

# APPENDAGES OF THE ARTHROPOD *AGLASPIS SPINIFER* (UPPER CAMBRIAN, WISCONSIN) AND THEIR SIGNIFICANCE

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**ABSTRACT.** A single specimen of *Aglaspis spinifer* is unique in having the appendages preserved approximately in place. Re-examination has shown that the cephalic region bore four (perhaps five) pairs of appendages, and not six as Raasch (1939) claimed. The first pair was uniramous, apparently cylindrical and jointed, but cannot be confirmed as being chelate. The remaining pairs on the cephalic region were like those on the anterior half of the trunk, uniramous walking legs composed of five podomeres. The aglaspids are therefore not chelicerates, and we do not consider them to be closely related to trilobites. The order is not assigned to any higher taxon. The record of Chelicerata in the Cambrian is dramatically reduced.

THE majority of specimens used by Raasch (1939) to describe the arthropod *Aglaspis spinifer* came from a single locality in the Lodi Member, St. Lawrence Formation, Trempealeau Stage, Upper Cambrian, Wisconsin. This account deals with only one of Raasch's specimens, which is unique in that appendages are preserved approximately in place beneath the dorsal exoskeleton. Raasch (1939, pp. 12-13, pl. 1; pl. 2, fig. 11; pl. 4) stated that six pairs of appendages were present on the carapace (cephalic region), the first being chelate, with those posterior to it and those on the trunk being simple, unspecialized 'walking legs'. In the light of these observations Raasch (1939, pp. 69-84) reviewed the systematics of aglaspids and concluded that they were merostomes, a conclusion widely accepted by subsequent workers (Størmer 1944, pp. 74-77, fig. 14, 16a, b; 1955, pp. P10-P12, fig. 7, 4a, b; in Grassé 1949, p. 217; Waterlot in Piveteau 1953, p. 546; Novojilov in Orlov 1962, p. 389; Bergström 1968, p. 501; Eldredge 1974, p. 38). The accepted classification of *Aglaspis* and its allies thus hinges on this single specimen (Størmer's 1944, fig. 14, 16b, is misleading in that it portrays appendages taken from this specimen and transferred to a different species, *Aglaspella eatoni*), and our aim was to re-examine the basis for Raasch's statements. We are most grateful to Dr. Robert M. West, Milwaukee Public Museum (abbreviated as MPM), Milwaukee, Wisconsin, for the opportunity to examine and prepare the specimen. The 'part' (Pl. 22, fig. 1) is an internal mould of the dorsal exoskeleton, which shows also the external mould of parts of the ventral exoskeleton, and portions of appendages beneath the internal mould; the 'counterpart' (Pl. 23, fig. 1) is an external mould of the dorsal exoskeleton. We do not follow Raasch in dividing the body into 'cephalothorax', and 'abdomen', preferring to use the terms 'cephalic region' and 'trunk', as carrying fewer implications of supposed affinities. The use of other terms is indicated in the explanatory text-figs. 1 and 2.



## SYSTEMATIC PALAEONTOLOGY

Family AGLASPIDIDAE Miller, 1877

Genus AGLASPIS Hall, 1862

*Aglaspis spinifer* Raasch, 1939

Plates 22–25; text-figs. 1, 2A, 2B

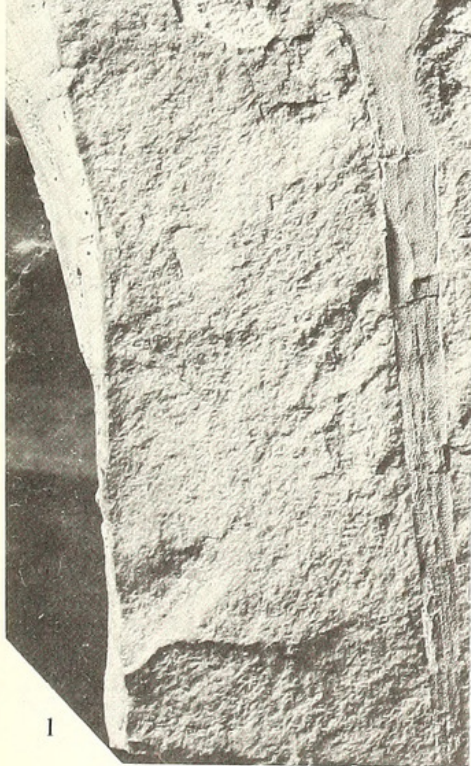
The original description and discussion by Raasch (1939, pp. 10–14, 62, 63, 65, 66, pls. 1–4, pl. 7, figs. 1–4, pl. 9, figs. 9, 10, pl. 10, figs. 8–10) is based on sixty specimens, most of which came from what he termed the merostome parting, in the Lodi Member, St. Lawrence Formation, at Point Jude, three miles east of Gotham, Richland County, Wisconsin. We have studied only the unique specimen from this locality which has the appendages preserved approximately in place (MPM 11154, 11155, part and counterpart respectively). Raasch (1939, fig. 6) gave a composite section at the locality, and subsequently (1951, p. 141) explained that the trilobite *Dikelocephalus gracilis ovatus*, which occurs at this horizon, is a synonym of *D. oweni*. Other trilobites, a lingulid brachiopod, and species of four other genera of aglaspids occur with *A. spinifer*. Current stratigraphical terminology is given by Ostrom (1970, fig. 4). Our comments on the unique specimen amplify or emend Raasch's original description.

