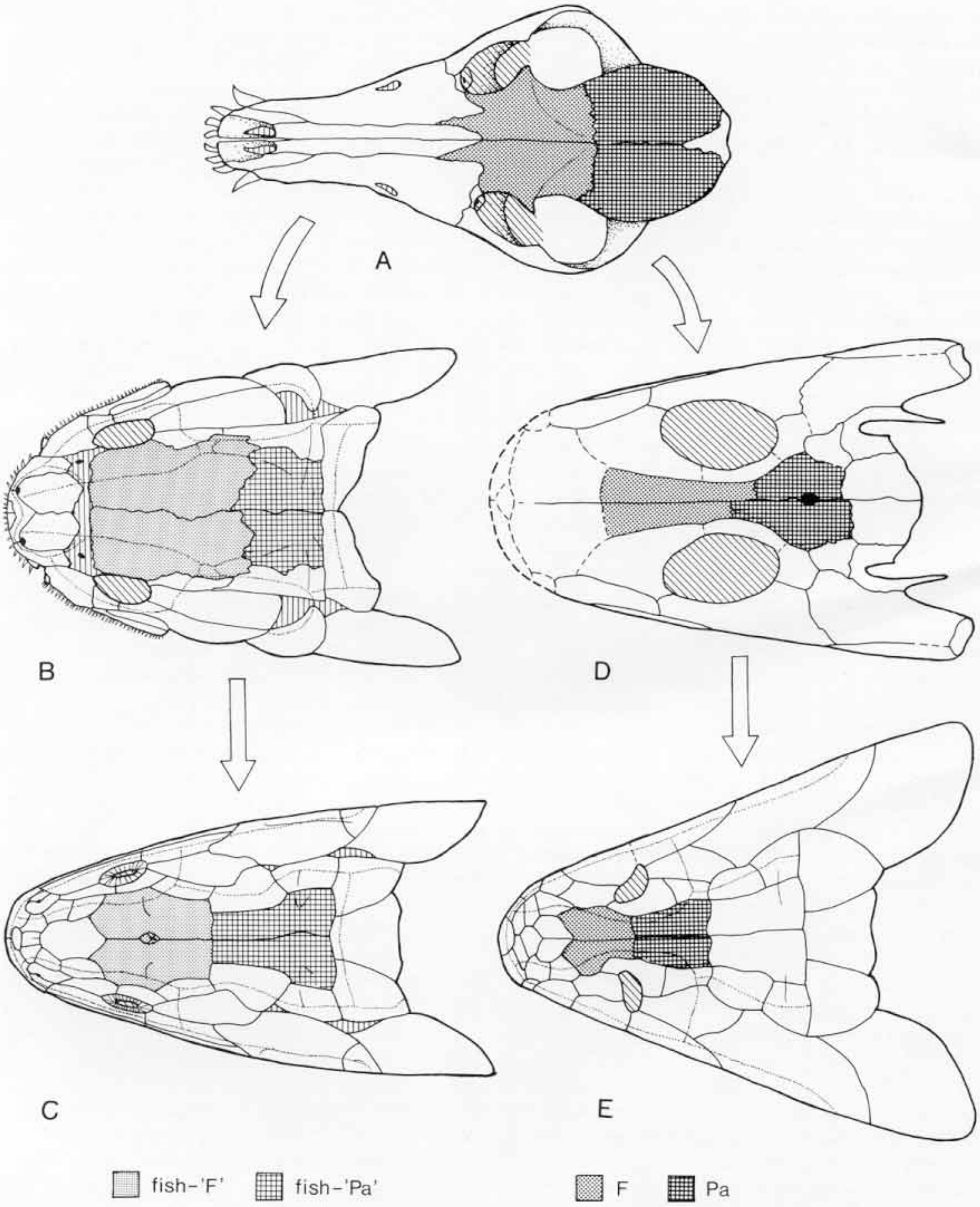
Jarvik (1967, fig. 12A, B) and Borgen (1983, figs. 2D, C, 5) showed that the same relationship exists between endocranial structures and overlying dermal bones of osteolepiforms, labyrinthodonts, and reptilomorphs. Contrary to Jarvik (1967), Borgen (1983) accepts identical terminology for skull roofing bones with the same relation to underlying endocranial structures in labyrinthodonts and reptilomorphs as does Shishkin (1973). However, Borgen did not follow Westoll (1938, 1943), Shishkin (1973) or Vorobyeva (1977*b*), all of whom applied the same terminology to skull roofing bones based on their relation to endocranial structures in osteolepiforms. Instead, Borgen made comparisons between distantly related forms (using mammals, specifically the young rabbit as did

Jarvik 1967, and *Eusthenopteron*). In mammals, despite the fact that the relationship between exocranial bones and endocranial structures varies between taxa (Parrington 1967), the exocranial bones have essentially the same relationships to endocranial structures in primitive placental mammals as in mammal-like reptiles and in early tetrapods (Parrington 1967; Borgen 1983, fig. 2A), except that the postparietals extend further anteriorly over the otic region in the earliest tetrapods. This change in position between parietal and postparietal was explained by Westoll (1943) and strongly supported by Shishkin (1973) by correlated shortening of the otico-occipital region of the endocranium and the dermal bones above it during the transition from osteolepiforms to tetrapods. A close correlation exists between endocranial structures and exocranial bones in early tetrapods and osteolepiforms. Nevertheless, Borgen (1983) refers to the bone over the otic region as the postparietal in *Paleoherpeton* and the parietal in *Eusthenopteron*, and to the bone over the exit of the optic nerve (cranial nerve II) and the basipterygoid process as the parietal in *Paleoherpeton* and the frontal in *Eusthenopteron*. The change in relationships between endocranial structures and dermal bones referred to by Borgen (1983) occurs in more advanced tetrapods; still, the relationships would hold if he had compared closely related forms.

The parietal foramen, another often disputed point in consideration of the relationship between exocranial and endocranial structures, lies between the parietals in all labyrinthodonts and reptilomorphs, independent of how far posteriorly the parietal foramen moves (Jarvik 1967, fig. 3B; Shishkin 1973, fig. 66*a–d*). In most mammals (except *Bos*, as stated by Borgen 1983, p. 742) the epiphysis (homologous to the parietal foramen) lies below the parietals. This constant relationship between parietal foramen and parietals exists throughout tetrapods. The condition in placoderms (Jarvik 1967, fig. 3A) is irrelevant. The skull roof pattern of placoderms is not comparable to that of osteichthyans and tetrapods despite Graham-Smith's (1978) attempt to construct a common ancestral pattern for placoderms and osteichthyans. We argue here for step-by-step comparison of closely related forms, but placoderms are only distantly related to osteichthyans (e.g. Denison 1978).

