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The Late Silurian Anaspid Genus *Rhyncholepis* from Oesel, Estonia, and Ringerike, Norway

ALEXANDER RITCHIE¹

ABSTRACT

Re-examination and further preparation of the original material of the Silurian anaspid *Saarolepis oeselensis* (Robertson) from the Ludlovian Paadla Formation of Oesel, Estonia, has led to the discovery of an almost complete and uncrushed head of this species. In the structure of its cranial and ventral (gular) shields the Oesel form closely resembles the well-known *Rhyncholepis parvulus* Kiaer from the Upper Silurian of Ringerike, southern Norway, and it must now be assigned to that genus, with the suppression of

Saarolepis (Robertson). There are sufficient differences of specific importance between the forms from Norway and from Oesel to justify the retention of *Rhyncholepis oeselensis* (Robertson) as a separate species, the second of this genus to be recognized. Details are also given of the discovery of well-developed, paired, ventrolateral finfolds in the Norwegian species, *R. parvulus* Kiaer, reinforcing earlier evidence that the presence of such fins is the rule rather than the exception in anaspids.

INTRODUCTION

The Anaspida are a small, diverse order of Siluro-Devonian ostracoderm agnathans most closely related to the Osteostraci (cephalaspids) with which they are usually grouped to form the Cephalaspidomorphi, and to at least one major division of the extant cyclostomes—the Petromyzontida (lampreys).

To date 10 genera of anaspids have been described: *Birkenia*, *Lasanius* (Traquair,

1899, 1905) Silurian, Scotland; *Euphanerops* (Woodward, 1900), Upper Devonian, Canada; *Ctenopleuron* (Matthew, 1900), Silurian, Canada; *Pharyngolepis*, *Pterygolepis* (*Pterolepis*), and *Rhyncholepis* (Kiaer, 1924), Upper Silurian, Norway; *Endeiolepis* (Stensio, 1939), Upper Devonian, Canada; *Saarolepis* (*Anaspis*) (Robertson, 1941, 1945), Silurian, Estonia; *Jamoytius* (White, 1946), Silurian,

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Scotland. In addition to these there are other, as yet undescribed, new anaspids recovered from the Middle Silurian of Cornwallis Island in the Canadian Arctic archipelago, from the Downtonian of Stonehaven, eastern Scotland and from the Lower Old Red Sandstone (Lower Devonian) of Argyllshire, western Scotland.

Of the described genera the least known is, unquestionably, *Saarolepis oeselensis* (Robertson) based on a handful of fragmentary specimens collected by Patten in the 1920s and 1930s. The present paper presents new information gained during re-examination and subsequent preparation of the original material of *Saarolepis* following which it became clear that the Estonian anaspid material can now be assigned to *Rhyncholepis*, the smallest of the three well-known Norwegian Silurian anaspids from Ringerike near Oslo. The generic name *Saarolepis* must therefore be suppressed. It is proposed, however, that the Estonian form be retained as a separate species of *Rhyncholepis*—*R. oeselensis* (Robertson).

The small island of Oesel (or Saaremaa) off the western coast of Estonia in the Baltic has long been famous for the abundance, diversity, and preservation of its Silurian ostracoderm faunas. One of the most active early workers in this area was Professor William Patten of Dartmouth College, New Hampshire, U.S.A. who made four separate visits to the island to organize and direct sizable excavation projects in the vertebrate-bearing horizons; the most productive years were 1930 and 1932, and a total of more than 3500 specimens was recovered and taken back to the United States for preparation and study. The collection included superb material of various cephalaspids (*Tremataspis*, *Dartmuthia*, *Thyestes*, *Rotsiküllaspis*, *Witaaspis*, *Procephalaspis*, etc.), thelodonts (*Phlebolepis*) and rare, fragmentary specimens of anaspids. Patten himself described some of the fauna but after his death in 1932 the study and description of the remaining material was carried out by G. M. Robertson and later by R. H. Denison; some of the material was investigated on loan by E. Jarvik,

Stockholm and by T. S. Westoll, Newcastle, England (Denison, 1952).

In 1938 the collection was moved to Dartmouth College Museum, given the accession number 38-71 and recatalogued. There it remained until 1975 when the Dartmouth College authorities decided to dispose of the systematic collections and the Patten Collection was presented in its entirety to the American Museum of Natural History, New York, where it has now been incorporated into the palaeoichthyological collections of that institution.

The scarce anaspid specimens among the Oesel vertebrate remains were first noted by Robertson (1937) who later published a brief account and description of the very incomplete material (Robertson, 1941, p. 314, fig. 1). He assigned the form to a new genus and species, *Anaspis oeselensis*, on the grounds that there was insufficient evidence to place it in an existing genus, and that this course would avoid confusion if further study of this (or additional) material should result in an identification with a known form. When it was later realized that *Anaspis* was preoccupied Robertson (1945) proposed *Saarolepis* as an alternative, a name derived from Saarema, the Estonian name for the island of Oesel. *Saarolepis oeselensis* (Robertson) is the only member of the group described from the Silurian sediments of the Baltic to date.

I have been involved in a study of the Scottish and Norwegian anaspids for many years (Ritchie, 1960, 1964, 1968) and visited Estonia in 1976 to attend the Inter-Union Colloquium on Middle Palaeozoic fishes held in Tallinn. The collections of the Estonian Academy of Sciences contain a few fragmentary specimens of *Saarolepis* but nothing that added significantly to Robertson's account. The return trip to Australia via the United States provided a long-awaited opportunity to examine some North American ostracoderm collections and, during a brief stay in New York, I was able to study the original *Saarolepis* specimens from the Patten Collection now housed in the American Museum of Natural History. It was observed

that some of the specimens had not been completely prepared. With permission of Dr. Bobb Schaeffer of the American Museum of Natural History, Patten's original *Saurolepis* material was forwarded to Australia for further preparation and study. The results exceeded all expectations and clarified for the first time, the taxonomic relationships of "*Saurolepis*."

ACKNOWLEDGMENTS

The present paper is dedicated to the late Professor Anatol Heintz, Oslo, who encouraged and assisted me in my studies on the Scottish and Norwegian Silurian ostracoderms and freely made available the Ringerike material for study, loan, and preparation.

Thanks are also extended to his daughter, Dr. Natascha Heintz, Palaeontological Museum, Oslo, for similar cooperation; to Dr. Bobb Schaeffer, American Museum of Natural History, New York, for permission to borrow and prepare the *Saurolepis* material from the Patten Collection; to Dr. Elga Mark-Kurik, Institute of Geology, Estonian Academy of Sciences, Tallinn, for the opportunity to examine *Saurolepis* material in the Estonian collections; to the Director and Trustees of The Australian Museum, Sydney, for financing the visit to Estonia and to the United States in 1976 which led to the discovery of the material described here. The 1973 *Rhyncholepis* discoveries were made possible by financial assistance from the C.S.I.R.O. Science and Industry Development Fund, the Ian Potter Foundation, and the Bushell Trust.

DESCRIPTION

Over the years the various specimens of Oesel anaspids have been given a variety of numbers which are listed here to avoid confusion. Robertson's preliminary numbers (An. 1–An. 9, based on the original generic name, *Anaspis*) were superseded in 1938 by Dartmouth College Museum numbers (DCM 38-71-12648–12656).

They have now been assigned American

Museum of Natural History numbers, as follows:

An. 1 (a, b)	= DCM 38-71-12648 = AMNH 6698
	Holotype
An. 2 (a, b)	= DCM 38-71-12649 = AMNH 6699
An. 3 (a, b)	= DCM 38-71-12650 = AMNH 6777
	Complete headshield
An. 4	= DCM 38-71-12651 = AMNH 6771
An. 5	= DCM 38-71-12652 = AMNH 6772
An. 6 (a, b)	= DCM 38-71-12653 = AMNH 6773
An. 7	= DCM 38-71-12654 = AMNH 6774
An. 8	= DCM 38-71-12655 = AMNH 6775
An. 9	= DCM 38-71-12656 = AMNH 6776

The most informative specimen of "*Saurolepis*" is not the holotype (An. 1) but another specimen (An. 3) preserved in part and counterpart. The larger portion, a block about 7 cm. square and 3–4 cm. thick, had been struck to remove a smaller flake. This flake (fig. 1C) displayed a narrow strip of anaspid dermal skeleton, seen in visceral view, which extended from the dorsal to the ventral margin. The exposed area lay between the left orbit and the anterior end of the branchial row. When the counterpart was examined the writer observed that (a) the left dermal skeleton continued anteriorly into the limestone matrix and (b) the opposite (right) side of the dermal skeleton was still present, buried deeper in the block and visible only in cross-section.

