

Arthropods of Burgess Shale type from the Middle Cambrian of Bohemia (Czech Republic)

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Abstract. Rare non-trilobite arthropods, mostly with affinities with the Burgess Shale fauna, are described from the Middle Cambrian Jince Formation of the Barrandian area, Central Bohemia (Czech Republic): *Tuzoia* sp., another large *Tuzoia*-like arthropod (probably a new genus), *Proboscicaris hospes* sp. n., *Helmetia? fastigata* sp. n., and *Forfexicaris?* sp. The status of *Pilocystites primitius* Barrande, 1887, formerly ranged with echinoderms but here recognized as a *Tuzoia* fragment, is discussed. Most of described arthropods (except *Forfexicaris?* sp.) are thought to be nekto-benthic animals of a shallow-water environment, possibly tolerant to some salinity fluctuations. Relationships, particularly to North American faunas, indicate open migration possibilities between Laurentia and peri-Gondwana regions during the Middle Cambrian.

Abstrakt. Ze středního kambria Barrandienu (převážně jineckého souvrství) jsou popsány vzácné zbytky arthropodů se vztahy k burgesským břídlíci z západní Kanady. Jde o zástupce rodu *Tuzoia* Walcott (zde označené *Tuzoia* sp., sem patří i zbytek popsáný jako *Pilocystites primitius* Barrande, 1887, dosud s rezervou řazený k ostnokožcům), dále zbytek jiného velkého členovce příbuzného rodu *Tuzoia* (patrně nový rod), první mimoa-merický zástupce rodu *Proboscicaris* Rolfe (*P. hospes* sp. n.) a čeledi Helmetiidae – *Helmetia? fastigata* sp. n. K arthropodům nejistého systematického postavení jsou řazeny kruhovitě štítky prozatímně označené jako *Forfexicaris?* sp. Většina popsáných zbytků pochází ze svrchní části jineckého souvrství z okolí Jinců (blízké podloží zóny *Paradoxides gracilis* až zóna *Ellipsocephalus hoffi-Rejkocephalus*), přibližný ekvivalent baltické trilobitové zóny *Paradoxides paradoxissimus* a báze zóny *P. forchhammeri*. Organismy jsou hodnoceny jako nektobentózní, snad tolerantní i k salinitním výkyvům, *Forfexicaris?* sp. mohl patřit k pelagickým formám. Vztahy k severoamerickým faunám svědčí o otevřených možnostech migrací mezi Laurentií a perigondwanskými oblastmi během středního kambria.

Key words: Arthropoda, Phyllocarida and incertae sedis, Middle Cambrian, Barrandian area, Czech Republic

Introduction

The marine Middle Cambrian strata of the Jince Formation in the Barrandian area, Central Bohemia, are world-famous particularly for well preserved trilobite and echinoderm faunas, accompanied by locally frequent ichnofossils, hyolithids, brachiopods, and acritarchs. Representatives of other fossil groups such as ostracods, gastropods, foraminifers, and algae as well as of some problematical groups are rare. Remains of large non-trilobite arthropods are also very rare finds and mostly were not correctly recognized in the past.

Collecting activity during the last fifty years, particularly in the Jince area, has revealed some remarkable finds of non-trilobite arthropods with relationships to the famous Middle Cambrian Burgess Shale fauna of North America. These are the subjects of the present report.

Regrettably, the new materials are incomplete in many respects, frequently allowing only a tentative determination at the generic level. Consequently, open nomenclature is commonly used.

The reference material is housed in the collections of the National Museum, Prague (inventory numbers prefixed by L), in the collections of the Czech Geological Survey, Prague (inventory numbers prefixed by VK = collection of Vratislav Kordule, SZ = coll. M. Szabad). Three specimens from the collection of the late Mr. J. Bouška are deposited in the West Bohemian Museum in Plzeň (numbers prefixed by MP-S).

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Systematic part

Phylum Arthropoda

Class Malacostraca Latreille, 1806

Subclass Phyllocarida Packard, 1879

Order and Family uncertain

Genus *Tuzoia* Walcott, 1912

Type species: *Tuzoia retifera* Walcott, 1912, Burgess Shale, Middle Cambrian.

Diagnosis (comp. Rolfe 1969): Carapace bivalve, hinge line distinct. Outline of carapace valves subelliptical, with distinct anterior carapace horn. Sculpture reticulate, prominent lateral ridge, carinate, with smaller reticulae than on main areas of valves. Spines or spinules of different length and number protrude from the margin of valves (except the anterior margin, spines may occur also on the lateral ridge). Doublure along the ventral margin is flat.

Remarks. *Tuzoia* was introduced by Walcott (1912) in describing the Burgess Shale fauna. Other species of this genus were described later from North America (particularly by Resser 1930, Robison and Richards 1981), China (Endo and Resser 1937, 1957) and South Australia (Glaessner 1979). No representatives have been so far reported

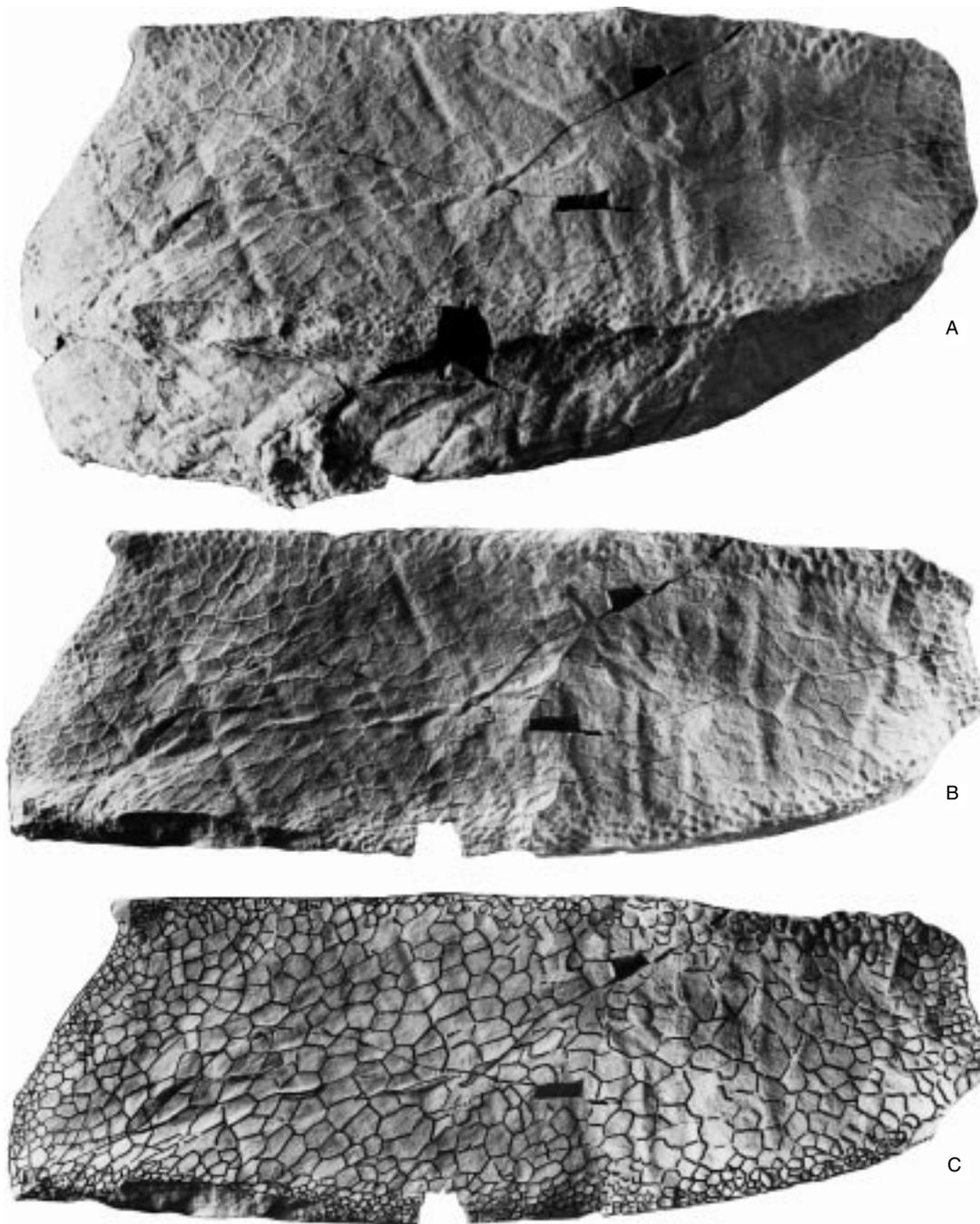


Fig. 1. *Tuzoia* sp., incomplete right carapace valve MP-S01748 (length 155 mm). Jince Formation, Jince. A – entire fossil remain; B – dorsolateral part of the same specimen with the dorsal margin and dorsolateral part of the lateral ridge; C – the same with the reticulate sculpture accentuated by drawing. Scale 1:1.

from Europe, though Barrande (1887) described under the name *Pilocystites primitius* a fragment with characteristic reticulate *Tuzoia*-like sculpture, which he regarded as an echinoderm remnant (discussion in this paper).

Tuzoia was classified by Raymond (1935) as a separate family Tuzoioidea, raised by Simonetta and Delle Cave (1975) to the rank of a separate order. This was followed by Hou and Bergström (1997), who ranged this order with arthropods of uncertain class within the Phylum Schizoramia. However, Rolfe (1969) classified *Tuzoia* as Phyllocarida of uncertain order and family that seems to be the

most appropriate approach (the abdomen and appendages are not known; see discussion in Glaessner 1979).

Species: *Tuzoia retifera* Walcott, 1912 (synonyms: *T. burgessensis* Resser, 1930, *T. canadensis* Resser, 1930), Middle Cambrian, Burgess Shale; *T. australis* Glaessner, 1979, Lower Cambrian, South Australia; *T. bispinosa* Yuan et Zhao, 1999, Lower or Middle Cambrian, China (Guizhou); *T. getzi* Resser, 1930, Lower Cambrian, Pennsylvania; *T. guntheri* Robison et Richards, 1981, Middle Cambrian, Utah;

T. magna Yuan et Zhao, 1999, Lower or Middle Cambr., China (Guizhou);
T. manchuriensis Resser et Endo in Resser, 1930, Middle Cambr., China (Manchuria);
T. nodosa Resser, 1930, Lower Cambr., British Columbia;
T. ? parva (Walcott, 1912), Middle Cambr., Burgess Shale;
T. polleni Resser, 1930, Lower Cambr., British Columbia;
T. praemorsa Resser, 1930, Middle Cambr., Burgess Shale;
T. sinensis P'an, 1957, Lower Cambr., South China (Yunnan).