In early reptilomorphs and some labyrinthodonts, the postparietal lies laterally to the tabular, with the supratemporal and intertemporal lateral to the parietal; the intertemporal is lost or fused with other elements in most labyrinthodonts. The tabular and supratemporal have the same relationship to endocranial features in early tetrapods as they do in osteolepiforms (Shishkin 1973), while the extrascapulars of osteolepiforms lie behind the endocranium. Säve-Söderbergh (1932) and Borgen (1983) postulated a shift of the extrascapulars onto the skull roof in tetrapods to become the postparietals. Such a change in the position of these bones is in the opposite direction to that occurring in the phylogeny of labyrinthodonts and reptilomorphs where postparietals and tabulars moved posteriorly onto to occipital region (Panchen 1972). Borgen (1983, p. 746) gave no explanation or indication for this proposed change in relationship between dermal and endocranial structures. However, Säve-Söderbergh (1932) and Jarvik (1967) considered the position of occipital commissure to be indicative of such a transition. Changes in the position of lateral lines from one bone to another are known to have occurred in early tetrapods (e.g. Shishkin 1973) and have even been accepted by Borgen (1983, p. 750). Thus, the shift of the occipital commissure to a pair of bones anterior to the extrascapulars was possible for early tetrapods (see Graham-Smith 1978).

If we accept that homologies are best recognized in closely related forms, then Borgen's (1983) argument for the use of traditional terminology in early tetrapods and osteolepiforms can be tested by comparing forms close to the fish-tetrapod transition. These include *Ichthyostega*, *Acanthostega*, *Elpistostege*, and *Panderichthys* (text-fig. 8). Borgen (1983, p. 748/749) drew support for his use of the traditional osteolepiform terminology from the position of the 'frontals' between the orbits in mammals, reptilomorphs, and advanced batrachomorphs, i.e. the primary reason for use of the traditional terminology in fishes and osteolepiforms (text-fig. 2A, B, C). He uses contrary to his proposition to clarify what happened at this transition, a comparison between distantly related forms (i.e. position of bones in relation to the orbits in mammals and fishes). Other supporting evidence is a consequence of his acceptance of the topographic criterion for the homology of the frontal. On the other hand, the bones of *Ichthyostega* and *Acanthostega* can easily be compared with those in other



TEXT-FIG. 2. The 'traditional' way of transferring the terminology of skull roofing bones in mammals (A. *Vulpes vulpes*) to fishes (B. *Amia calva*; C. *Eusthenopteron foordi*, after Jarvik 1972, fig. 61D) and, alternatively, by comparison of forms most closely related to early amphibians (D. *Paleoherpeton decorum*, after Panchen 1970, fig. 1*a*) to panderichthyid osteolepiforms (E. *Panderichthys rhombolepis*, after Vorobyeva 1977*b*, fig. 2B).

early tetrapods (Jarvik 1952). In *Ichthyostega*, the 'parieto-extrascapular' of Jarvik (1972, 1980) and Säve-Söderbergh (1932) lies over the otico-occipital region as does the postparietal in early tetrapods and the 'parietal' of Jarvik (1972, 1980) in osteolepiforms. Borgen (1983) argues that there is no close functional or embryological correlation between skull roofing bones and endocranium. That permits the change in their position relative to each other from osteolepiforms to reptilomorphs and to mammals as postulated by Westoll (1943). Still, the constant topographic relationship between endocranial structures and related dermal roofing bones in closely related forms is a more reliable indication of bone homology than a topographic relation to the orbits alone. The 'frontals' of Jarvik (1967, 1972, 1980) surround the parietal foramen, as do the parietals in all other tetrapods.

Borgen (1983) presents a defence of two opposing terminologies, one derived from phylogenetic step-by-step comparison from mammals back to early tetrapods (text-fig. 2A, D, E). The other, he derives solely by topographic comparison between mammals and fishes (text-fig. 2A, B, C). The topographic relationships between bones and the orbits often changes during ontogeny within one species (Boy 1972, Shishkin 1973) and may also differ between members of closely related groups. For example, the rostral margin of the 'frontal' in osteolepiforms lies in front (*Eusthenopteron*, *Elpistostege*), between (*Osteolepis*, *Panderichthys*), or close to the posterior margin of the orbits (*Eusthenodon*).

In early tetrapods, the suture between frontals and parietals shifted from a position between the orbits (*Ichthyostega*, *Acanthostega*, and others) to the level of the posterior margin of the orbits (*Paleoherpeton*, *Colosteus*, *Benthosuchus*, some specimens of *Greererpeton*, and others), and finally to the most common position behind the orbits (*Greererpeton*, most labyrinthodonts and reptilomorphs). Contrary to Borgen (1983, p. 744), a posterior, not a forward movement of this suture relative to the orbits has been observed in ontogenetic series of *Branchiosaurus*, *Micromelerpeton*, *Sclerocephalus*, and *Pelosaurus* (Boy 1972, Shishkin 1973). In *Eusthenopteron* this suture (which equals the anterior margin of the 'frontals') moved anteriorly during ontogeny when compared to the orbits, while the parietal foramen migrated posteriorly (Schultze, 1984). Extreme ontogenetic lengthening of the postorbital region is a typical rhipidistian feature which is not paralleled in early tetrapods (contrary to Borgen's statement, p. 744).

We believe it is unnecessary to repeat all the reasons for applying the terminology of skull roofing bones used for early tetrapods to osteolepiforms (see Shishkin 1973). It follows from Borgen's (1983) presentation of the different views that the traditional terminology of either tetrapods (Westoll 1938, 1943) or osteolepiforms (Jarvik 1967) should be used in both closely related groups. The possibility of transferring, step-by-step, the widely used terminology applied to mammals, back to early tetrapods (as accepted by Borgen 1983), favours the use of the traditional tetrapod terminology for osteolepiforms and actinopterygians as employed by Romer (1945) and Jollie (1962). In addition, *Panderichthys* and *Elpistostege* have paired frontals in front of the parietals, thus making their skull roof pattern much more tetrapod-like than that of other osteolepiforms.

SYSTEMATIC PALAEONTOLOGY

Order OSTEOLEPIDIDA Boulenger 1901 correct.