The two surfaces of the exoskeleton of the pre-branchial and head region were separated by 0.5–1.0 cm. of matrix and it seemed possible that as a result the entire head region was preserved uncrushed in such a way that it could be prepared from both sides.

Preparation of this specimen, carried out by the writer with the aid of a vibrotool and pneumatic engraving pen, provided the first information on the dorsal, lateral, and ventral regions of the headshield of "*Saurolepis*."

The entire left surface of the head region was found to be preserved virtually intact and in considerable relief (fig. 2A). The limestone matrix in which the head was embedded was excavated to a depth of about 1 cm.

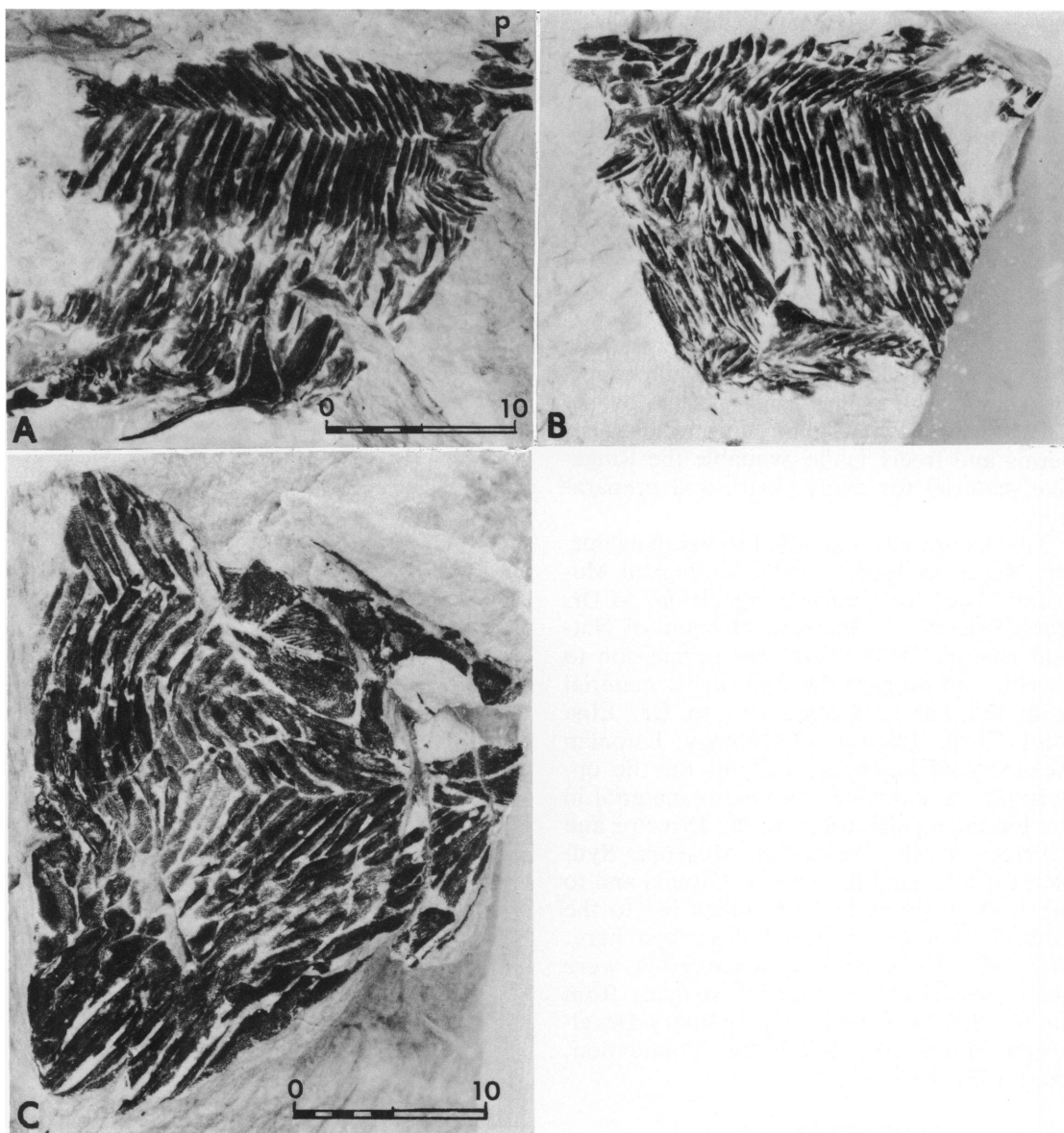


FIG. 1. *Rhyncholepis (Saarolepis) oeselensis* (Robertson), Upper Silurian (Middle Ludlow) Oesel, Estonia, U.S.S.R. A. Holotype, AMNH 6698 (formerly DCM 38-71-12648). Left flank of trunk posterior to orbit, seen in visceral view. Pineal plate (p) visible (top right), postbranchial and pectoral plates (bottom center). B. Counterpart of holotype showing considerable portion of posterior cranial roof, right pectoral plate, visceral surface of right trunk scales, ventral scales. C. Left lateral surface of head and anterior portion of trunk, AMNH 6777b, with anterior portion rebuilt from flakes removed from counterpart, AMNH 6777a during preparation. Scale in mm.

all round, leaving the anaspid head on a narrow pillar of matrix. The head was then flaked off the main block in the hope that much of the still-buried right lateral surface could be recovered both as an external and an internal mould. The approach was successful, the anaspid head was detached safely but it was discovered that the right surface had been crushed inward during burial (fig. 2D) and was less complete than the left side.

Despite the postmortem damage this beautifully preserved specimen provides sufficient information to enable a reconstruction of the entire head region (fig. 7A–C). Although much of the original dermal skeleton was preserved as a translucent, deep brown substance most of it had split through the middle or flaked off the specimen in such a way that it could not be recovered. It was therefore decided to remove all remains of the exoskeleton from the various parts of this specimen to obtain detailed impressions of both the dermal and visceral surfaces. This seemed the course likely to yield the maximum amount of information. A latex cast of the dorsal, left lateral, and ventral surface was prepared, unrolled and attached to flat card for study and photography.

The most striking discovery was that the entire anterior ventral surface—the gular region—of the head was covered with a distinctive arrangement of very large plates and scales (fig. 2A, C, D, figs. 3, 5) quite unlike the pattern seen in the other armored anaspids such as *Birkenia* (Heintz, 1958, fig. 4b, c), *Pharyngolepis* (Kiaer, 1924, fig. 37; Ritchie, 1964, fig. 1a–c) and *Pterygolepis* (Kiaer, 1924, fig. 35). However, the gular pattern revealed in “*Saareolepis*” is so similar to that present in *Rhyncholepis parvulus* Kiaer (1924, figs. 24, 25, 36; this paper fig. 6), the smallest and in many ways the most specialized of the three anaspid genera in the Silurian fauna from Ringerike, that it must now be considered to belong to that genus.

The left half of the dorsal surface of the headshield is virtually complete but the right half is mostly missing (fig. 2A, B, figs. 3, 4). The basic pattern is not unlike that of *Rhyncholepis parvulus* Kiaer but with differences

in detail. The rostral area is covered with several pairs of largish plates but it is difficult to determine with certainty whether the anteriormost plate is single or paired; the latter interpretation is depicted here (fig. 7B).

One of the most distinctive plates on the anaspid head, the large, Y-shaped pineal plate, is present in the midline dorsal and slightly posterior to the left orbit which is completely preserved. The deep, rounded notch which formerly housed the pineal organ is open anteriorly, suggesting that the anterior portion of the pineal plate which normally separates the pineal aperture from the much larger, single, naso-hypophysial foramen has become detached and lost (figs. 3, 4).

