THE DORSAL SHIELD OF *PSAMMOLEPIS PARADOXA* AGASSIS.

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Abstract—A complete dorsal shield of *Psammoilepis paradoxa* Ag., collected by the author in 1927 in Latvia, is described and depicted. It is probably the most complete dorsal shield of *Psammoilepis* yet known. The growth of the dorsal shield is discussed on the basis of investigations of the scales-pattern around the margins of the shield. It is most probable that the scales which surround the dorsal shield, gradually become incorporated in the shield. Lastly the traces of wear on the surface of the dorsal shield and on some fragments of other shields are described and discussed.

Introduction

During a visit to Latvia and Estonia in 1927, I collected in different localities some Middle Devonian Agnathes and fishes. The majority of the fossils represented only fragments, but a few were more complete bones and shields. Among the latter was also a large shield of *Psammoilepis paradoxa* Ag. I discovered it in a section along the shore of the Livland AA river, near Zellen-dorf.

Originally, only a small part of the shield protruded from the section, and I could not imagine that the shield in reality was almost complete; I therefore, unfortunately, carved out only one piece after another, without clearing the whole shield first. As a result I obtained a great number of relatively small pieces which I could assemble only after my return to Oslo. Only then did it become clear to me that I had found an almost complete dorsal shield of *Psammoilepis* (Pl. 17).

As will be known, complete dorsal shields of *Psammoilepis* are very rare. As far as I can see from the relevant literature, more or less complete dorsal shields of *Psammoilepis* have hitherto never been described. The only illustration known is a reconstruction published by Gross (1933) (fig. 1 A). In the text, Gross mentioned only two dorsal shields of *Psammoilepis*—one from the Palaeontological Museum, Oslo, and the other from Riga Museum. It is difficult to decide from Gross' description, how complete the Riga specimen is. He mentions only that the length of the shield is 28 cm. and the width 23.5 cm., and adds "Die ganze etwas schwacher gewobte Platte ist vorn eingeschnitten, etwas so wie die von *Drepanaspis*" (Gross, 1933, p. 6).

During my visit to Riga Museum in 1927, I made a sketch of a large fragment of a dorsal shield collected by professor Küpfner and determined as "*Psammosteus* Ag. Dorsalplatte, 1922, 23." There is, however, no doubt that this shield in fact belongs to *Psammoilepis*. I do not know whether the shield mentioned is the same as Gross has studied, but that is not at all probable. The specimen I saw was only a large fragment of a dorsal shield, with a well-preserved central part and a more or less complete front part.

In 1944, Obrutchev published a reconstruction of *Psammoilepis paradoxa* (fig. 1 B), but he mentioned in the description that the shape of the dorsal shield is taken from Gross' drawing mentioned previously. It is evident that Obrutchev himself has not known any other more or less complete dorsal shield of *Psammoilepis*. In a yet unpublished paper, Dr. E. Mark gives a new
and very interesting reconstruction of *Psammolepis venskovi* (Obrutchev). I would here like to express my deep thanks to Dr. Mark for permission to publish in my paper her reconstruction, drawn by Professor Bystrov (fig. 1, C).

**Description of the Dorsal Shield**

The dorsal shield of *Psammolepis paradoxa* in the Paleontological Museum, Oslo (P.M.O.A. 172) (Fig. 2, Pls. 17, 18) is 271 mm. long and 252 mm. broad. Gross (1933) mentioned slightly diverging figures:—ca. 26 cm. long and ca. 25 cm. broad. The shield is moderately convex—the greatest height being ca. 45 mm. and this point is situated not in the centre, but a little nearer the back edge of the shield. The anterior

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**Fig. 1**—Three different reconstructions of the dorsal shield of *Psammolepis*.

A. *P. paradoxa* Ag. After Gross, 1933.
B. *P. paradoxa* Ag. After Obrutchev, 1941.
C. *P. venskovi* (Obrutchev). After a yet unpublished paper by Mark (1957), with kind permission from the author. The drawing is made by Professor A. Bystrov.

