

Anatomy of the Silurian thelodont *Phlebolepis elegans* Pander

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Abstract. The Silurian thelodont *Phlebolepis elegans* Pander from Saaremaa, Estonia, is one of the most-often illustrated early vertebrates, yet its external morphology has remained poorly known and experts seldom agree about its probable body form. We examined hundreds of articulated specimens from the type locality (Himmiste Quarry) to reconstruct its morphological features. We found that a reconstruction published more than four decades ago by A. Ritchie was the best available till now. We disagreed mostly in that the mouth is not terminal, but subterminal, and there is a slight development of a rostrum dorsal to the mouth. The pectoral fin originates close behind the orbits, but is otherwise similar to Ritchie's reconstruction. We also found the caudal fin to be much larger, more flexible and more symmetrical (though not perfectly symmetrical) than earlier reconstructions, with a large dorsal lobe and an even larger ventral lobe, and a fin web supported by slender 'ray-like' scale-covered lobes. The shape, number and location of the branchial openings are notably still not certainly known. Our preferred morphological features are represented by an artist's restoration. With this revised understanding, future representations of *Phlebolepis elegans* can be based on more reliable information and its morphology can be compared more accurately with that of other early vertebrates.

Key words: *Phlebolepis elegans*, Silurian, Saaremaa, Estonia, Thelodonti, morphology, reconstruction.

INTRODUCTION

Phlebolepis elegans Pander, 1856, is one of the most-often illustrated early vertebrates (e.g., Carroll 1988). It has often been the only thelodont illustrated in books of vertebrate palaeontology, comparative anatomy or general biology. While other well-preserved thelodont fossils have become better understood in recent years (e.g., Wilson & Caldwell 1993, 1998; Märss & Ritchie 1998; Märss et al. 2006), the morphology of thelodonts described in earlier decades has not been as well understood as that of *Phlebolepis*. However, despite their frequent use to illustrate thelodont morphology, published reconstructions of *Phlebolepis elegans* have taken a great variety of forms, and there has been an apparent lack of consensus about the major features of its body (Fig. 1).

The species was originally named by Pander (1856) based on isolated scales from Saaremaa Island, Estonia, and it was only much later that articulated specimens were found. In 1929, A. Luha, University of Tartu, discovered a mass-mortality deposit of articulated specimens in the Himmiste-Kuigu Quarry on Saaremaa. Luha produced only a short paper on osteostracans of Saaremaa (Luha 1940), but more than 70 examples were studied in Oslo and named *Coelolepis luhai* Kiaer, 1932, in a paper that was edited by A. Heintz after Kiaer

died in 1931. Hoppe (1933) later synonymized Kiaer's genus and species with Pander's taxa, and the scales and articulated specimens have been considered synonymous ever since, under the name *Phlebolepis elegans* Pander.

Numerous papers have been devoted to the morphology, variability and microstructure of the scales (Hoppe 1931; Bystrow 1949; Gross 1967, 1968; Karatajūtė-Talimaa 1978; Märss 1986a, 1986b), the lateral line system (Gross 1968; Märss 1979), the body morphology (Fig. 1) often accompanied by reconstructions (Westoll 1945; Bystrow 1949; Stensiö 1964; Obruchev 1964; Ritchie 1968; Janvier 1975; Blicek & Janvier 1999; Wilson & Märss 2004) and the taphonomy of the fossil occurrence, which is interpreted as a fossilized school (shoal) subjected to a mass-death event (Robertson 1938; Märss et al. 2003).

After 1929, several excavations of the quarry, most notably those by W. Patten (e.g., 1931), produced additional specimens, exhausting the quarry; in recent decades, no articulated agnathans have been found apart from a few shields of *Tremataspis mammillata* Patten and *Dartmuthia gemmifera* Patten. Many specimens of *P. elegans*, as well as of osteostracans, have been exported to museums in Europe (e.g., BMNH, London) and North America (e.g., AMNH, New York), but the largest collection of *P. elegans* in the world is the Luha

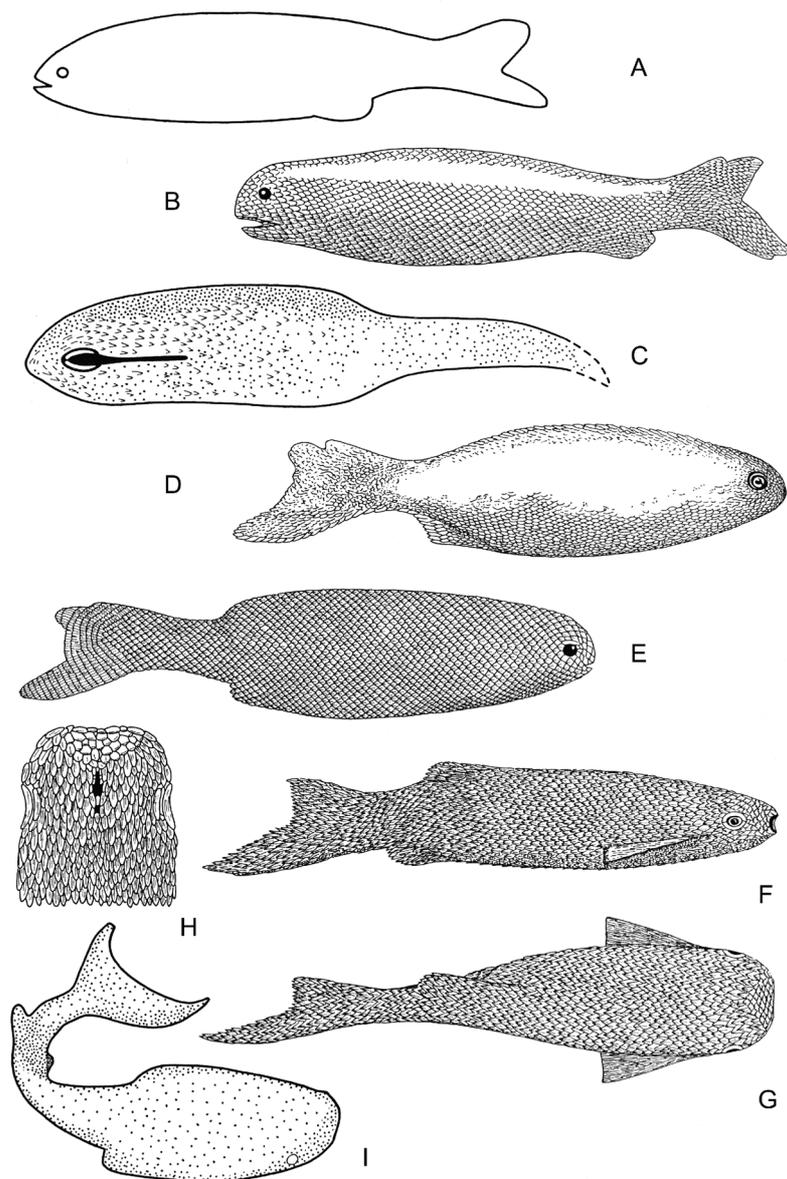


Fig. 1. History of reconstructions of body shape of *Phlebolepis elegans*. **A**, Westoll 1945, fig. 5A; **B**, Bystrow 1949 (figure taken from Berg 1955); **C**, Stensiö 1964, fig. 110C; **D**, Obruchev 1964, fig. 10; **E**, Gross 1968, fig. 3A; **F**, **G**, Ritchie 1968, fig. 3; **H**, Janvier 1975, fig. 3G; **I**, Blicek & Janvier 1999, fig. 9.3H. Body length of *Phlebolepis* is ca 7 cm. Reproduced from Märss et al. (2007) by permission of the publisher, Verlag Dr Friedrich Pfeil.

collection that belonged originally to the University of Tartu. In 1947 it was given to the Institute of Geology of the Academy of Sciences of Estonia in Tallinn, where over 250 specimens were studied and numbered (Märss 1979, 1986a, 1986b). Then, in 1995, it was decided to return the vertebrate collection to the University of Tartu. That plan prompted a re-examination of the articulated specimens of *P. elegans* for study of their taphonomy (Märss et al. 2003) and for a revision of

their anatomy (Wilson & Märss 2005) by the present authors. During that re-examination, several unstudied slabs with beautifully preserved specimens were discovered. A few additional specimens were discovered also in the E. Bõlau collection in Tartu, which mainly contains osteostracan head shields.