T. spinosa Resser, 1930, from the Lower Cambrian of British Columbia is based on insufficient material. *T. nitida* Resser et Howell, 1938, and *T. vermontensis* Resser et Howell, 1938, from the Lower Cambrian of eastern North America (Appalachians), are poorly known as commented by Glaessner (1979). *T. ? parva* can be regarded as a juvenile ontogenic stage of *Tuzoia* as reported by Briggs (1977).

Probable of separate generic position are *Tuzoia ? dunbari* Resser, 1930, from the Lower Cambrian of Pennsylvania (marked by extremely developed spines, comp. Resser 1930, Resser and Howell 1938) and *Tuzoia ? peterseni* Robison et Richards, 1981, from the Middle Cambrian of Utah, with a very long posterodorsal spine (lateral ridge and sculpture are unknown).

Stratigraphic range: late Lower up to late Middle Cambrian.

Geographic distribution: North America (western and eastern parts), China, Australia, Central Europe (Barrandian area, here reported).

Tuzoia sp.

Pl. I, figs A-D; pl. II, figs A-H; text-figs 1-4

Material: 6 incomplete carapace valves showing diagnostic features of *Tuzoia*, other 8 carapace fragments with characteristic reticulate sculpture and few other characters.

Description. The most completely preserved specimen (MP-SO1748, fig. 1) represents the right carapace valve with almost complete dorsal margin (length 120 mm), broken anterodorsal horn, well traceable lateral ridge and incomplete ventral part of the valve. The raised longitudinal ridge (preserved length 139 mm) shows a sharp crest-like apex for most part of its course. Posterodorsal termination is protruded into a short and broad horn-like projection, not prolonged into a spine. Anterior and ventral margins are broken off; posterior margin forms a gently posterior-bent arc. The characteristic sculpture consists of marked reticulation of the whole surface. Individual reticulae are of polygonal, most commonly pentagonal and hexagonal outline, obvious diameter 4-6 mm (maximum 7 mm). Reticulae gradually diminish towards the margins of the valve and a still more pronounced diminishing of reticulae is marked close to the lateral ridge and on its surface (observable up to the distance of 4-5 mm from the apex of the carina in dorsal and ventral direction). Apart from wrinkles caused by compaction, unsharp, longitudinally projected depressions, interpreted as probable traces of scavengers, radiate from the lateral ridge in dorsal, posterodorsal and posteroventral directions.

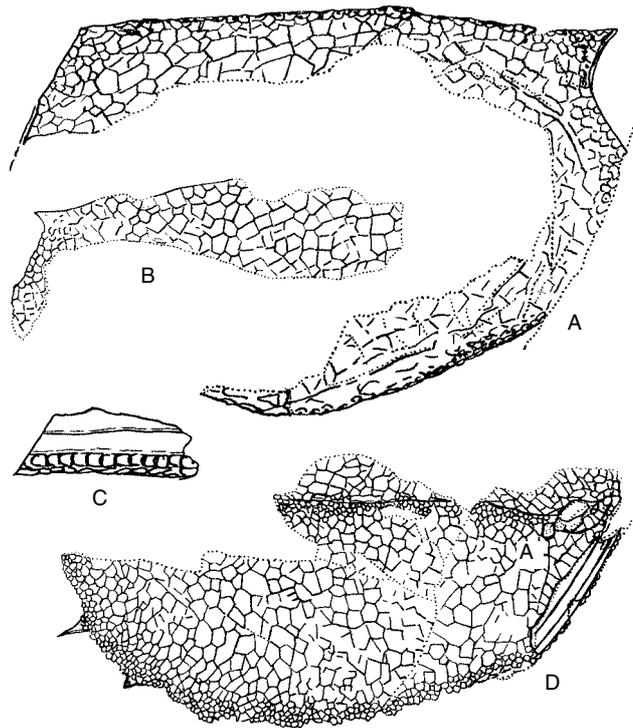


Fig. 2. *Tuzoia* sp. from the Jince Formation, Jince area. A – incomplete right carapace valve VK41, Vinice; B – fragmentary right carapace valve, L36483, counterpart, Vinice; C – fragment of the ventral doublure showing the external transition into the reticulate sculpture, SZ169; D – incomplete right carapace valve with partly preserved lateral ridge, posteroventral spines and exposed doublure, VK40, Vinice. Scale A, B, D $\times 0,5$, C $\times 2$. Comment to all drawings: dotted lines indicate secondary damages of the specimens (broken limits etc.).

The other two more completely preserved specimens (VK40 – fig. 2D, pl. I, figs A-C, VK41 – fig. 2A, pl. II, figs A-D) show at least partly preserved subelliptical outline of carapace valves. A moderately developed anterior horn projection and the straight dorsal margin is shown in VK41, the lateral ridge with sharp apex and markedly smaller and densely packed reticulae, and two spines (8.2 and 3.1 mm long) partly preserved on the posteroventral margin can be observed in VK40. The typical reticulate sculpture, consisting of reticulae of polygonal, markedly

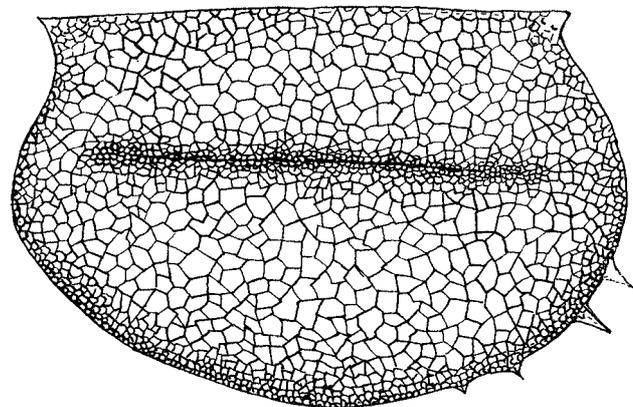


Fig. 3. *Tuzoia* sp., reconstruction of the left carapace valve from the Jince Formation, presumed length 110-180 mm.

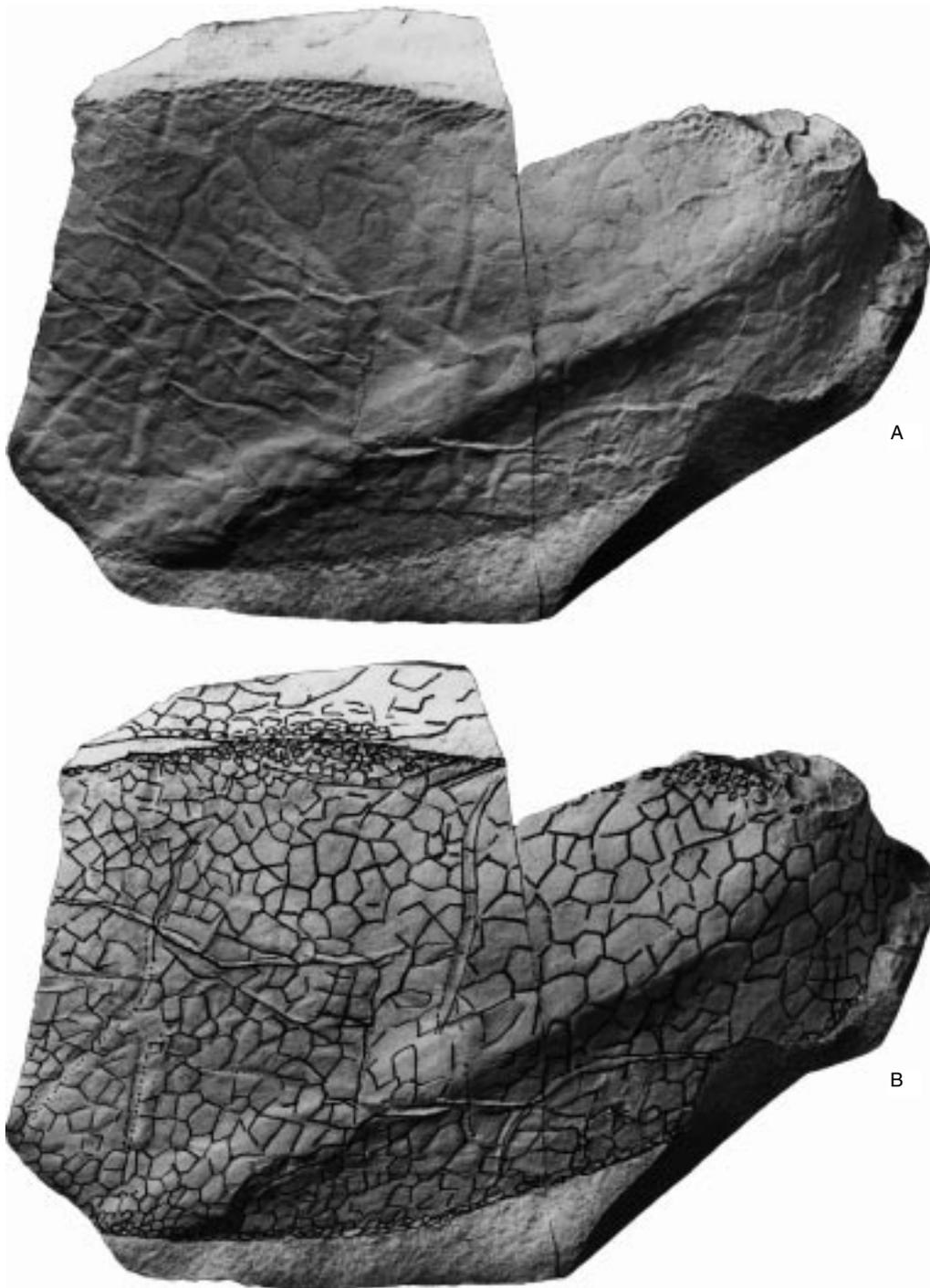


Fig. 4. *Tuzoia* sp. incomplete right carapace valve MP-S01749, Jince Formation, Jince. Large specimen of preserved incomplete diameter 150 mm. A – lightened from the dorsal side; B – the same with reticulate sculpture accentuated by drawing. Scale around 1:1.

variable outline (pentagonal and hexagonal shape obvious, maximum diameter around 5 to 6 mm) is distinctive and well observable in both specimens. Remarkable is the presence of doublure in the anterolateral border region of the valve of VK40 (fig. 2D, pl. I A, C), where it is exposed in the anterolateral border region 33 mm long. The doublure is smooth – except for two very narrow sharp lines (ridges) parallel to the outer margin of the valve. The connection of the doublure with the outer reticulate side of the exoskeleton is indicated by imprints of small reticulae bor-

dering the outer margin (the same situation is in the doublure fragment SZ169, fig. 2C, pl. ID).