*Dorsal exoskeleton.* The internal mould (Pl. 22, fig. 1) is of the size given by Raasch (1939, p. 10; his plate 1 is approximately  $\times 0.75$  natural size). The counterpart (Pl. 23, fig. 1) shows the division of the dorsal exoskeleton into cephalic shield, eleven trunk tergites, and the twelfth portion a long terminal spine ('telson segment' of Raasch, 1939, p. 12). The spine was presumably circular or oval in cross-section before compression, and there is no evidence that it was other than horizontal in life. A relatively short anterior portion of each trunk tergite is set off by the articulating ridge as an articulating flange; the flange is smooth, the main portion of the tergite faintly tuberculate (Pl. 23, fig. 1). The posterior margin of the tergite bears a conspicuous narrow band of close-packed, coarser tubercles, similar to those on the posterior margin of the cephalic shield. It appears that tergites 1–11 freely articulated with each other, the cephalic region, and the terminal spine (Pl. 25, fig. 1; text-fig. 2A). Raasch (1939, p. 12) considered that tergite 11 was considerably longer than the first, but much narrower than those preceding it, and so regarded somite 11 and the terminal spine as comprising the 'postabdomen'. Tergites 1–11 appear to change progressively in form, the pleural regions becoming narrower backwards and more

## EXPLANATION OF PLATE 22

Figs. 1–3. *Aglaspis spinifer* Raasch, 1939. Holotype, MPM 11154, part, internal mould, Lodi Member, St. Lawrence Formation, Trempealeau Stage, Upper Cambrian, Point Jude, 3 miles E of Gotham, Richland County, Wisconsin, U.S.A. 1, entire part,  $\times 1.05$ . 2, posterior portion of part, showing post-ventral plates and ventral view of proximal portion of terminal spine,  $\times 2$ . 3, latex cast, anterior portion of part, showing appendages in ventral view,  $\times 1.5$ .





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strongly curved, and tergite 11 (the pleural regions of which (Pl. 25, fig. 1; text-fig. 2A) appear to have been crumpled by flattening of original convexity) seems to belong in this gradational series. There is thus little evidence for a subdivision of the trunk. Some separation of trunk tergites has occurred, so that part of the articulating flange is exposed axially between them (Pl. 23, fig. 1). Laterally the posterior margin of an individual tergite diverges from the articulating ridge on the succeeding tergite (against which it would have abutted), and the entire articulating flange of the pleural region may be exposed (Pl. 23, fig. 1; text-fig. 1). This is presumably the result of flattening of the original convexity, combined with the evident separation of the tergites in the axial region.

*Appendages.* The anteriormost appendage (Pl. 22, fig. 3; Pl. 23, fig. 2; Pl. 24, fig. 1; text-fig. 1) runs forward and outward from beneath the eye-lobe on each side of the cephalic region to the margin. Raasch (1939, pl. 4, fig. 1) outlined four podomeres of the left anterior appendage (the distal two forming the chela) in thick, black lines. The lines of fracture or change in level traced by Raasch may be identified in Pl. 22, fig. 3 and Pl. 23, fig. 2. The margins of a parallel-sided structure are preserved, traversed by changes in level which curve from longitudinal to transverse in direction. These impressions may represent a probably cylindrical, possibly jointed appendage which has been flattened during preservation, but are not sufficient to conclude that the preserved portion of the appendage was chelate. A featureless strip outlines the position of the right anterior appendage (Pl. 22, fig. 3; Pl. 24, fig. 1), the margins not clearly outlined and transverse lines lacking.