The pattern of largish plates surrounding the orbit and covering the postorbital region can be restored by combining the information from the external (fig. 1A–C) and internal (figs. 3, 4) impressions. The differences in shape and proportions from the plates covering the same areas in *Rhyncholepis parvulus* are considered here to be mainly of specific importance.

The ventral (gular) region of the exoskeleton is more completely preserved than the dorsal surface, with only a small area near the anterior end damaged as the result of a fracture (fig. 2C, figs. 3, 5). The plate pattern can be restored with confidence (fig. 7C). The central plate, a five-sided unit, is pointed posteriorly and tapers anteriorly to a narrow, blunt end; the anterolateral margins are concave. In this latter feature and in the relatively smaller size of the median gular plate *Rhyncholepis oeselensis* differs from *R. parvulus* (Kiaer 1924, figs. 24, 25, 39; this paper fig. 6). The median gular plate is flanked anteriorly, laterally, and posteriorly, respectively, by three pairs of plates of approximately the same, or slightly smaller, size. Dorsolaterally, the plates become longer and narrower merging into the smaller, obliquely directed scales covering the cheek area.

The gular region includes several other median plates which should be noted. The ventral shield is terminated posteriorly by a large, transversely oriented, semicircular

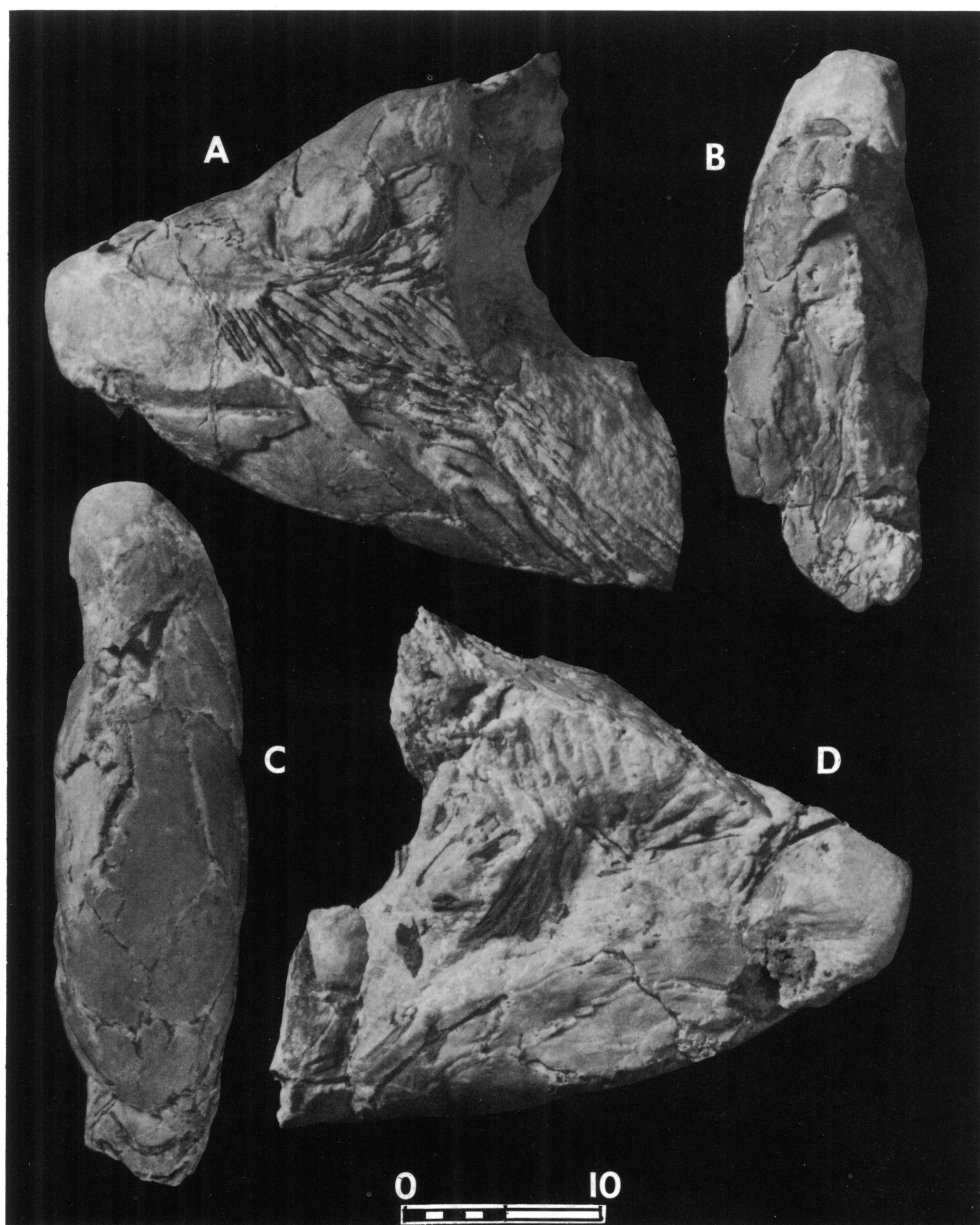


FIG. 2. *Rhyncholepis* (*Saarolepis*) *oeselensis* (Robertson), Upper Silurian (Middle Ludlow), Oesel, Estonia, U.S.S.R. AMNH 6777a. Four views of isolated head, preserved in three dimensions. A. Left lateral view. B. Dorsal view (anterior to top). C. Ventral view (anterior to top). D. Right lateral view.

plate with a convex posterior margin. This is followed posteriorly by several similar, but much narrower, median plates or scales.

One of the most interesting features of the

entire ventral surface, however, is a relatively small, median plate which forms the anterior ventral margin of the oral opening. This plate, exposed as a mould of the vis-