Remarkable is the specimen MP-S01749 (fig. 4), which is interpreted as an incomplete right carapace valve, with partly preserved lateral ridge with sharp crest and crowded smaller reticulae in its proximity. The broadly arcuate ventral margin lacks spines (they were evidently more posterior).

All reported specimens exhibit the characteristic reticulate sculpture consisting of polygonal reticulae, cover-

ing the entire surface, becomes markedly denser and composed of smaller reticulae near the margins and in proximity of the lateral carina, where the ridges, forming the characteristic reticulae, are thickened.

The specimen L36481 (pl. IIH, preserved incomplete length 71.5 mm, coll. Dr. M. Široký) represents fragments of two carapace valves approached along the straight hinge line. The very distinct polygonal reticulate sculpture diminishes and becomes denser close to the dorsal margin and near the presumed lateral ridge (the ridge itself is broken off). It may be recalled that this specimen was figured and misinterpreted as a fish fragment by Michálek (1978) in a popular journal, which caused some erroneous stories about fish remains in the Jince Cambrian.

All other specimens of *Tuzoia* sp. are fragmentary but show a typical reticulate sculpture consisting of polygonal fields of different shape and density (most obvious pentagonal and hexagonal polygons, maximum diameter 6–7 mm).

Among these specimens, L36484 (pl. IIE, coll. Dr. R. J. Prokop) shows the straight dorsal margin preserved at a length of 49 mm long. The area of denser and smaller reticulae, delimited by stronger ridges near the dorsal margin, is locally up to 8 mm wide, but the increase of marginal density is typical and comparable e.g. with MP-S01748 (fig. 1) or L36481 (pl. IIH).

A remarkable remain is L36483 (text-fig. 2B, coll. Dr. M. Široký). It is a negative counterpart of the dorsal and posterodorsal parts of a large carapace valve (total preserved length 111 mm), which shows damaged dorsal margin terminated by a stout, horn-like spine (length 6 mm). Configuration of this spine differs in form and suppressed sculpture from the spine interpreted in VK41 as the anterodorsal. Consequently, the spine in L36483 is interpreted as the posterodorsal, very similar to the termination of the fragmentary remain described by Barrande as *Pilocystites primitius* (see discussion below). The polygonal reticulate sculpture shows only a slight tendency to diminish near the margins (influenced by preservation).

Remarks. Although assigned to *Tuzoia*, the available specimens do not show the entire outline of carapace valves and the number and configuration of all marginal spines. Consequently, a full diagnosis cannot be given and open nomenclature is used.

Among the species described, *T. retifera* Walcott, 1912, *T. guntheri* Robison et Richards, 1981, and *T. polleni* Resser, 1930, show analogies in reticulate sculpture, presence of a marked lateral ridge with diminished and denser reticulae and configuration of the anterodorsal region. Although the diminishing of the reticulation near and on the surface of the lateral ridge is more marked and occupies a broader band in our specimens, the individual variability of sculpture and its changes during ontogeny has not been studied in any larger set of individuals of *Tuzoia*, and, consequently, its systematic significance cannot be precisely evaluated. In our view, the increase of reticulation density, especially near the lateral ridge, can increase during the ontogeny, being more marked in large individuals. This is another reason for leaving our specimens in open nomenclature.

All our specimens referred to *Tuzoia* sp. indicate large dimensions: the extrapolated length of the carapace valves ranges between 110 and 160 mm, or even more (in MP-S01749 is the preserved length of the incomplete carapace valve 145 mm, the total extrapolated length 170–180 mm). These dimensions are larger than in specimens described from other areas and exceed even the measurements of the type species *T. retifera* from the Burgess Shale.

Occurrence: Jince Formation, mostly the middle part. The lowermost find (VK41) derives from the upper part of the *Eccaparadoxides pusillus* Zone, about 3 m below the *Dawsonia bohémica* “Horizon” at Vinice near Jince. Most specimens come from the interval between the *Eccaparadoxides pusillus* and *Paradoxides gracilis* Zones, namely from its upper part at Vinice and Vystrkov near Jince (the single specimen from Velká Bába near Hostomice probably came from the same level). Later specimens occur in the *Paradoxides gracilis* Zone (Vinice) and the latest fragments come from the *Ellipsocephalus hoffi*-bearing layers at Koniček.

Comments on *Pilocystites primitius* Barrande, 1887
Text-fig. 5

Barrande (1887) based the genus *Pilocystites* on a single fragmentary specimen named *Pilocystites primitius* Barr. from the shales with “*Paradoxides*” belonging to his “faune primordiale” from Ginetz (*recte* Jince). He regarded the fossil as an incomplete calyx of a cystoid and in its description he stressed the composition of irregular polygonal plates without distinct pores (Barrande 1887, p. 185). Barrande’s interpretation was understandable, as no similar arthropod remains with marked reticulate sculpture were known in his time from strata of comparable age (the problematic *Dictyocaris* Salter, 1860 from much younger, Downtonian, strata, was no firm base for comparison).

Jaekel (1899) regarded *Pilocystites* as a doubtful root of a crinoid, Ubahgs in Beaver et al. (Treatise, 1967: S493, fig. 323, 2) expressed doubts about the echinoderm nature of the fossil.

The original specimen of *P. primitius* is not deposited in the Barrande collection in the National Museum, Prague, and only the plaster cast – the plastotype L9049 – exists (Barrande noted that the specimen is contained in a block of shales with a large “*Paradoxides*” he found about forty years ago, i.e. in the 1840’s). Regrettably, all attempts to find the original specimen were unsuccessful.

In our interpretation, based on the plastotype of the original specimen figured by Barrande (1887) in pl. 2, fig. 26 and refigured here in text-fig. 5, this is a fragment of a carapace valve of a tuzooid arthropod, most likely conspecific with *Tuzoia* sp. as reported here.

The plastotype proper is not of very good quality but it shows a straight edge 51 mm long, representing in our opinion the incomplete dorsal margin of a carapace valve. The horn-like process on the left edge of the cast can be interpreted as the posterodorsal spine, comparable with that preserved in the specimen L36483 of *Tuzoia* sp. The

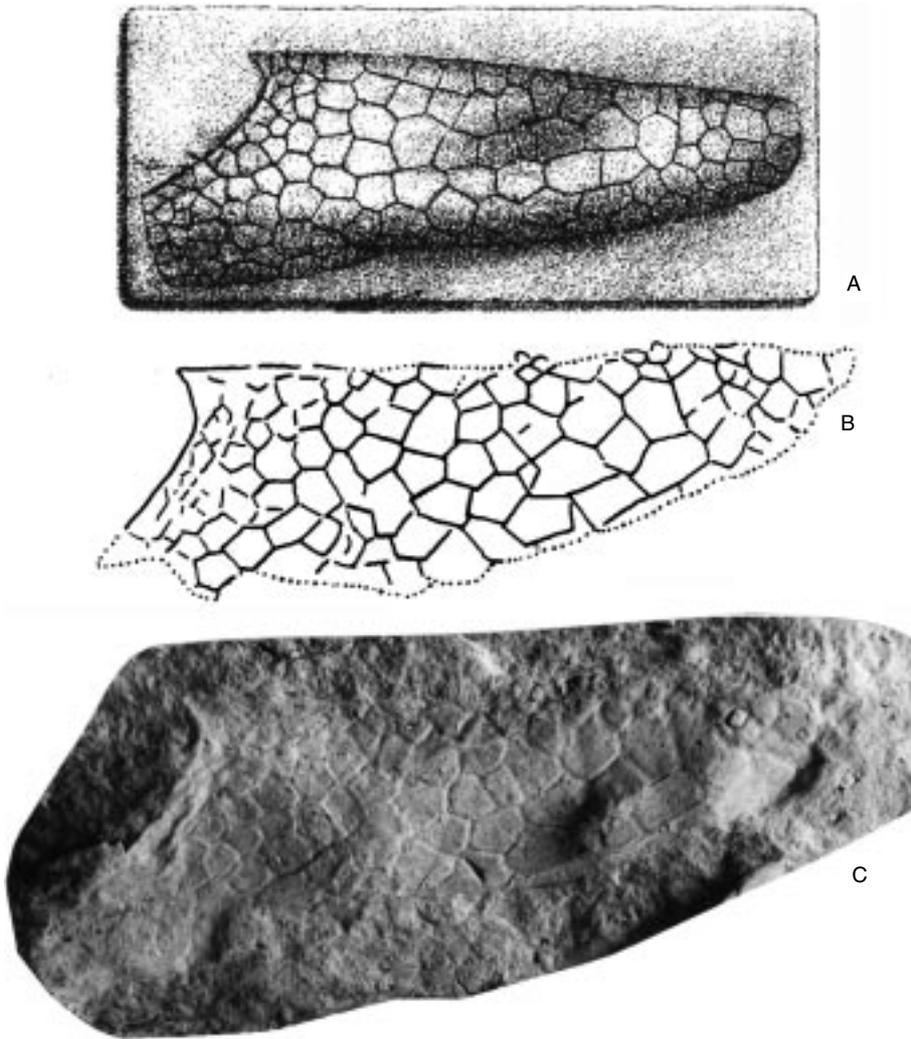


Fig. 5. Plaster cast (plastotype) of *Pilocystites primitius* Barrande, 1887, spec. Nr. L9049, length 51 mm, Jince. A – original drawing figured by Barrande (1887, pl. 2, fig. 26); B – recent schematic drawing according to the plastotype; C – recent photograph of the plastotype.

oblique margin on the left side is interpreted as a fragmentary posterodorsal margin, all other edges of the remnant being secondary. The most characteristic feature – the reticulate sculpture consisting of polygonal reticulæ of unequal size (maximum diameter 5–6 mm) and shape, in which pentagonal and hexagonal fields are obvious – fully agrees with *Tuzoia*. Also the diminishing reticulæ near the inferred dorsal and posterodorsal margins are analogous as observed e.g. in our specimen VK41 or in other specimens of *Tuzoia* sp.

