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Traces of *Augoichnus dituberculatus* gen. et sp. nov. on *Hypermorphocrinus magnospinosus* from the Lower Permian of Cisuralia

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Abstract—Traces of *Augoichnus dituberculatus* on *Hypermorphocrinus magnospinosus* and some other crinoids are described from the reef deposits of the Sarginian Horizon near the village of Ryabinovka, in the vicinity of Krasnoufimsk. Usually these are groups of shallow depressions, egg-shaped in outline, 4–5 mm long, similarly oriented, with a marginal groove, paired tubercles, and a deeper subcentral region. Less commonly the depressions are deep and occasionally even can perforate the skeleton. It is possible that these traces were left by gastropods, which could have moved on the surface of crinoids and fed at their expense.

Keywords: traces, new taxa, *Augoichnus dituberculatus*, *Hypermorphocrinus magnospinosus*, Lower Permian, Cisuralia

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INTRODUCTION

The remains of very large reef-associated crinoids *Hypermorphocrinus magnospinosus* Arendt, 1968, which I discovered in an outcrop of Sarginian (Upper Artinskian) rocks near a railway tunnel above the village of Ryabinovka near the town of Krasnoufimsk, show numerous traces described below. They are found on stems, cups, and very large spines of crowns extending from the lowermost arm segments and the apex of the anal sac, and on other arm segments. Usually, these are shallow or moderately deep bilaterally symmetrical depressions, ovoid in outline, with a deeper subcentral region and small paired tubercles posteriorly. The traces can be rather deep and sometimes the skeleton is perforated throughout up to the places of the supposed location of soft tissues. The depressions are characteristically located on the borders between the adjacent crown plates, arm and stem segments where soft tissues were more accessible and chains of similarly oriented depressions are observed on the spines, with the narrower anterior side and paired tubercles posteriorly. They are also occasionally found on other crinoids and also can be deep and even perforate the skeleton.

On the cups, these traces are rather irregular but they are grouped closer to the plane of symmetry and especially to the anal area of these rheophilic forms, generally forming one or several longitudinal lines upon spines. Occasionally rounded or oval traces can be observed. A large assemblage of current-associated forms, including the microcrinoids Hypocrinacea and Allagicrinacea, is found in association with the depressions. The organisms that left the traces apparently lived on the crinoids in places where many food particles brought by the currents, and crinoid faeces, accumulated. They most likely fed on ectoderm and substances on its surface and less commonly (in the case of perforated skeletons) on the soft tissue of the organisms they lived on. The soft tissue was more accessible by penetration into the marginal areas of plates and segments. These organisms were apparently able to remain stationary in the regions most suitable for penetration, but when looking for a more favorable place they were probably capable of active movement. Sometimes previous traces are overlapped by newer ones. Together with crinoids, the locality contains many platyceratid gastropods, the only skeletal organisms that could possibly have left these traces.

Similar traces were found on the holotype of *Arrectocrinus abruptus* (Moore and Plummer, 1940) from the Beattie Limestone (Lower Permian, Kansas). These are most commonly rounded rather than ovoid, 4–5 mm across, apparently without paired tubercles. Ten depressions surround the cup along the border between the basal and radial circlets, and according to Moore and Plummer, they are apparently formed by a shell-boring gastropod. The traces described in this article can also possess the above features and in one of the cups of *Hypermorphocrinus magnospinosus* are arranged in nine depressions also surrounding the cup, along the border between the circlets (basal and infrabasal). Moore and Plummer (1940, p. 290), note that

"This type of marking on crinoid plates and stems is not uncommon.... The borings are very much like those made by carnivorous gastropods on shells of other marine animals, and association of gastropods and crinoids in which the gastropod is attached to the crinoid near the anal vent.... these gastropods appear to have fed on the refuse from the crinoids rather than on the soft parts of the animal itself."

Genus *Augoichnus* Arendt, gen. nov.