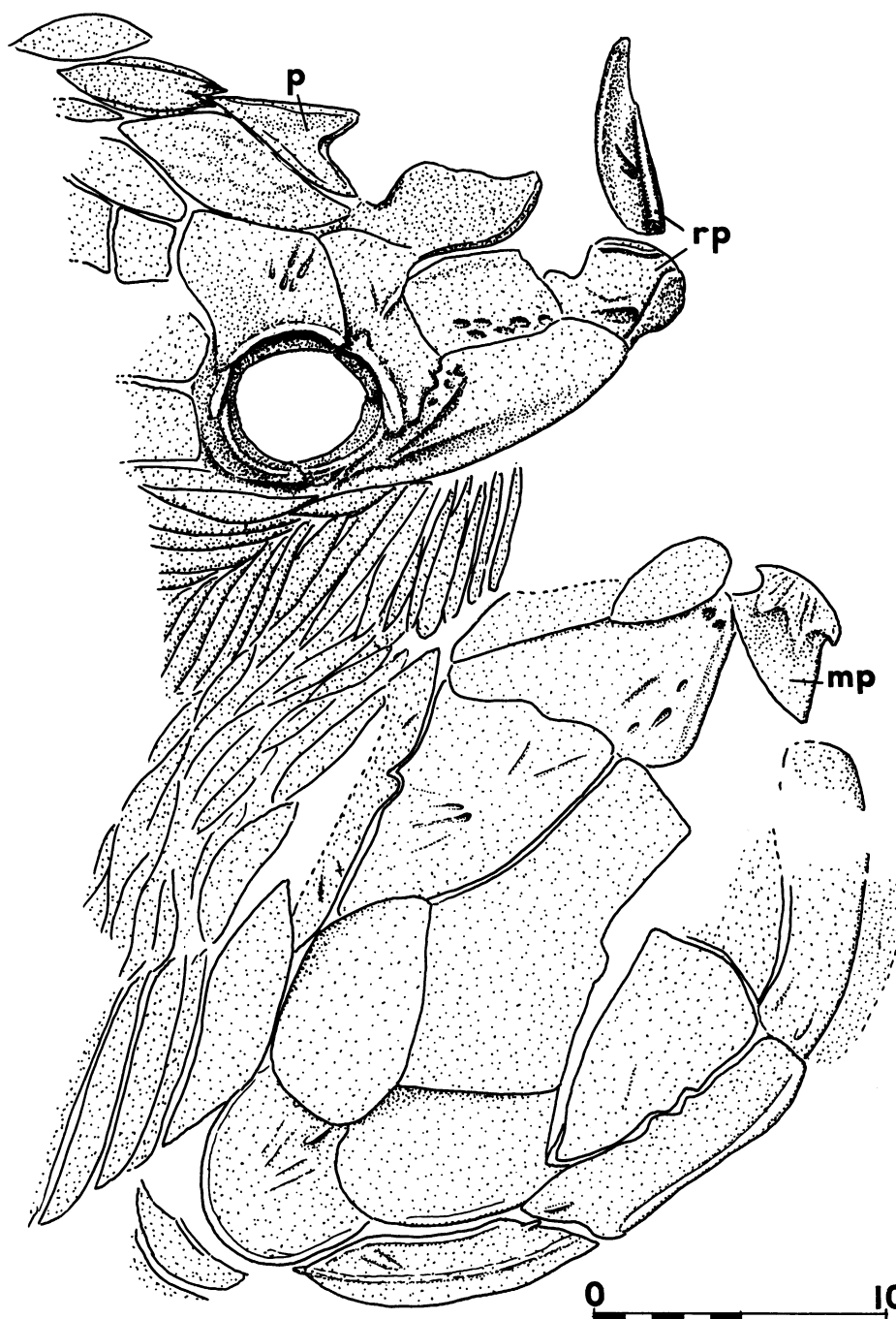


FIG. 3. *Rhyncholepis (Saarolepis) oeselensis* (Robertson). Dermal skeleton of head region of AMNH 6777a (fig. 2A–D), from latex cast, split along right lateral margin and unfolded in one plane. Cast shows visceral surface of cranial roof (left half only; cf. fig. 4), left cheek scale covering, and ventral (gular) shield (cf. fig. 5). mp = mandibular plate; p = pineal plate; rp = left and right rostral plates. Scale in mm.

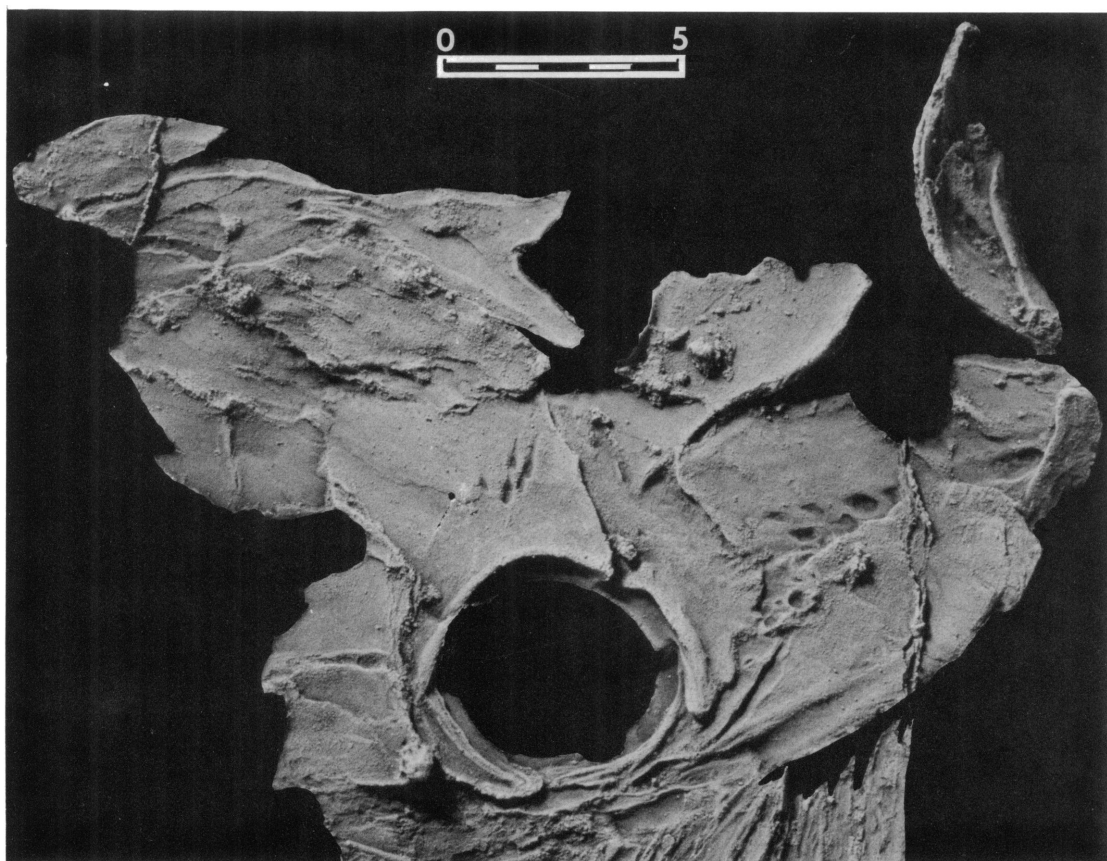


FIG. 4. *Rhyncholepis* (*Saarolepis*) *oeselensis* (Robertson). Cranial shield (left half), AMNF 6777a (fig. 2A, B), visceral surface as seen in latex cast (fig. 3). Portion of pineal plate anterior to pineal foramen has been lost and the right rostral plate has also been dislodged relative to the left rostral plate which remains *in situ*. Scale in mm.

ceral surface, displays an intriguing arrangement of anteriorly converging grooves and ridges (fig. 3, fig. 5, *mp*, fig. 7C) and immediately brings to mind the strange, well-developed T-shaped "mandibular plate" of *Pharyngolepis oblongus* Kiaer (1924, p. 48, figs. 22, 37, pl. X). Although this was later reinterpreted by Stensiö (1958, p. 226, figs. 126, 127; 1964, figs. 27, 28) as part of a rasping tongue apparatus, I concluded, after examining the type *Pharyngolepis* material in the Oslo collections, that Kiaer's original interpretation was the correct one and restored

the plate to an external position on the ventral oral margin (Ritchie, 1964, pp. 9–13, figs. 1a, b, 2a, b, pl. VI, figs. 1, 2).

The anterior median ventral plate of *Rhyncholepis oeselensis* (Robertson) is almost certainly homologous to the large, mandibular plate of *Pharyngolepis oblongus* Kiaer and both probably served to reinforce the lower buccal margin. The interpretation of the buccal region and the dermal skeleton of *Rhyncholepis parvulus* Kiaer has posed a problem since it was first described but, after careful examination of all the original *Rhyn-*