Although the conspecificity with *Tuzoia* sp. seems evident, the plastotype cannot in our opinion affect the validity of the generic name *Tuzoia* Walcott, 1912, even though *Pilocystites* Barrande, 1887, has priority. The reason is that *Pilocystites* in its original concept (now based exclusively on the plastotype) shows no characteristic features that unambiguously demonstrate the identity of both genera: the plastotype does not show the lateral ridge and marginal spines diagnostic of *Tuzoia*. Similar reticulate

sculpture is developed even in some other Cambrian arthropods, e.g. *Hurdia* Walcott, 1912, from the Burgess Shale, the remains of a large tuzoiid arthropod described in this paper, or the curious Lower Cambrian *Retifacies* Hou-Chen et LU, 1989, from the Chengjiang fauna (Hou and Bergström 1997). A similar sculpture also occurs in much later arthropods, e.g. the enigmatic, late Silurian *Dictyocaris* and the Lower Carboniferous phyllocarid *Kulmocarid* Hahn et Brauckmann, 1977, from the Viséan of Germany (Hahn and Brauckmann 1977).

We cannot therefore see any sufficient proof to replace, for nomenclature reasons, the well established and widely used *Tuzoia* Walcott, 1912, by the older but ambiguous *Pilocystites* Barrande, 1887. It is recommended to use *Pilocystites* only for the reported plastotype (eventually for the original specimen, should that be found in future).

Occurrence: After Barrande (1887) *Ginetz*, i.e. Jince, evidently the Jince Formation (according to the large “*Paradoxides*” reported by Barrande), exact locality unknown (for discussion of Barrande’s localities see Chlupáč 1999).

Large tuzoiid arthropod (n. gen.)

Pl. III, figs A–C, text-fig. 6

Material: The single specimen L36595 from Jince.

Description: The specimen is represented by two separated, strongly sculptured parts interpreted as remnants of two very large carapace valves in parallel position, without preserved margins.

Each of the valve remnants – the left and the right parts of the fossil – shows an analogous and symmetrical arrangement of sculptural elements. The main median area of both “valves” that occupies most of the surface is flat and marked by a typical sculpture consisting of polygonal reticulæ analogous to those of *Tuzoia*: individual polygons of quadrangular, pentagonal and hexagonal outline form a network of reticulæ 4–7 mm (exceptionally up to 8 mm) in diameter, delimited by narrow ridges. Flat areas with this kind of reticulation are bordered on both sides (peripheral = outer, median = inner) by areas with clearly different sculpture, consisting of blunt and thickened ridges encircling distinct-

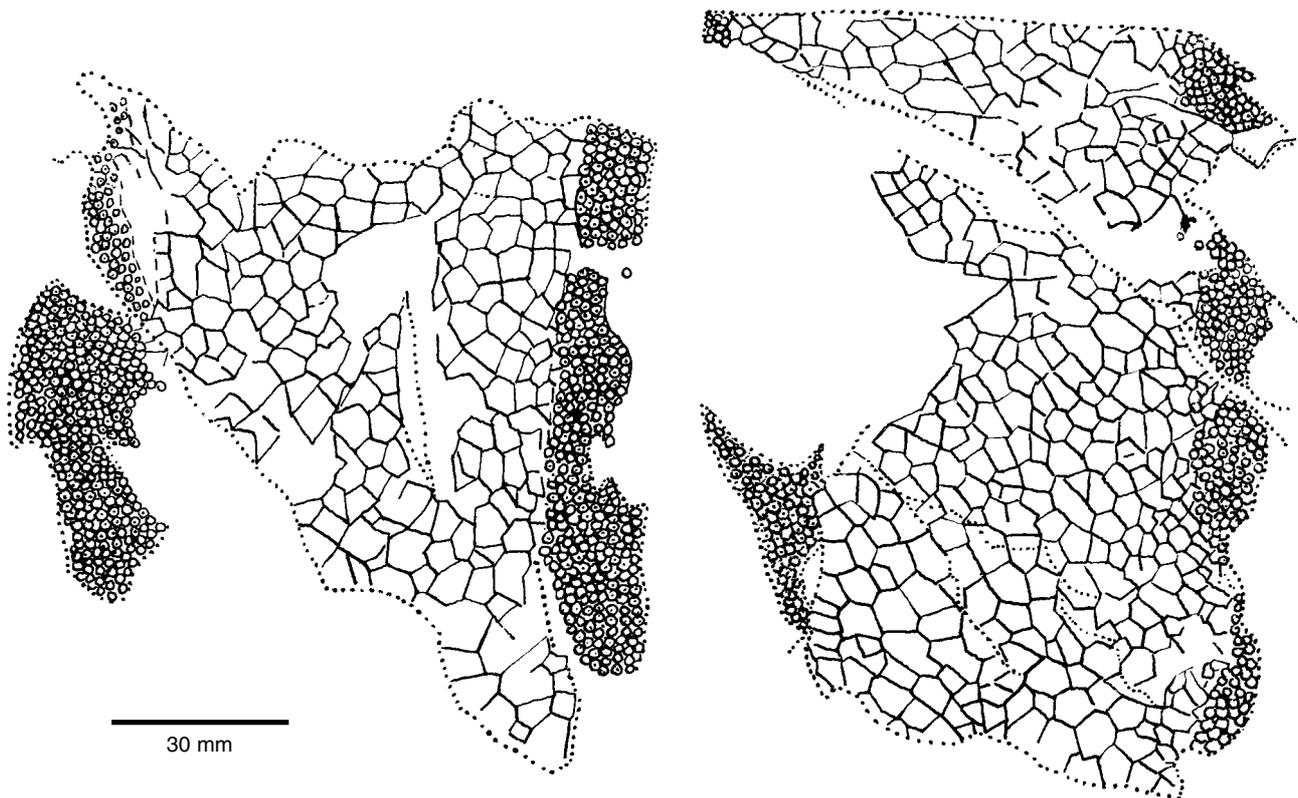


Fig. 6. Schematic drawing of remains of the large tuzoiid arthropod *Tuzoidae* n. gen.? (L36595) from Vinice near Jince, *Paradoxides gracilis* Zone (coll. M. Široký).

ly concave subcircular depressions terminated by median pits (pl. IIIC). The density of depressions is around 6–8 in 10 mm. The areas with large polygons and those with pitting are connected and distinguished by smaller reticulæ but the differences are very marked.

Although the fossil is flattened, traces of the primary morphology are partly preserved: the two median bands with dense sculpture are slightly raised, the main reticulate areas are flat and the outer, marginal bands with dense sculpture are moderately bent downwards on both sides of the specimen. Remains of paradoxidid trilobites (librigenae, thoracic segments, parts of cephalae) are imprinted into the evidently thin reticulate areas of the shield.

Measurements: The total width of the fossil is 227 mm; maximum length, measured parallel to the bands of different sculpture, is 123 mm. The preserved transverse width of bands with dense sculpture on the outer sides of both presumed valves is 26 mm and the inner bands with dense sculpture attain a maximum width of 17 mm.

Remarks. As the original margins are not preserved, the interpretation of the fossil is ambiguous. Even in interpretation as two valves of a bivalve arthropod exist two possibilities:

1. The areas with dense sculpture situated in median part of the fossil indicate areas in proximity and along the dorsal margins of valves, the large flat areas with large reticulæ represent most of the surface of both carapace valves, and the densely sculptured outer bands correspond to marginal parts of valves near their ventral margin. In this case, the presumed dorsoventral width of

individual valves can be calculated as c. from 100 to 110 mm, length as 150 to 170 mm.

2. The second possibility differs in interpretation of the main flat reticulate areas which would represent only the dorsolateral sectors of the valves, while the areas with dense sculpture on the outer margin of the fossil indicate merely bands along the lateral longitudinal ridge (analogous to *Tuzoia* in which the ridge area is distinguished by a denser reticulation). In this case, the calculated dimensions would be substantially larger than in the first interpretation (the minimal dorsoventral width would be estimated as c. 170–180 mm, length as 220 to 250 mm).

As for sculpture, namely the broad bands with dense sculptural elements, they differ from all known representatives of *Tuzoia* and point to a separate generic status. However, the lack of primary margins prevents from making an unambiguous and sufficient diagnosis. Therefore, the fossil, representing one of the most remarkable findings in the Middle Cambrian of Jince, is here left under informal designation.

Occurrence: The single find, made by Dr. M. Široký at Vinice near Jince (lower part of the hillside), derives from the upper part of the *Paradoxides gracilis* Zone of the Jince Formation.

Genus *Proboscicaris* Rolfe, 1962

Type species: *Proboscicaris agnosta* Rolfe, 1962.