Etymology. From the Latinized Greek *augo* (egg) and *ichnus* (trace) to reflect the ovoid (egg-shaped) outline.

Type species. *A. dituberculatus* Arendt, sp. nov.; Lower Permian, Upper Artinskian, Sarginian Horizon, Cisuralia.

Diagnosis. Traces of varying, usually shallow depth, on skeletons of *Hypermorphocrinus* and occasionally other crinoids. Ovoid in outline (less commonly oval and round), bilaterally symmetrical, rimmed by marginal groove or two grooves, with a relatively deeper subcentral depression and as a rule, paired tubercles between it and the posterior margin. Sometime skeleton was perforated.

Species composition. Type species.

Remarks. At present it is difficult to give a formal comparison for the traces described. Clearly delineated, ovoid bilaterally symmetrical traces with paired tubercles to my knowledge are not found in either fossil or extant species. Fossil crinoids of various geological ages often possess round borings, varying in size from very small to larger ones, sometimes penetrating the skeleton through, but usually very small in diameter. Occasionally, they are paired, e.g., on the arms of the Upper Carboniferous *Cromyocrinus simplex* Trd., penetrating the latter from outside to the ambulacral grooves. These are called *Schizoproboscina ivanovi* Yak. (Arendt, 1961; Yakovlev, 1939).[1]

The author has shown this material to Academician A.V. Ivanov who responded on April 4, 1965 saying: "... I checked the imprints on the spines of Cidaridae when the parasitic mollusk is removed (e.g., *Thyca* and *Capulus*). It became apparent that the traces are very similar to what you showed to me on the spines of your fossil crinoids." Unfortunately I was not able to see that material. Traces of attachment of some gastropods to the spines of extant Cidaridae, which are presently interpreted as depressions, lack features of the traces described in this paper. In addition, my own observations of various attachments and boring traces on fossil crinoids of various geological ages and extant echinoids, as well as literature data show that all previously known material bears little resemblance to traces described herein (Arendt, 1985; Yakovlev, 1939, 1964; Bowsher, 1955; Breimer, 1978; Franzen 1974; Häntzschel, 1975; Hyman, 1955; Lane, 1978; etc.). The previously described traces never showed a typical for our objects combination of egg-shaped shape, distinct outline, bilateral symmetry, and paired tubercles.

Attachment and encrustation traces of organisms using crinoids as substrate are simpler in morphology. These are areas, often depressed, bored or following the original relief, lacking morphological features similar to those described for *A. dituberculatus*. It appears that these animals used some chemicals to bore through the crinoidal skeletons. In the case of deep penetration, they could also use ligament, muscular, nervous, and other tissues for feeding. Organisms that fed on crinoids and received sufficient amount of food could stay in the same place, without any movement. The traces described in this paper most likely belonged to gastropods, which were not always tightly attached or encrusting, but often moved along the crinoids in search of richer or more diverse feeding grounds. A mollusk could feed on epidermis, on food particles brought to rheophilic crinoids by currents, and possibly on faeces produced by *Hypermorphocrinus* and other crinoids. Reefal regions of the Sarginian sea typically supported rheophilic biotas, as is clearly indicated by the appearance of diverse crinoids from these regions. Yakovlev (1964) noted that platyceratids could possibly drill into the anal vent of crinoids to facilitate coprophagy.

Stems of *Hypermorphocrinus* could "creep" along the bottom in the intrareefal depressions with erect crowns bending up and laterally to follow the current. The crown was not erected very high up and was not supported on the bottom by the cup, which was weakly convex at the base, and by the spines on the arm bases. These very specialized crinoids hosted some very specialized platyceratids that fed mainly at their expense, and possibly also some other organisms that left the traces described in this paper. In relation to the dominant current, the crinoids were apparently oriented with the A^2 ray facing forward and interray CD facing backward. The spines at the arm bases during normal