Family PANDERICHTHYIDAE Vorobyeva 1968

Diagnosis (*emended*): Osteolepiform fishes with tetrapod-like skull roof pattern; paired frontals followed by paired parietals and paired postparietals, paralleled by elongate prefrontal (equals supraorbital 1), postfrontal (equals supraorbital 2), intertemporal, supratemporal, and tabular. Snout composed of many bones, medial rostral(s) followed by anterior, medial, and posterior postrostrals, three paired nasals, first nasal fused with premaxillary. Large postorbital can reach spiracular notch; cheek without extratemporal or postspiracular plate. Lateral rostral and anterior tectal surrounding the external nasal opening, the prefrontal does not reach the posterior margin of the external nasal opening. One large median gular between a series of broad submandibulars, followed by a pair of lateral gulars.—Nasal capsules close to the lateral wall of the posterior part of ethmoid; solum nasi and nasal walls well ossified; length of ethmoid about half ethmosphenoid length.—Vomers with posterior process in contact with each other; lateral ethmoidal contact of palatoquadrate absent, medial contact synchondrosal.—Anterior lower jaw with tusks; teeth with deep infolding at their base, internally polyplocodont.—Dermal bones and scales without cosmine. Lateral line canals in trabecular layer of bone, sensory pores sometimes joining in grooves. Rhombic scales with coarse bony ornamentation.—Scapulocoracoid connected by single contact with cleithrum.

Elpistostege Westoll 1938

Type species. Elpistostege watsoni Westoll 1938.

Diagnosis. Panderichthyid fish with elongate, broad, paired frontals meeting the parietals anterior to the orbits, parietals narrow between orbits expanding posterior to the orbits, postparietals embayed at posterior margin, frontals, parietals and postparietals very close to the same rostroposterior length. Long narrow prefrontals (equals supraorbital 1) reaching as far, or even further rostral, than the frontals. No separate intertemporal (probably included into postorbital), postorbital broad, jugal contact with ventral margin of orbit brief, or lacking. Rounded dorso-ventrally elongated orbits.

Time. Late Devonian.

Elpistostege watsoni Westoll 1938

Text-figures 3–7

Diagnosis. As for genus.

Type horizon and locality. Escuminac Formation, Frasnian, upper Devonian; shore of river Ristigouche at Miguasha, Province of Quebec, Canada.

Holotype. BMNH P60526a, b (posterior half of skull roof).

Additional material: MHNM 538 (head without posterior portion), ?MHNM 537 (postcranial skeleton without fins or head).

Description. The holotype was the only known specimen of *Elpistostege* until 1981; casts of it were used for the identification of MHNM 538. Specimen MHNM 538 will be described here before comparisons are made with the holotype.

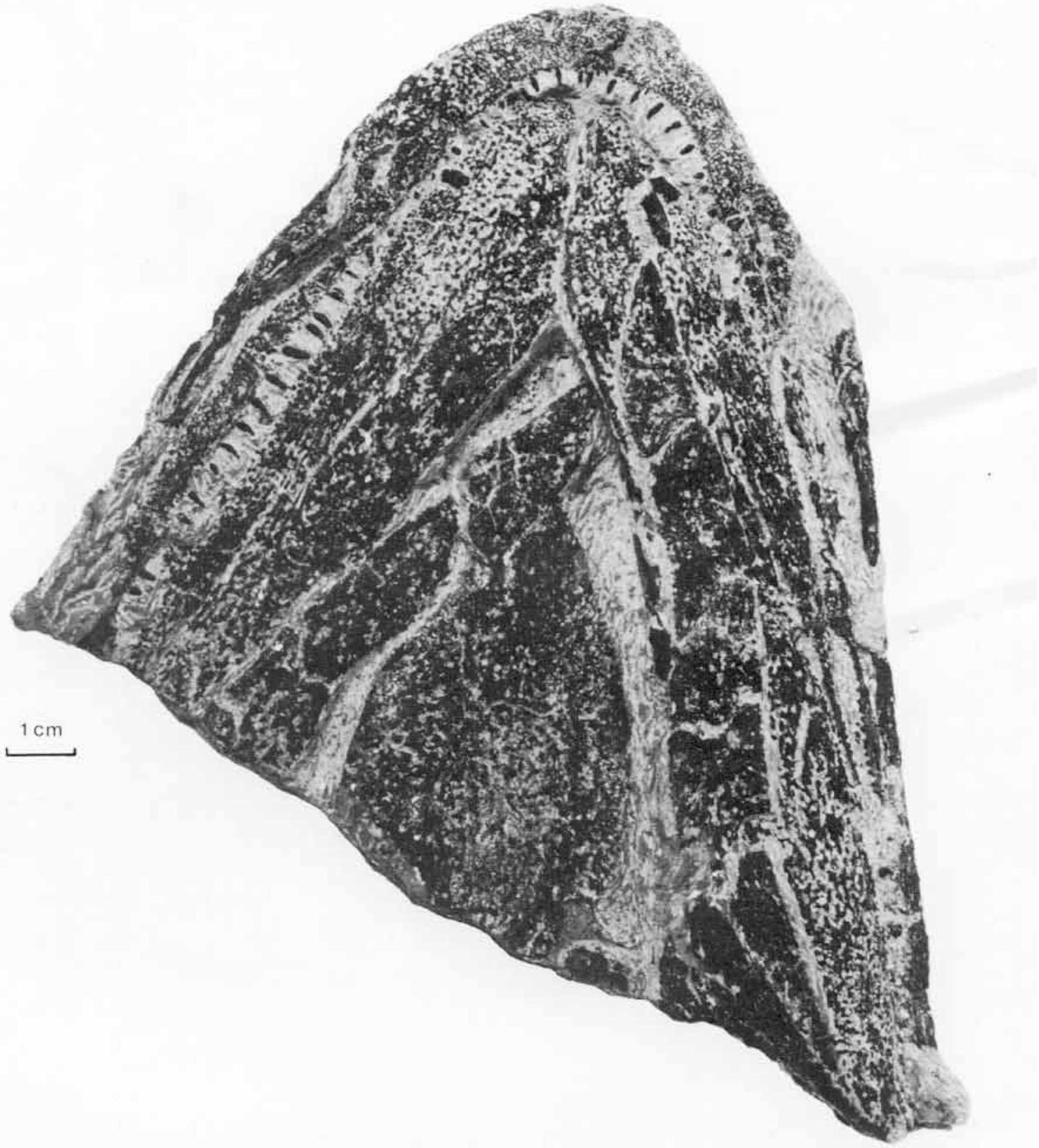
The head of specimen MHNM 538 is flattened post-mortem so that gular plate and lower jaw are in close contact with the palate region (text-fig. 5D). The skull roof is pressed down into one plane, only the 'eye brows' are elevated above that plane. From the snout back to the posterior part of the parietals is all that is preserved of the skull. The posterior margin is broken obliquely so that the jugal is complete and the postorbital nearly so on the left side; both bones are only partially preserved on the right side. The postcranial specimen MHNM 537 is assigned to *Elpistostege* with reservation. The surface sculpture of the scales are similar to that of the skull roof of *Elpistostege*. The distance between dermal ridges on the skull roof is comparable to that of similar ridges on the anterior scales; both are 1·4–1·7 mm apart. Depth of ornament (up to 0·8 mm) is also closely comparable. Only the discovery of a complete specimen could definitely prove the association. Nevertheless, the fact that there is no other form known from the locality of Miguasha with this type of ridge and furrow dermal ornament favours our association of these two specimens.