Diagnosis: Carapace valves subovate to subrectan-

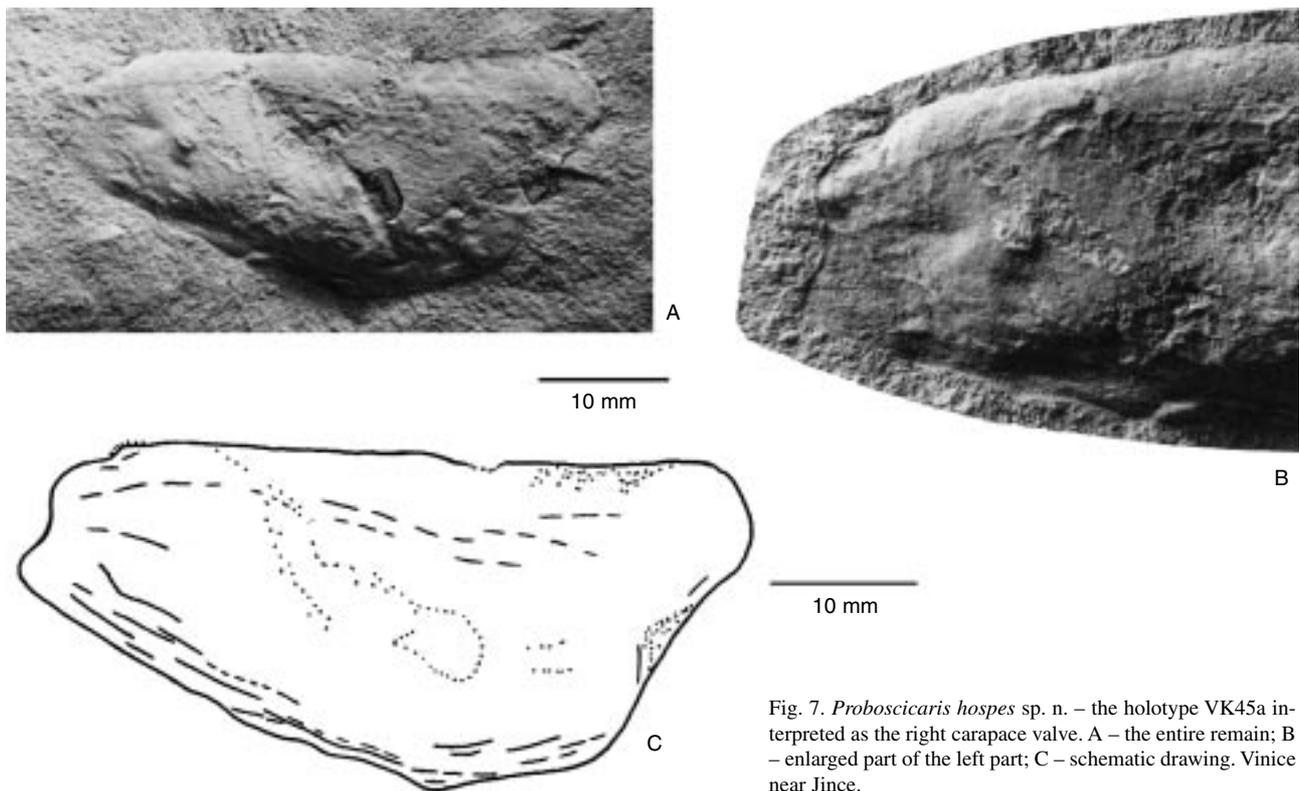


Fig. 7. *Proboscicaris hospes* sp. n. – the holotype VK45a interpreted as the right carapace valve. A – the entire remain; B – enlarged part of the left part; C – schematic drawing. Vinice near Jince.

gular, with carapace horn anterior-produced into spatulate beak (Rolfe 1969).

Remarks. With one exception, only isolated carapace valves are preserved, reaching in the type species the length of more than 100 mm and in the other species – *P. ingens* Rolfe, 1962 – up to 156 mm. The reticulate sculpture, resembling *Tuzoia*, is less marked and only locally preserved on the carapace valves of the type species as reported by Rolfe (1962). The genus has been so far known exclusively from the Middle Cambrian of North America (Burgess Shale and Utah). Its occurrence in Bohemia is the first of this kind in the Old World.

Proboscicaris hospes sp. n.

Text-fig. 7 A–C

Holotype: right carapace valve VK45a, b moderately deformed by pressure and preserved with its counterpart.

Derivation of name: from Lat. *hospes* = guest (subst.).

Type locality: Vinice near Jince.

Type stratum: Jince Formation (middle part), interval between the *Eccaparadoxides pusillus* and *Paradoxides gracilis* Zones, Middle Cambrian.

Material: The holotype.

Description. Carapace valve prolonged, semielliptical in outline, tapering posteriorly. Dorsal margin in most part of its course straight, without spines, anterodorsal part of the valve protruded into broad, anterior-rounded “beak”. Anteroventral margin gently curved, ventral margin gently curved with some irregularities: a slight ventral

projection at about the mid-length of the carapace valve, other irregularities could be due to pressure deformation. The valve is markedly posterior-tapered. It reaches the maximum dorsoventral width of 23 mm slightly anterior of the mid-length of the valve and attains a width of only 9–10 mm near the posterior margin. The posterior margin exhibits two rounded projections the posteroventral of which is slightly longer and more markedly curved than the posterodorsal one. The arcuate notch between both projections is moderately anterior-curved. The convexity of the valve was modified by pressure but according to mode of preservation it was moderate.

Remarks. The assignment to *Proboscicaris* is based on the presence of the anterodorsal “beak” and general shape of the carapace valve without any marked spines. The diagnostic features of our species are the shape of the prolonged valve, the broad anterior “beak” and two rounded posterior projections separated by an arcuate notch. The last feature resembles *Pseudoarctolepis* Brooks et Caster, 1956, in which two posterior projections are also developed but the notch between them is more marked and the posterodorsal projection is sharp and spin-formed (comp. Brooks and Caster 1956, Robison and Richards 1981). The most characteristic feature of *Pseudoarctolepis* – the anteroventral-situated and posteroventral-directed hollow spine – is lacking in *P. hospes*.

Secondary pressure deformations are expressed in the holotype as irregular wrinkles parallel with the ventral margin and as irregular depressions and elevations on the valve surface. No patterns of reticulate sculpture are developed and only very faint and small ridges near the posterior margin (especially on the posteroventral projection) may be regarded as sculptural elements.

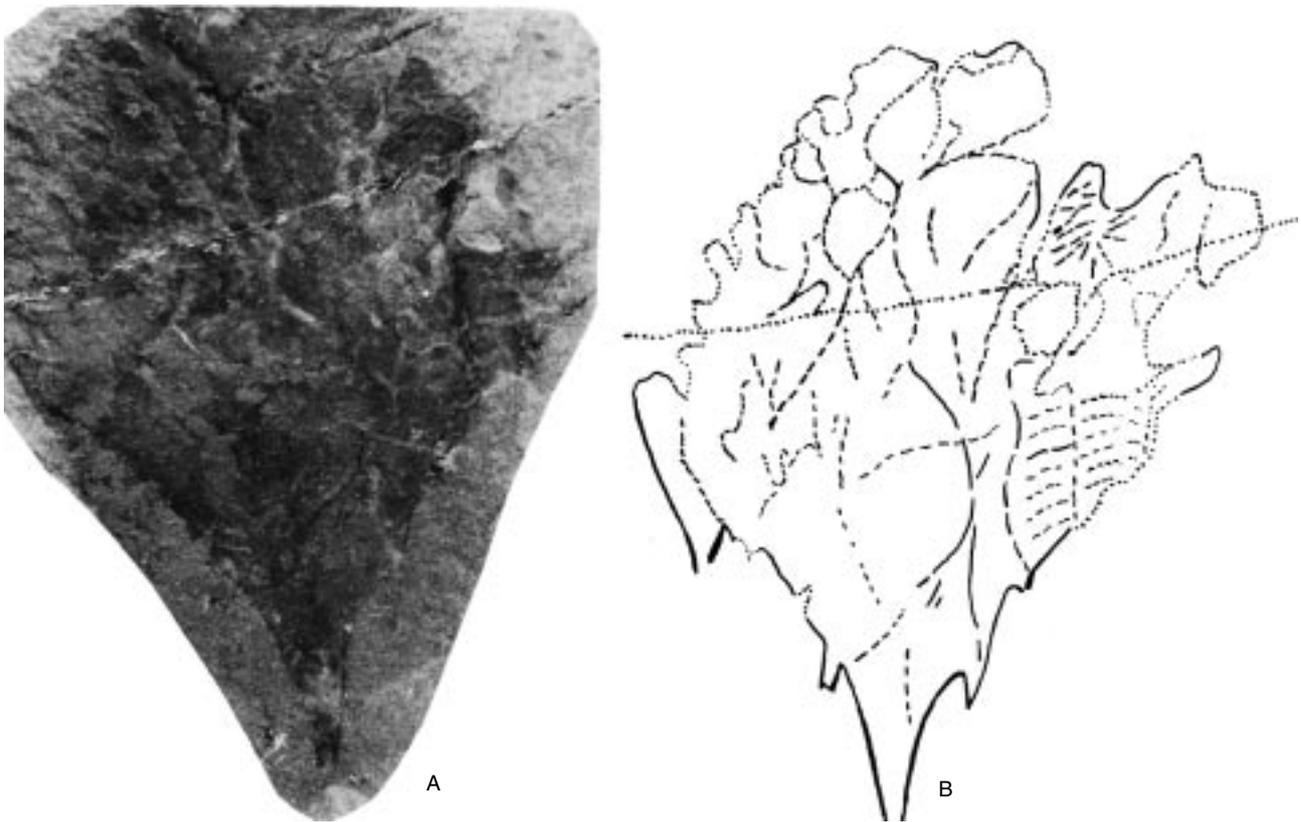


Fig. 8. *Helmetia? fastigata* sp. n. – the holotype VK42a (A) and its schematic drawing (B) supplemented by features preserved on the counterpart. Rejkovice, *Ellipsocephalus hoffi* – *Rejkocephalus* Zone. Total width 37 mm.

Occurrence: The only known specimen comes from Vinice near Jince, middle part of the Jince Formation, the uppermost part of the interval between the *Eccaparadoxides pusillus* and *Paradoxides gracilis* Zones (coll. V. Kordule).

Class Artiopoda Hou et Bergström, 1997
 Subclass Conciliterga Hou et Bergström, 1997
 Order Helmetiida Novozhilov, 1969
 Family Helmetiidae Simonetta et Delle Cave, 1975
 Genus *Helmetia* Walcott, 1918

Type species: *Helmetia expansa* Walcott, 1918, Burgess Shale, Middle Cambrian, British Columbia.

Diagnosis: see Störmer in Harrington et al. (1959).

Helmetia? fastigata sp. n.
 Text-fig. 8A, B

Holotype: Crushed tail shield VK42a, b (with counterpart) figured in text-fig. 8A, B.

Derivation of name: From Latin *fastigatus* = pointed (adj.).

Type locality: Rejkovice near Jince, railway cutting.

Type stratum: Upper part of the Jince Formation, Zone with *Ellipsocephalus hoffi*, level with *Lindinella kordulei*.

Material: The holotype and two fragmentary specimens possibly conspecific.

Description. Only the tail shield is known. It is in-

terpreted as prolonged, bearing characteristic marginal spines. The posterior, median spine is long and strong, moderately tapering, pointed. The paired posterolateral marginal spines are markedly smaller and shorter. The posterior pair is approached to the median spine, the next, more anterior-placed pair is poorly preserved as a still smaller projection. On one side of the shield, another longer and stouter, more anterior-placed spine is indicated and posterior-directed. However, this part of the shield is separated from the main part by a secondary fold, which makes the connection unclear. The whole tail shield is flattened and crushed, showing secondary folds and fissures, which also form its evidently secondary anterior delimitation.

Measurements of the holotype: Sagittal length of the preserved part of the shield: 60.5 mm, width c. 37 mm (dimensions affected by crushing), length of the median spine 13.5 mm, length of the posterolateral spines 2.5–3 mm.

Remarks. Although the preservation of the holotype is not sufficient for a full diagnosis, the configuration and position of marginal spines on the tail shield differs from all previously described representatives of Helmetiidae and allows the establishment of a new species.