[1] A fragment of an arm of *Cromiocrinus simplex* Trd. with six perforations *Schizoproboscina ivanovi* Yak. extending on the external surface of the arm to the ambulacral groove (no. 1641/299) was found by A.V. Stupachenko in a quarry near the village of Myachkovo in the same beds that yielded Yakovlev's (1939) material. Similar large perforations are evenly spread along the ambulacral groove. Externally on the arm, there are similar large paired perforations with one rounded ridge, also a group of three small perforations with one rounded ridge and one small perforation in the depression between them. It appears that all "Myachkovian" perforations on the arms, cups, and stems, penetrating the skeleton, or shallower unpaired or paired perforations with a shared ridge or lacking it belonged to *Schizoproboscina ivanovi* Yak. (Arendt, 1961, text-figs. 1, 2, pl. 14).

[2] Here and below I use the letter indices: (A, B, C, D, E) rays, (AB, BC, CD, DE, EA) interrays, (IBB) infrabasals, (BB) basals, (RR) radials, (RA) radianal plate, (RX, X) anals, (IBr_1) the first brachial of the first order arm, (L) length of the trace, (W) maximum width, (H) maximum depth, (l) distance between the paired tubercles, (l_1) distance between the adjacent traces, (bp) back part, (fp) front part, (ir) interieur reduce, (mg) marginal groove, (ps) plane symmetry, (pt) pair tubercles, (sh) subcentral hollow.

feeding opened together with the arms, and when the feeding was discontinued they were closed in such way that the tops of the arm spines and those of distal spines on the anal sac were positioned at the same level, almost completely converging. The damaging organisms were located mainly inside the space between the spine on the dorsal cup, in the anal sac, and on the on the cup surface. *A. dituberculatus* were located above the lower spines and below the upper spines.

Penetration of the skeleton, aiding more effective feeding on soft tissues in the most accessible places, primarily along the plate margins, was performed in the zones where two, three, or more plate margins come together (Pl. 4, figs. 1, 5, 9). Plate 4, fig. 5 shows a relatively thick skeleton penetrated by a depression with a cylindrical wall reaching the ligament cavity.

The expanded bases of spines typically possess two or three traces oriented distally by the narrow end. Further on, on the tapering part of the spines the traces are arranged in a linear chain, always with the narrow end oriented distally. They reach approximately half the length of the spine, with one–three distal traces being considerably narrower than the previous ones (Pl. 4, figs. 3–6, 8). The arm spines possess traces on their upper side, but in one instance a short chain of five small traces is located on the left side of the spine (Pl. 4, fig. 6). On the anal spines, the traces are located on the lower surface. However, one of these spines possesses on the lower surface a pair of weakly discernible traces and a large longitudinal depression (Pl. 4, fig. 7). Laterally and on the top, apart from several irregularly arranged traces, there are four rows of longitudinal traces, with two basal rows arranged very densely, and with an incomplete alternation in the adjacent traces. The traces on the spines of arms and of the anal sac are almost always similarly oriented, arranged linearly along the plane of symmetry, on the top surface of the arm spines and on the lower surface of the anal sac spines, and many of them were probably left by the same animal. The traces are usually terminated at a distance of half to a third of the spine's length from its base, and the organisms that left these traces should have moved distally. Initially, traces left by the animals damaging the crinoid were small and later they usually expanded and deepened. On the spines, the traces are always oriented with their wider end towards the base of the spine. Paired tubercles and a peripheral groove allowed the animal to fix more tightly than it would be if it was fixed on the even surface. If these animals were not detrimental to the crinoids and were just passively attached, they would have been oriented with their "upside down" on the surface of the annals spines and on the cup, whereas on the brachial spines they would have been oriented "downside up," which is unlikely. In addition, in most cases they would have been oriented excessively close to each other.

***Augoichnus dituberculatus* Arendt, sp. nov.**

Plate 4, figs. 1–9, Plate 5, figs. 1–4

Etymology. From the Latin *di* (two) and *tuberculae* (tubercle); i.e., with two tubercles.