While the squamation of *P. elegans* is well known, and the body form was often illustrated, very little has been published about the internal structure of this

animal. Märss & Wilson (2008) described internal structures of *Phlebolepis* for the first time. The denticles and denticulate platelets discovered, along with rostral, cephalo-pectoral and lateral scales, give evidence that they come from the anterior part of the body, from the lining of the bucco-pharyngeal and branchial regions (i.e., the mouth and throat, and the branchial ducts and chambers).

The present study is based on nearly all the available specimens from the Himmiste Quarry and is designed to re-evaluate the external morphology of *Phlebolepis elegans*. This study concentrates on the mouth, caudal fin and the branchial region of *P. elegans*, where new information has led to a revised interpretation of the body form. It is hoped that the new data will allow more accurate reconstructions to be prepared for this often-illustrated and iconic early vertebrate.

MATERIAL AND METHODS

We studied altogether 48 slabs of different sizes (see Märss et al. 2003, table 1) belonging to the Museum of Geology, University of Tartu (TUG 865 + slab + specimen number). These contained more than 450 specimens (one labelled GIT 211-1). One of us (M. V. H. W.) also examined additional specimens at the AMNH, New York. However, the best-preserved specimens are in the Tartu collection.

The preservation of *P. elegans* specimens on different slabs is highly variable. Specimens are found on the slabs either in dorsal, ventral or lateral view, or in a variety of oblique views, and usually with some curvature of the body. Some degree of distortion is apparent in most specimens. The original slabs were split apart by pioneer discoverers yielding part and counterpart specimens. In most specimens, there are large numbers of the original scales present in articulation or semi-articulation, while in others the scales are missing and their natural molds remain. When present, the colour of the scales varies from white through light beige to dark coffee-brown.

Because of the variable preservation, no single specimen was well preserved in many respects. Therefore, it was necessary to examine numerous specimens and to base our anatomical conclusions on the best-preserved parts of the best specimens.

Based on these results, we also worked with an artist to create preliminary sketches and eventually a colour painting illustrating the most likely body features of *P. elegans* swimming in a school over a marine carbonate seafloor. Although the orientation of the specimens was likely taphonomic rather than biological, Märss et al.

(2003) found that there was often one slightly more strongly preferred orientation on most slabs for the heads and tails of the specimens, and attributed this to very weak wave or current action.

RESULTS

Order PHLEBOLEPIDIFORMES Berg, 1937

(= KATOPORIDA Karatajüte-Talimaa, 1978)

Family PHLEBOLEPIDIDAE Berg, 1940

Genus *Phlebolepis* Pander, 1856

Phlebolepis elegans Pander, 1856 (= *Coelolepis luhai* Kiaer, 1932)

General morphology

Phlebolepis elegans was a small jawless vertebrate about 7 cm in length. It possessed paired lateral (pectoral, suprabranchial) fins extending from close behind the orbits and ending at the posterior end of the cephalobranchial region. There was also a small, posteriorly situated dorsal fin and a small anal fin (Fig. 2). Paired pelvic or abdominal fins were absent. The caudal fin was large and clearly hypocercal, the main ventral lobe being noticeably more stout than the dorsal lobe, although the dorsal and ventral lobes were nearly equal in posterior extent.

Phlebolepis elegans had a generally fusiform body in life, with a somewhat depressed (dorsoventrally flattened) cephalobranchial region that comprised about half the total body length, and a laterally compressed trunk and tail (Figs 2, 3).

The degree of dorsoventral flattening (depression) of the cephalothorax was modest, as judged by preserved shape and by the orientation of the specimens on the bedding plane (Fig. 3). Concerning preserved shape, most specimens preserved in dorsoventral view are slightly wider than most of those preserved with the cephalobranchial region in lateral view (compare Figs 2 and 3). With respect to orientation of specimens, we noted the approximate proportion of specimens preserved in dorsoventral as opposed to lateral view. The trunk and tail were moderately to strongly laterally compressed, as seen in some specimens where the tail was preserved mainly dorsoventrally (Fig. 3A, B). If the cephalobranchial region had been approximately circular in cross section, the compressed trunk and tail would have caused specimens to be found mainly as lateral compressions. However, approximately 40% of all specimens are preserved with their cephalobranchial region in dorsoventral compression (as tallied from Märss et al. 2003, figs 6–9). We conclude that the cephalobranchial region was slightly to moderately depressed in life, and

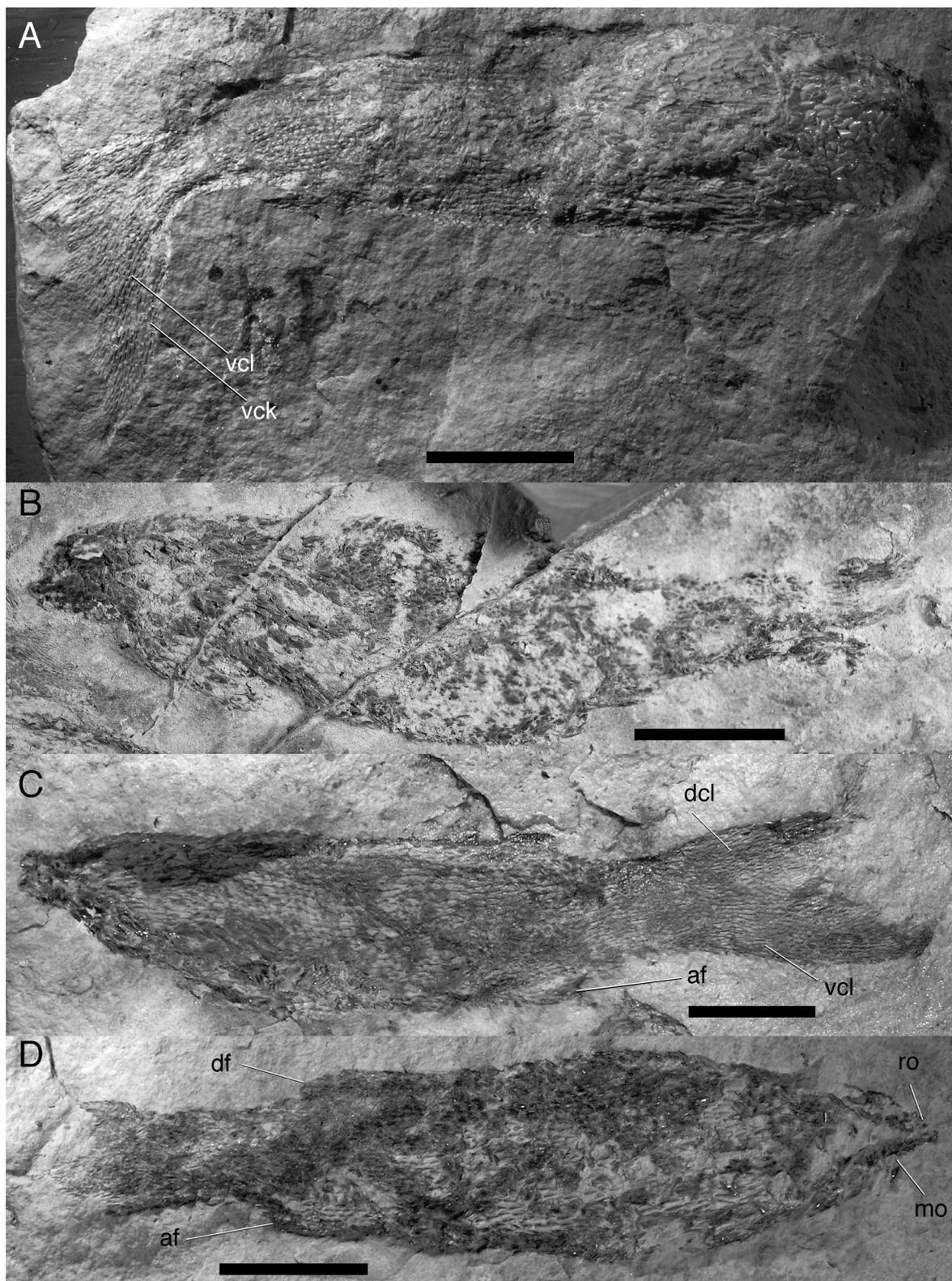


Fig. 2. *Phlebolepis elegans* Pander. Specimens preserved in lateral view, from Himmiste-Kuigu, Saaremaa, Estonia. **A**, GIT 211-1 (previously numbered as Pi 6682); **B**, acid-prepared specimen TUG 865-42; **C**, TUG 865-5-26; **D**, TUG 865-4-3. C, D imaged wet. Scale bars are each 1 cm. Abbreviations: af, anal fin; dcl, dorsal caudal lobe; df, dorsal fin; mo, mouth; ro, rostrum; vck, ventral caudal keel; vcl, ventral caudal lobe.