The secondary deformations strongly affect particularly the anterior part of the holotype. They are manifested as asymmetrical curved folds and small ridges of two kinds and dimensions: the larger curved traces of more or less longitudinal (exsagittal) direction strongly suggest the ichnofossil trails *Helminthopsis*, the markedly smaller ridges

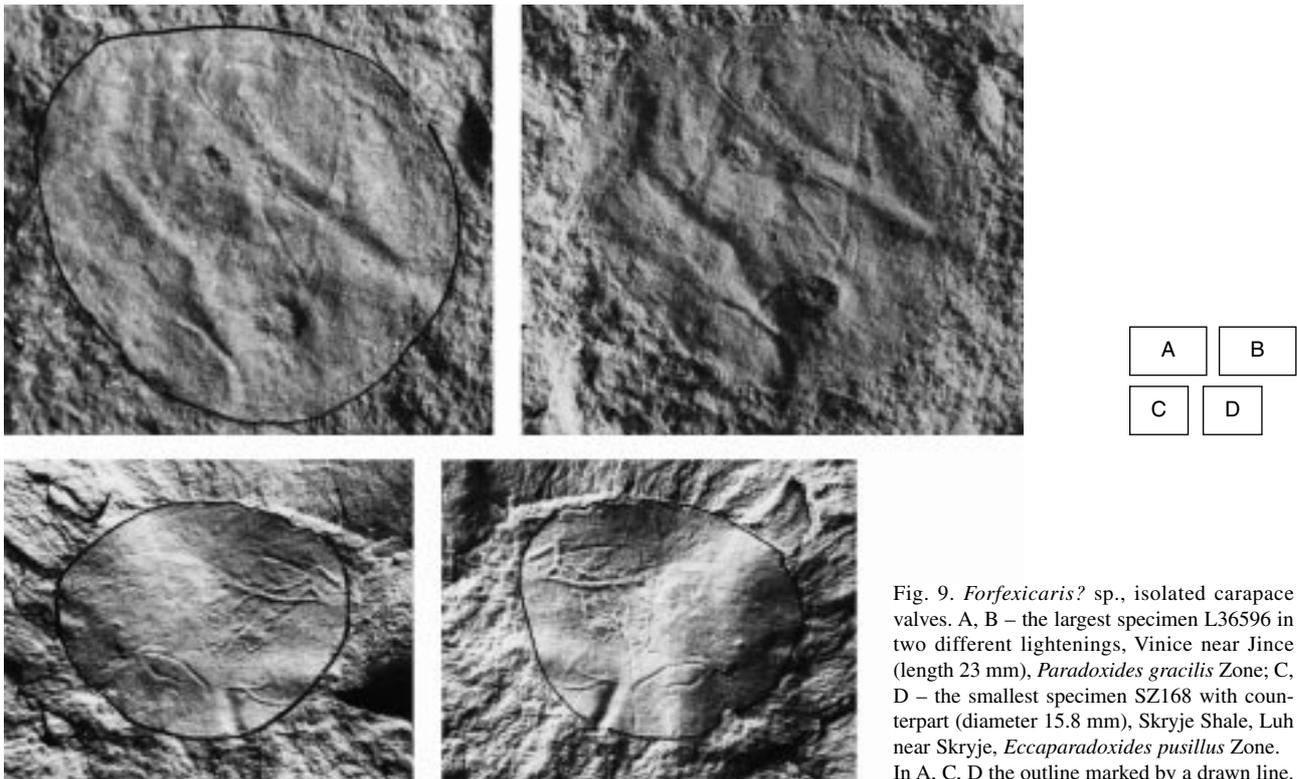


Fig. 9. *Forfexicaris?* sp., isolated carapace valves. A, B – the largest specimen L36596 in two different lightnings, Vinice near Jince (length 23 mm), *Paradoxides gracilis* Zone; C, D – the smallest specimen SZ168 with counterpart (diameter 15.8 mm), Skryje Shale, Luh near Skryje, *Eccaparadoxides pusillus* Zone. In A, C, D the outline marked by a drawn line.

and irregularly curved traces are comparable with *Gordia*. All these structures be of evidently organic origin represent traces of worm-like animals, possibly scavengers concentrated on the surface of or near the shield at the time of its burial (the traces are developed exclusively on the remnants of the shield and do not continue into the surrounding rock). Other deformations are caused by a clear imprint of a thorax of *Ellipsocephalus* in the lateral part of the shield and by secondary crushing which caused a strong breakage of the anterior part of the fossil.

The family *Helmetiidae* includes in its present concept three genera: *Helmetia* Walcott, 1918, *Kuamaia* Hou, 1987, and *Rhombicalvaria* Hou, 1987 (Hou and Bergström 1997). As indicated by both authors, the separate position and generic status of *Kuamaia* and *Rhombicalvaria* are questionable, and this also concerns their relations to *Helmetia*, which has nomenclature priority. Owing to this, our specimen is tentatively ranged with *Helmetia*.

The type species of *Helmetia* – *H. expansa* Walcott, 1918, as figured by Walcott (1931, cf. also figure in Conway Morris et al. 1982, Briggs et al. 1994), shows a clearly greater distance between the posterior median spine and the more anterior-placed lateral ones. The same difference concerns both the so far described species of the Lower Cambrian *Kuamaia* – *K. lata* Hou, 1987, and *K. muricata* Hou et Bergström, 1997, which also show a shorter and broader tail shield and a smaller median spine. The type and the only known species of *Rhombicalvaria* – *R. acantha* Hou, 1987 (comp. Hou 1987) exhibits – in contrast to *Kuamaia* – considerably longer and slender marginal spines, the distance between the median and the last posterolateral spine being substantially longer.

H.? *fastigata* is the first representative of *Helmetiidae* outside North America and southwest China.

Occurrence. Rejkovice near Jince, olive-green silty shales of the upper part of the Jince Formation, Zone with *Ellipsocephalus hoffi* and *Rejkocephalus*, level with *Lindinella kordulei*. In association with *Ellipsocephalus hoffi* (Schlotheim), *Rejkocephalus rotundatus* (Barrande), hyolithids, *Lindinella kordulei* Mergl et Šlehoferová, rare *Konicekion tix* Šnajdr and ichnofossils.

Arthropoda incertae sedis
Genus *Forfexicaris* Hou, 1999

Type species: *Forfexicaris valida* Hou, 1999, Lower Cambrian, Yunnan, China.

Forfexicaris? sp.
Text-fig. 9A-D

Material: 8 subcircular plates interpreted as isolated carapace valves flattened in silty shale.

Description: Valves subcircular, gently asymmetrical in outline. Carapace very thin. Dorsal margin (at the supposed hinge-line) slightly curved up to rectilinear for some distance, thus differing from the broadly arcuate and markedly curved ventral margin. Anterodorsal corner rounded, somewhat narrower than the broadly arcuate posterodorsal one. Maximum length of valves in about 1/4 of the maximum width of valves measured perpendicularly from the presumed dorsal margin. Surface of valves smooth, only slight indications of lines parallel with the margins (except the dorsal one).

Measurements: The best-preserved specimen (L36596) shows the dorsoventral width of the valve as 21.5 mm, its length being 23 mm. The maximum diameters of other specimens range between 30 and 17 mm. The smallest specimen SZ168 is 15.8 mm in diameter at the most.

Remarks. As the extremities and the thorax remain unknown, the interpretation and assignment are doubtful. The rounded outline and smooth surface of carapace valves are shared with several Cambrian arthropod taxa of diverse relationships. Most morphologically similar are carapace valves of the genera *Forfexicaris* Hou, 1999, *Occacaris* Hou, 1999, and *Clypecaris* Hou, 1999, all from the Lower Cambrian Chengjiang fauna (Hou 1999). Among them, *Forfexicaris* seems to show greatest analogy in available features, and, therefore, the remnants are tentatively assigned to it with reserve.

Though the flattening cannot be excluded in all specimens so far collected, the absence of any marked coarse and irregular wrinkles on the evidently very thin cuticle points to the valves being originally flat in life.

The described fossils were previously figured from the Jince Formation of the Jince area by Mergl and Šlehoferová (1991, pl. 11, figs 4, 5, MM284, YA1305), who classified them with reserve as brachial valves of a possible but doubtful inarticulate brachiopod *Acrothele gigantea* Želízko of uncertain systematic position (even with possibility of exclusion from Brachiopoda). Mikuláš (2000) in his revision of Bohemian Middle Cambrian ichnofossils figured in pl. 13, figs 3, 4 and pl. 34, figs 6, 7 also subcircular very thin valves, which he also regarded with some reserve as shells of inarticulate brachiopods with superficial ichnofossils designated as *fodinichnion* igen. et isp. indet.

These subcircular thin shells are best interpreted as arthropod carapace valves designated here as *Forfexicaris?* sp. Almost all show also analogous trace fossils on their surface – possibly traces of scavengers (the relationships between arthropod remnants and associated ichnofossils will be discussed elsewhere). However, the rocks of the Jince Formation also contain thicker-shelled subcircular fossils with indicated apices whose brachiopod (inarticulate) nature is very probable – this concerns e.g. some specimens designated as *Acrothele gigantea* Želízko deposited in collections of the National Museum, Prague.

The described thin-shelled subcircular fossils probably do not occur so sporadically as the available material suggests. Their unattractive nature probably meant that they were in most cases overlooked by fossil collectors, even at classic localities.

Occurrence: Jince Formation, Jince area: the slope of Vinice, *Paradoxides gracilis* Zone, Rejkovice (railway cutting) and Koníček near Jince, the *Ellipsocephalus hoffi* – *Rejkocephalus* Zone, Skryje-Týřovice area: Luh and Plazy near Skryje, *Eccaparadoxides pusillus* Zone.

Biostratigraphy and accompanying fauna

The Jince Formation, introduced in the literature by Lipold and Krejčí (1860) for Barrande's *étage C* of his "Silurian System" (1852) and later moderately redefined (Havlíček in Chlupáč, ed. 1968), corresponds too much of the Middle Cambrian.

According to recent state of knowledge, it can be subdivided into several biostratigraphic zones and subzones ("horizons"); see Fatka and Kordule (1992), Kordule (1996), Fatka (2000). The distribution and character of faunas clearly reflect the cycle of marine ingression, starting with low-diversity brachiopod and trilobite-dominated assemblages and continuing over two maxima of abundance distinguished by the presence of higher diversity faunas (even with miomerid = agnostid trilobites) and declining into the regressive phase in the uppermost part of the Jince Formation with dominating lingulids.

