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AULACOPLEURID TRILOBITES FROM THE UPPER ORDOVICIAN OF VIRGINIA

JONATHAN M. ADRAIN
Department of Geoscience, University of Iowa, 121 Trowbridge Hall, Iowa City 52242, <jonathan-adrain@uiowa.edu>

ABSTRACT—Five species of aulacopleurid trilobites occur in rich, silicified trilobite faunas from the Upper Ordovician of Virginia: *Harpidella triloba* (Hu, 1975a), *Strasburgaspis cona* (Hu, 1971), and *Strasburgaspis*? n. sp. A, all from the Turinian Edinburg Formation, *Harpidella whittingtoni* new species, from the overlying Turinian Oranda Formation, and *Harpidella evitti* new species, from the Chatfieldian Martinsburg Formation. The species of *Harpidella*, similar to other sets of congeneric taxa known from the formations, are subtly but pervasively differentiated. In addition to qualitative differentia such as the expression of the eye socle and of pygidial tubercle rows, the species are shown to differ in cranidial and librigenal shape via landmark-based geometric morphometric analysis. The genus *Strasburgaspis* (type species *S. cona*) is new. It is assigned to Aulacopleuridae on the basis of its micropygous morphology, but it shares potential apomorphies with Brachymetopidae and could prove to be the most plesiomorphic representative of that family.

INTRODUCTION

UPPER ORDOVICIAN silicified trilobite faunas of the Lincolnshire, Edinburg, Oranda, and Martinsburg formations in the Shenandoah Valley of Virginia are among the best-preserved ever discovered. Unfortunately, the faunas have been described in rather piecemeal fashion. Some groups have been given comprehensive attention in now-classic monographs whereas others remain essentially undocumented. The primary goal of the present work is to describe members of the family Aulacopleuridae, which have thus far received only limited treatment.

This work is one of a series describing or revising aulacopleuroidean species in preparation for a comprehensive phylogenetic analysis. It follows revisions of the genera *Otarion* Zenker, 1833 (Adrain and Chatterton, 1994), *Harpidella* M'Coy, 1849, and *Maurotarion* Alberti, 1969 (both Adrain and Chatterton, 1995a), *Aulacopleura* Angelin, 1854 and *Songkania* Zhang, 1974 (both Adrain and Chatterton, 1995b), and *Cyphaspis* Burmeister, 1843 (Adrain and Chatterton, 1996), along with papers describing species on a regional basis (Adrain, 1996; Adrain and Edgecombe, 1996; Adrain and Kloc, 1997).

Many aulacopleurid genera (including *Aulacopleura*, *Harpidella*, *Maurotarion*, and *Otarion*) have Silurian type species, and Silurian and Devonian species of the family include most of the really well-described taxa. As noted by Lespérance and Weissenberger (1998), the Ordovician species remain poorly known. Most named Ordovician species are inadequately described, and are typically known only from small photographs of cranidia. In the present state of knowledge, there is limited potential for working out the phylogeny and classification of Ordovician aulacopleurids and for determining their phylogenetic relationships to the better-known Siluro–Devonian taxa. This state of affairs can only be rectified via thorough revision and description of taxa, including all exoskeletal parts available, and the present mainly descriptive study is directed toward that end.

LOCALITIES AND STRATIGRAPHY

The Upper Ordovician stratigraphy of the Shenandoah Valley was studied by Cooper and Cooper (1946), who named the Edinburg and Oranda formations as successive units overlying the Lincolnshire and overlain by the Martinsburg. The formations dealt with herein have often been referred to as ''Middle Ordovician,'' but this is archaic. The GSSP for the base of the Upper Ordovician Series and the fifth, as yet unnamed, stage of the Ordovician was ratified by the IUGS in 2002 as the lowest occurrence of *Nemagraptus gracilis* (Hall, 1847) at the Fågelsång section in Scane, southern Sweden. This level is within the upper Whiterockian in Laurentian terms. The Laurentian Mohawkian consists of a lower Turinian and upper Chatfieldian Stage (Leslie and Bergström, 1995, 1997). The base of the Chatfieldian is the Millbrig K–Bentonite bed, and in the Shenandoah Valley this level corresponds roughly to the contact between the Oranda and Martinsburg formations (Leslie and Bergström, 1995, fig. 3; Leslie, 2000, fig. 2). The upper Lincolnshire, Edinburg, and Oranda are all of Turinian age, while the lower Martinsburg is Chatfieldian. In British terms, these correspond approximately to the Burrellian and Cheneyan of the Caradoc Series, sensu Fortey et al. (2000).