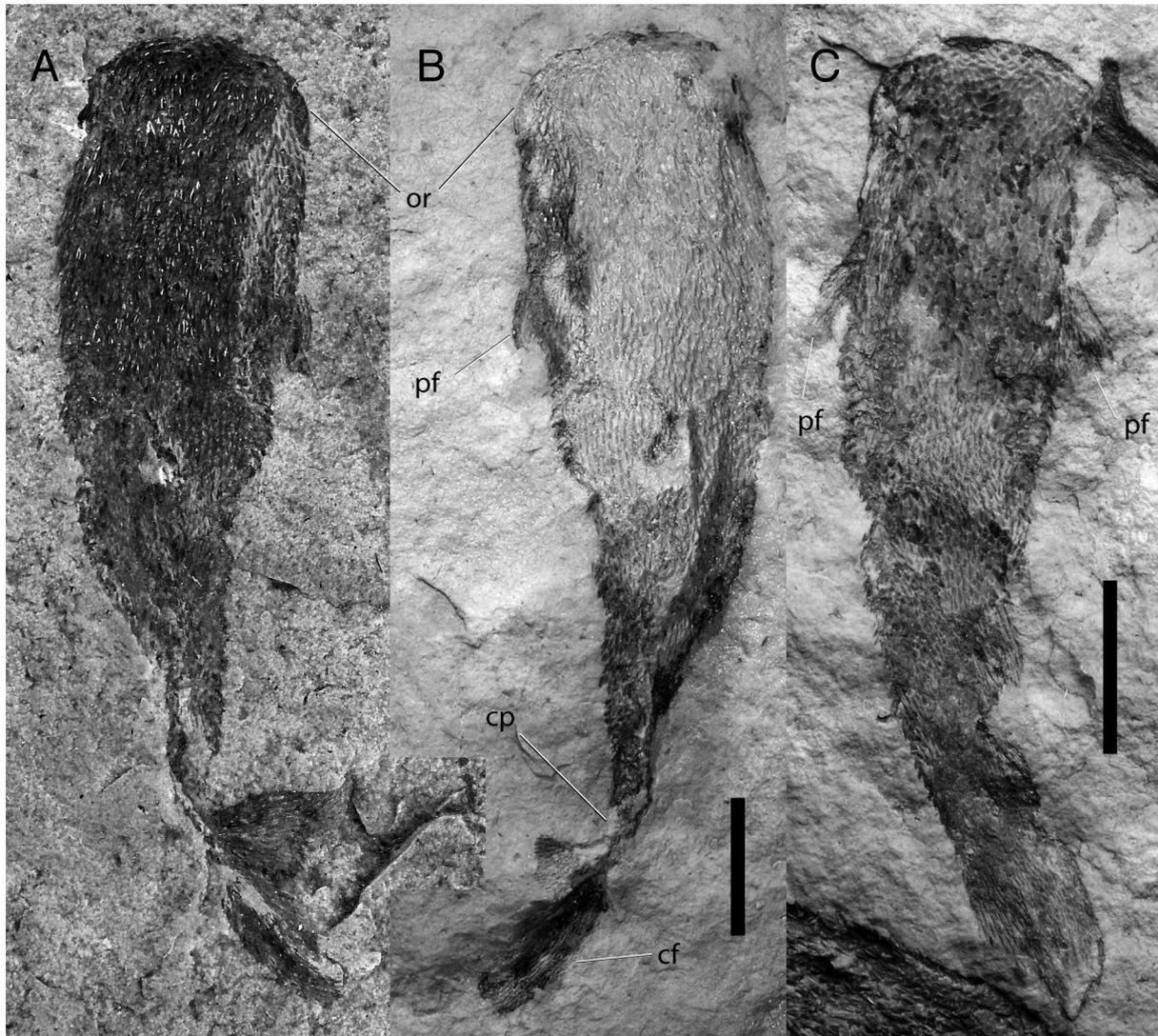


Fig. 3. *Phlebolepis elegans* Pander. Specimens preserved in dorsal view, from Himmiste-Kuigu, Saaremaa, Estonia. **A**, TUG 865-14-1, counterpart of B; **B**, TUG 865-14-6, counterpart of A; **C**, TUG 865-14-2. Scale bars are each 1 cm. Abbreviations: cf, caudal fin; cp, caudal peduncle; or, orbital scales; pf, pectoral fin.

that the ultimate orientation of each specimen depended on whether the depressed cephalobranchial region or the compressed trunk and tail determined the orientation of the carcass.

Squamation

Scale morphology varies on the body; different scale types have been defined and described several times (Märss 1986a, 1986b; Märss et al. 2007; Märss & Wilson 2008) and will not be repeated here. Sculpture (elements of ornament larger than 50 µm) on the crown of typical body scales consists of posteriorly converging

ridges that meet in a central raised crest (Märss et al. 2007, fig. 80). Rostral and cephalopectoral scales have marginal ridges and smooth crowns. Ultrasculpture (the finest sculpture known so far, up to 25 µm wide and up to 50 µm in length) on the crown surface of body scales consists of fine longitudinal striations (Märss 2006). The predominant orientation of the rows of scales and the main ridge on each scale is longitudinal (Figs 2A, 3A, B). Exceptions include the rostral region (Fig. 4A, B) and the rows of small scales surrounding the mouth (Fig. 4E), where transverse and oblique rows occur, and the branchial region ventral to the pectoral fins (Fig. 5), where the more posterior scales are oriented obliquely, anterodorsally to posteroventrally.

Head

The head is slightly to moderately depressed so that it is broader than it is deep. The anterior margin of the head is slightly convex and the anterolateral corners immediately anterior to the orbits are pronounced (Figs 3, 4A, B). There is a narrow rostral area located anterodorsal to the subterminal mouth (Figs 2D, 4A, C–E, 5). In some specimens, the rostral scales are taphonomically displaced anteriorly as a unit, but still attached to the head posteriorly (Fig. 4D).

Orbits

The orbits, located just posterior to the anterolateral corners of the head (Figs 3A, B, 4A, B, E, 6B–D), were bordered by two pairs of larger, lunate orbital scales, one above each orbit and one below. The orbital scales resemble body scales but the surface has reduced ornament. The orbits between the orbital scales were not circular, but in the shape of an elongate oval. We saw no evidence of scleral bones within the orbit.

Pineal

The pineal region is marked in some but not all specimens by a specific ring-shaped arrangement or symmetry of scales. There is no pineal foramen. Typically there is not a well-defined macula, pineal spot or specialized scale, but rather the location of the pineal is inferred as the centre of the scale pattern (Fig. 4A, B).

Rostrum

In earlier reconstructions, the mouth was often omitted or scarcely illustrated (e.g., Fig. 1D), or shown as terminal (Fig. 1F). The best-preserved specimens that we examined seem to show the modest development of a rostrum dorsal to the mouth (Fig. 4C, D), occasionally seen also in ventral view (e.g., Fig. 4E), although it is not as much developed as the rostrum of many basal heterostracans (e.g., *Athenaegis*; Soehn & Wilson 1990, fig. 7). In well-preserved specimens seen in dorsal view, the mouth is not visible (Fig. 4A). The scales on the rostrum are small and slightly transversely elongated. In ventral view, the mouth is often visible, though usually very distorted, and in well-preserved specimens (Fig. 4E), there is a pre-oral field of small transversely elongated scales. Post-oral scales are usually not well preserved, but there are remnants of small scales in this area in some specimens.