Holotype. PIN, no. 1786/88574, the fourth trace from the top, in a chain of eight traces on the lower surface of the spine on the anal sac of *Hypermorphocrinus magnospinosus*; the right bank of the Ufa River, above the village of Ryabinovka near Krasnoufimsk in the Middle Cisuralia; 15 m from the left edge of the railway tunnel; Lower Permian; Upper Artinskian, Sarginian Horizon, Divja Formation (basal part).

Description (Figs. 1, 2). The traces are usually ovate in outline, bilaterally symmetrical, shallow, 4–5 mm long, rimmed externally by a narrow marginal groove, sometimes with an adjacent narrow ridge, a stepped depression, and commonly also by a second groove. Posteriorly, traces possess narrow, high paired tubercles, narrowly spaced and symmetrical to the sagittal plane, and anteriorly of them, in the narrower zone, a relatively deep subcentral pit is located.

Sometimes, the traces can be oval, less commonly and mainly the smallest ones are almost rounded

Explanation of Plate 4

Figs. 1–8. Traces *Augoichnus dituberculatus* Arendt, gen. et sp. nov. on the cup (1), brachial spines (6, 8), and anal sacs (2–5, 7) of *Hypermorphocrinus magnospinosus* Arendt, 1968, ×1: (1) no. 1786/242, cup of *Hypermorphocrinus magnospinosus*, basal view, with 23 traces near the plane A-CD and the anal interray; stemless crinoid *Eopilidiocrinus heckeri* (Arendt) is attached on the basal BC' Cisuralia, village of Ryabinovka near Krasnoufimsk, railway cutting; Lower Permian, Upper Artinskian, Sarginian Horizon, Divja Formation; (2) no. 1786/11801, anal sac spine (with a small base), basal view, with 10 linearly oriented traces; the same locality; (3) holotype, no. 1786/88574, fifth from the bottom trace; anal sac spine with 8 linearly oriented traces and one trace on the side on a spine's base; the same locality; (4) no. 1786/88575, anal sac spine with 8 linearly oriented traces and another six traces; the same locality; (5) no. 1786/88578, anal sac spine with two traces at the base, of these, the left half-trace is deep, apparently, penetrating the spine up to the ligament soft tissue, and a third trace slightly above the base; the same locality; (6) no. 1786/1180, spine at the arm base with a chain of seven traces, upper view; the small traces are the most distal; the same locality; (7) no. 1786/242, anal sac spine with four longitudinal chains of traces, on the top and on the sides and other traces, altogether 33 traces; compressed longitudinally upper view; the same locality; (8) no. 1786/88572, spine of the arm base with a chain of five small traces on the right side; the same locality.

Fig. 9. Traces *Augoichnus dituberculatus* Arendt, gen. et sp. nov. (two traces) on *Ulocrinus* sp; no. 1786/1111, cup with two uneven deep adjacent (on three plates) traces in the interray B and C, ×5: (9a) basal view of the cup; (9b) lateral view of the cup, ray B; (9c) posterior view; interray CD; (9d) upper view; the same locality.

Plate 4

(Figs. 1, 2). The marginal groove is in some places interrupted on the sides and continues with a small displacement. The paired tubercles are closer to one another or are further apart and from the external border of the traces, strongly or weakly developed. Both or one of the tubercles may be absent. The subcentral depression is rounded or irregular in shape; indistinctly or less commonly distinctly outlined. Occa-