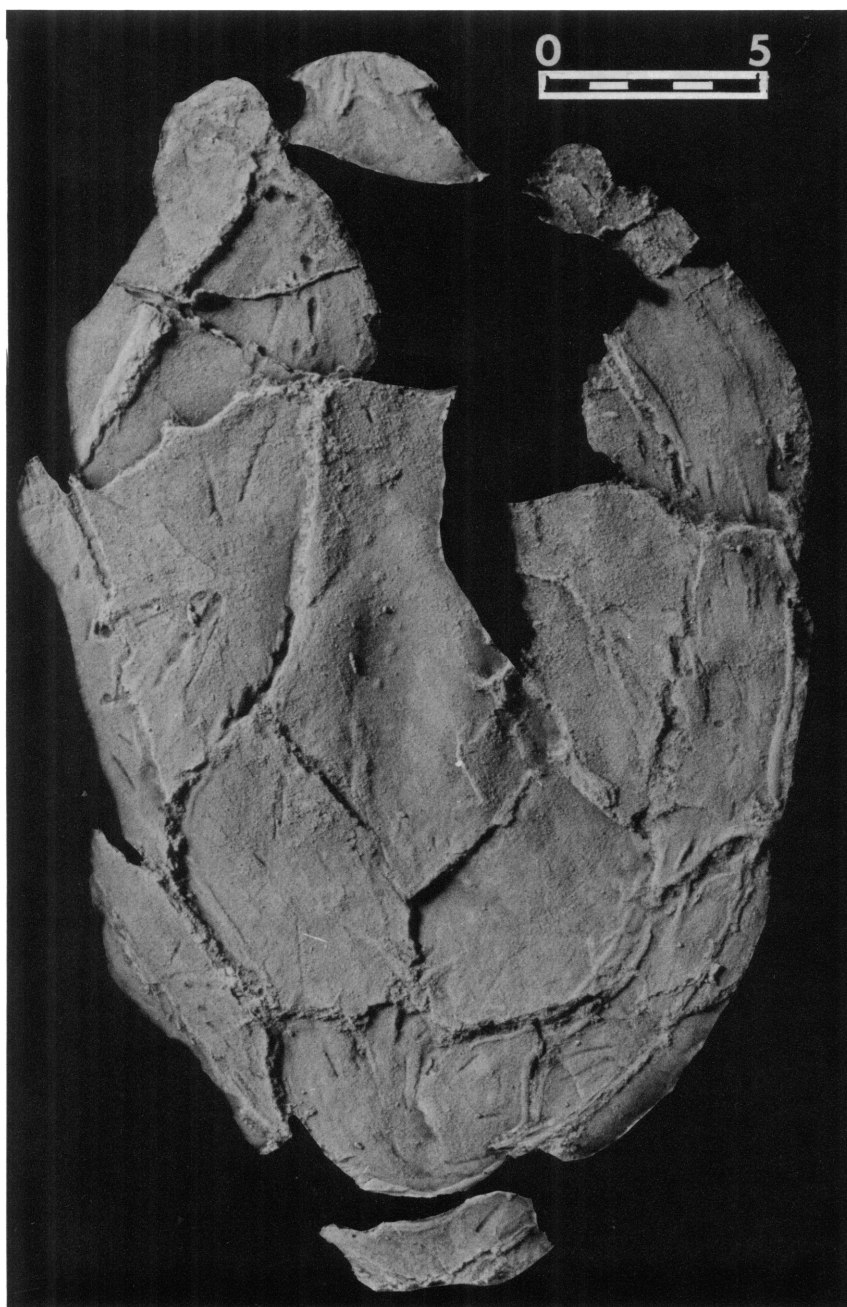


FIG. 5. *Rhyncholepis* (*Saarolepis*) *oeselensis* (Robertson). Ventral (gular) plates of head seen in visceral view (cf. fig. 2A, C, D). Latex cast whitened with ammonium chloride, from AMNH 6777a (cf. fig. 3). Scale in mm.

cholepis material in the Oslo and other museum collections, I am convinced that, with a few minor modifications, Kiaer's restoration is quite accurate (1924, fig. 36; this paper, fig. 10). Unlike most of the other armored anaspids, such as *Birkenia* (Heintz, 1958, fig. 4) and *Pharyngolepis* (Ritchie, 1964, fig. 1a-c) which appear to have had a vertical, oval buccal opening, *Rhyncholepis* seems to present an example of an agnathan which partly overcame the absence of true jaws by a specialized development of the gular and mandibular skeleton. The new material from Oesel confirms and enlarges our understanding of this region in *Rhyncholepis*.

The dorsal and ventral shields in *Rhyncholepis oeselensis* are separated laterally by an area of obliquely directed, narrow, lancet-shaped scales covering the cheek region and merging posteriorly into the scale covering of the branchial region and trunk (figs. 1C, 3). This pre-branchial scale-covered area is considerably larger in *Rhyncholepis oeselensis* than in *R. parvulus* but the basic pattern is similar. The lancet scales extend below, and considerably anterior to, the orbit, terminating some 7 mm. short of the rostral and mandibular margins, leaving a deep unarmed notch in the lateral buccal margin. Whilst this area may well have been bridged in life by soft tissues not preserved in the fossil it is also possible that the lateral buccal margin was indented deeply and that the ventral shield and the mandibular plate were sufficiently mobile to be brought against the ventral rostral margin with a nipping or biting action.

The lateral scale covering of *Rhyncholepis oeselensis* (Robertson) is developed basically as in the other scaled anaspids and can be reconstructed from information provided by the holotype (AMNH 6698, fig. 1A, B), the detached flake (AMNH 6777b, fig. 1C) associated with the head region and some of the other fragments in the Patten collection.

Two specimens have the branchial region preserved but with the surrounding scale covering disturbed and the branchial apertures are not as clearly displayed as in the

Norwegian *R. parvulus* (fig. 9). From the position and proportions of the branchial row and the associated plates it can be estimated that the original number of openings was probably around eight, the number present in *R. parvulus* (and in *Birkenia*), and was certainly fewer than in *Pterygolepis* (10 apertures) or in *Pharyngolepis* (12-15).

The associated dermal skeleton is of the standard anaspid type, a long, narrow, L-shaped postbranchial plate and a large, triangular pectoral plate (figs. 1A, B, 7A); in the holotype the latter has been further uncovered by me to expose the full extent of the long, needle-sharp pectoral spine. From the evidence of *Pharyngolepis oblongus* Kiaer and *P. heintzi* Ritchie (Ritchie, 1964, fig. 1a-c) it is now known that, in anaspids, this pectoral spine originally formed the anterior margin of a paired ventrolateral finfold which extended along part or all of the ventrolateral ridge between the branchial row and the anus.

Evidence for such a paired fin in *Rhyncholepis* was discovered by the writer during studies on the original Ringerike material in the Palaeontologisk Museum, Oslo, during 1966 and 1973 and is described below.

The remainder of the trunk and caudal skeleton of *Rhyncholepis oeselensis* (Robertson) remains unknown. Only one of the dorsal ridge scales has been observed in the available material (Robertson, 1941, 316) but it was apparently similar to those present in the Norwegian species *Pterygolepis*. It is unlikely that the caudal fin differed significantly from *R. parvulus* but it would be of interest to discover whether the anal fin in *R. oeselensis* was quite as specialized as the long, low, spinous structure observed in *R. parvulus* (figs. 9, 10).

In the light of the evidence provided by the recently prepared head of the Oesel Silurian anaspid previously assigned to *Saareolepis oeselensis* (Robertson) there seems little doubt that this form must now be considered to be a species of the better known genus *Rhyncholepis* from the Upper Silurian of southern Norway, which has precedence (Kiaer, 1924). In several respects (the longer

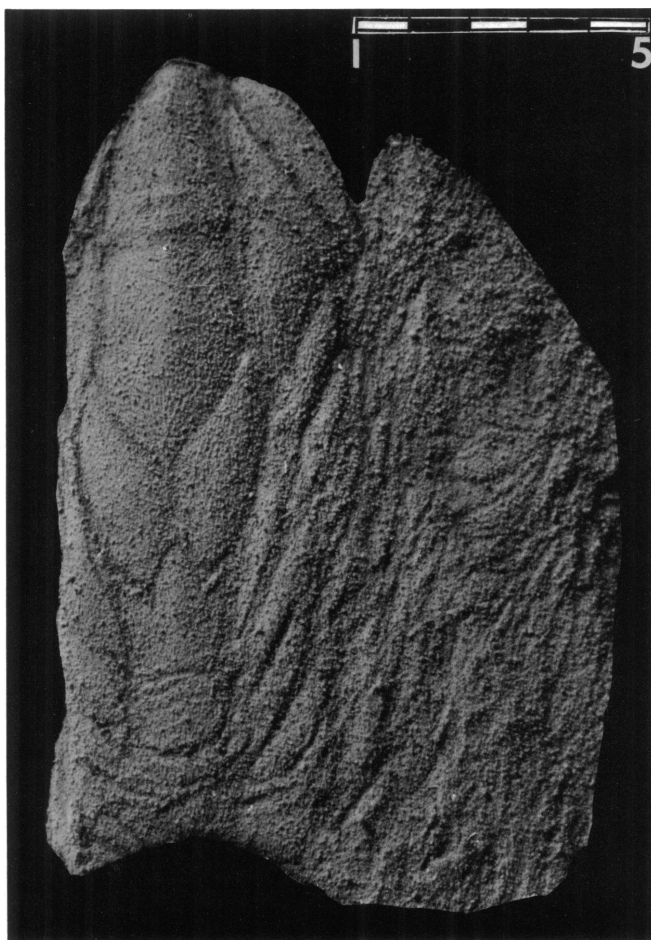


FIG. 6. *Rhyncholepis parvulus* Kiaer, Late Silurian (Ludlow), Rudstangen, Ringerike, Norway. Palaeontological Museum, Oslo EO169. Silicone rubber cast of gular plates and left cheek scale covering, whitened with ammonium chloride. Scale in mm.

pre-orbital region, the pattern of the cranial roof and the gular region, the greater development of lancet scales of the cheek area) the Baltic form is sufficiently distinct from *Rhyncholepis parvulus* Kiaer to justify continued separation in a second species of the same genus, *R. oeselensis* (Robertson).