It is thus clear, that the dorsal shield in the possession of the Paleontological Museum in Oslo is the only almost complete dorsal shield of *Psammolepis paradoxa* known hitherto. It is therefore, of some interest to give a more detailed description of it.
part of the shield is thus flatter than the posterior. Besides, the posterio-median point of the shield (D) is placed somewhat

The shape of the shield is more or less pentagonal. The front margin (B-A-B') is just slightly concave, not so much by far

higher (ca. 10 mm.) than the lateral sides (C), thus it is bent more from side to side, than from front to rear.

as depicted by Gross (1933) and Obrutchev (1944) (Fig. 1, A,B). In the centre of the front margin there is developed a small, but

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**Fig. 2—Psammelepis paraopena Ag. (P.M.O.A 172).** The dorsal side of the dorsal shield. Drawn after a photograph of the shield and compared with the original. Explanation of the letters—see in the text.
well-marked point (A), limited on both sides by small impressions (a–a'). The left anterio-
lateral corner (B') is lost, on the right side, the corner (B) is partly damaged; but it is
certain that the anterio-lateral corner was not so pointed as is drawn on Gross' and
Obrutchev's reconstructions.

The anterio-lateral margins (B–C, B'–C')
are slightly concavo-convex and the lateral
corners (C–C') more rounded than shown by
Gross. The shield is broadest between
the lateral corners (C–C') and the line
between them goes almost through the mid-
point of the shield.

The posterio-lateral sides (C–D, C'–C')
are moderately convex, somewhat irregular.
The posterio-median corner of the shield (D)
is moderately rounded, but well-expressed.
Gross mentioned in his description of the
shield that “Hinterrand ist konvex, mit einer
kurzen, median verdickten Spitze, die an
einem Exempler des Osloer Museum gut zu
sehen ist” (1933, p. 6). It is true that our
shield has an expressed short posterio-median
spine (D), but it consists only of the basal
and partly median (spongiosa) layers, but
lacking the superficial layers (fig. 2, Pl. 17,2).

It was thus, in the living animal, situated
under the surface of the skin and was invisible;
it was probably even covered by isolated
median scales, and therefore can not be
compared with the median-dorsal spines, for
instance, in Pteraspis. It is, however,
uncertain that the presence of such a “median
spine” is characteristic for Psammolepis para-
doxa. On a small fragment of another
specimen of the shield of Psammolepis in my
possession (P.M.O.A. 178, Pl. 19, 1), the
posterio-median corner is preserved, but the
“median spine” is not developed. I suppose
the presence or absence of the “median
spine” is more casual and is connected with
the different growth-stages of the shield.
This question will be discussed later (p. 158).

The shield is comparatively thin in front
and anterio-lateral parts, and is here between
2.8–3.5 mm. In the median part it is about
3.5 mm., but the posterior part, especially
along the posterior margin, is thicker—about
4.0–4.5 mm.

The surface of the shield is usually covered
with fine, stellar, almost rounded teeth,
placed close together (Pl. 17, 2; Pl. 18). The
shape and size of the single tooth varies
moderately. The teeth in the median part
of the shield, however, are smaller than those
placed more peripherally, but there is not
much difference (Pl. 18, 1).

Somewhat in front of the actual centre of
the shield, there is situated a well-marked
and comparatively clearly bounded central
area. (Fig. 2, Pl. 17, 1; Pl. 18, 1). It too, is
approximately pentagonal and shows a some-
what confused, concentric arrangement of the
teeth. On Gross' and Obrutchev's recon-
structions, these “central areas” are clearly
depicted, and in the description Gross men-
tioned that “Das Zentrum der Platte ist
ungefeldert, von ovalen Umrisse.” In both
reconstructions the central areas are placed
in the actual centre of the shield and are
relatively large. In each, it comprises about
0.4 of total length and 0.3 of the total width
of the shield. In my specimen, however,
the central area is considerably smaller. Its
length comprises only about 0.24 and the
breadth not more than 0.2 of the total
length and breadth of the shield, respectively.
On the reconstruction made by Dr. Mark
(Fig. 1, C), the “central area” is situated at
the same place as in our shield. The poster-
ioar angle of the central area lies somewhat
in front of the actual centre of the shield.
The distance from the front margin of the
central area to the front margin of the shield
is only about one half of the length from the
posterio corner of the central area to the
posterio corner of the shield (Fig. 1).