Skull roof (text-figs. 3, 5A). A tongue of the parietals extends between the elevations ('eye brows') formed by the postfrontals (equals supraorbital 2), medial to the orbits. Behind the postfrontals, the parietals extend a short lateral wing before they widen again posteriorly. The parietal foramen lies through an elevation through which the median suture between the parietals runs anteroposteriorly; lateral to it the parietals are depressed. The postfrontal forms the dorsal or medial margin of the orbit, but reaches anteriorly further than the parietal. Parietal and postfrontal border the posterior margin of the frontal. The frontal is the broadest bone of the skull roof, anteriorly widening and interdigitating with postrostral and nasal. Lateral to the frontal lies the long narrow prefrontal (equals supraorbital 1) which reaches from the anterior margin of the orbit forward to the anterior tectal, extending beyond the anterior margin of the left frontal. The snout is covered by a mosaic of bones in which all sutures are not completely distinguishable. A series of nasals, three on the left and two on the right side, surround paired posterior, medial and anterior postrostrals; together these form the roof of the snout which is elevated above surrounding elements by the tusks in the anterior lower jaw. The orbits are wider dorsolaterally than antero-posteriorly. Each orbit is situated lateral to the high ridge ('eye-brow') that runs on both sides of the parietals and frontals.

Cheek and upper jaw (text-figs. 3, 5A, C). The cheek lies in the same plane as the skull roof; it bends ventrally at the margin to the upper jaw. Most of the broad postorbital, a jugal that reaches far anteriorly, and part of the

TEXT-FIG. 3. Skull of *Elpistostege watsoni*, specimen MHNM 538; dorsal view.

squamosal are preserved on the left side, while only the anterior part of postorbital and jugal remain on the right. The postorbital widely overlaps the parietal (text-fig. 5D) which was traversed by the supraorbital sensory canal. This indicates that the parietal may incorporate the intertemporal as suggested by Borgen (1983) for *Ichthyostega*. The right jugal briefly contacts the posterolateral border of the orbit; it is separated from the left orbit by the lachrymal which borders the postorbital. The lachrymal is a large bone widening anterolaterally. At the extreme lateral border of jugal and lachrymal and near the middle of the anterior tectal, the cheek region bends sharply downwards. At this bend, the upper jaw is crushed into the ventral plane with the lower jaw.

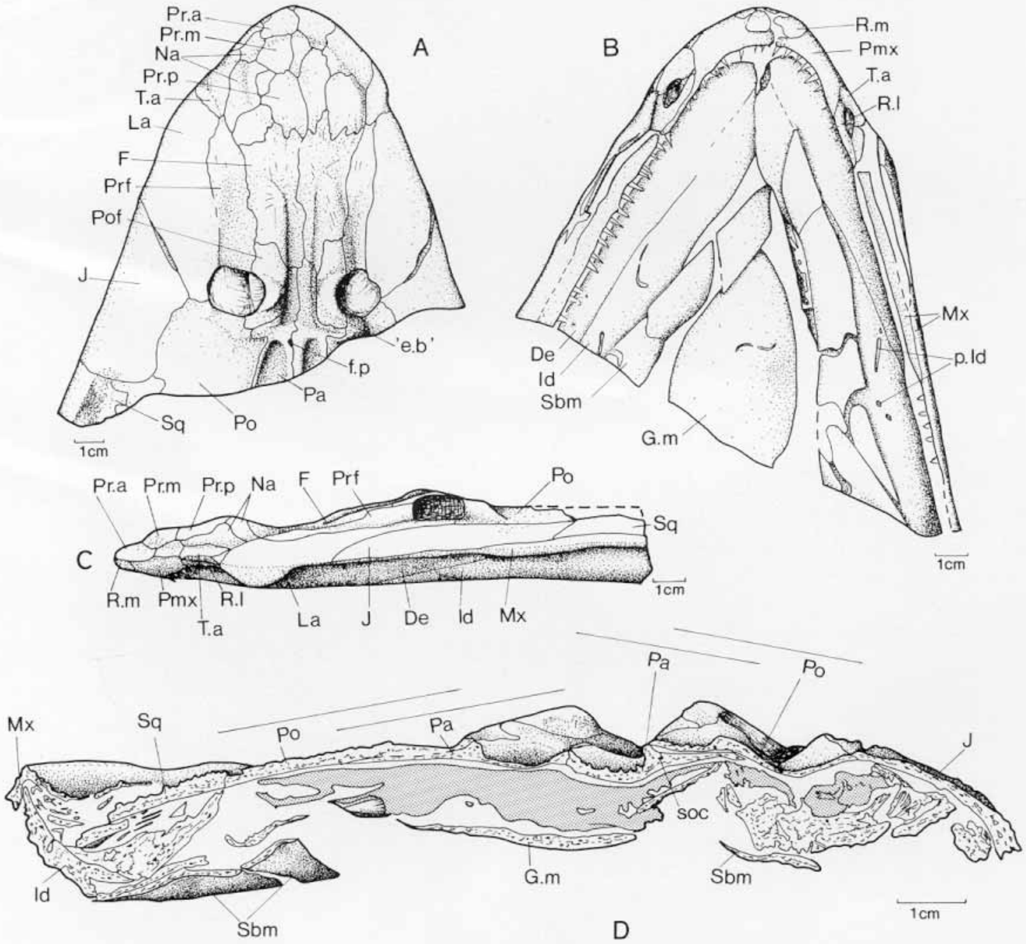


TEXT-FIG. 4. Skull of *Elpistostege watsoni*, specimen MHNM 538; ventral view.

A narrow maxilla forms the middle part of the upper jaw; it reaches to the lateral rostral which is separated from the jaw margin by a narrow posterior extension of the premaxilla. In front of the lateral rostral and anterior tectal, the premaxilla expands and then narrows again at the symphysis to accommodate a pair of median rostrals. Small, evenly spaced, pointed teeth sit on the margin of the maxilla and premaxilla.