Behind the first appendage (numbered 1 in text-fig. 1) a series of nine similar pairs (numbered 2 to 10) are exposed. The distal podomeres are best preserved, all appendages except the last on the right showing two or three of them. The fourth podomere from the distal end is evident in right appendage 2, in pair 5, and in left 6 and those posterior to it. A fifth podomere (the coxa) is apparent only in appendages right 5 and left 8. Small spines are visible in places along the margins of some of the appendages (right 2, left 5, 6, right 8) but the limbs do not appear to have borne an armature of heavy spines. The proximal ends of the appendages are poorly preserved, presumably because they lay close to the dorsal exoskeleton and were pressed against it during preservation. As a result the two layers are difficult or impossible to separate by preparation. In contrast, the thicker layer of matrix which intervenes distally between appendages and exoskeleton makes preparation easier. The proximal podomeres of appendages 2 to 10 are aligned more or less normal to the trunk axis, the majority of the limbs flexed so that the distal two podomeres are preserved directed backward or forward. The appendages were probably flattened antero-posteriorly

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#### EXPLANATION OF PLATE 23

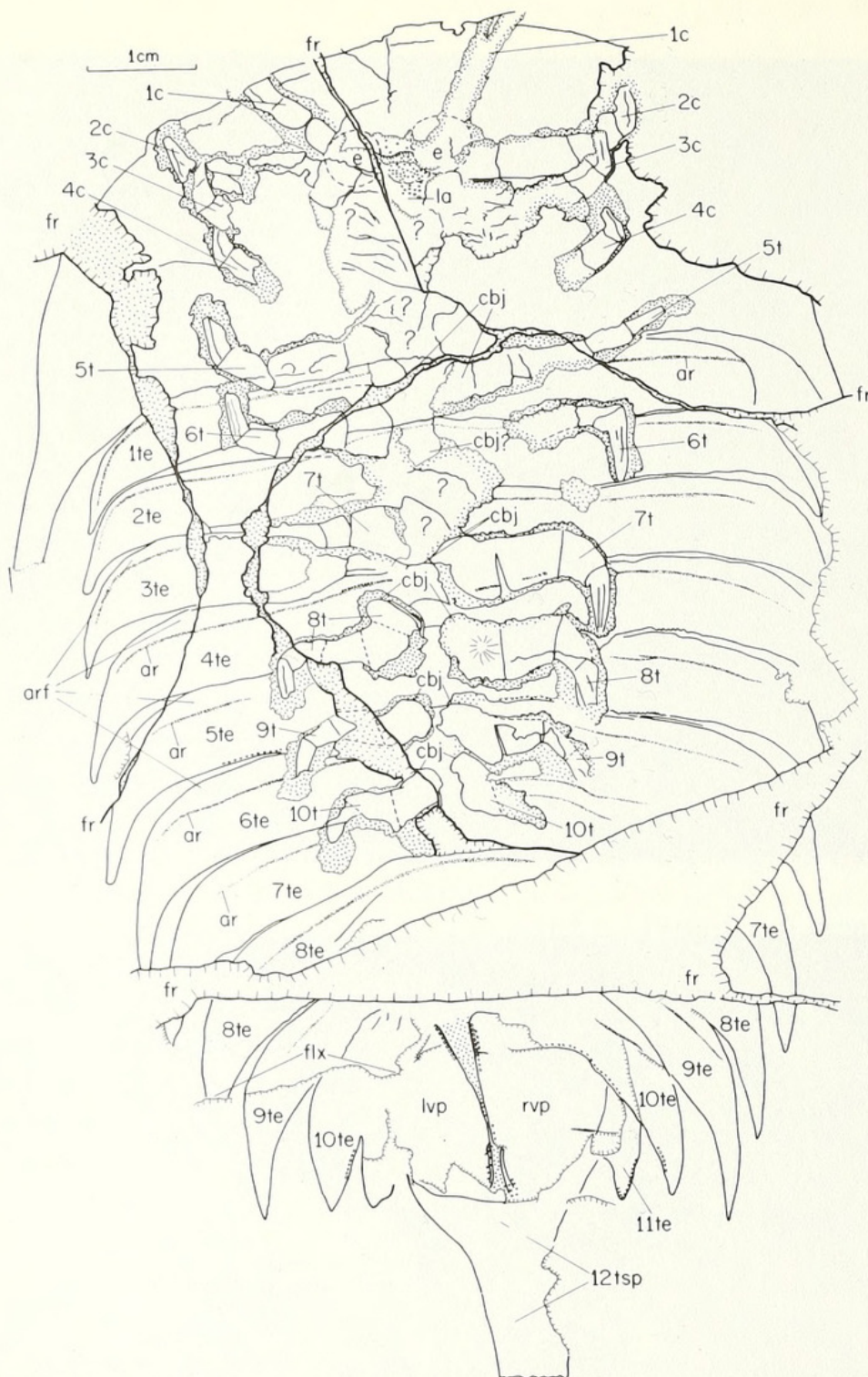
Figs. 1, 2. *Aglaspis spinifer* Raasch, 1939. 1, Holotype, MPM 11155, counterpart, showing posterior portion of cephalic shield and portions of trunk tergites 1-7,  $\times 2$ . 2, holotype, MPM 11154, part, median and left anterolateral portion of cephalic region, for comparison with Raasch 1939, pl. 4, figs. 1, 2. Symbols as text-fig. 1, those for appendages placed immediately to left of particular appendage.  $\times 5$ . Horizon and locality as Pl. 22.