PAIRED FINS OF *RHYNCHOLEPIS*

In 1962 when I first visited Oslo to carry out comparative studies on the Norwegian

Silurian anaspids from the quarry at Rudstangen, Ringerike described by Kiaer [1924; *Pharyngolepis*, *Pterygolepis* (*Pterolepis*), *Rhyncholepis*] evidence for the presence of paired ventrolateral finfolds was discovered in several specimens of *Pharyngolepis*, the largest of the three Ringerike genera (Ritchie, 1964, pp. 4-9, fig. 1a-c, pls. I-V). Ventrolateral finfolds had earlier been described in the late Devonian *Endeiolepis* from Scaumenac Bay, Quebec, Canada by

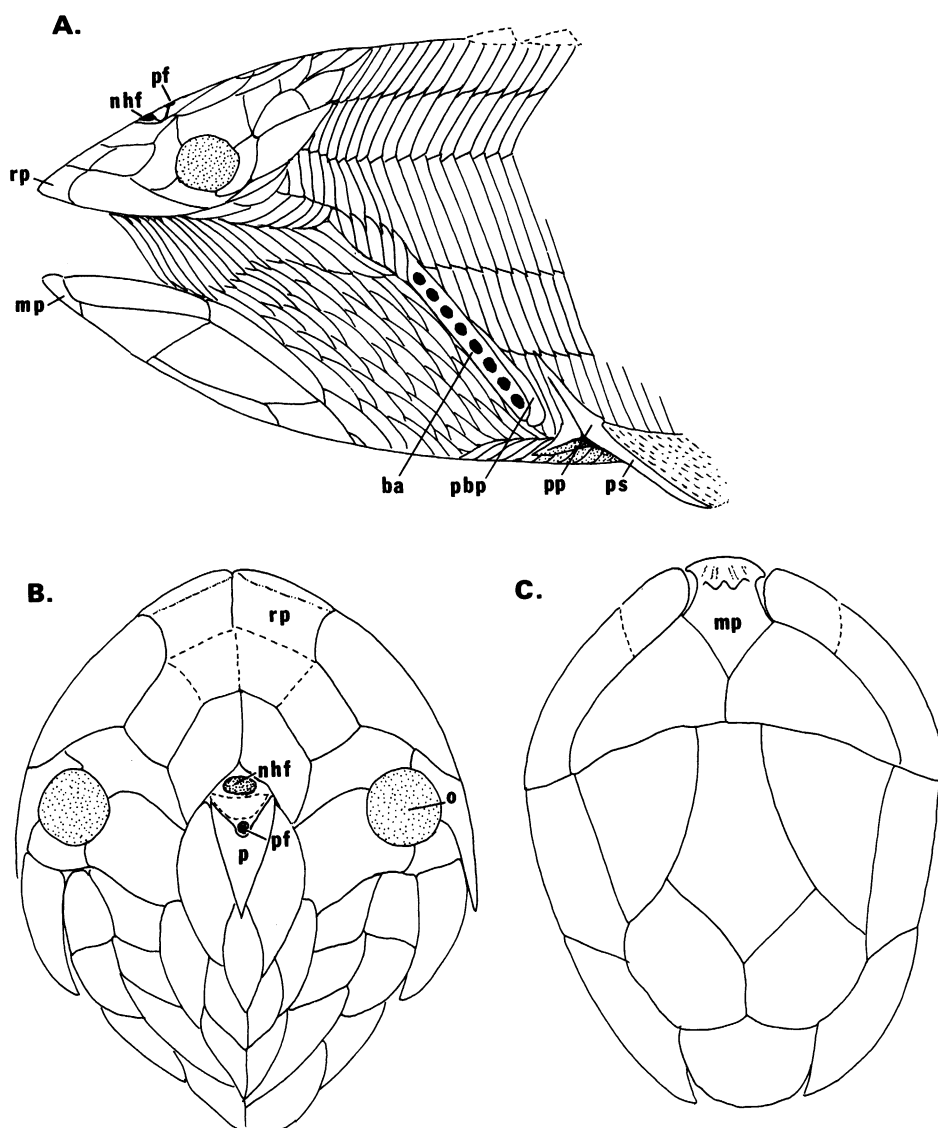


FIG. 7. *Rhyncholepis (Saarolepis) oeselensis* (Robertson), Late Silurian, Oesel, Estonia, U.S.S.R.; A. Reconstruction of head and anterior trunk, based largely on AMNH 6777a (fig. 2A), counterpart AMNH 6777b (fig. 1C) and part and counterpart of the holotype, AMNH 6698a, b (fig. 1A, B), branchial apertures restored after *R. parvulus* Kiaer (figs. 9, 10). B. Cranial shield, flattened; composite reconstruction from AMNH 6698a, b, AMNH 6777a, b. C. Ventral (gular) shield, flattened; reconstructed after AMNH 6777a, b (figs. 3, 5).

Abbreviations: ba = branchial aperture; mp = mandibular plate; nhf = nasohypophysial foramen; o = orbit; p = pineal plate; pbb = postbranchial plate; pf = pineal foramen; pp = pectoral plate; ps = pectoral spine; rp = rostral plate.

Stensiö (1939, fig. 7, Pl. 1, figs. 1, 2) but this was the only anaspid known to possess such structures. Kiaer had noted a small row of needle-sharp projecting spines along the ventrolateral ridge in *Pterolepis* (now *Pterygolepis*) *nitidus* (1924, p. 71, fig. 31b). Despite careful examination I was unable, in 1962, to detect any evidence of fins similar to those of *Pharyngolepis* in the associated material of *Pterygolepis* or *Rhyncholepis* which consist of hundreds of specimens in various states of completeness and preservation.

On two subsequent visits to the Palaeontological Museum, Oslo, in 1966 and 1973, re-examination of the *Rhyncholepis* material did reveal several specimens which, after some preparation, were discovered to possess faint, but unmistakable, remains of a delicate fin membrane. In each case this lay immediately behind the projecting pectoral spine of the large, triangular pectoral plate, the same relationship already known to be present in *Pharyngolepis oblongus* Kiaer and *Pharyngolepis heintzi* Ritchie (Ritchie, 1964, fig. 1a–c).

The specimen of *Rhyncholepis parvulus* Kiaer which best displays the ventrolateral finfold is a small, almost complete individual (Pal. Mus. Oslo, EO140, fig. 8A, B) seen from the ventral aspect with the gular region of the head twisted sideways. The ventral scales of the trunk are clearly visible, converging anteriorly and the long, sharp posterior spines of the pectoral plates project clear of the trunk on both sides. The pectoral spine on the right margin (as the specimen lies inverted in the rock) is the more fully extended. In the area immediately posterior to this spine a faint but definite stain can be distinguished, most clearly when the fossil is immersed in alcohol (as in fig. 8A). This stain thus represents a delicate, membranous fin, some 2–3 mm. wide extending along the ventral margin for about 5 mm. and terminating short of the anal fin. The outer margin is strongly convex. There are traces of a similar, but less completely preserved, fin membrane behind the other pectoral spine on the same individual.

Two other specimens of *Rhyncholepis parvulus* Kiaer in the Oslo collections (EO128 and EO168) also display faint traces of the delicate finfold behind the pectoral spine, confirming the presence, probable shape and proportions of the lateral fin of *Rhyncholepis* as shown here (fig. 10) in a modified version of Kiaer's (1924) restoration.

It has now become obvious that the presence of well-developed, paired ventrolateral finfolds was the rule, rather than the exception, among the anaspids, and the presence of such features makes anaspid swimming habits somewhat easier to understand than had originally been the case. For a long time after their first discovery, the swimming abilities of anaspids were the subject of controversy (Heintz, 1935, Parrington, 1958, Westoll, 1958, Nursall, 1962) because of the unusual combination of a hypocercal caudal fin with the notochord extending into the ventral (hypochordal) lobe and the apparent absence of paired fins. Following the discovery of paired finfolds in the geologically late *Endeiolepis aneri* Stensiö (1939) and, more recently, in *Pharyngolepis oblongus* Kiaer and *Pharyngolepis heintzi* Ritchie (1964) it became somewhat easier to understand the swimming mechanics. However, it was mistakenly assumed that the finfold in *Pharyngolepis* increased positive pitch and assisted the caudal fin which had a similar effect.