The external nasal opening lies close to the margin of the upper jaw. It is surrounded by the lateral rostral and anterior tectal. The lateral rostral lies ventral and posterior to the nasal opening, while the anterior tectal extends from the dorsal and anterior margin of the nasal opening onto the dorsal side of the specimen, where it meets the prefrontal.

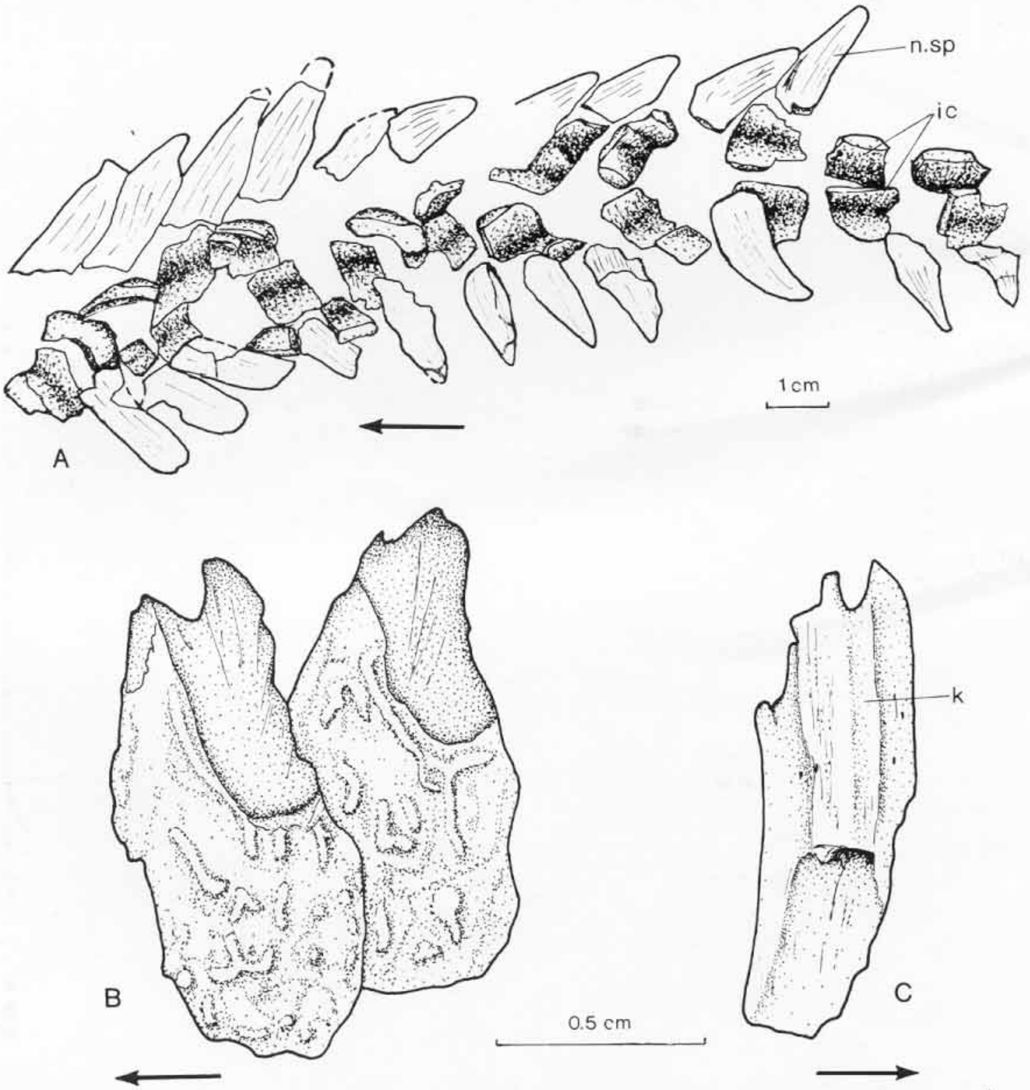
Lower jaw and gular region (text-figs. 4, 5B). The lower jaw is pressed nearly into one plane with the submandibular series and median gular plate; only the left jaw is directed upwards so that the teeth meet the teeth of the maxilla (text-fig. 5D). The boundary between dentary and infradentary series is distinguishable, but the boundaries between the infradentaries are not. Pit lines indicate that three infradentaries of the infradentary series are



TEXT-FIG. 5. Skull of *Elpistostege watsoni*, specimen MHNM 538. A, Dorsal view, B, ventral view, C, lateral view, D, posterior view (oblique cross section, on the left side further posterior than on the right; endocranial part stippled).

preserved. Three right, and four left submandibular bones lie dislocated over the lower jaw and median gular. A large median gular fills the space between the submandibular series.

Skull shape. The skull is post-mortem flattened, still it can be assumed from the cross section (text-fig. 5D) that the skull was, like that of *Panderichthys*, not greatly arched. The orbits are elevated above the skull roof with a deep depression between them. The main arching occurs close to the upper jaw; maxillae and premaxillae lie on the ventral side. The rostral part of the skull reaches far forward so that the mouth becomes subterminal. Orientation of the left lower jaw, with its oblique dorsolateral to ventromedial direction, may correspond closely to its original position. As a whole, the skull is very much like that of a labyrinthodont.