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TEXT-FIG. 1. *Aglaspis spinifer* Raasch, 1939. Camera-lucida drawing of MPM 11154, holotype, part, internal mould; ar—articulating ridge, shown in fine stipple; arf—articulating flange; c—appendage of cephalic region; cbj—coxa-body junction; e—area of eye-lobe outlined by dashed line; flx—flexure; fr—fracture; la—labrum; lvp—left ventral plate; rvp—right ventral plate; t—appendage of trunk; te—tergite of trunk; tsp—terminal spine. Appendages are numbered 1–10, with suffix; tergites are numbered 1–11, with suffix. Coarser stipple indicates matrix along fractures, around appendages, and between post-ventral plates, hachures run down-slope from line indicating break in slope. Query indicates areas in which interpretation is uncertain.

#### EXPLANATION OF PLATE 24

Fig. 1. *Aglaspis spinifer* Raasch, 1939. Holotype, MPM 11154, antero-median portion of part to show appendages,  $\times 2.5$ . For interpretation see text-fig. 1. Horizon and locality as Pl. 22.





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in life, oval in cross-section, tapering distally so that the terminal podomere was elongate-conical in form. This podomere shows one or two longitudinal grooves or ridges, which may have served to strengthen it. In the course of burial the flexed limbs have been rotated about the coxa-body junction (text-fig. 1) into the plane of bedding, so that either the anterior (pairs 2 to 4) or posterior (pairs 8 to 10) surface is uppermost. In pair 5 the left has been swung forward, while the right is unusual in being extended straight, and may be compressed with the dorsal surface uppermost. In pairs 6 and 7 the left has been rotated forward, the right backward. The outline of the appendages suggests that when extended the dorsal margin was straight. A narrow triangular area separating some of the podomeres (e.g. the two most proximal in right 7 and 9) presumably represents the less sclerotized arthrodial membrane of a hinge joint, articulating dorsally. The terminal podomere is never sufficiently well preserved distally to confirm that the extremity of the appendages was a blunt point and did not bear a spine or spines.

Raasch (1939, p. 123) considered that the mid-portion of the cephalic region, adjacent to the prominent fracture, shows the crushed remains of the basal joints of appendages. This region lies below the level of the dorsal exoskeleton, and lacks the characteristic external sculpture (Pl. 22, fig. 3; Pl. 23, fig. 2; Pl. 24, fig. 1). Some poorly defined ventral structures appear to be preserved, and are also evident in the mid-region of tergites 1 to 4 (indicated by ? in text-fig. 1). They may represent proximal parts of appendages, but the number of podomeres in each limb does not appear to have exceeded five (it is considered unlikely that further podomeres are concealed as a result of folding or overlap during burial). Raasch (1939, pl. 4, fig. 2) outlined a possible ventral plate ('epistoma') in the cephalic region between the eye-lobes. The margins of this supposed labrum are evident (Pl. 23, fig. 2; Pl. 24, fig. 1; text-fig. 1) posteriorly and posterolaterally, but are not as clearly defined anteriorly as suggested by Raasch.