Hopson (1974, pp. 83–93), in a closely reasoned analysis, has reviewed the functional significance of the hypocercal caudal fin in the active, fusiform anaspids and has cleared up earlier misconceptions about the hypocercal tail–lateral finfold combination. He showed that equilibrium in the pitching plane could only be achieved by increasing negative pitch, and that this was what the finfold, because of its position, was adapted to do. For a fuller understanding one must take into account the relative positions of the center of gravity, center of buoyancy, and center of lift (from the finfolds and from that portion of the trunk between them).

In a heavier-than-water fish with a hetero-

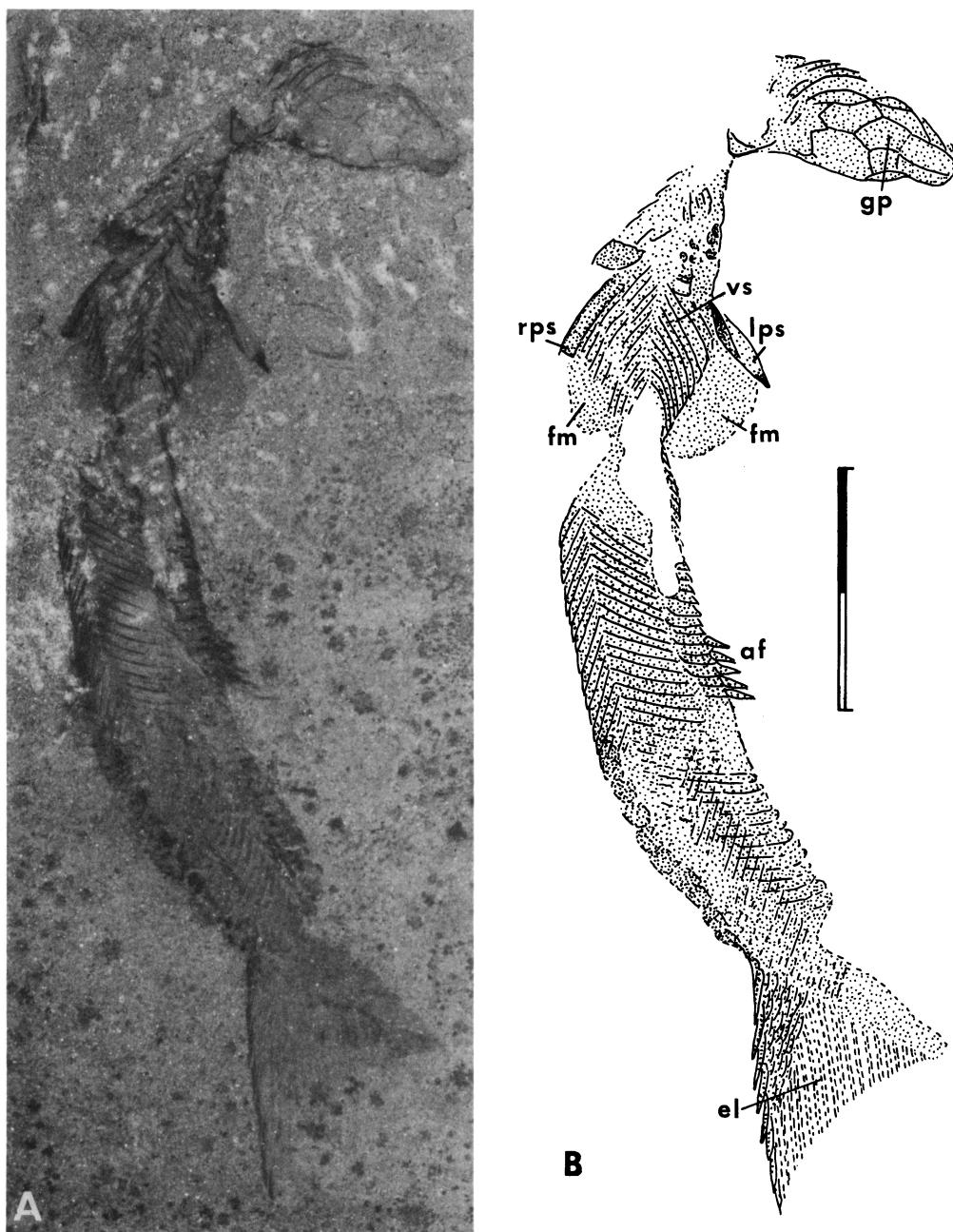


FIG. 8. *Rhyncholepis parvulus* Kiaer, Late Silurian (Lower Ludlow), Rudstangen, Ringerike, Norway. Palaeontological Museum, Oslo, EO140, smallish individual seen mainly in ventral view, with remains of delicate fin membranes preserved immediately posterior to the posterolaterally projecting pectoral spines. A. Specimen photographed under alcohol; B. Interpretation of specimen shown in figure 8A.

Abbreviations: af = anal fin scales; el = epichordal lobe (of caudal fin); fm = fin membrane; gp = gular plates; lps, rps = left and right pectoral spines; vs = ventral scales (of trunk).

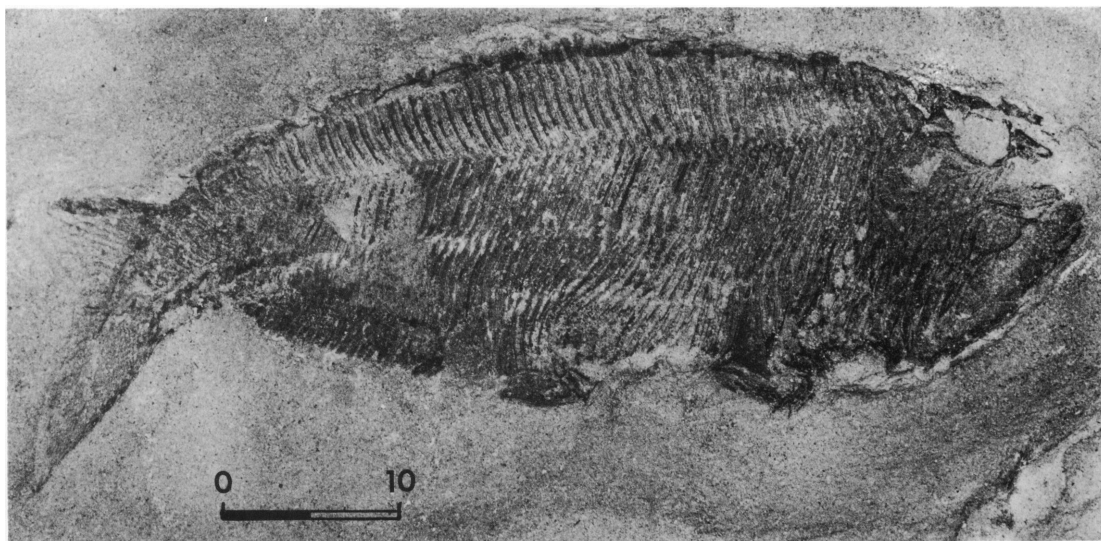


FIG. 9. *Rhyncholepis parvulus* Kiaer, Late Silurian (Lower Ludlow), Rudstangen, Ringerike, Norway. Palaeontological Museum, Oslo EO44, figured by Kiaer (1924, pl. XIV, fig. 1). Specimen photographed immersed in alcohol. Note the extension of the anterior cheek scale covering between the cranial shield and the lateral gular plates immediately ventral to the orbit, as in *Rhyncholepis oeselensis* (Robertson) (cf. figs. 2A, 7A), and horizontal orientation of preanal plate. Scale in mm.

cercal caudal fin (eg., a shark; Hopson, 1974, fig. 1A) these three centers are quite widely separated and the paired fins lie well anterior to the centers of gravity and buoyancy. In *Pharyngolepis oblongus* the situation is quite different (1974, fig. 1B) with all three centers placed close together.