Explanation of Plate 17

Pasammolepis paradoxus Ag. (P.M.O.A 172)

Fig. 1—The dorsal side of the dorsal shield. Explanation of the letters—see in the text.

2—The posterio part of the dorsal shield to show the development of “posterio median scale” (m)
and posterio-median “spine” (D). (Photo. B. Mauritz).

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HEINTZ: PSAMMOLEPIS PARADOXA AG. FROM LATVIA
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is thus evident that the growth of the shield takes place more rapidly in the posterior-lateral than in the anterior direction. This is in fact remarkable. In the majority of the Heterostraci, where the growth of the shield can be studied it is, as a rule, the front part of the shield which grows most rapidly.

As is well known, Gross, (1930, 1933) the dorsal shield of Psammolepis, with the exception of the central area, shows a more or less clear “scaled” pattern. The single “scales” are very distinctly seen along the margin of the shield, but become more blurred towards the centre (Fig. 2, Pls. 17, 18). Along the posterior-lateral margin the single scales are especially distinct (Pl. 17; 18; 2,3). They are sharply defined, often with more or less deep furrows, but also partly overlapping one another. (Pl. 18, 2). One can often see two or three rows of single, more or less rhombic, scales arranged very regularly (Fig. 2). On the other side, the shape of the scales along the antero-lateral margins is more irregular; the scales are not arranged in pronounced rows, nor do they “overlap” one another. Along the margin of the front part of the shield one can only distinguish one row of clearly bounded “scales” (Fig. 2; Pl. 18, 1).

In the direction towards the centre of the shield the “scales” become smaller and the boundaries between them more and more obscure (Fig. 2; Pls. 17, 18). It is not always easy to determine the shape with certainty. In the posterior and the posterior-lateral parts of the shield, one can still trace well-arranged rows, of rhomboid scales even at some distance from the margin (Fig. 2; Pl. 18, 2,3). In antero-lateral and especially anterior parts, the scale-pattern becomes more indistinct even close to the margin (Fig. 2; Pl. 18, 1).

Close to the central area, the scale-pattern disappears more or less completely and one can only see elongated impressions or furrows, radiating from the central area in all directions, but most clearly towards the anterior side (Pl. 18, 1). Here one can see, more or less, well-expressed concentric lines, arranged parallel to the central area—kind of “growth-lines” (Fig. 2; Pls. 17, 1; 18, 1).

The greatest part of the shield-border of our specimen is very well preserved (Pl. 17, 1). The appearance of the margins varies a great deal in different parts. Generally one can recognise three different types of marginal structures.

The first type is only to be found at few places. From the boundary of the sculptured surface of the shield the unsculptured margin declines gradually forwards and downwards and becomes thinner. Here and there is developed a kind of “overlapping-margin”. This type of margin is seen on both sides of the antero-median point of the shield (a, a’) and also on a few isolated parts of the shields (Fig. 2; Pl. 17, 1).

The most common type of the shield-border has a more or less rounded margin, almost perpendicular to the surface. The boundary of the sculptured part is not always sharply defined and runs into the upper declining part of the margin. The unsculptured part of the margin is practically invisible from the dorsal side. These types of margins are developed from the antero-median to about the middle of the antero-lateral part of the margin (a–b, a’–b’) and from somewhat behind the lateral corner (c–c’) to somewhat in front of the antero-median “spine” (C–d, C’–d’). (Fig. 2, Pl. 17, 1; Pl. 18).

The last type is most marked. Here the sculpture continues to the very limit of the shield surface, but the basal part runs still further forwards, and composes a kind of relatively thin brim beneath and in front of the sculptured surface. Between the surface and the basal part, a more or less
deep cavity is developed. This remarkable type of margin is especially clearly developed around the lateral angle (b-C-c; b'-C'-c') (Fig. 2; Pl. 17, 1; Pl. 18) and around the posterio-median "spine" (d-D-d'). The posterior "spine" is in fact a strongly developed basal part of the shield.