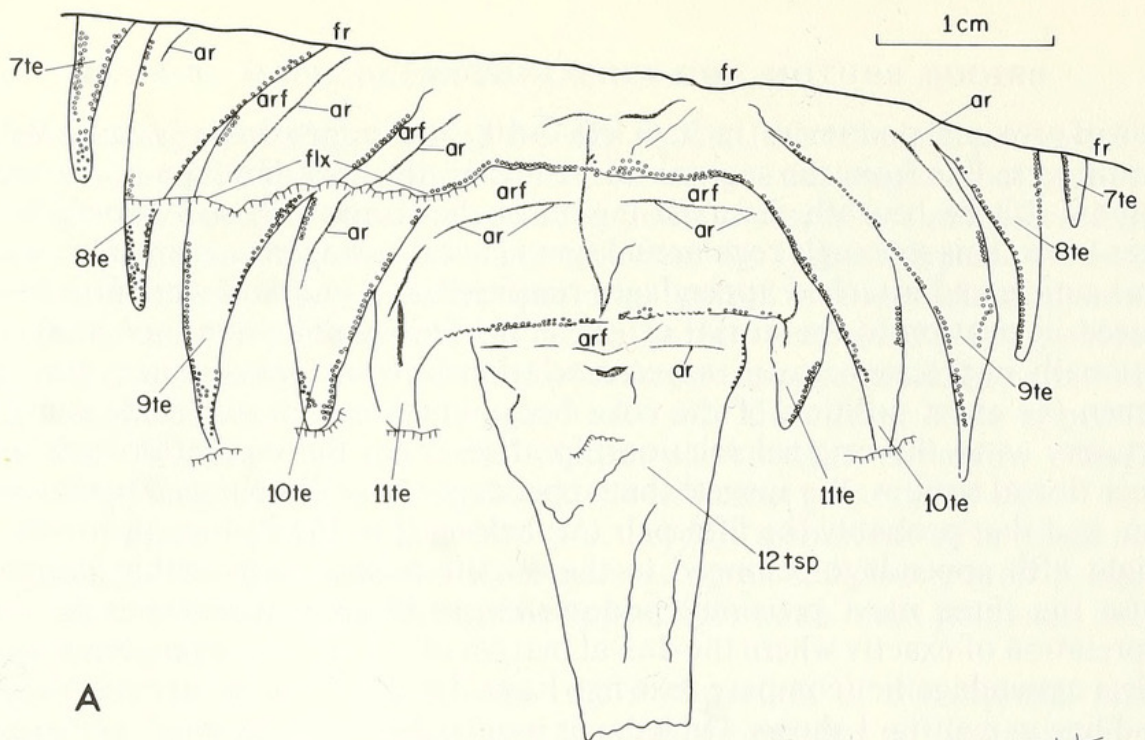
The configuration of the ten paired appendages, including the similarity of spacing between them, leads us to consider that, despite the portions missing and uncertainties of outline, no further limbs remain to be exposed within the series. However, if the original relation between dorsal exoskeleton and appendages is to be assessed, a second assumption must be made, that each appendage is now in the same, or little modified, position relative to the dorsal exoskeleton as it was in life. In other words, it is assumed that decay of soft parts, burial, and compaction of the sediment did not lead to displacement of the ventral cuticle and attached appendages relative to the dorsal exoskeleton, but merely to the rotation of each appendage 2-10 about the coxa-body junction so that it came to lie anterior or posterior face upward. This is a large assumption for two reasons. Firstly, in the only other specimen of *Aglaspis* showing appendages, *A. barrandei* (Raasch 1939, pl. 5, figs. 1-4), they are detached and displaced. Secondly, in a study of a trilobite with appendages, *Olenoides serratus* (Whittington 1975, pp. 102-104), it was shown that in all specimens displacement relative to the dorsal exoskeleton occurs, despite the evidence that ventral cuticle and appendages were not broken up but remained a unit. In the present specimen of *A. spinifer*, the configuration of the appendages in relation to the dorsal exoskeleton does, however, provide evidence which appears to favour the above assumptions. Text-fig. 1 shows that the proximal ends of 1c, and the coxa-body junction (dorsal