Facies distinctions within the Edinburg Formation have led to the application of several different names. Cooper and Cooper (1946) recognized two facies, a Lantz Mills facies of cobbly to nodular buff-weathering limestone, and a Liberty Hall facies of black limestone and shale. They also proposed a Botetourt Limestone Member at the base of the formation for brown-weathering granular limestone immediately above the Lincolnshire. Cooper (1956) elevated the Botetourt to formational status. This usage was followed, for example, by Evitt and Tripp (1977) in their monograph on Encrinuridae from the formations. It was not used by Whittington (1959), nor by Tripp and Evitt in subsequent papers (1981, 1983, 1986). All Lantz Mills, Liberty Hall, and Botetourt horizons are referred to the Edinburg Formation herein.

Locality descriptions for the collections have been detailed by Whittington (1959) and summarized by Evitt and Tripp (1977). Those relevant to the present work are repeated here, supplemented by collection information and designations. Whether or not separate collection designations at a given locality have any stratigraphic or spatial import is in most cases not clear. In his classic works, Whittington (1956, 1959) made no distinction and did not report them, listing only localities, which indicates that the separate designations may not have any particular meaning. As the collection information is available, though, it seems prudent to report it in the present work. The collections used in this study were made by G. A. Cooper, A. R. Loeblich Jr., M. Kay, W. R. Evitt and his wife, and H. B. Whittington.

Locality 3.—Whittington (1959, p. 381): ''Lower part of Edinburg limestone, section in field on south side of road, 0.2 mile east of Strasburg Junction, just west of Strasburg, Shenandoah County, Virginia.'' Collections: 600p (made by G. A. Cooper and A. R. Loeblich Jr., 26 April 1947)—0–10 ft below Botetourt coarse granular limestone, 20–30 ft above base of Edinburgh Formation; 600o (made by G. A. Cooper and A. R. Loeblich Jr., 26 April 1947)—Botetourt limestone; also W6, W7, Evitt 70, precise position unknown. A block collected by M. Kay is also from Locality 3.

Locality 6.—Whittington (1959, p. 381): ''Edinburg limestone, lower part, Hupp Hill, at entrance to Battlefield Crystal Caverns, and in field on opposite (east) side of U. S. Highway 11, about 11/2 miles north of Strasburg, Shenandoah County, Virginia.'' Collection: 600a.

Locality 8.—Oranda Formation; Whittington (1959, p. 382): ''Lower 5 feet of formation, cobbly limestone, in band and pasture on north side of Virginia secondary highway 777, just west of its junction with Virginia secondary highway 910, and circa 300 yards north of Greenmount church, five miles north of Harrisonburg, Rockingham County, Virginia.'' Collections: 600k, Evitt 77, evidently from the same horizons (material is figured from 600k, though large Evitt 77 collections are also available).

Locality 10.—Martinsburg Formation; Whittington (1959, p. 383): ''Pasture on north side of Virginia secondary highway 772, about 1 mile east of Greenwood church, five miles north of Harrisonburg, Rockingham County, Virginia.'' Collections: Evitt 153, Evitt 153a.

HISTORY OF STUDY OF THE FAUNAS

Whittington (1941) was first to illustrate silicified trilobites from the Virginia localities, working on a collection from the Martinsburg Formation (Locality 11 of Whittington, 1959). This included an aulacopleurid figured by Whittington in open nomenclature which is described below as *Harpidella evitti* n. sp. Evitt (1951) named some species belonging to the families Cheiruridae, Harpetidae, and Lichidae. Cooper (1953) named several silicified species from the Edinburg formation, with generally sparse illustration. Whittington and Evitt (1954) dealt with a range of genera with representatives in both the Edinburg and older Lincolnshire formations, with Whittington responsible for photography of the former and Evitt the latter. Whittington then produced magnificent and comprehensive monographs of the odontopleurids (Whittington, 1956) and the remopleuridids, trinucleids, raphiophorids, and endymioniids (Whittington, 1959) from all of the formations. The only comparable subsequent work has been Evitt and Tripp's (1977) monograph of the encrinurids. Hu (1971, 1974a, 1974b, 1975a, 1975b, 1976) published a series of works restricted to the Edinburg Formation and based on collections provided to him by Franco Rasetti. Hu's work is notable for the high level of basic misassociation of exoskeletal parts. In addition to common confusion of sclerites belonging to different families, Hu considered that most species were sexually dimorphic. This led to further misassignment of two ''morphs'' of many sclerite types, which clearly belong to separate and often unrelated species. Nevertheless, Hu introduced several species names and, despite the confusion, his illustrations of some taxa, such as the styginids and illaenids, are nearly the only ones presently available in the literature. Tripp and Evitt (1981, 1983, 1986) published on, respectively, the lichids, *Dimeropyge* Öpik, 1937, and the asaphids (the latter following an earlier paper on asaphid ontogeny by Evitt [1961]). These short papers suffered from a lack of material, with most species left in open nomenclature. Chatterton (1994) illustrated material of *Dimeropyge virginiensis* Whittington and Evitt, 1954, from the Edinburg. Chatterton et al. (1990) and Chatterton et al. (1994) incorporated material from the formations into their studies on the ontogeny and systematics of calymenoideans and trinucleoideans, respectively. Finally, Tripp et al. (1997) described two new species of *Sphaerocoryphe* from the Edinburg Formation.