These three types of margins are developed more or less symmetrically on both sides of the shield. It is thus natural to suppose that they are not occasional occurrences, but correspond in one way or another to the different kind of scales or plates which surrounded different parts of the dorsal shield. It seems improbable that any of these three margin-types can be regarded as really overlapping-margins, covered by larger neighbouring plates.

On the underside the shield is relatively smooth, with clear lines, radiating from the centre. Some of these lines are very thin, others somewhat coarser and thicker. On the posterior part of the shield an expressed, narrow keel is developed, especially high on the posterio-median "spine", becoming markedly lower and thinner in the anterior direction, but which can still be traced as a very thin weak crest nearing the front of the centre of the shield.

Besides the radiating lines one can also see, on the inner surface, concentrically arranged lines or diminitive thickenings, running more or less parallel to the margin of the shield. They are especially clear along the lateral and posterio-lateral border.

On the underside, no traces of the scale-pattern, so clearly developed on the dorsal surface of the shield—can be seen, not even in places where the single scales are very sharply divided from each other. No expressed overlapping-margin can, on the whole, be seen on the margins from the underside. Only along the front margin, on both sides of the median point, two relatively short, but well-expressed and marked margins are developed.

**THE GROWTH OF THE DORSAL SHIELD**

There cannot be any doubt that the dorsal shield of *Psammolepis paradoxa* increased in size during the life of the animal. It is clearly seen on the arrangement of the "scale-pattern" on the surface of the shield (Fig. 2). It is, however, quite obvious that the growth does not take place as a more or less continuous enlarging of the shield by appositional growth along the margins, e.g. in *Drepanaspis*, but probably by periodical incorporation of a smaller or larger number of single scales.

Gross (1930, 1933) and Obrutchev (1944, 1947) mention that the arrangement of the single shields, plates and scales in *Psammo- stoids* is most probably more or less the same as in *Drepanaspis*. On the reconstruction of the dorsal side of *Psammolepis* made by Dr. Mark (Fig. 1, C) one can see that this interpretation is correct. The dorsal and ventral shields thus do not come into direct contact with the other body plates such as branchials, eventually rostrals, orbitals and cornals, but there was developed a zone with minute plates or scales between them. They are the small plates and scales which surround the dorsal shield which gradually become incorporated into the shield, while the new scales at the same time most probably come into existence in the zone between the dorsal shield and the other body plates.

The growth of the dorsal shield took place probably in the following way:—The single

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**EXPLANATION OF PLATE 19**

*Psammolepis paradoxa* Ag. (P.M.O.A 178)

Fig. 1.—A fragment of the posterior part of the dorsal shield. m—"posterior median scale", ls—"posterior-lateral scales".

*Psammolepis (?) paradoxa* Ag. (P.M.O.A 173)

2.—The whole shield fragment.
3, 4, 5.—Greatly enlarged parts of the same shield, showing the secondary teeth, partly worn (3, lower part).
6.—An enlarged part of the shield, showing the scale-pattern and the worn areas with the secondary teeth. (Photo, B. Mauritz).
HEINTZ: PSAMMOLEPIS PARADOXA AG. FROM LATVIA
scales surrounding the shield were thin, much thinner than the shield itself. Their spongiosa and basal layers especially were quite minute. I have in my possession some scales in which the basal layer barely covers the thin spongiosa. Gross (1933) mentioned also such thin scales. These thin scales lay close to the border of the shield. The basal layer grows underneath the scales so that they gradually become attached to the basal layer by the developed spongiosa. I suppose, therefore, that the boundary between the shield and surrounding scales was not always clearly defined, and the reconstructions of Obrutchev (1944) are perhaps therefore not entirely successful.