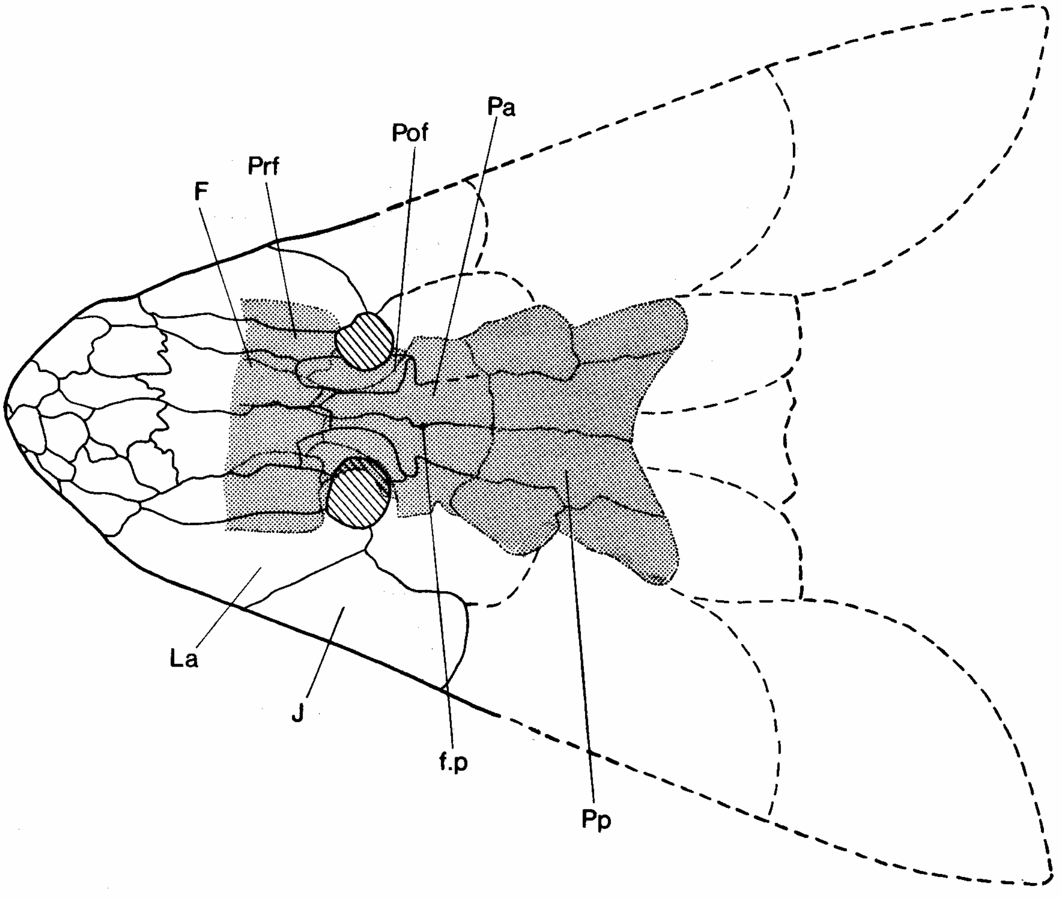


TEXT-FIG. 6. Postcranial skeleton of presumed specimen of *Elpistostege watsoni*, MHNM 537. A, Vertebrae, B, scales in external view, C, scale in internal view. Arrows point anteriorly.

Postcranial skeleton (text-fig. 6). Specimen MNHM 537 is a piece 26–27 cm long and up to 15 cm wide with scales and vertebrae. The specimen is assigned to *Elpistostege watsoni* based on the scale ornament (text-fig. 6B) which is similar to that of the skull bones (text-figs. 3, 4). Comparable rhombic scales are found on the body of complete specimens of *Panderichthys rhombolepis* (Vorobyeva 1980, fig. 1).

A string of sixteen to seventeen vertebrae runs the length of the specimen. Neural arches and intercentra (text-fig. 6A) can be identified; the neural arches, with their smooth perichondral surface, are distinct from the intercentra, which show endochondral bone tissue on the internal surface. As preserved, the vertebrae are compressed dorso-ventrally so that left and right half of the neural arches lie 'dorsal' and 'ventral' to the intercentra, which are seen from their inside or from their anterior or posterior border. The intercentra form broad half rings so that right and left intercentra together completely surround the notochord. Pleurocentra were not identified.

Portions of the scales (text-fig. 6B, C) are preserved in normal contact, and internal and external surfaces can be observed. These rhombic scales are very deep (at least twice as deep as wide). They extensively overlap each other within the dorsoventral scale rows as seen by the unsculptured part of the external side, which occupies up to half of the scale depth. The deep area, ventral to the keel on the internal surface, corresponds to the overlapped area on the external surface. Scales only narrowly overlap each other from scale row to scale row (from anterior to



TEXT-FIG. 7. Comparison of specimen MHNM 638 (solid lines) with holotype BMNH 60526 (dotted lines) of *Elpistostege watsoni*. Posterior part (broken lines) reconstructed after *Panderichthys rhombolepis* (after Vorobyeva 1977*b*, fig. 2B).

posterior). The free external scale surface is covered with irregular, strong bony ridges. On the internal surface, a distinct keel can be seen, but it does not end dorsally in a pronounced peg. The dorsal border forms a broadly based expansion ('peg') with irregular margin.

Comparison with holotype (text-fig. 7).

The holotype (BMNH P60526a, b) comprises the posterior half of the skull roof including the posterior end of the frontals and prefrontals and extending back to the posterior margin of the postparietals. The bones are seen in internal view, and were accurately figured by Westoll (1938). Specimen MHNM 538 agrees with the holotype in shape and form of the orbits, in the external ornament (preserved as an imprint in the holotype), in the position of the parietal foramen, the shape and extent of the anterior part of the parietals, and the posterior part of the frontals. These congruences and the fact that there are no other similar fish known from the Escuminac Formation at Miguasha, corroborate the assignment of the new specimen to *Elpistostege watsoni*. Differences occur in the width of the prefrontal, the postfrontal, and the posterior part of the parietal. These differences are the effect of overlap between bones because size and shape of skull roof elements varies widely between internal and external surfaces. This means that the prefrontal extensively underlies frontal and lachrymal, and that the parietal extensively underlies the postorbital (compare text-fig. 5D).