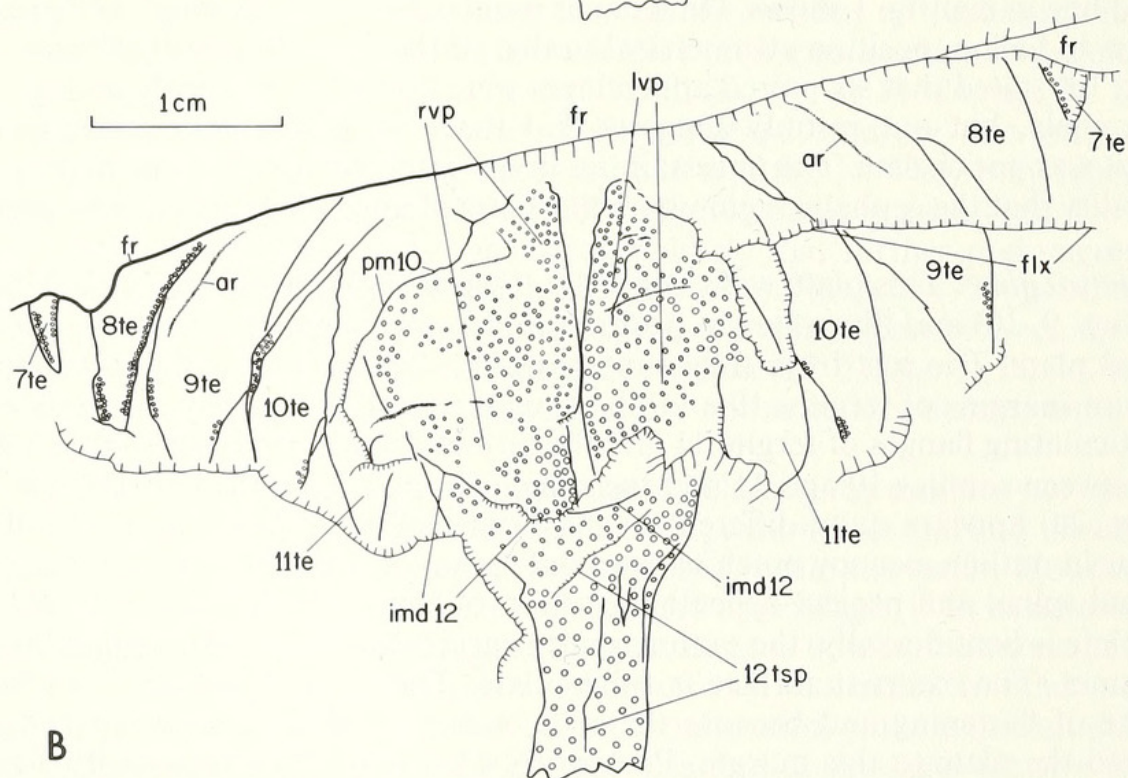
margin of proximal podomere) in 5t, 6t left, 7–10t, lie at approximately equal distances in a transverse line from the sagittal line. Further, the coxa-body junctions of 5t, 6t left, and 7–10t lie beneath the axial region of the trunk, and successively beneath tergites 1 to 6. This strikingly regular and symmetrical arrangement can only mean that ventral cuticle and attached appendages remained as a unit and were not markedly displaced in relation to the dorsal exoskeleton. The qualification ‘not markedly’ is intentionally imprecise because the exact relationship must remain uncertain. In this specimen the exact position of the coxa-body junction is not defined, and further uncertainty as to the original relationship arises from the separation now evident between dorsal tergites. We suggest that appendages 1c to 4c belonged to the cephalic region, and that probably the fifth pair (5t) belonged to the first trunk somite. That the right fifth appendage belonged to this somite seems a reasonable assumption, because the three most proximal podomeres lie beneath the first trunk tergite. Interpretation of exactly where the dorsal margin of the equivalent podomeres of the fifth left appendage lie (compare text-fig. 1 and Pl. 24, fig. 1) is less certain, as the dashed line in text-fig. 1 shows. On balance we conclude that the coxa-body junction appears to lie in a position symmetrical to that of the right fifth limb. Raasch (1939, pp. 12, 13) stated that six paired appendages were present in the cephalic region, the first a chela, but our restudy suggests that there were only four pairs, and that the first was not chelate. The uncertainties in our interpretations are evident, and the possibility that the cephalic region bore five pairs of appendages cannot be excluded.

*Postventral plate.* This plate was defined by Raasch (1939, p. 12; pl. 1; pl. 2, fig. 12; pl. 9, figs. 9, 10) and illustrated in position in this specimen, in one other, and as an isolated plate. The cast from the counterpart (Pl. 25, fig. 1; text-fig. 2A) shows the posterior margins of tergites 10 and 11, straight medially, coarsely tuberculate, and the articulating flanges of tergite 11 and the terminal spine, evidence of free articulation between somites 10 and 11 and the spine. The cast from the part (Pl. 25, fig. 2; text-fig. 2B) appears quite different in the axial region. A pair of plates, subsemi-circular in outline, occupy much of the axial region of somite 11 and the base of the terminal spine, and project beneath a portion of somite 10. The adaxial margin of each plate is bent dorsally, the outline gently curved convexly, and medially they are in contact. The external surface is tuberculate. The abaxial margin is ill defined, because of flattening and because the split between part and counterpart has not followed the plate to this margin. Posteriorly each plate may have abutted against the curved inner margin of the doublure of the terminal spine (imd in text-fig. 2B). Because of compaction and flattening of the specimen, the curled (and therefore more resistant to flattening) edge of the exoskeleton tends to be impressed into the exoskeleton of the opposite side. Thus in the counterpart (Pl. 25, fig. 1) the impression made by the adaxial margin of each plate is marked, as is the impression in the part (Pl. 22, fig. 2; Pl. 25, fig. 2) of the posterior margin of tergites 10 and 11, crossing the plates. This specimen thus provides the type of evidence on which Raasch (1939, p. 65) based his postventral plate, which he regarded as ‘divided into two longitudinal halves presumably united anteriorly by a connecting membrane’. In *A. spinifer* Raasch (1939, p. 12) described the plate as ‘almost completely bisected longitudinally’, considering that the posterior cleft was open, the anterior possibly closed