One may, as mentioned previously, clearly follow this incorporation of the scales by studying the surface of the shield. The scale-rows along the margins of the shield are clearly expressed and divided from each other by marked furrows or they overlap one another (Fig. 2; Pl. 18, 2,3). Towards the centre of the shield the boundaries between the scales become more and more obscure, and disappear more or less completely near the central area (Pl. 17, 1; 18, 1).

As has been mentioned, the boundaries between the single scales are only seen from the dorsal side. From the ventral side no trace of them can be seen. This fact supports the suggestions that the new scales become incorporated in the shield by means of the basal layer. Investigating the scale-pattern of the surface of the shield, we may state that the rows of scales are not incorporated equally along the whole margin of the shield, but in smaller groups at different places (Fig. 2, C; Pl. 18, 2,3). The parts along the margin where the basal layer especially protrudes, are probably the places where the scales would be incorporated next time. It has been mentioned that the posterior-median part of the shield has a relatively long “spine” protruding backwards (Fig. 2; Pl. 17, 2). It consists only of the basal layer of the shield and was certainly in the living animal covered by a median scale. I have in my possession a small fragment of another dorsal shield (P.M.O.A. 178) in which the posterior-median part of the shield is probably preserved immediately after the incorporation of the new scales (Pl. 19, 1). It may be seen that the median scale (m), which corres-
ponds to the median scale of our shield (Pl. 17, 2,m), is surrounded on the posterior side by two lateral scales, growing from the sides towards the median line (l). No traces of the basal brim or spine are seen here.

As mentioned previously, the scales which became incorporated into the shield, were probably originally isolated scales situated in the intermedian zone between the dorsal and lateral shield plates. The shape and arrangement of these incorporated “scales” along the margin of the shield can thus tell us about the shape and position of the scales and minute plates in the intermedian zones. One may suppose that the anterior and anterio-lateral part of the intermedian zones were covered by relatively flat, more or less irregular small plates, which do not overlap each other (Pl. 18, 1). On the other side in the posterio-lateral and posterior part, the intermedian zone probably contained expressed scales overlapping each other, having on the dorsal side a more or less clear diagonally thickened ridge (Pl. 18, 2,3). Comparing this arrangement with the conditions known from Drepanaspis, we find that it corresponds perfectly (Traquair, 1903).

TRACES OF WEAR ON THE SURFACE OF THE SHIELD
Traces of more or less heavy wear are earlier described from the ventral and branchial (coronal) plates of various Psammolestids (Gross 1930, 33, 36; Obrutchev 1944, 47; Bystraw 1956; Mark 1956 and Preobraschenskij 1910). At many places on the shield the wear could be very heavy and the whole upper layer, consisting of teeth, could disappear and the spongiosa be filled secondarily with dentin (Gross 1933, 36). In many cases it is also described that new, secondary layers of teeth are developed on the worn areas, covering them completely and in some cases also spreading over the more or less well-worn older teeth (Bystraw 1956, Gross 1935).

On our shield the traces of wear are clearly seen in many places. Firstly, the actual central part of the central area is more or less considerably worn (Pl. 18, 1). Secondly, all the more thickened and protruding parts of the shield, e.g., the boundaries and median ridges on the “scales” etc.
are torn (Pl. 17, 2; 18, 2, 3). The wear is, on the whole, quite moderate and only the highest parts of the teeth became ground down—partly, however, very heavily, so that nearly all the traces of the teeth have disappeared. I have, however, only at some very few and small areas, confirmed that the spongiosa has become exposed, and I have never seen that secondary teeth have developed.

On another shield-fragment which I collected in Latvia in 1928 (P.M.O.A. 173, Pl. 19, 2–6), the traces of wear are, however, much heavier. The piece is about 11 cm. long and 7.5 cm. broad and belonged to a relatively flat, bilaterally symmetrical shield, with a more or less completely preserved central area (Fig. 3, Pl. 19, 2). It is most probable that the fragment belongs to either a dorsal or a rostral shield (Fig. 1, C), as it is too flat to be a part of the ventral shield. The shape of the central area differs, however, considerably from the central area, in our form. The single teeth in the superficial layer are also clearly smaller. The arrangement of the “scale-pattern” seen in the extreme lateral part of the fragment is, however, quite similar to that in Psammoletis paradoxa (Pl. 19, 2, 6). It is thus at present difficult to determine with certainty whether the fragment belongs to P. paradoxa or perhaps represents another Psammoletis species.