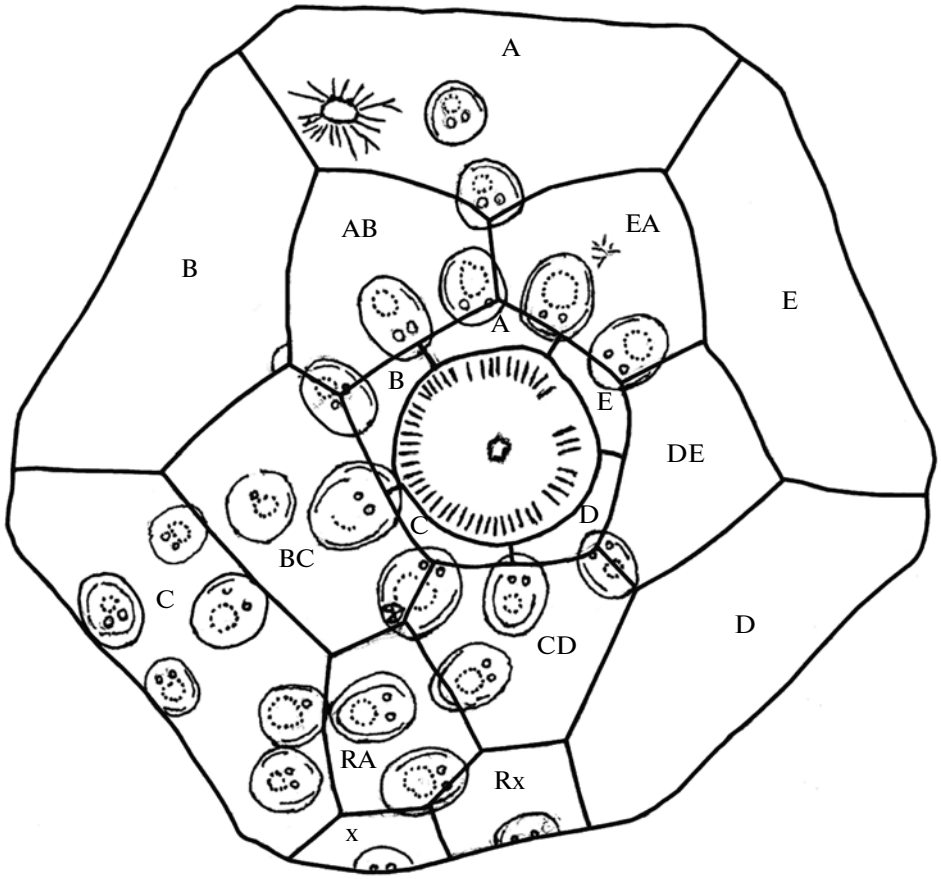


Fig. 1. Traces *Augoichnus dituberculatus* gen.et sp. nov. (23 traces) on the aboral side of the cup of *Hypermorphocrinus magnospinosus*; no. 1786/8857, ×3. For explanation of indexes see the text.

sionally the traces are particularly deep and perforate the skeleton up to the soft tissues. Let's note some features of particular specimens.

The cup of *Ulocrinus* sp. possesses a pair of relatively deep, closely spaced, rounded, variously sized traces on the borders of three adjacent plates: a relatively small on the borders of the radials B, C, and the basal BC, and a large trace on the border of the radial B and the basals AB and BC (Pl. 4, figs. 9a, 9b).

The most seriously damaged spine of the anal sac on the top of the right side possesses a long longitudinal depression, deeper anteriorly, probably a trace of a shark bite (Pl. 4, fig. 7a; Fig. 2). Discharge from the injury could have attracted organisms feeding on crinoids. To the left of the depression and on its distal continuation, there are three shallow, longitudinal traces. The image on Pl. 4, fig. 7b shows six slightly deeper linearly arranged and similarly oriented depressions, whereas the seventh (second proximal) trace is largely shifted to the right. The lower surface of the spine possesses two longitudinal rows of similarly oriented traces arranged almost next to each other. The adjacent traces on the left and right rows tend to alternate (Pl. 4, fig. 7c, Fig. 2). On the widened base of the spine, the traces are more widely spaced, are larger and shallow. The right lateral row consists of eight medium-sized shallow, densely spaced traces. Most traces on the spine are rather deep, some lacking paired tubercles. The distal half of the spine is broken off, apparently during life, due to intense drilling through it.