A



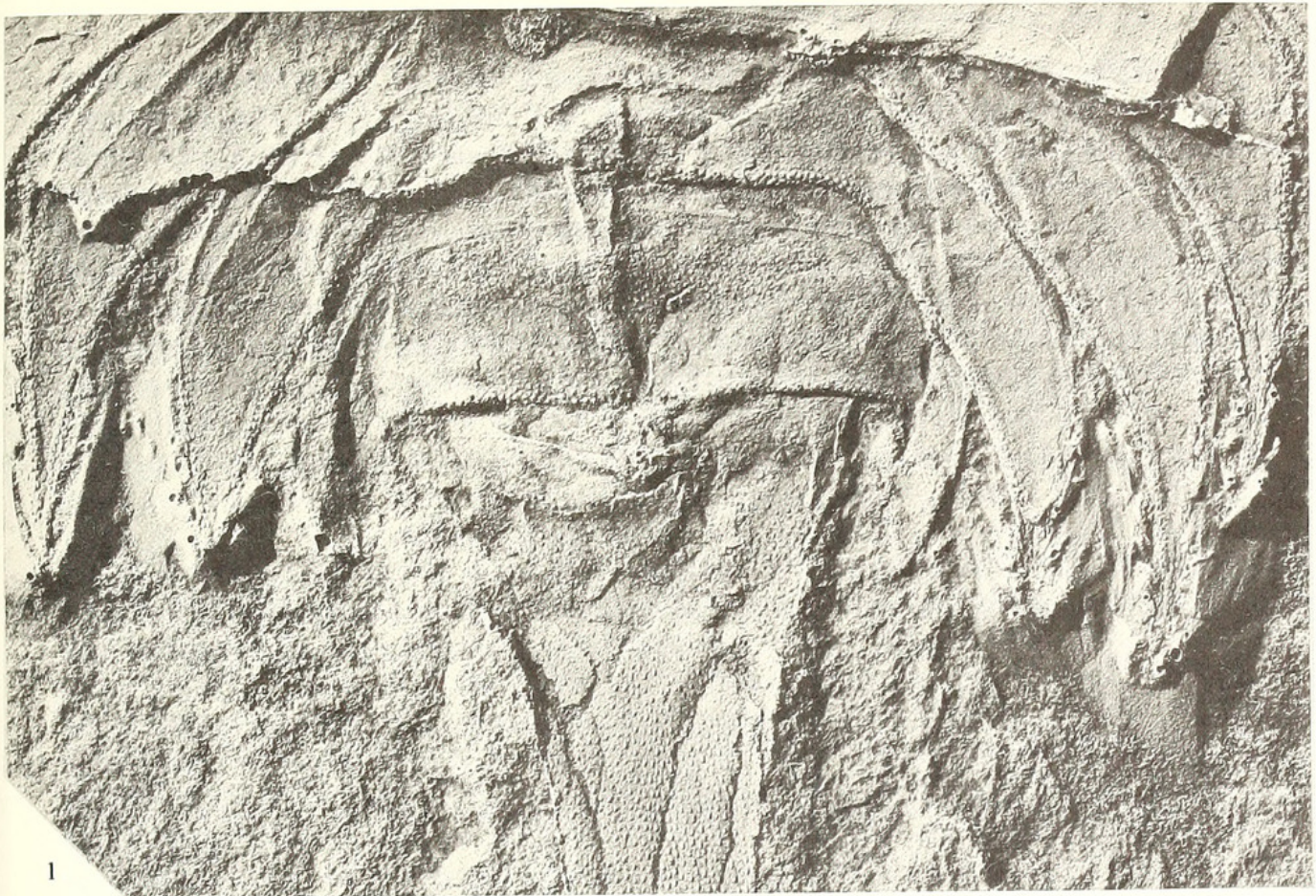
B

TEXT-FIG. 2. *Aglaspis spinifer* Raasch, 1939. Camera-lucida drawings. A, MPM 11155, latex cast of posterior portion of counterpart. B, MPM 11154, latex cast of posterior portion of part. ar—articulating ridge; arf—articulating flange; flx—flexure; fr—fracture; imd—internal margin of doublure; lvp—left ventral plate; pm—posterior margin; rvp—right ventral plate; te—tergite; tsp—terminal spine. Tergites numbered 7–11, 12 is terminal spine. Tubercles indicated by open circles. Lines with hachures indicate break in slope, hachures are directed down-slope.