The finds of described non-trilobite arthropods belong mostly to the upper parts of the Jince Formation, i.e. within the sequence with common trilobite and other faunas.

The occurrence of *Tuzoia* sp., however, does not fully correspond with the abundance and diversity maxima of other fossils. The oldest find derives from the upper part of the *Eccaparadoxides pusillus* Zone. Most remains, however, come from the interval between the *E. pusillus* and *Paradoxides gracilis* Zones, particularly from its upper part (designated by Kordule 1996 as the Subzone with *Acanthocystites* and *Akadocrinus*), where also *Proboscicaris hospes* was found, but the total faunal diversity is low. The common accompanying trilobite is here *Hydrocephalus minor* (Boeck), frequently found even as complete exoskeletons. It is joined by *Rejkocephalus rotundatus* (Barrande), *Peronopsis integra* (Beyrich), *Acanthocystites briareus* Barrande, *Akadocrinus jani* Prokop, *Stromatocystites pentangularis* Pompeckj, rare *Konicekion radion* Šnajdr, and very few other fossils. According to Mikuláš (2000), *Planolites* and *Teichichnus* dominate among ichnofossils.

Rare remains of *Tuzoia* sp., carapace valves of *Forfexicaris?* sp. and the unique find of the large tuzooid arthropod (*Tuzoidea* n. gen.?), as described here, were found within the upper part of the Jince Formation with the second maximum fossil abundance, namely in the *Paradoxides gracilis* Zone. They occur together with numerous trilobites with strongly dominant *Paradoxides gracilis* (Boeck), frequent *Conocoryphe sulzeri* (Schlotheim), *Ptychoparia striata* (Emmrich), *Hydrocephalus minor* (Boeck), *Peronopsis integra* (Barrande), echinoderms *Lichenoides priscus* Barrande, *Stromatocystites* sp., *Etoctenocystis bohemia* Fatka et Kordule, rare ostracods *Konicekion radion* Šnajdr, hyolithids, *Tommotium* sp. etc.

In the present zonal subdivision of the Middle Cambrian according to agnostid trilobites, the above mentioned beds with arthropod remains can be roughly correlated

with the *Ptychagnostus atavus* and particularly with the *P. punctuosus* Zones (sensu Robison 1984), i.e. the higher part of the major *Paradoxides paradoxissimus* trilobite biozone of the Baltic scheme.

The latest described arthropods come from the *Ellipsocephalus hoffi* – *Rejkocephalus* Zone, especially from the locality at Rejkovice, where *Helmetia?* *fastigata* sp. n., *Tuzoia* sp., *Forfexicaris?* sp. and some other problematical remains were found in association with *Ellipsocephalus hoffi* (Schlotheim), *Rejkocephalus rotundatus* (Barrande), frequent small hyolithids (often with opercula), brachiopods *Lindinella kordulei* Mergl et Šlehoferová, rare *Konicekion tix* Šnajdr, and few other fossils. Ichnofossils (Mikuláš 2000) belong to *Skolithos*, *Planolites*, *Teichichnus* and *Daedalus*. The *E. hoffi* – *Rejkocephalus* Zone might correspond to the lower part of the *Paradoxides forchhammeri* Zone of the Baltic zonal scheme (the correlation, however, is still problematic).

Rare remains tentatively reported as *Forfexicaris?* sp. from the Skryje-Tyřovice Cambrian in the NW flank of the Barrandian, belong to the *Eccaparadoxides pusillus* Zone of the Skryje Shale, corresponding roughly to the lower (but not the lowest!) part of the Jince Formation of the Jince area.

To summarize, the representatives of *Tuzoia* and allied tuzoid arthropods occupy together with thin-shelled remains designated as *Forfexicaris?* sp. a rather long stratigraphic interval within the Middle Cambrian, particularly in its higher part correlatable with the *Paradoxides paradoxissimus* Zone. Rare finds of *Helmetiids* and other exceptional arthropods occurring in later strata with the index trilobite *Ellipsocephalus hoffi* can be correlated with the lower part of the *Paradoxides forchhammeri* Zone of the Baltic scheme.

Palaeoecological notes

All the arthropods described here come from the Middle Cambrian siliciclastic rocks, namely from siltstones and silty-clayey shales. They occur in sequences marked by alternating influx of silt-clay-sand (greywacke) material in irregular intervals of mm to tens of cm thickness (lithologic characteristics of the Jince Formation: Kukul 1971, Havlíček and Kukul in Chlupáč et al. 1998). Interbeds of dark grey or grey-green greywackes are locally frequent but they are persistent on individual outcrops. Described remains of arthropods derive exclusively from shale or siltstone beds, they were never found in greywacke layers. This suggests that the presence of such arthropods corresponds to intervals of more stable conditions reflected in the fine-grained sedimentation.

Frequent remains of marine benthic animals, namely large polymerid trilobites and less common but typical echinoderms (carpoids, eocrinoids, edrioasteroids) and hyolithids, accompany the described arthropods. Agnostids are also present, though they are not dominant. According to the scheme established for the Jince Middle Cambrian by Fatka (2000) our arthropods belong in the shallow-wa-

ter life zone, dominated by polymerid trilobites.

The ichnofossils marked by common epi- and intrastratal traces indicate the widely distributed shallow-water environment of the *Cruziana* and/or *Skolithos-Cruziana* Ichnofacies (comp. Mikuláš 2000).

The co-occurrence with complete exoskeletons of small and large trilobites and non- or incompletely disarticulated echinoderms and the preservation of even thin shields exclude any longer transport of the studied remains. In our view, the tuzoid, helmetid and probably also proboscicariid arthropods could be regarded as nektobenthic animals whose habit might be compared with some trilobites: they might be scavengers or filter-feeders rather slowly moving above the sea floor (cf. consideration of *Helmetia* by Briggs in Conway-Morris et al. 1982).

A different habit can be presumed in *Forfexicaris?* sp. with very thin cuticle. It might represent a pelagic element less dependent on bottom conditions and shallow-water realms (this can be supported by its occurrence in the Skryje Shale in association with more common agnostids).

Conclusion

Rare remains of large non-trilobite arthropods in the Middle Cambrian of Bohemia are confined to the later phase of the marine transgression cycle.

The described arthropods show clear resemblances to other, particularly North American, Middle Cambrian faunas (especially the Burgess Shale of British Columbia and coeval strata of Utah). Their rare occurrence and incomplete preservation, however, prevent adequately based palaeogeographical and biostratigraphical conclusions from being drawn. The relationships indicate open migration possibilities and faunal exchange over vast areas, probably even between Laurentia and the presumed shelves of Gondwana, to which also the Barrandian area belonged.

All described arthropods lived in marine environment with marked terrigenous influx. However, their remains are contained in finer-grained siltstone and combined siltstone-claystone layers pointing to temporary intervals of relative stable and quieter sedimentation. These conditions could be generally more suitable for preservation of thin carapaces of described arthropods. The occurrence of *Helmetia?*, *Tuzoia*, and *Forfexicaris?* in siltstones of the *Ellipsocephalus hoffi* Zone with less diversified benthos may indicate a tolerance to conditions of decreased salinity.

A nektobenthic habit and a rather shallow-water environment are presumed for the discussed arthropods (except *Forfexicaris?* sp. as a possible pelagic element).

Biostratigraphical conclusions are premature, but the available finds come mostly from the upper part of the Jince Formation, where some decrease of diversity in benthic fauna is already observed. The correlation with the middle and upper parts of the *Paradoxides paradoxissimus* Zone (most finds) and possibly with the lowest part of the *Paradoxides forchhammeri* Zone (the youngest finds) of the Baltic biostratigraphical scheme is most probable.

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Explanation of plates

Plate I ⇒
Tuzoia sp., Jince Formation (upper part), Vinice near Jince (A-C), Rejkovice (D).
 A, B, C – incomplete right carapace valve VK40 with partly preserved lateral ridge, posteroventral part and doublure; (B – enlarged figure without the anterior part, C – enlarged anterior part with partly exposed doublure); D – fragment of doublure SZ169.

Plate II ⇒ ⇒
Tuzoia sp., Jince Formation near Jince (except F – Velká Bába near Hostomice).
 A, B, C, D – incomplete right carapace valve VK41, Vinice; A – enlarged posterodorsal part, B – enlarged anterior part, C – enlarged dorsal part, D – the overall view showing the covered median part and broken antero- and

posteroventral parts); E – fragmentary dorsal part of the right carapace valve with posterior edge, L36484; F – fragmentary specimen SZp5964, a tooth-like projection is probably a hyolithid shell attached to the *Tuzoia* fragment; G – fragment of a large specimen showing the typical reticulate sculpture, L36482; H – two fragmentary and approached carapace valves showing configuration of the dorsal margins and increasing density of reticulate sculpture near the broken lateral ridges, L36481.

Plate III ⇒ ⇒ ⇒
 Large tuzooid arthropod (n. gen.), Jince Formation, Vinice near Jince, *Paradoxides gracilis* Zone. L36595 (coll. M. Široký), maximum diameter 227 mm.
 A, B – overall views in different light, with different sculpture and imprinted remains of paradoxidid trilobites; C – strongly enlarged part of the left medium sector showing the marked difference between the “tuzooid” polygonal sculpture and the thicker and pitted parts.