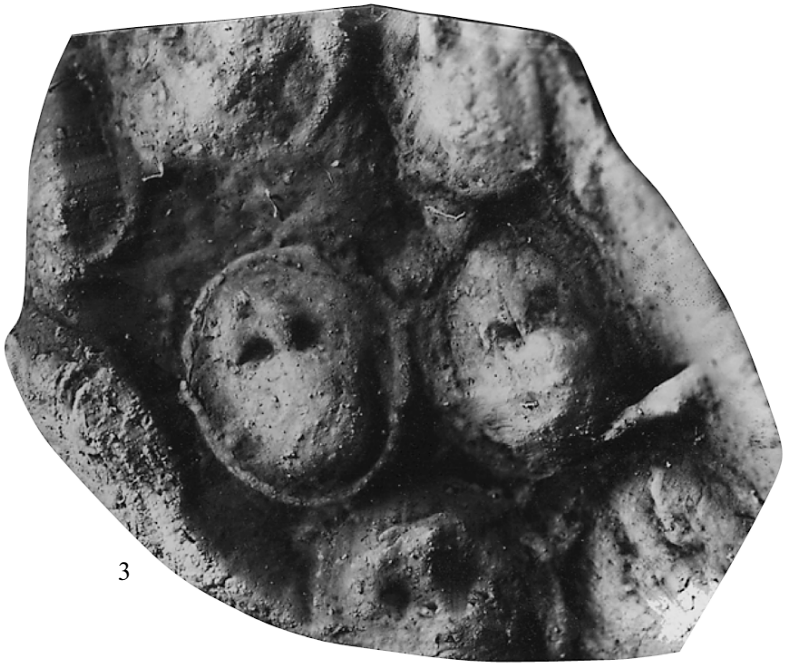
The proximal part of the spine on the base of the arm possesses a row of seven traces (Pl. 4, fig. 6). The bottom traces are more prominent than the upper ones and are adjacent to one another. Paired tubercles are observed on three traces only. The uppermost trace is small and deep. The proximal part of another spine of the arm base possesses a chain of six shallow unconnected traces (Pl. 4, fig. 8). All of them are present on the left side of the spine only. Probably, the crown of this crinoid was unusually oriented, and this part of the spine was facing upward or downward. Small

Plate 5

1

4

2



3

Explanation of Plate 5

Figs. 1–4. Traces *Augoichnus dituberculatus* Arendt, gen. et sp. nov. on the anal sac spines, (1, 2), ×5, and on the cup (3, 4), ×10, of *Hypermorphocrinus magnospinosus* Arendt, 1968. Plasticine casts: (1) no. 1786/242; Cisuralia, village of Ryabinovka near Krasnufimsk, railway cutting; Lower Permian, Upper Artinskian, Sarginian Horizon, Divja Formation; (2) no. 1786/8857; the same locality; (3, 4) no. 1786/242; the same locality.