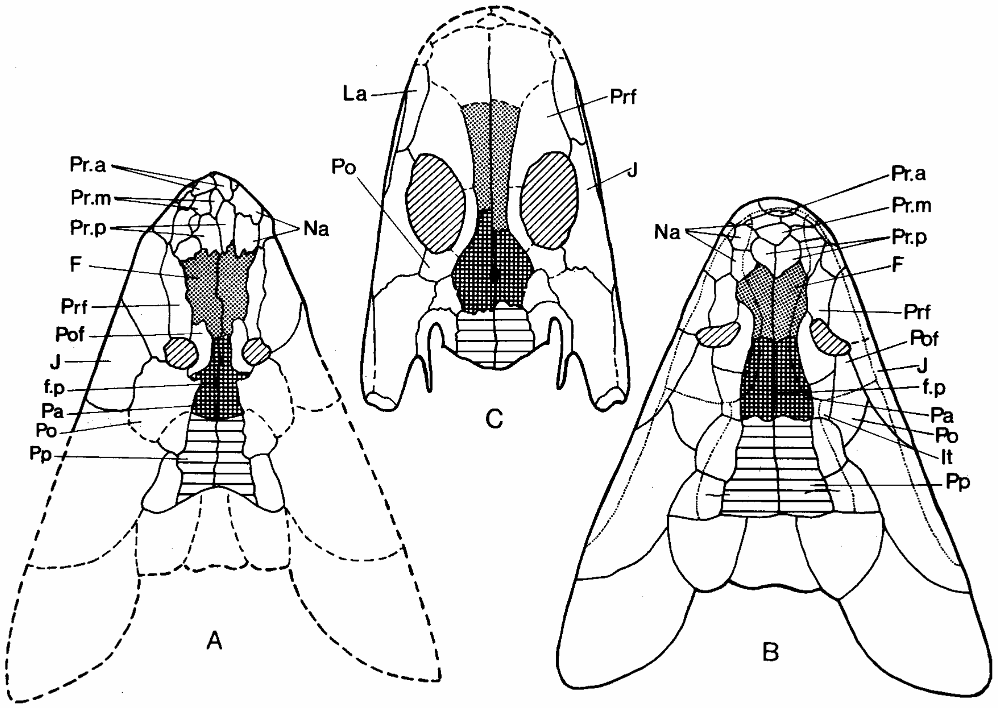
SYSTEMATIC POSITION OF *ELPISTOSTEGE*

Elpistostege was considered by Westoll (1938) as a labyrinthodont with 'a perfect transition between Crossopterygian and Ichthyostegid patterns of dermal bone'. The similarities to which Westoll (1938) referred still hold even though Vorobjewa (1973) correctly placed *Elpistostege* within the Panderichthyidae. Comparison of *Panderichthys*, *Elpistostege*, and *Ichthyostega*, with the rhipidistian, *Osteolepis*, and the labyrinthodont, *Greererpeton* (Table 1), indicates a close relationship between panderichthyids and early tetrapods, and agrees with placement of *Elpistostege* within panderichthyids (Vorobjewa 1973).

TABLE 1. Comparison of skull and cheek bones between three osteolepiforms and two labyrinthodonts

	Osteolepis	*Panderichthys*	*Elpistostege*	*Ichthyostega*	*Greererpeton*
skull roof	arched	flat	flat	flat	flat
orbits	lateral	high dorsal	high dorsal	high dorsal	high dorsal
external naris	above margin	marginal	marginal	marginal	marginal
parietal opening	between orbits	behind orbits	behind orbits	behind orbits	behind orbits
intracranial joint	external	not external	not external	not external	not external
sensory canals	in bone	in bone	in bone	in bone	in grooves
ornament	cosmine	bony ridges	bony ridges	bony ridges	bony ridges
snout shape	vertical	prominent	prominent	vertical	vertical
rostrals	?	unpaired	one pair	unpaired	none
postrostrals	?	1 pair, 2 single	3 pairs	none	none
position frontals	anterior orbits	between orbits	anterior orbits	between orbits	between orbits
frontals	?unpaired	paired, broad	paired, broad	paired, narrow	paired, long
parietals	between orbits	narrow between and wide behind orbits			behind orbits
postparietals	very long	paired, long	paired, long	unpaired, short	paired, short
anterior tectal	present	present	present	present	none
lateral rostral	present	present	present	reduced	septomaxillar
prefrontal	?	elongated	very elongated	broad	broad
postfrontal	narrow	broad posterior	narrow	narrow	broad posterior
intertemporal	present	present	missing	missing	sporadic
jugal	at orbit	at orbit	not or at orbit	wide at orbit	wide at orbit
squamosal	large	large	?large	medium	medium, long
median gular	small	large	large	none	none
submandibulars	present	present	present	none	none
operculum	present	present	present	none	none
preoperculum	present	present	present	reduced	none
extrascapularia	present	present	present	none	none

The flat skull with high dorsally situated orbits links the panderichthyids and labyrinthodonts. The external nasal opening lies very close to the margin of the upper jaw. An external intracranial joint is not developed. The parietal foramen has a position behind the orbits even though the parietals reach between the orbits as in osteolepiforms and ichthyostegids. A pair of frontals extending from between (*Acanthostega, Ichthyostega, Panderichthys*) or just in front of the orbits (*Elpistostege*) is common to all these forms (text-fig. 8).



TEXT-FIG. 8. Comparison of skull roofs of A, *Elpistostege watsoni*, B, *Panderichthys rhombolepis* (after Vorobyeva 1977*b*, fig. 2B), and C, *Acanthostega gunnari* (after Jarvik 1952, fig. 34A).

On the other hand, features such as many bones in the snout region, submandibular series, gular plates, opercular series (Vorobyeva 1977*b*), extrascapular series (Vorobyeva 1977*b*), heavy bony rhombic scales, and fins (known from *Panderichthys* only) are clearly osteolepiform piscene features of the panderichthyids. Some piscene features can still be found in ichthyostegids, such as sensory canals enclosed in bone, and an external nasal opening surrounded by the anterior tectal and lateral rostral.

The large median gular and the subterminal mouth (prominent snout) are the main features uniting *Elpistostege* with *Panderichthys*. The three pairs of nasals, anterior, medial; and posterior postrostrals, elongate prefrontals, and the elevation ('eye brows') dorsomedial to the orbits are further indication of a close relationship between these two genera. They are distinct from each other in the presence (*Panderichthys*) or lack (*Elpistostege*) of the intertemporal, the shape of parietal, prefrontal, and the postfrontal, and in the position of the suture between parietal and frontal. The jugal always reaches the orbit in *Panderichthys*, but not always in *Elpistostege*. The shape of the orbits is quite different, and the postorbital seems to be much larger in *Elpistostege*.

In conclusion, *Elpistostege* is a member of the Panderichthyidae, and the Panderichthyidae are closely related to early tetrapods. We suppose that the loss of the intertemporal occurred independently in *Elpistostege* and ichthyostegids and other labyrinthodonts many times in parallel. The single, fused postparietal is an autapomorphy of *Ichthyostega*, while paired postparietals are present in the ichthyostegid *Acanthostega*.

TABLE 2. Relation between length of frontal (fr), orbit (orb), parietal (pa), postparietal (pp), distance anterior border parietal to snout (sn), and skull roof (sk)

	sn/sk %	fr/sk %	pa/sk %	pp/sk %	orb/sk %	pp/pa %	fr/pa %
Osteolepis	32	—	23	45	18	198	—
Panderichthys	45	20	24	30	5	125	83
Elpistostege	51	29	26	22	9	84	88
Ichthyostega	50	28	26	25	19	95	108
Greererpeton	56	41	24	19	14	81	176

Relative proportions of skull bones changed at different rates in the transition from osteolepiforms to early tetrapods (Table 2). The parietal had an equal length in these forms, about one quarter of skull roof length, while the frontal enlarged gradually from panderichthyids to ichthyostegids (longer in *Acanthostega* than in *Ichthyostega*) to labyrinthodonts. The postparietal reduced its length markedly, a point especially noted by Westoll (1938, 1943). The greatest change in the relationship between length of postparietal to length of skull or parietal occurred during the transition between osteolepid and rhizodontid osteolepiforms on one hand and panderichthyid osteolepiforms and labyrinthodonts on the other. All these proportional changes reflect the change in snout proportion. The snout is longer in panderichthyids and labyrinthodonts than in other osteolepiforms. The typical ontogenetic postorbital growth in osteolepiforms is reduced in panderichthyids and labyrinthodonts. Postorbital growth in osteolepiforms is correlated with ontogenetic reduction of orbital size (Schultze 1984). *Osteolepis* (text-fig. 1A) is a small osteolepiform where the orbit size does not differ much between juvenile and adult, while it does in the large *Panderichthys* and *Elpistostege*. Ontogenetic change in the size of the orbit of *Eusthenopteron* is intermediate between *Osteolepis* and *Panderichthys—Elpistostege*. Relative size of the orbit in tetrapods is similar to that of juvenile osteolepiforms.