All photos R. J. Duda

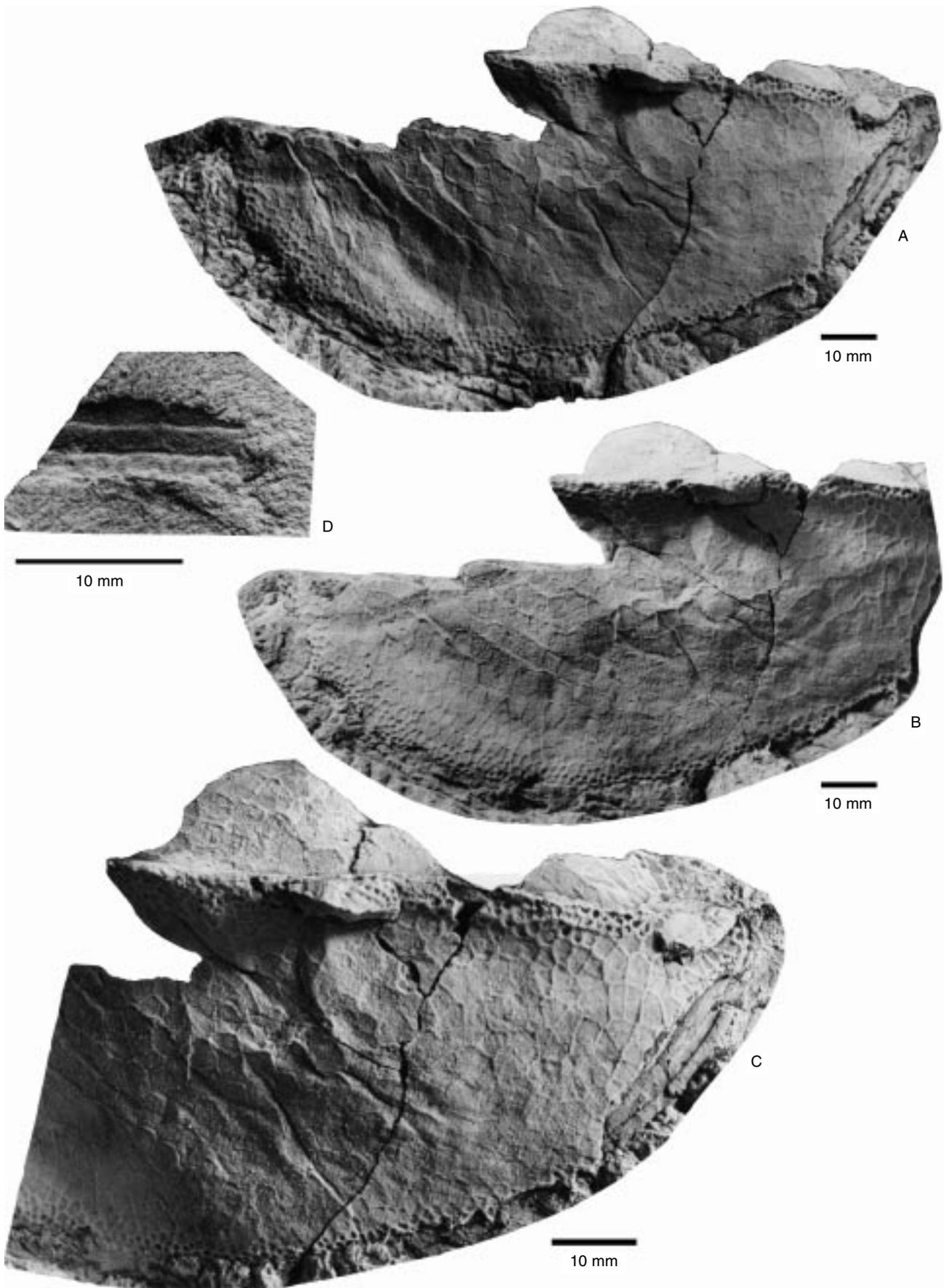


Plate I

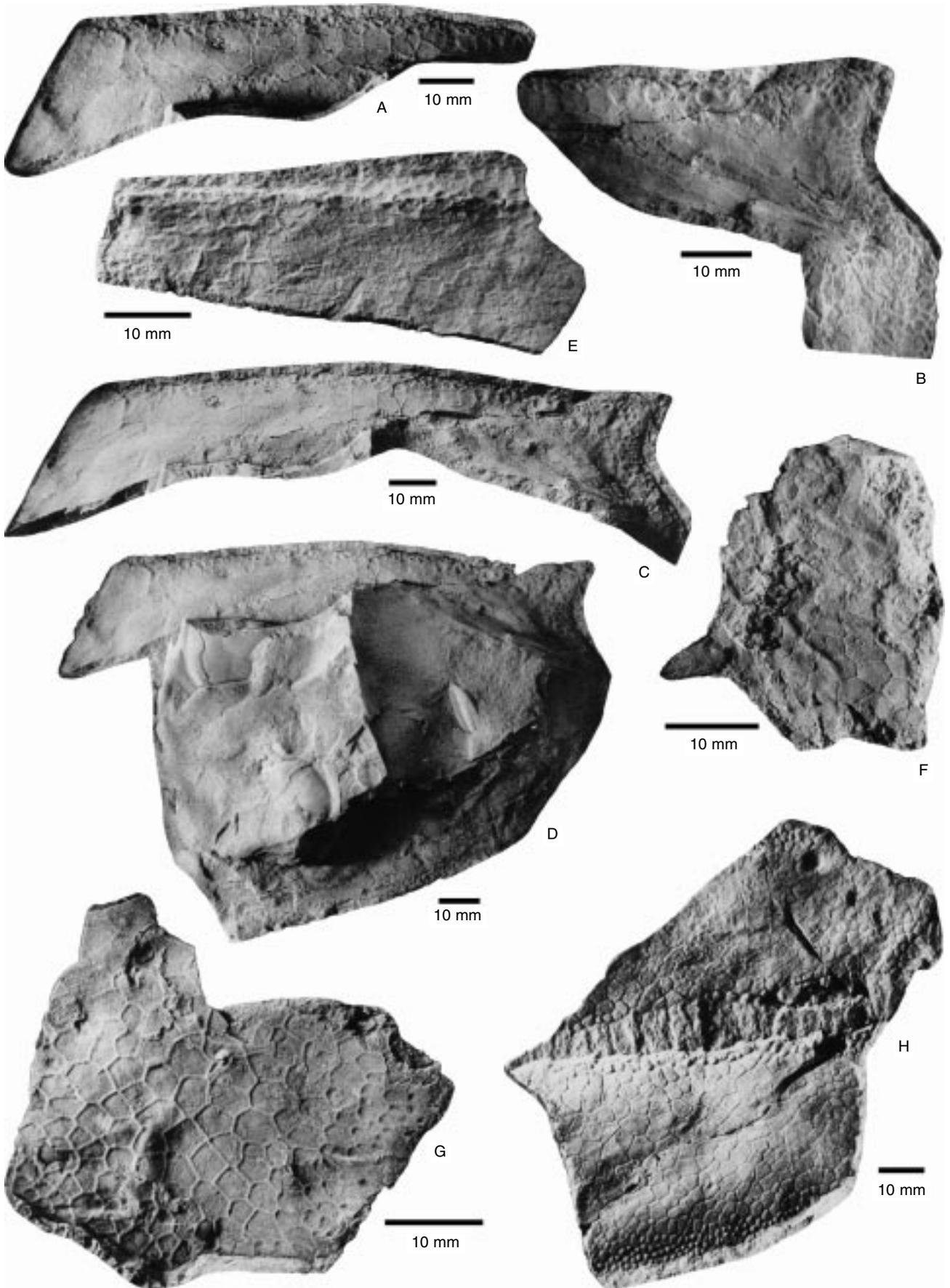


Plate II

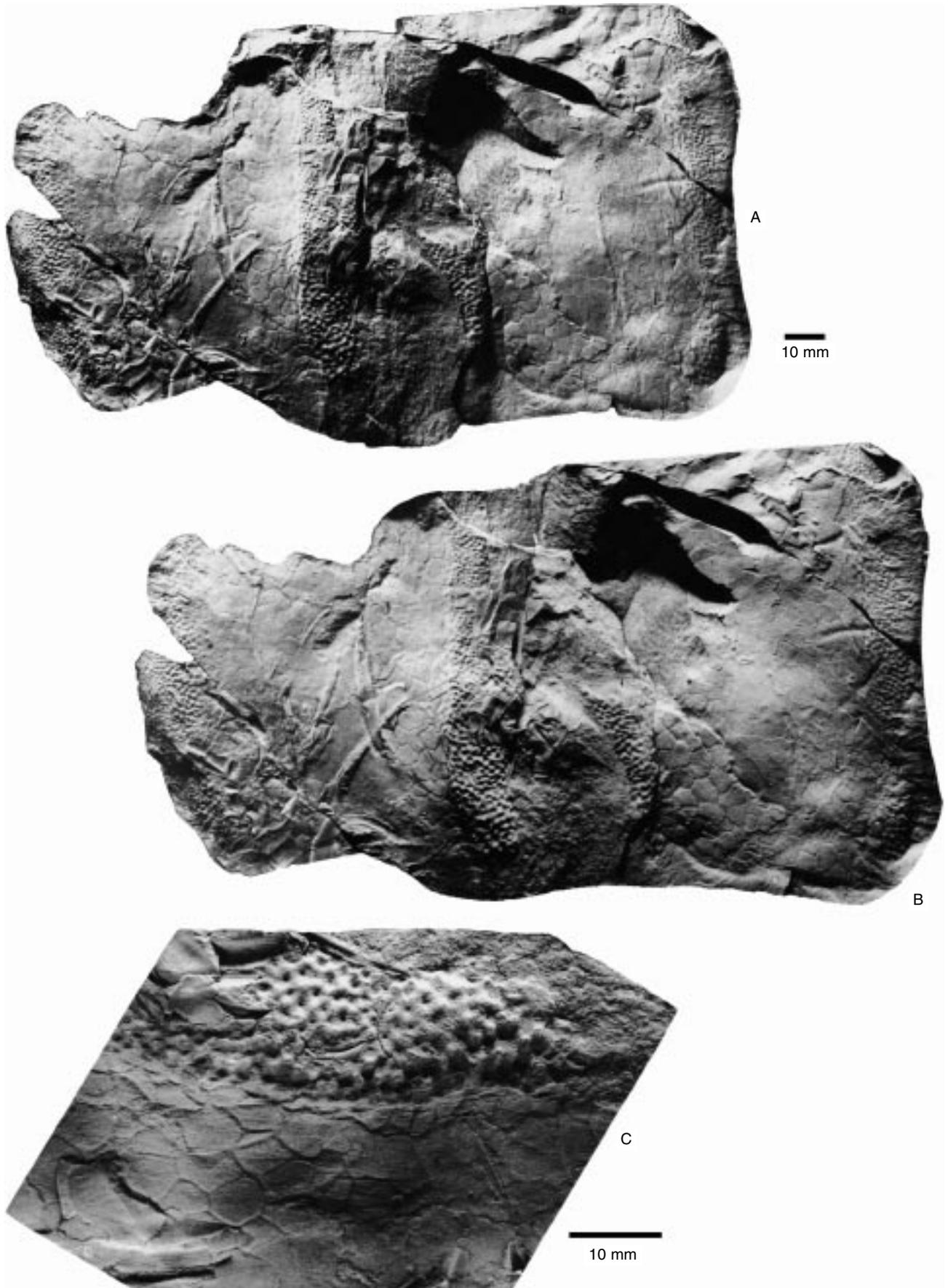


Plate III