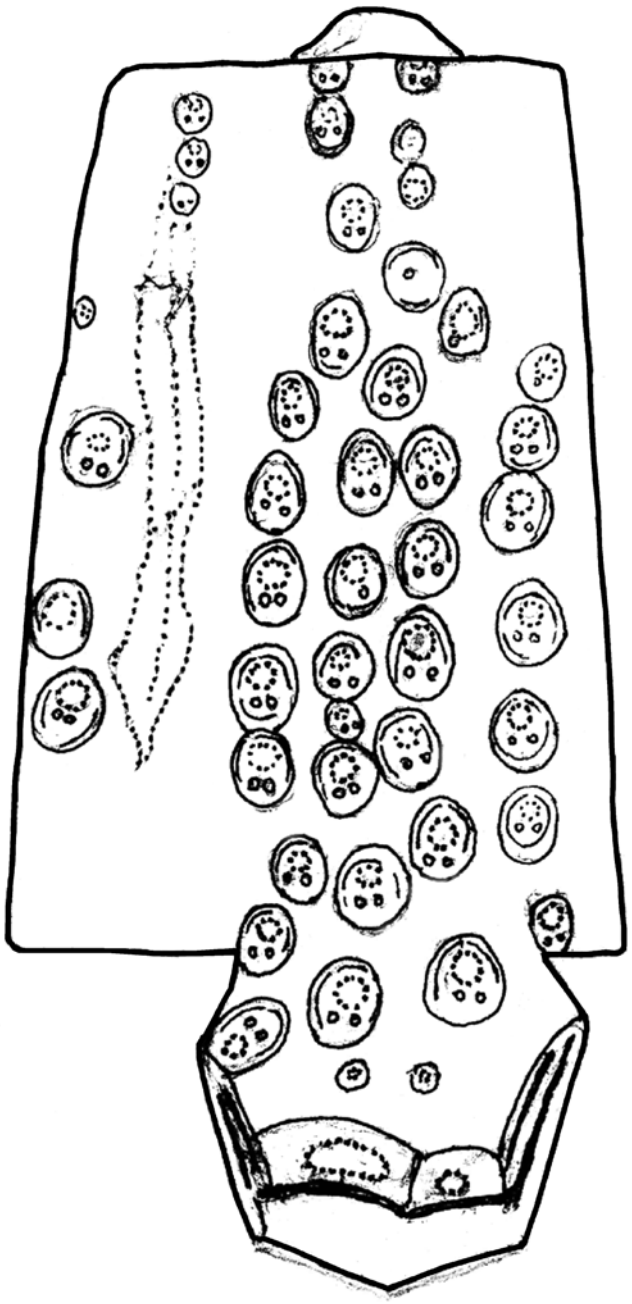


Fig. 2. Traces of *Augoichnus dituberculatus* gen. et sp. nov (33 traces) on the fragment of spine in the distal portion of the anal sac of *Hypermorphocrinus magnospinosus*; developed view (except the spine base with no traces on the sides and on the top); no. 1786/242, ×3.

paired tubercles are discernible on three traces only. Immediately above the base of the brachial spine, there are eight small (2.0–3.5 mm) traces (specimen no. 1786/88571). Of these, three traces form a longitudinal chain, and four traces form an oblique chain, at 30° to the former chain. On another small brachial spine (specimen no. 1786/88572) eight similar traces are densely grouped in the upper lateral regions of the spine, adjacent to its base.

Near the base of the anal sac spine there are five deep, large, densely spaces spines (Pl. 4, fig. 4). A wide ramp or a ridge is observed immediately outside the external margin of each. Two distal traces are small and the last one lacks paired tubercles. The specimen also shows the beginning of a second longitudinal row consisting of two traces. The lower half of the anal sac spine shows a chain of eight longitudinal traces, one of each is broken through to reveal a large cavity with a thin external wall located within the spine (Pl. 4, fig. 3). A longitudinal chain of ten traces adjacent to one another or set slightly apart extends along the lower side of the anal spine (Pl. 4, fig. 2). A cup of *Eopolidiocrinus* (an attached, stemless, and armless crinoid) is observed on the second trace from the bottom. A theca of another specimen is observed to the left of this cup. A similar cup is also present on the narrow end of the spine on the left. The same is observed in the center of the fourth trace from the bottom. In half of the traces no distinct paired tubercles are observed. The stem can be covered with such traces.

The cup of *Hypermorphocrinus magnospinosus* possesses 23 traces, which are grouped nearer to the plane of symmetry A–CD, with a slight shift to ray C (Pl. 4, fig. 1, Fig. 1). There is a trend to variation in trace orientation, although most of them are oriented with their narrow end towards ray C. No traces are oriented radially, between the infrabasal and basal circlets and all are similarly oriented, i.e., with their wider side towards the circles IBB and the stem. There are no traces near the border of the infrabasals D and E, in the middle of the basal DE, and on the radials B, D, and E. The base of a trace is preserved on the border between the cup and the missing stalk. The traces radially diverging near the stem are slightly deeper than the others. Paired tubercles are present in almost all traces. A single trace is half the size of the others, and lacks tubercles. One of the traces between the anals RA and X contains an armless attached crinoid *Eopilidiocrinus heckeri* with a completely preserved skeleton (Pl. 4, fig. 1, Fig. 1). Another cup (half of which is preserved) contains one trace in each of the central areas of the plates bordering each other (the basal CD and anal RA and X); the traces are differently oriented (specimen no. 1786/1471).