Mouth

The mouth is usually preserved distorted in some way. It can be preserved obliquely and can take on various

shapes, suggesting that it was surrounded by easily distorted soft tissue. In a very few well-preserved specimens (e.g., Fig. 4E), the mouth appears to be about half as wide as the head, with a slightly convex anterior margin and a moderately convex posterior margin. It is bordered by small, diamond-shaped pre-oral scales. Posteriorly the scales bordering the mouth are mostly lost from the specimens, but remnants of these post-oral scales were also of small size (Fig. 4E).

Lateral line system

The lateral line system consists of scales penetrated by pore-canal and one or more large external pores on the scale crown. Pore scales are arranged in rows, forming dorsomedian, dorsolateral and supraorbital canals on the dorsal surface of the head, and ventrolateral canals on the ventral surface; short commissures were distributed between the canals (Märss 1979).

Pharyngobranchial region

The pharyngobranchial region, the part of the animal posterior to the mouth and ventral to the orbits and pectoral fins, is generally not well preserved, and the number of branchial pouches and branchial openings is uncertain. Märss & Wilson (2008, fig. 6) found evidence for the existence of four pairs of pouches in an inclined row, but without more evidence, the number of branchial pouches and openings must remain uncertain. Variations in profile are interpreted as variation in the inflation of the pharyngeal chamber and/or the branchial pouches. Some specimens seem to have little or no inflation of the pharyngeal region (Fig. 5), whereas others have a convex, seemingly highly inflated profile suggesting a pharynx that could be inflated significantly (Figs 2A, 6C, 7A). This inflated profile is something like that seen in the Silurian thelodont *Pezopallichthys* from northern Canada (Wilson & Caldwell 1998).

Unlike the predominantly longitudinal orientation of the scales on most of the body, at least some of the scales covering the pharyngobranchial region have an oblique long axis, being aligned anterodorsally to posteroventrally (Figs 5A, B, 6D) in a manner that suggests that the branchial pouches or row of branchial openings was also oblique, as it is in anaspids (Blom et al. 2002) and in the fork-tailed thelodonts (Wilson & Caldwell 1998). The oblique orientation of the scale rows is less pronounced immediately posterior to the mouth, but more pronounced towards the posterior end of the branchial region (Fig. 5B), and perhaps the branchial openings were concentrated more posteriorly, as also in anaspids.

Pectoral fins

A single pair of pectoral fins (suprabranchial fins, considered precursors of and homologous at least in part with pectoral fins; see Wilson et al. 2007) is visible on many specimens (Figs 3A–C, 4A, 6A, B), though usually only on one side and usually not the complete fin. As reconstructed from numerous specimens, the fin is extremely thin and composed of radiating ray-like rows of very small scales. The outermost ray is composed of slightly larger scales than the rays within the fin web (Fig. 4A). The fin is triangular, the inner edge being attached to the body, the outer (leading) edge being usually straight, and the posterior or trailing edge also nearly straight or slightly convex. The fin originates close to but posterior to the orbits (Fig. 4A, 6D), and terminates at its trailing edge at or anterior to the posterior end of the branchial region. It is rare for the entire length of the pectoral fin to be visible on a specimen, in most cases only the posterior half or third being visible extending from the side of the body (Fig. 3B). In Fig. 4A it is possible to trace the enlarged scales of the outermost ‘ray’ to their origin immediately posterior to the orbital scales. Certain specimens preserved in lateral view show a slightly oblique line of small scales extending posteriorly from the orbital region (Fig. 6C, D), dorsal to the branchial region. This is the line of attachment of the pectoral fin to the body.

Branchial openings

Unfortunately, despite transfer (acetic acid) preparation of specimens that might be expected to show branchial openings (e.g., Fig. 2B), no definitive branchial openings have been seen. In an earlier study, we identified crescent-shaped sets of lateral scales that remained attached to each other after acid dissolution of matrix and that are thought to originate from the branchial region (Märss & Wilson 2008). These scale sets have a sculptured surface on the edge of the concave side that might have been the margin of a branchial opening. We have not identified these scale sets in any articulated specimens. In that study we also identified very fine platelets consisting of two or three small denticles joined in a linear series, and in one specimen we found (Märss & Wilson 2008, fig. 2h) some such platelets just beneath the pectoral fin base, distributed stepwise in rows. In summary, we suggest that branchial openings of *P. elegans* were small, in an oblique row located beneath the pectoral fin, posterolaterally on the branchial region, and covered externally by skin bearing scales little different from those around them.

Trunk, tail and median fins

Trunk

The trunk of *Phlebolepis elegans* was approximately cylindrical in cross section immediately posterior to the branchial region, but became very laterally compressed posteriorly (Fig. 3). The trunk region of the body occupied about one-quarter of the total body length (the latter including the caudal fin) and bore the dorsal fin at about three-quarters of its length (Fig. 2D), with the anal fin marking the trunk’s posterior extremity. Only one specimen (Fig. 7A) provides evidence of a sediment infilling within the pharynx and gut or body cavity. We assume that the anus was located immediately anterior to the anal fin but we have not found direct evidence for it.

Dorsal and anal fins

Both the dorsal and anal fins were small and little elevated above the profile of the already tapering caudal peduncle (Figs 2D, 7B, C). The dorsal fin is located at an anteroposterior distance slightly anterior to that of the anal fin. Both fins are covered with scales having their long axis arranged longitudinally, and diminishing only slightly in size towards the posterior margin of the fin (Fig. 7B). These fins do not vary greatly in size or preservation, and we conclude that they were not very flexible in life.

Caudal peduncle

The caudal peduncle (Fig. 8C) is defined as the portion of the body posterior to the anal fin and anterior to the first expansion of the caudal fin. Posterior to the median fins, the peduncle continues to taper dorsoventrally until the first expansion of the caudal fin is reached (Figs 2D, 8C).

Caudal fin

The preservation of the caudal fin is highly variable and usually very incomplete. No single specimen has what can be described as a complete caudal fin. Therefore, our reconstruction of the shape of the fin in the living animal is based on the most completely preserved fragments (e.g., Figs 7C, 8).

Overall, the fin is large, with strongly diverging dorsal and ventral margins in many specimens (Fig. 8B, C), an emarginate posterior edge (Fig. 8B, C), and it is supported by a stout ventral body lobe and a prominent but slightly shorter and considerably less stout dorsal lobe, both covered with diamond-shaped scales that decrease in size posteriorly (Fig. 8). Between

these two main lobes, the fin was supported by narrow ‘rays’ covered by even smaller scales. Only traces of some of these ‘rays’ are seen in any one specimen (e.g., Fig. 8A, D), and the emargination of the reconstructed tail (Fig. 9) is extrapolated from these traces. About five ‘rays’ clearly arose from the inner margin of the main ventral lobe (Fig. 8D) and supported the ventral half of the fin web, and about four supported the dorsal half of the fin web but their origin is less clear. They arose either from the inner margin of the main upper lobe or else were parallel to the dorsal lobe and arose from the most anterodorsal part of the lower lobe. The main lobes and inner ‘rays’ were highly flexible, so that in addition to the examples with strongly diverging dorsal and ventral margins (Fig. 8C), there are other examples in which the margins are nearly parallel and the posterior tips of the main lobes converge (e.g., Figs 7C, 8A), and an example in which an interior ‘ray’ is folded ventrally and overlaps the ventral lobe (Fig. 8D).

Ventral to the ventral lobe, a ‘keel-like’ expansion of the fin is evident in numerous specimens (Figs 2A, 8C). This ventral caudal keel had a gently convex dorsal margin and a gently convex ventral margin and was covered by diamond-shaped scales smaller than those covering the main ventral lobe. No such keel occurs on the dorsal edge of the dorsal lobe. In the absence of well-preserved dorsal and anal fins, the ventral caudal keel can be used to orient fragmentary specimens correctly.