#### EXPLANATION OF PLATE 25

Figs. 1, 2. *Aglaspis spinifer* Raasch, 1939. 1, holotype, MPM 11155, portion of latex cast of counterpart,  $\times 3$ ; for interpretation see text-fig. 2A. 2, holotype, MPM 11154, portion of latex cast of part,  $\times 3$ ; for interpretation see text-fig. 2B. Horizon and locality as Pl. 22.





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by a membrane. It is thus not clear whether Raasch thought the plate was divided into two separate portions (as Størmer 1955, p. P10 implies). If it were, the occurrence of isolated examples implies that the two halves were held together by a less sclerotized membrane which was not preserved. In the specimen studied here the inner edges of the two halves, which are dorsally upturned, appear to be separated by matrix along almost the entire length (Pl. 25, fig. 2; text-fig. 1), the two edges in contact medially for a very short distance. It does not appear that the two halves were fused medially. The anus may have opened in the posterior portion of the cleft in the postventral plate (Raasch 1939, p. 65).

#### DISCUSSION

Our objective was limited to the re-examination of the single specimen on which depended the view that *Aglaspis* and its allies were to be assigned to Class Merostomata; we have not studied other specimens of *A. spinifer*, nor searched for any which also may have appendages preserved approximately in place. Without such further work, and a wider study of aglaspidids, we would not attempt a restoration of the animal. What we consider may be inferred about appendages of *A. spinifer* is summarized in text-fig. 1. This knowledge is both equivocal and incomplete, reflecting the preservation of the specimen. We contend that the left anterior appendage (1c in text-fig. 1; compare Pl. 23, fig. 2) is too poorly preserved to be interpreted as a chela, and that the cephalic region bore fewer than six pairs of appendages. If we are correct, then *Aglaspis* and presumably other genera constituting the family Aglaspidae are not Merostomata nor Chelicerata. Størmer (1955) included three other families with the Aglaspidae in the Order Aglaspida, and placed the order in Subclass Xiphosura of the Merostomata. Various modifications to this taxonomy have been proposed since 1955. Genera have been added to the family Aglaspidae or the order by Chlupáč (1965), Chlupáč and Havlíček (1965), Novojilov (*in* Orlov 1962), and Repina and Okuneva (1969), a new family added by Flower (1969), while Bergström (1968, 1971) has suggested subtractions from this grouping. Our work bears only marginally on these matters. Now that we know the number of pairs of appendages in the cephalic region of *Aglaspis* is 4 or 5, not 6, the force of Bergström's (1971) arguments for removing the families Strabopidae and Paleomeridae from the Aglaspida are diminished, and we doubt their validity. Further, the work in progress by Bruton does not support the attribution by Bergström of these two families to the Subclass Merostomoidea Størmer, 1959, resemblances between them and genera placed in this Subclass by Størmer being only superficial. The Cambrian specimens of *Khankaspis bzhnovi* described as an aglaspidid by Repina and Okuneva (1969) show structures beneath the exoskeleton which they have interpreted as lamellate gill branches, but show no traces of the segmented limbs of Raasch's specimen. It appears to us an unwarranted inference (Bergström 1975, p. 291) to state that aglaspidid appendages are biramous, for no trace of a branch is preserved in the Wisconsin specimen, and the limb appears uniramous. More information is needed on the nature of aglaspidid appendages, and the content of the order remains uncertain.



If our restudy had unequivocally shown only four pairs of appendages in the cephalic region of *Aglaspis*, the same number as in the cephalon of certain trilobites (Cisne 1975; Whittington 1975, 1977), we might have argued for some relationship between them. Such a relationship has been considered (Raasch 1939, pp. 69, 70; Størmer 1944, pp. 76, 115, 116), but cannot be argued for on the similarity of the body regions or of the appendages. The resemblance between olenellid trilobites (in which only antennae are known) and aglaspidids appears to us superficial. For example, the furrowed olenellid glabella, the long, curved eye-lobe, the opisthothorax and pygidium, are exoskeletal features having no parallel in aglaspidids, and the postventral plate is unique to the latter. Whatever genera and families may be grouped with *Aglaspis* into the Order Aglaspida, present knowledge excludes it from merostomes and we prefer not to assign it to any higher taxon. Bergström (1968; 1975, pl. 1, fig. 1) described a fragmentary early Cambrian xiphosuran, and gave a diagram (1968, fig. 8) of main evolutionary lines among early merostomes. The removal of aglaspidids from the Merostomata widens the gap between these lines, and dramatically reduces the Cambrian record of this class.

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