The most seriously damaged part of the entire collection is one of the anal sac spines (Pl. 4, fig. 7, Fig. 1). Due to the damage produced by *A. dituberculatus* a distal third, and possibly even a half of the spine's length has been lost; and it had begun to regenerate in the upper part, where it was broken off. The traces densely cover the lower and lateral surfaces of the spine. More commonly they are closely adjacent and have paired tubercles and a relatively deep subcen-

tral depression in the adjacent rows. The traces are grouped in longitudinal chains, with two such chains on the lower side of the spine and one on either side.

The lower side of the anal sac spine, there are three shallow traces separated from one another with hardly discernible paired tubercles (Pl. 4, fig. 5). The anterior part of the fourth trace (which is deep, with a vertical lateral wall penetrating the walls of the spine up to the soft tissue cavity) is on the left of the above three traces, on the border with the next spine base. The remaining fragment of the anal spine possesses three relatively deep traces occurring in a line along the plane of symmetry. Spaces between the traces are small. The cavity at the spine base is wide, whereas the external wall of the spine is thin (Pl. 4, fig. 3).

There is a thick arm spine constricted and compressed at the base (specimen no. 1786/11805). There is also a short and wide spine of the lower arm segment with a depression at the base, possibly a shark bite mark. Distally, the spine had regenerated after it was broken off (specimen no. 1786/ 11804).

The anal sac spine possesses ten traces with spaces between them of various sizes. Distally, on the right there is an attached cup of the microcrinoid *Eopilidiocrinus*. The complete attached thecae (degenerated crowns) or cups of *Eopilidiocrinus* are commonly found, i.e., on the lower side of the distal region of the broken spine with a chain of ten traces (Pl. 4, fig. 1, no. 1786/11805), separately or in the traces described here.

The depressions, which are possibly shark bite marks, are commonly found either separately or in association with *Augoichnus* (specimen no. 1786/11803-1805). The traces could be located on the lower, or upper, or lateral surfaces of the spines and often led to moderate deformations.

Plasticine imprints show some features of the organisms which damaged the crinoids (Pl. 5, figs. 1–4). The most peripheral part (external margin of the border of external groove) was convex. In place of paired tubercles, there were paired depressions densely embracing tubercles, which together with the external groove housing a portion of the body, mainly accommodated the animal feeding on the crinoid. The central, deeper part of the trace accommodated a portion of the soft body, which was most responsible for penetration. The spines possess similarly oriented chains of traces (Pl. 5, figs. 1–3). On the cup, the traces are more regularly arranged (Pl. 5, fig. 4). The traces are occasionally superimposed by new growths and are in places partly overlapped (Pl. 5, fig. 2). Areas without traces posses ornamentation represented by small tubercles and ridges, merged or detached, prominent or hardly discernible. Casts on Plate 4 show longitudinal rows of traces on the brachial and anal spines, and a more prominently expressed irregular arrangement of traces on the cup. The adjacent or detached traces, growth of new traces over the old ones are observed.

Dimensions in mm

Specimen PIN, no.	L	W	H	l	L_1	L/W
1786/88574 holotype	5.0	3.2	1.5	0.4	0.5–1.3	1.56
1786/88572 distal trace	3.8	3.0	1.2	0.4	1.3	1.27
1786/1111 small trace	4.0	3.8	1.5	1.0	0.3	1.50
1786/1111 large trace	4.0	5.0	2.0	1.0	1.0	0.80

O c c u r r e n c e: Lower Permian, Upper Artinskian, Sarginian, Divja Formation; Cisuralia.

M a t e r i a l. Traces on thee stems, three cups, and 30 brachial and anal spines (broken or complete).

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