RECONSTRUCTION

The *Phlebolepis* school or shoal perished in a lagoon in the Himmiste-Kuigu area, which was connected with the open sea over the reef belt; *Phlebolepis* inhabited waters on both sides of the reef belt (Märss et al. 2003). We have commissioned an artist’s impression of *Phlebolepis elegans* to illustrate our new information about its external morphology (Fig. 9B), reconstructing it as a living animal in a habitat similar to that represented by the Himmiste Quarry (Fig. 9A). Although there are no plants preserved with *Phlebolepis* in the mass-mortality beds at the Himmiste Quarry, we have shown a small group of aquatic plants (Fig. 9A) representing two of the species that are known to occur in the Llandovery of the Kalana Quarry, central Estonia (Tinn et al. 2009).

DISCUSSION

Although *Phlebolepis elegans* is one of the most-often illustrated early vertebrates and often used as repre-

sentative of thelodonts (e.g., Carroll 1988, figs 3–7c; Turner 1991), its external morphology (except for its scales) has been little studied apart from the work of Kiaer (1932) and Ritchie (1968). It is the reconstruction of Ritchie (1968, fig. 3; see Fig. 1F, G) that has been most often reproduced as typical of thelodonts in general and of *Phlebolepis* in particular. Our results differ from those of Ritchie (1968) in two major ways and in some minor ways. We emphasize that we also agree with his results in many respects and give credit to that reconstruction as the most accurate produced to date.

The first important difference is that we find evidence for the existence of a small rostral area anterior to the subterminal mouth. The mouth itself is not precisely terminal, nor is it circular, as illustrated by Ritchie (1968), but rather it is subterminal and somewhat oval (horizontally wider than it is vertically). The rostrum was not as highly developed as that of many heterostracans such as *Athenaegis* Soehn & Wilson, 1990, but it was present. The mouth itself was surrounded by very flexible tissue and often preserved in a distorted shape. It was bordered anterodorsally by fine, diamond-shaped pre-oral scales, and posteroventrally by fine post-oral scales but of less certain arrangement and shape.

The second important difference concerns the shape and construction of the caudal fin, which Ritchie (1968) illustrated as highly asymmetrical (hypocercal) and not very flexible. The specimens that we examined show that the caudal fin was large and highly flexible, and that the main ventral lobe was only slightly longer than the main (albeit less robust) dorsal lobe. We also found evidence for scale-covered ‘rays’ supporting the fin web, which we reconstruct as emarginate (slightly forked). We further found evidence for a ventral keel beneath the main ventral lobe.

A small difference concerns the orbits. We find in numerous specimens that the orbits are located immediately posterior to the anterolateral corners of the head, whereas Ritchie (1968) located them slightly more posteriorly.

Another small difference concerns the pectoral fins. Ritchie illustrated them as originating posteroventral to the orbits. We actually agree almost completely with Ritchie’s (1968) reconstruction of the pectoral fins, but we suggest that they were located slightly more dorsally, originating posterior and close to the orbits.

Apart from these differences, we have found Ritchie’s (1968) reconstruction (Fig. 1F, G) to be by far the most accurate of those published over the years since the discovery of the articulated specimens of *Phlebolepis elegans* (Fig. 1).

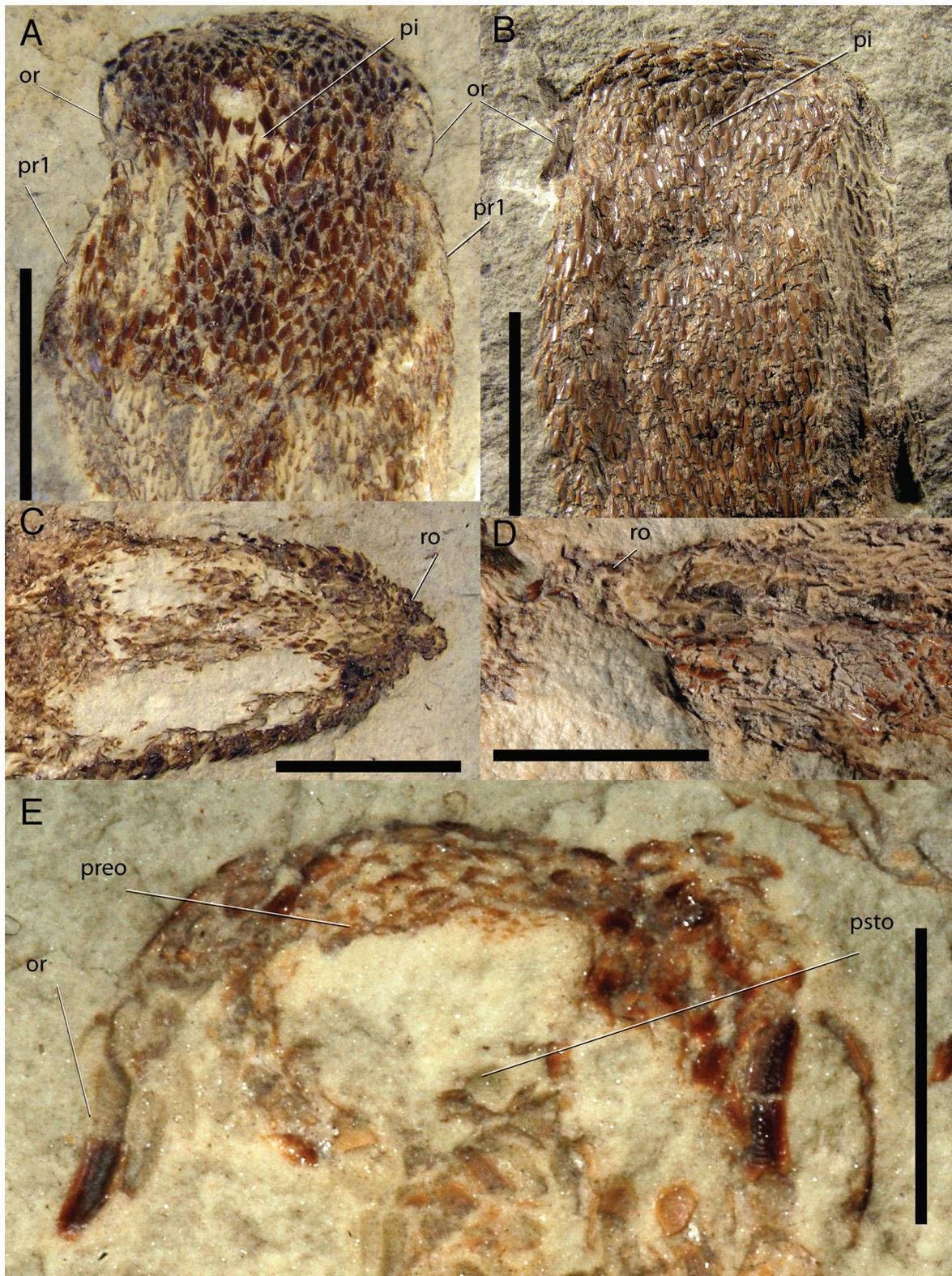


Fig. 4. *Phlebolepis elegans* Pander. Closeup images of the head, from Himmiste-Kuigu, Saaremaa, Estonia. **A**, TUG 865-9-2, part (previously numbered as Pi 6677); **B**, TUG 865-14-1; **C**, TUG 865-4-1; **D**, TUG 865-7-2; **E**, TUG 865-3-3. Scale bars for A–D, 1 cm; for E, 5 mm. A, C–E imaged wet. Abbreviations: or, orbital scales; pi, scales covering pineal organ; pr1, first (outer, leading edge) pectoral ‘ray’; preo, pre-oral scales; psto, post-oral scales; ro, rostrum.