These gradual changes make it difficult if not impossible to identify incomplete specimens as fish or amphibian (see Jarvik's 1981 critique of Rosen *et al.* 1981). Like Westoll (1938), the authors even considered the new skull of *Elpistostege* as that of a labyrinthodont before the ventral side was prepared. *Crassigyrinus* is another incompletely known form (cheek, preorbital region, cranial roof, vertebrae) 'intermediate between . . . a typical rhipidistian . . . and the Devonian amphibian *Ichthyostega* (Panchen 1973, p. 190)'. The proportions of the skull (long postorbital region), the composition of the snout, the course of the infraorbital line, the large preopercular and squamosal are fish-like (osteolepiform features). Shape (as in *Elpistostege*) and size of orbit, narrow anterior portion of parietal (as in *Elpistostege*), posteriorly widened postfrontals (as in *Panderichthys*), size of quadratojugal, quadrate, maxilla, and premaxilla are not unquestionably tetrapod features. The prefrontal is within the size range of panderichthyids, and the ornament could not be easily distinguished from osteolepiforms devoid of cosmine. The comparably small postorbital, the long border of the jugal with the ventral margin of the orbit, the lachrymal not reaching the orbit, the external nasal opening located away from the margin of the upper jaw, and snout not prominent, excludes *Crassigyrinus* from the Panderichthyidae, but not from other osteolepiform or rhizodont rhipidistians. Postparietals and tabulars are reduced to labyrinthodont size (Panchen 1980, fig. 8).

The 'two apparently adjacent centra' (Panchen 1980, p. 340 and fig. 9a, b) of *Crassigyrinus* are very similar to those in specimen MNHM 537, tentatively assigned to *Elpistostege*.

Campbell and Bell (1977) described a 'primitive amphibian' jaw from the late Devonian of New South Wales, Australia. It is difficult but not impossible to distinguish an osteolepiform jaw from one of an early amphibian. Campbell and Bell's (1977) reasons for placing *Metaxygnathus* within the ichthyostegids were based on the following features: size of the retroarticular process, the splint-like dentary, and the elongate and anteriorly acuminate surangular. We believe these characters are insufficient evidence of tetrapod affinities. A retroarticular process is normally missing in osteolepiforms (and in many labyrinthodonts), however, Vorobyeva (1977*b*) has figured a distinct retroarticular process in the osteolepiform *Lamprotolepis*. The ornament on the jaw of *Metaxygnathus* is fine, the symphysis weak, and the prearticular extends almost to the symphysis; these features are clearly those of a fish. Other characters found only in osteolepiforms include: a mandibular canal, enclosed by bone (no sulcus!), with three pores visible in infradentary 2 (equals postsplenial) and 4 (equals surangular), and an adsymphysial tooth plate. Distinct coronoids with tusks are typical of rhipidistians, still, they occur in some labyrinthodonts. Even though the characteristics of this lower jaw are insufficient to align *Metaxygnathus* with any specific osteolepiform, it clearly belongs within that group.

Elpistostege, *Crassigyrinus*, and *Metaxygnathus* are examples of the difficulties of distinguishing osteolepiform rhipidistians and early labyrinthodonts (Jarvik 1981). These numerous similarities of structure would be surprising convergences if they do not indicate a close relationship between rhipidistians and tetrapods.

Acknowledgements. The authors wish to express their gratitude to the Government of the Province of Quebec for purchasing the new *Elpistostege* skull for the Musée d'Histoire Naturelle de Miguasha and for continuing support for protection, services, and excavations at this famous locality. Norman Parent of Miguasha kindly draw the attention of the junior author to the specimen. We thank O. Bonner, Museum of Natural History, Lawrence, Kansas, for the difficult and careful preparation of the specimen, and J. Chorn for taking the photographs of the specimen. Dr. P. Forey, British Museum (Natural History), London, kindly supplied the senior author with casts of part and counterpart of the holotype of *Elpistostege watsoni*. The senior author thanks Dr. K. S. W. Campbell, Department of Geology, Canberra, Australia, for permission to examine the jaw of *Metaxygnathus*, and Dr. E. Vorobyeva, Institute of Morphology and Ecology of Vertebrates, Moscow, for the translation of parts of her 1977*b* publication. Finally, we thank J. Chorn and M. Gottfried, both Museum of Natural History, Lawrence, Kansas, for improving the manuscript stylistically.

ABBREVIATIONS

In text-figures: De, dentary; 'e.b.', 'eye-brow' (elevation medial to orbit); F, frontal; f.p, parietal foramen; G.m, median gular; Id, infradentary; It, intertemporal; i.c, intercentrum; J, jugal; k, keel; La, lacrimal; Mx, maxilla; Na, nasal; n.sp, neural spine; orb, orbit; Pa, parietal; p.ld, pit-line of infradentaries; Pmx, premaxilla; Po, postorbital; Pof, postfrontal; Pp, postparietal; Pr.a, anterior postrostral; Pr.m, median postrostral; Pr.p, posterior postrostral; Prf, prefrontal; R.l, lateral rostral; R.m, median rostral; Sbm, submandibular; soc, supraorbital canal; Sq, squamosal; St, supratemporal; T.a, anterior tectal; Ta, tabular.

Institutions: BMNH, British Museum (Natural History), London, England; MHNM, Musée d'Histoire Naturelle de Miguasha, Québec, Canada.

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HANS-PETER SCHULTZE

Museum of Natural History and
Department of Systematics and Ecology
University of Kansas
Lawrence, KS 66045
U.S.A.

MARIUS ARSENAULT

Ministère du Loisir, de la Chasse et de la Pêche
Musée d'Histoire Naturelle de Miguasha
P.O. Box 183
Nouvelle, Québec
Canada GOC 2EO

Typescript received 3 May 1984