The finfold condition now known to exist in *Rhyncholepis parvulus* (fig. 10) and, almost certainly also present in *R. oeselensis*, is closer to that in *Pharyngolepis heintzi* Ritchie (1964, fig. 1c) than to that in *P. oblongus*. The shorter finfold corresponds only to the anterior portion of the fin in *P. oblongus* but is relatively wider and subtriangular in shape. The center of lift force in *Rhyncholepis* (and in *P. heintzi*) lay closer to the center of gravity and thus the lift available for countering any downward thrust by the tail was virtually nil (fig. 11). Hopson suggested that the tail of *P. heintzi* (which is not known) was probably nearly or actually isobatic (producing level movement) rather than epibatic (producing upward movement) as in

P. oblongus. The net result was to decrease the dynamic stability of the fish but simultaneously increase its maneuverability. The lateral fins, lying directly below the center of gravity (as in some higher teleosts, e.g., gobies) would have produced very small turning movements and slight adjustments of the caudal fin would be relatively more effective.

The evidence therefore suggests that *Rhyncholepis*, like *Pharyngolepis* and most of the other anaspids, was an active, efficient swimmer able to operate and feed anywhere between the surface and the bottom, in contrast to the majority of the more heavily armored heterostracans and cephalaspids which appear to have been more suited to a bottom-dwelling mode of life.

STRATIGRAPHIC SIGNIFICANCE OF *RHYNCHOLEPIS*

The recognition of the anaspid genus *Rhyncholepis* in the Oesel ostracoderm faunas provides a useful link between the late Silurian vertebrate faunas of Estonia and

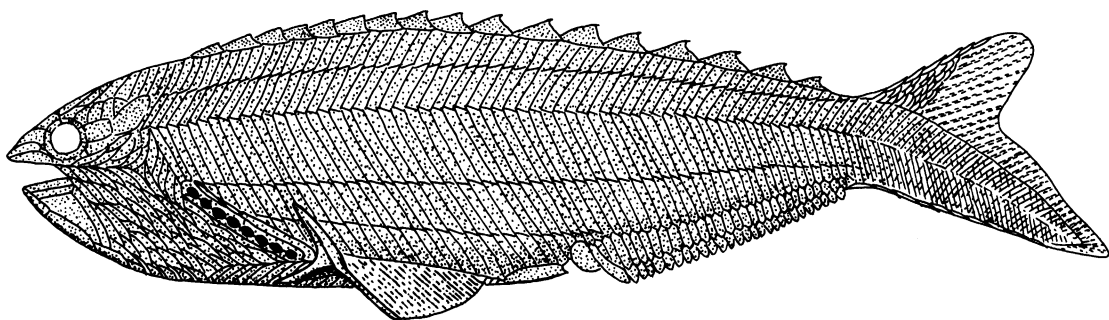


FIG. 10. *Rhyncholepis parvulus* Kiaer, Late Silurian (Lower Ludlow) Rudstangen, Ringerike, Norway. Reconstruction, modified after Kiaer (1924, fig. 36). Main differences are in the separation of the cranial and gular shields by the anterior insertion of lateral scales of the cheek, the addition of a paired "pectoral" finfold supported anteriorly by the long, slender flattened pectoral spine, and in the reorientation of the preanal ridge plate. The anteriorly converging ventral scales of the trunk terminate anterior to the preanal ridge plate.

southern Norway. Mark-Kurik (1969, pp. 145–152) has reviewed the distribution of Silurian vertebrates in Estonia whilst Heintz (1969, pp. 23–25) has reviewed the faunal and stratigraphic relationships of the Estonian, Norwegian and Scottish Silurian ostracoderm-eurypterid assemblages.

Patten's original material of *Rhyncholepis oeselensis* (Robertson) came from one very productive quarry at Himmiste (cf. Mark-Kurik, 1969, fig. 1) in western Oesel (or Saa-

rema) which was originally thought to expose the uppermost part of the Kaarma (now Rootsiküla) Stage (K_1) and the basal part of the overlying Paadla Stage (K_2); this was thought to mark the boundary between the Lower and Middle Ludlovian. Later investigations by Aaloe (1963) indicated that the ostracoderm fauna characterized by *Tremataspis mammillata* Patten (and also including *Rhyncholepis oeselensis*) came from dolomite layers higher up in the Paadla Forma-

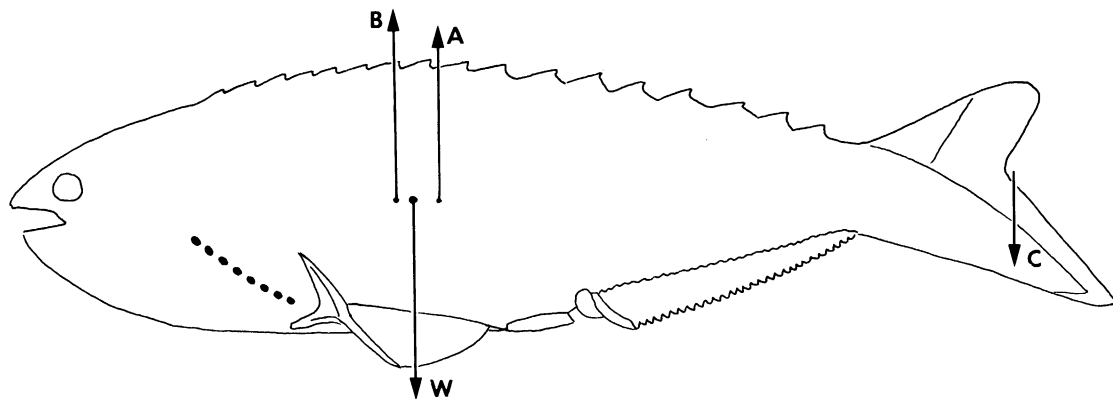


FIG. 11. *Rhyncholepis parvulus* Kiaer. Suggested vertical forces acting on the anaspid *R. parvulus* swimming horizontally (compare with Hopson, 1974, fig. 1A).

A, represents upthrust of water displaced, acting through the center of buoyancy; B, represents lift produced by snout, pectoral fins and area between them; C, represents lift produced by tail; W, represents fish's weight acting through center of gravity.

tion of probable Middle Ludlovian age. Associated with *Rhyncholepis* at Himmiste are abundant thelodont scales (*Thelodus laevis*, *T. schmidtii*, and *Phlebolepis elegans*), locally abundant articulated specimens of *Phlebolepis*, and various genera and species of cephalaspids (Mark-Kurik, 1969, fig. 3).

The Himmiste Beds (K₂H) are thought to represent sediments deposited in a semi-closed basin, temporarily freshened due to the discharge of a river (Obruchev, and Karatjute-Talimaa, 1967, pp. 6–7) whilst the preceding and following units, the Sauvere Beds (K₂S) and Uduvere Beds (K₂U), respectively, are generally represented by normal shelf deposits (Mark-Kurik, 1969, fig. 2).

Isolated anaspid scales attributable to *Rhyncholepis* (= *Saarolepis*) are now known to occur well below the Himmiste Beds and are locally abundant at Vesiku (K₁Vs) in the Rootsiküla Stage near the base of the Ludlovian.

The richest vertebrate assemblages in the late Silurian rocks of southern Norway come from the Ringerike Sandstone at Rudstangen (Kiaer, 1924) and at Nes, 1.5 km. to the northeast (cf. Heintz, 1969, fig. 1 for map). Both horizons apparently lie within Zone 10 of Kiaer, the lower part of which is now believed to be of Lower Ludlovian age.

Abundant well-preserved anaspid remains have only been found at the Rudstangen site, not at Nes, and it was the former site which produced *Pharyngolepis*, *Pterygolepis* and, of course, *Rhyncholepis parvulus* Kiaer. The occurrence of species of *Rhyncholepis* at Rudstangen, Norway and Himmiste, Oesel need not indicate that the two faunas are exactly contemporary, especially since the latest findings from Oesel indicate a Lower to Middle Ludlovian range for this little anaspid genus, but the new findings do strengthen the evidence for an early Ludlovian age for the Rudstangen ostracoderm fauna.

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