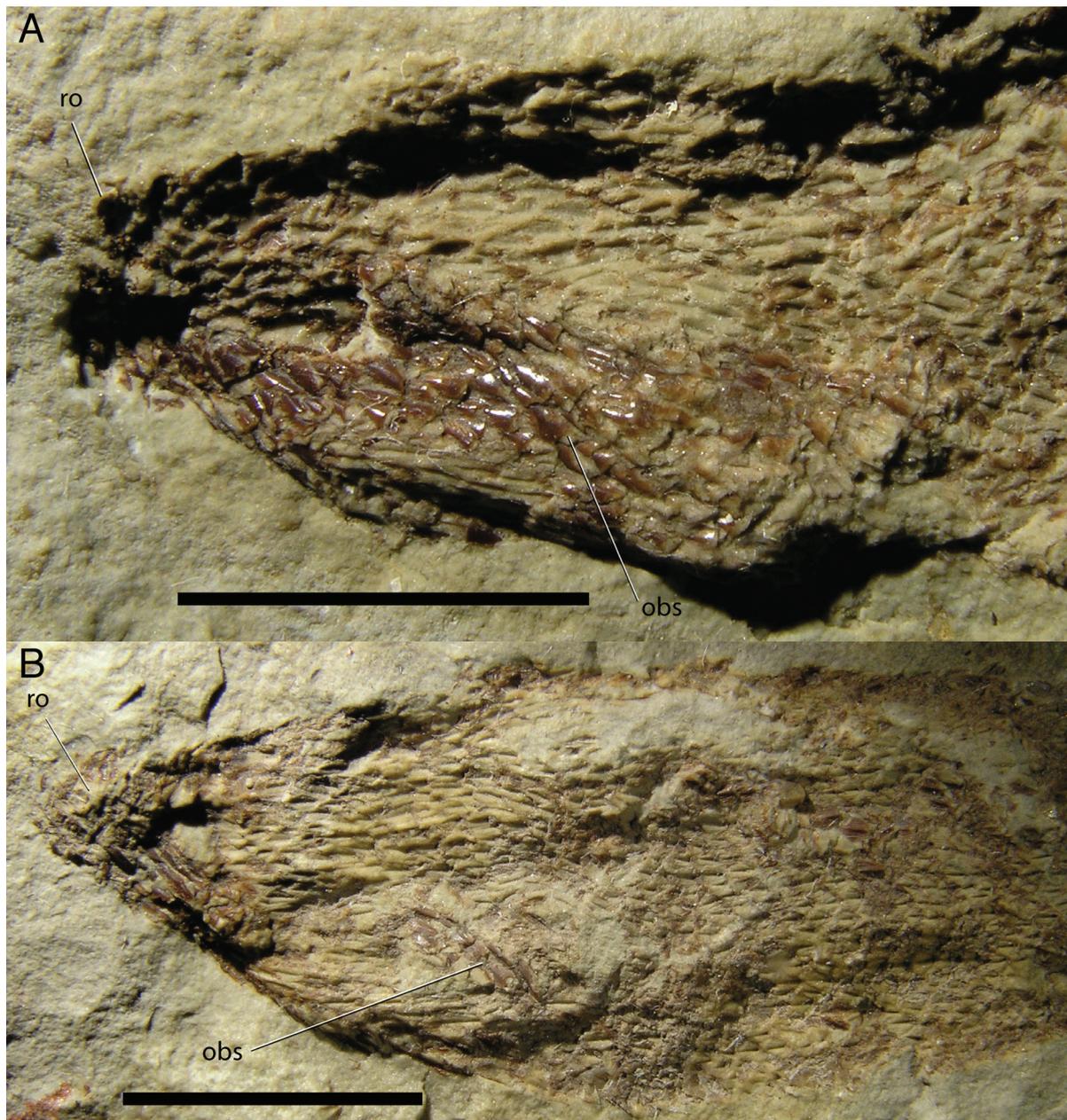


Fig. 5. *Phlebolepis elegans* Pander. Cephalobranchial region of specimens in lateral view, from Himmiste-Kuigu, Saaremaa, Estonia, imaged wet. **A**, TUG 865-27-2; **B**, TUG 865-16-2. Scale bars are each 1 cm. Abbreviations: obs, oblique branchial scales; ro, rostrum.

Among the remaining unanswered questions about the anatomy of *Phlebolepis*, several stand out. First, we must continue to try to find evidence for the number and arrangement of the external branchial openings and the internal branchial pouches or slits, the most significant remaining lack in our understanding. It is rather surprising that there is so little

evidence for the branchial openings on the external surface of the best specimens, contrary to the condition in, for example, furcacaudiform thelodonts (Wilson & Caldwell 1998).

Second, we have not located the anal opening definitively and we have not found specimens with gut infillings such as those that are so prominently seen in

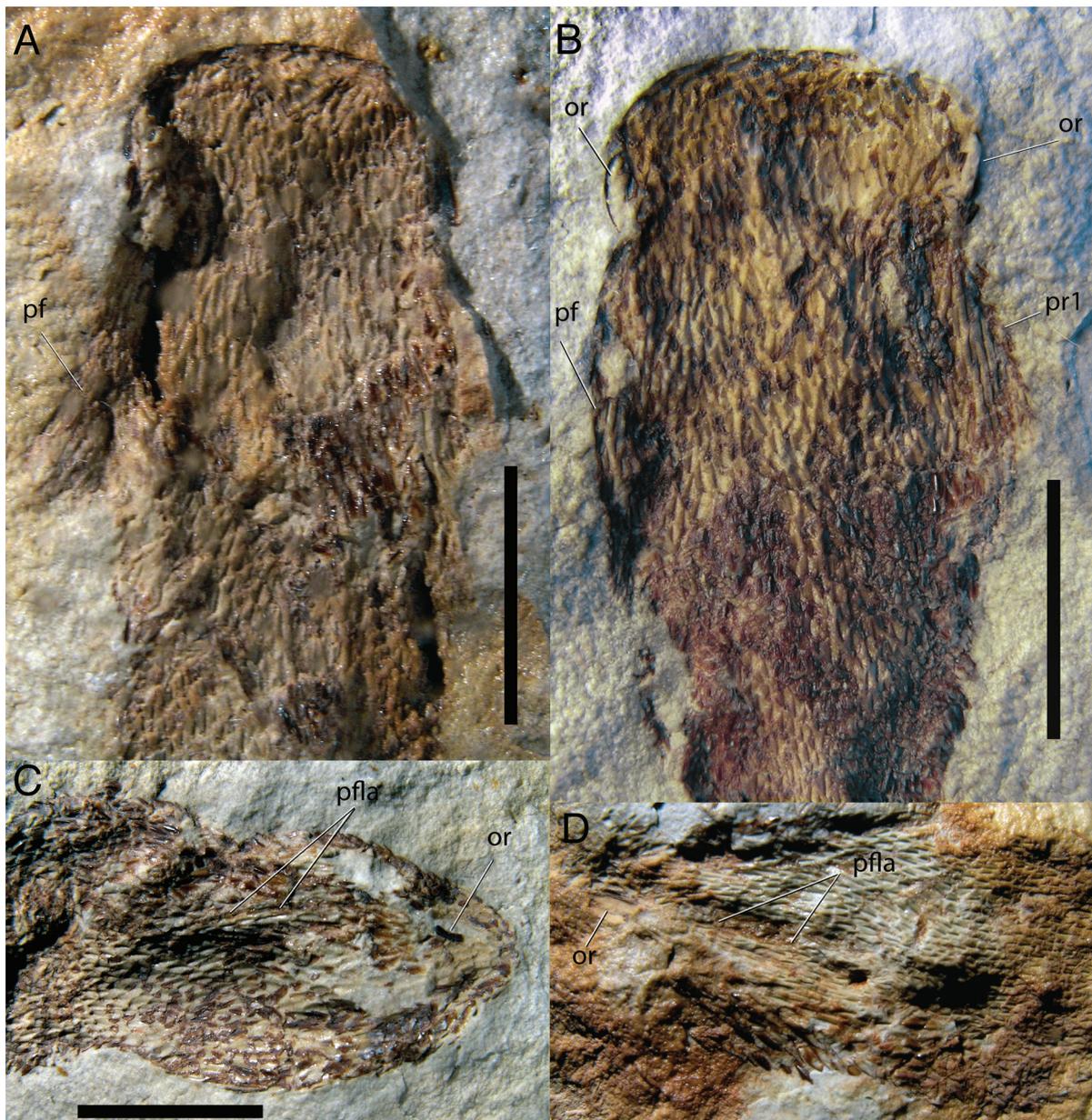


Fig. 6. *Phlebolepis elegans* Pander. Specimens showing pectoral fin, from Himmiste-Kuigu, Saaremaa, Estonia, imaged wet. **A**, TUG 865-28-4; **B**, TUG 865-9-2 (counterpart of Fig. 4A); **C**, TUG 865-1-3; **D**, TUG 865-16-10. Scale bars are each 1 cm. Abbreviations: or, orbital scales; pf, pectoral fin; pfla, pectoral fin line of attachment; pr1, first (outer, leading edge) pectoral fin ‘ray’.

furcacauid thelodonts (Wilson & Caldwell 1998). Therefore, we still do not know anything about the internal morphology of the gut.