As mentioned previously, the shape at the central area differs considerably from that of our dorsal shield. The “central area” is not pentagonal but oval, somewhat constricted from the sides (Fig. 3, Pl. 19, 2). A clear impressed line (a–a) on the lateral side, runs from the central area to the right, and it seems as if the corresponding line also was developed on the left side. Two other, not so marked lines (b,b) run symmetrically from the anterior (?) margin of the central area forwards (?) and somewhat outwards. Around the central area a broad, nearly plain zone is developed with expressed concentrically arranged growth-lines (Pl. 19, 2). The posterior (?) part, behind the above-mentioned impressed lateral lines (a–a), is considerably broader than the anterior. The “scale-pattern” is only seen on the most lateral part of the fragment and is sharply divided from the zone with growth-lines (Pl. 19, 2). The single “scales” are well marked off and are arranged in the same way as on the posterio-lateral parts of the dorsal shield of Psammoletis (Pl. 19, 2, 6).

It has been mentioned previously that our fragment is very heavily worn. In most of the central area the teeth are ground (Pl. 19, 2). On some places the spongiosa are seen, and some small groups of the secondary teeth are developed. At the zone with growth-lines the superficial teeth-layer is also worn down on the most protuberant places, and on some few points the secondary teeth are developed (Pl. 19, 2, 6). The area with “scale-pattern” is, however, partly very heavily worn. At all more protuberant and thicker parts, the original teeth-covering has completely disappeared, and more or less large collections of the secondary teeth are developed (Pl. 19, 3, 6). Even the secondary teeth are more or less heavily worn, which indicates that the grinding process continued also after the new teeth were developed (Pl. 19, 3, 5).

The development of the secondary teeth on the shields of different Psammosteids has been described earlier in detail (Gross 1935, Bystrow 1956) and will not be discussed here. In most of the earlier descriptions, however, the fragments with secondary developed teeth belong to the ventral shield or the corinal and branchial plates. All these plates are, during the life of the bentonic animal, in constant contact with the bottom, and are thus exposed to heavy wear.

In our case both shields are from the dorsal side of the animal, and it is not easy to understand how so marked wear can occur here. In a letter to me Professor Bystrow proposes two possible explanations:

1) *Psammoletis* lived most probably in rivers with strong currents. The animals did not move very much and according to Obrutchev (1949) lay mostly on the bottom of the streams with the head against the direction of the current. Sand and mud whirled by the stream could thus polish the dorsal shield.

It seems to me, however, that this explanation does not take into consideration why only the most protuberant parts of the shield are worn, and that the boundaries between the worn and unworn parts are so sharp.
Fig. 3—Psammolepis (P) paradoxa Ag. (P.M.O.A. 173). A fragment of the dorsal or nostral shield. The dotted area is the reflection of the fragment, drawn to give an idea of the structure of the whole shield.
The whirling sand would likely polish the whole shield to more or less the same degree.

2) *Psammolepis* could perhaps wriggle into the bottom sand. The sand would cover the whole animal and the dorsal shield could be more or less heavily worn.

This proposition, as far as I can judge, is not very probable. It would not be easy for such a large, and certainly not very mobile animal to wriggle into the bottom sand, and it would be surely still more difficult for it to get out again. Any wear should, in this case, be noticeable over the whole surface of the shield, not only on the most protuberant places.

As has been mentioned, the study of the surface of the dorsal shield of *Psammolepis* shows that only the more protuberant parts are worn, while the depressed areas have their teeth sculpture completely untouched. Thus it seems, that the wear is caused by rubbing or friction against a more or less firm, even surface. Perhaps the animal has in one way or other rubbed its shield against rocks and stones in an attempt to keep itself steady in the current, or it has scratched itself against the bottom, occasionally turning upside down, as the fish was certainly an extremely poor swimmer and very clumsy.

**REFERENCES**