With these revised interpretations, it will be possible for new reconstructions and artistic representations of *Phlebolepis elegans* to be based on more reliable information, so that it can continue to be used as

a prime example of both Silurian vertebrates and members of the Thelodonti. In addition, comparisons of the morphology of *Phlebolepis* with that of other early vertebrates will have a sounder basis, leading to improved understanding of the evolution of the vertebrate body plan, including the mouth and paired and median fins.

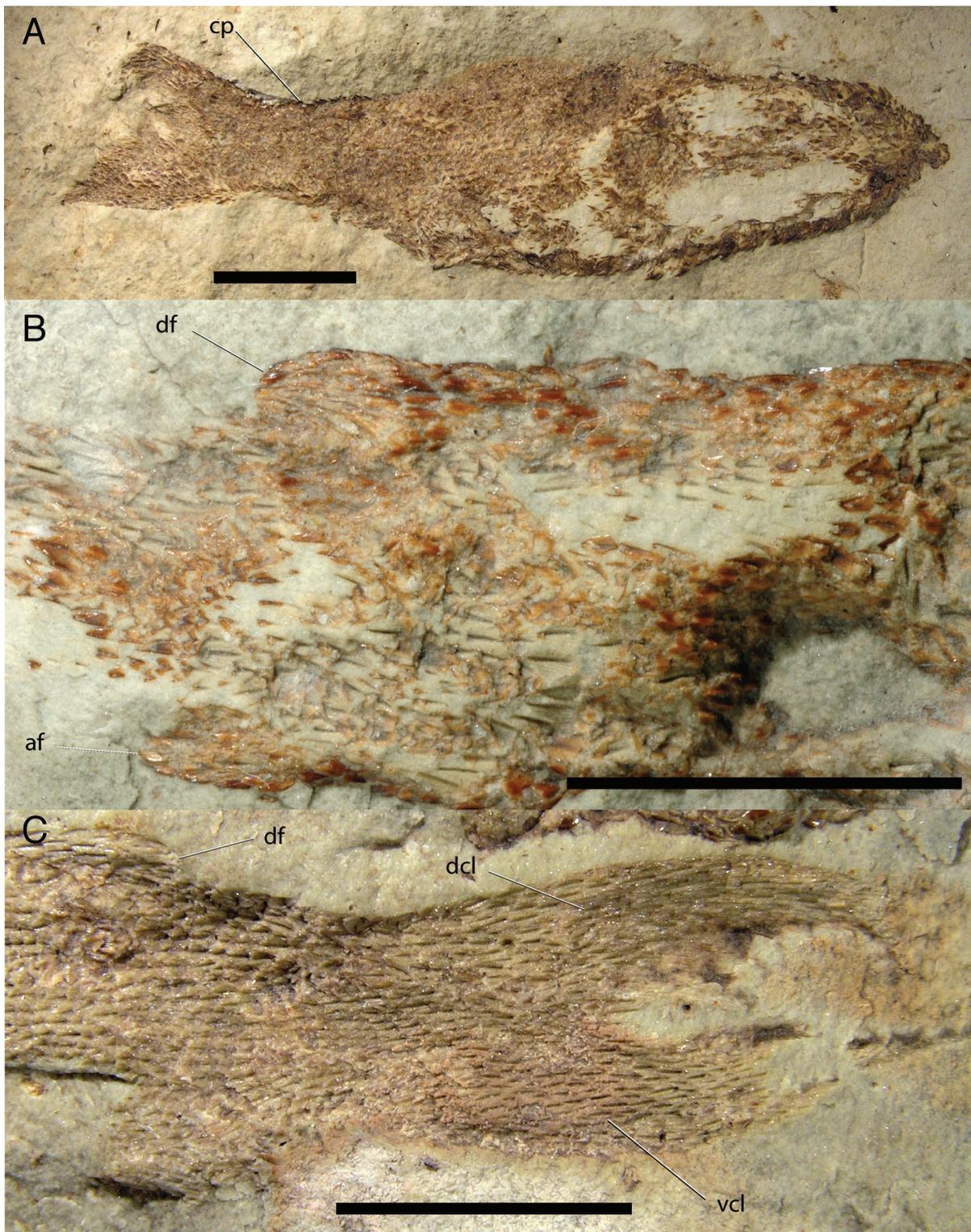


Fig. 7. *Phlebolepis elegans* Pander. Specimens illustrating the trunk and dorsal and anal fins, from Himmiste-Kuigu, Saaremaa, Estonia, imaged wet. **A**, TUG 865-4-1, illustrating the proportions and shape of the trunk and caudal peduncle; **B**, TUG 865-3-2, with dorsal and anal fins; **C**, TUG 865-5-21, dorsal fin, caudal peduncle and caudal fin with converging main lobes. Scale bars are each 1 cm. Abbreviations: af, anal fin; dcl, dorsal caudal lobe; df, dorsal fin; cp, caudal peduncle; vcl, ventral caudal lobe.

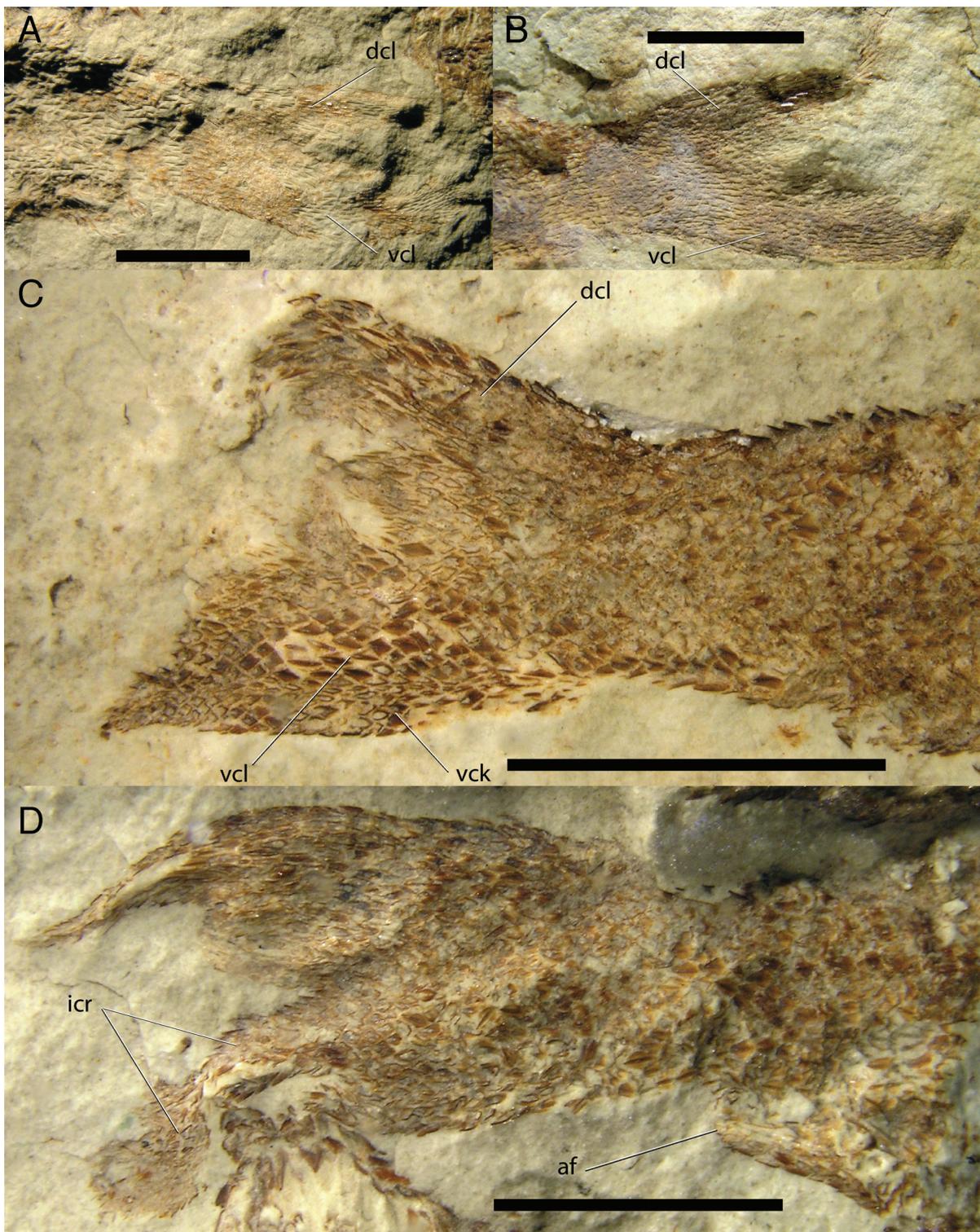


Fig. 8. *Phlebolepis elegans* Pander. Specimens illustrating caudal fin in lateral view, from Himmiste-Kuigu, Saaremaa, Estonia, imaged wet. **A**, TUG 865-3-7, caudal fin with converging main lobes; **B**, TUG 865-5-26, with diverging main lobes more completely preserved than most (note dorsally deflected termination of dorsal caudal lobe); **C**, TUG 865-4-1, with strongly diverging main lobes and fairly complete fin web; **D**, TUG 865-9-1, one large interior ‘ray’ folded down over top of the ventral lobe. Scale bars are each 1 cm. Abbreviations: af, anal fin; dcl, dorsal caudal lobe; icr, interior caudal ‘ray’; vcl, ventral caudal lobe; vck, ventral caudal keel.

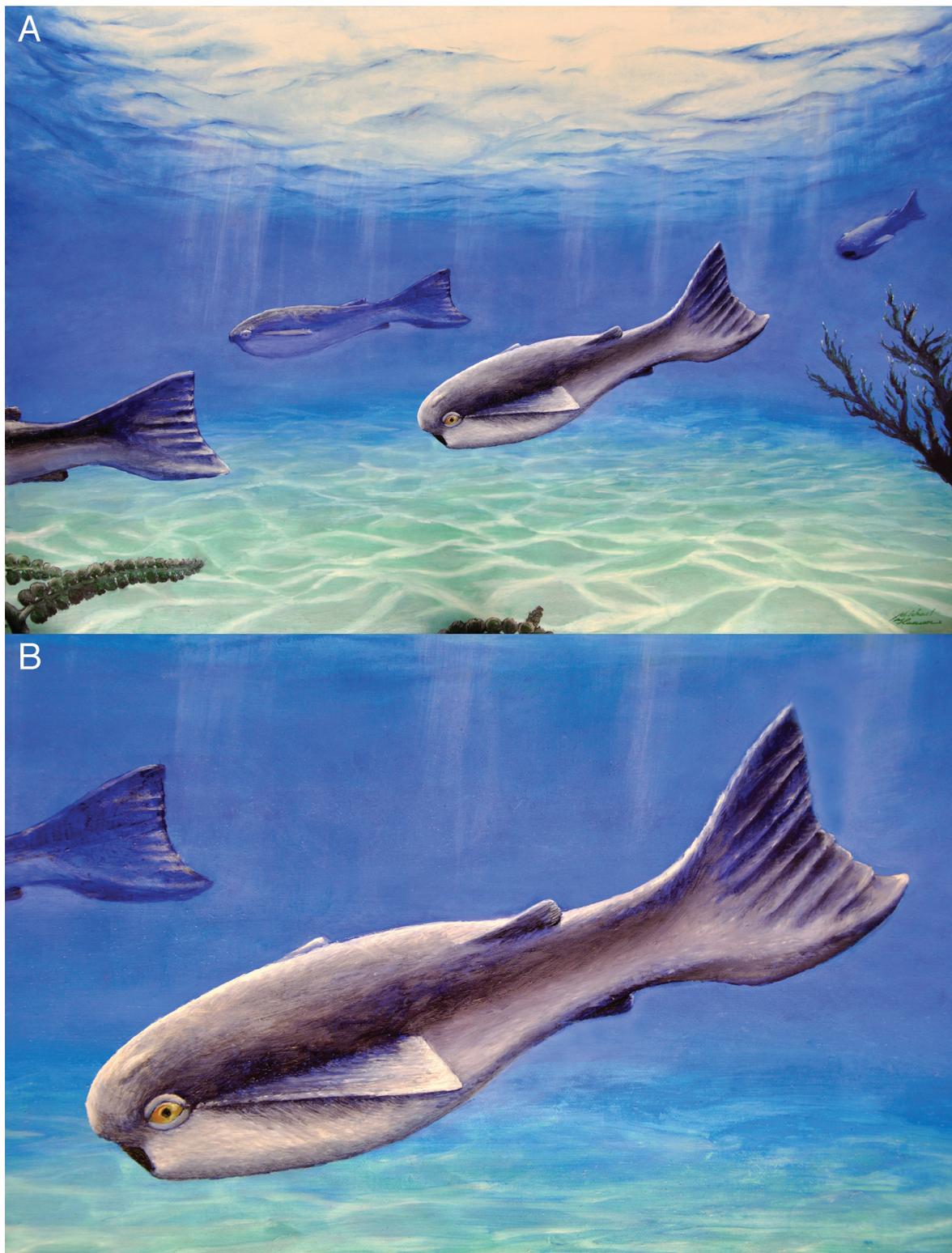


Fig. 9. Artist's conception of the Silurian thelodont *Phlebolepis elegans* Pander preserved in a mass-mortality layer in the carbonate-rich sedimentary rocks at Himmiste-Kuigu, Saaremaa, Estonia. **A**, members of the school swimming in a lagoon prior to suffering the mass mortality event. **B**, closeup of the foreground individual of *Phlebolepis elegans* Pander to illustrate revised concepts of its external morphology. Artwork for A and B by Michael Hanson, Chicago.

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Siluri telodondi *Phlebolepis elegans* Pander anatoomia

Mark V. H. Wilson ja Tiiu Märss

Siluri thelodont *Phlebolepis elegans* Pander Saaremaalt Eestist on üks sagedamini kirjanduses kujutatud varajane selgroogne, kelle väliskuju on siiski puudulikult teada ja spetsialistid nõustuvad harva tema kohta varem avaldatud kehakuju detailidega. Tema morfoloogiliste iseärasuste väljaselgitamiseks uurisime oma töös sadu selle kala tervelt säilinud eksemplare nende tüüpleiukohast Himmiste murrust. Leidsime, et Ritchie (1968) rekonstruktsioon on seni olemasolevatest parim. Siiski me ei nõustu Ritchiega selles, et *Phlebolepis*’e suu oli terminaalne, vaid see oli subterminaalne, veidi ventraalselt asetsev, ja mõned meie uuritud eksemplarid annavad tunnistust kalal dorsaalselt olevast veidi etteulatuvast rostrumist. Rinnauimed algavad vahetult silmade taga, muus osas sarnaneb *Phlebolepis*’e keha esiosa Ritchie antud rekonstruktsiooniga. Samuti leidsime sabauime olevat tunduvalt suurema, tugevama ja paindlikuma ning sümmeetrilisema (siiski mitte perfektselt sümmeetrilise) kui varasematel rekonstruktsioonidel. Sabauim on suhteliselt suure dorsaalse ja veelgi suurema ventraalse hõlmaga ning on toetatud peente, soomustega kaetud ‘kiirtega’. Lõpuseavade kuju, arv ja asukoht jäävad siiski ka meie töös lõpuni täpsustamata. Meie leitud uued morfoloogilised tunnused on esitatud kunstniku rekonstruktsioonil. Antud revisjon võib tulevastel *Phlebolepis elegans*’i kehakuju esitlustes aluseks olla ja tema keha kuju on täpsemini võrreldav teiste varajaste selgroogsete omaga.