The present work describes most of the aulacopleurid trilobites occurring in the formations. Through the generosity of H.B. Whittington, many of the original collections from the Edinburg, Oranda, and lower Martinsburg were made available for study, and for all but *Strasburgaspis*? n. sp. A there is abundant material of most exoskeletal parts. Of the five aulacopleurid species identified, two were named by Hu, albeit with gross misassociation of sclerites. *Harpidella triloba* (Hu, 1975a) was revised by Adrain and Chatterton (1995a). This treatment is accurate, but much better and more abundant material is now available, making feasible a complete written description. *Phaseolops conus* Hu, 1971 has been commented upon by several authors but never revised, and full treatment with corrected sclerite associations is provided below. The species is made the type of a new genus, *Strasburgaspis*. A single cranidium of a new species apparently most closely related to *S. cona* (Hu, 1971) is also described. New species of *Harpidella* from the Oranda and Martinsburg formations are formally described and named.

SYSTEMATIC PALEONTOLOGY

Repositories.—Type and figured material is housed in the United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., with specimen number prefix USNM. Reference is made to material in the University of Cincinnati Geology Museum, Cincinnati, Ohio, with specimen number prefix UCGM.

Imaging and data gathering.—Specimens were blackened with dilute india ink then mounted with gum tragacanth on the sharpened tips of blackened toothpicks. For photography, the base of the toothpick was set in modeling clay, allowing precise orientation of the specimen. Specimens were photographed using a digital camera coupled to a Leitz Aristophot system and an 80 mm Summar lens, and were whitened with ammonium chloride sublimate prior to photography. Images were sized and processed in Adobe Photoshop (typical image processing: levels correction, resizing, two passes of Unsharp Mask filter at 50% with radius 0.7 pixels). Landmarks were digitized with the freeware program NIH Image, version 1.63, using a millimeter scale to three decimal places. All morphometric analyses were carried out using H. David Sheets's (2003) IMP Suite.

Superfamily AULACOPLEUROIDEA Angelin, 1854
Family AULACOPLEURIDAE Angelin, 1854
Subfamily OTARIONINAE Richter and Richter, 1926
Genus HARPIDELLA M'Coy, 1849

Rhinotarion WHITTINGTON AND CAMPBELL, 1967, p. 458, *FIDE* ADRAIN AND CHATTERTON, 1995a, p. 307.

Type species.—*Harpes*? *megalops* M'Coy, 1846, from the Kilbride Formation, Llandovery (Telychian), Boocaun, Cong, County Galway, Ireland; see Whittington and Campbell (1967) and Adrain and Chatterton (1995a) for illustrations of syntypes and other material.

Other species.—See Adrain and Chatterton (1995a, p. 307).

Discussion.—Lespérance and Weissenberger (1998) followed Adrain and Chatterton's (1995a) revision of *Harpidella* but pointed out, correctly, that the glabella and occipital ring typically occupy around 80%, not 70%, of the cranidial sagittal length in dorsal view.

Morphometrics.—The three species of *Harpidella* present in the collections are similar to one another, but are clearly distinct based on a variety of qualitative characters as detailed in the species discussions below. To explore differences in shape using explicit quantitative methods, landmark-based geometric morphometric analyses were employed. Homologous landmarks were located on the dorsal surface of the cranidium and external surface of the librigena.

Thirty-nine cranidial landmarks were located (Fig. 1.1). Five lie on the sagittal axis, whereas 34 occur in symmetry pairs on either side of the axis. As trilobite cranidia are bilaterally symmetrical, landmarks were reflected across the axis of symmetry using the IMP program BigFix (Sheets, 2003). The position of each pair of landmarks was taken as their average value, reduced

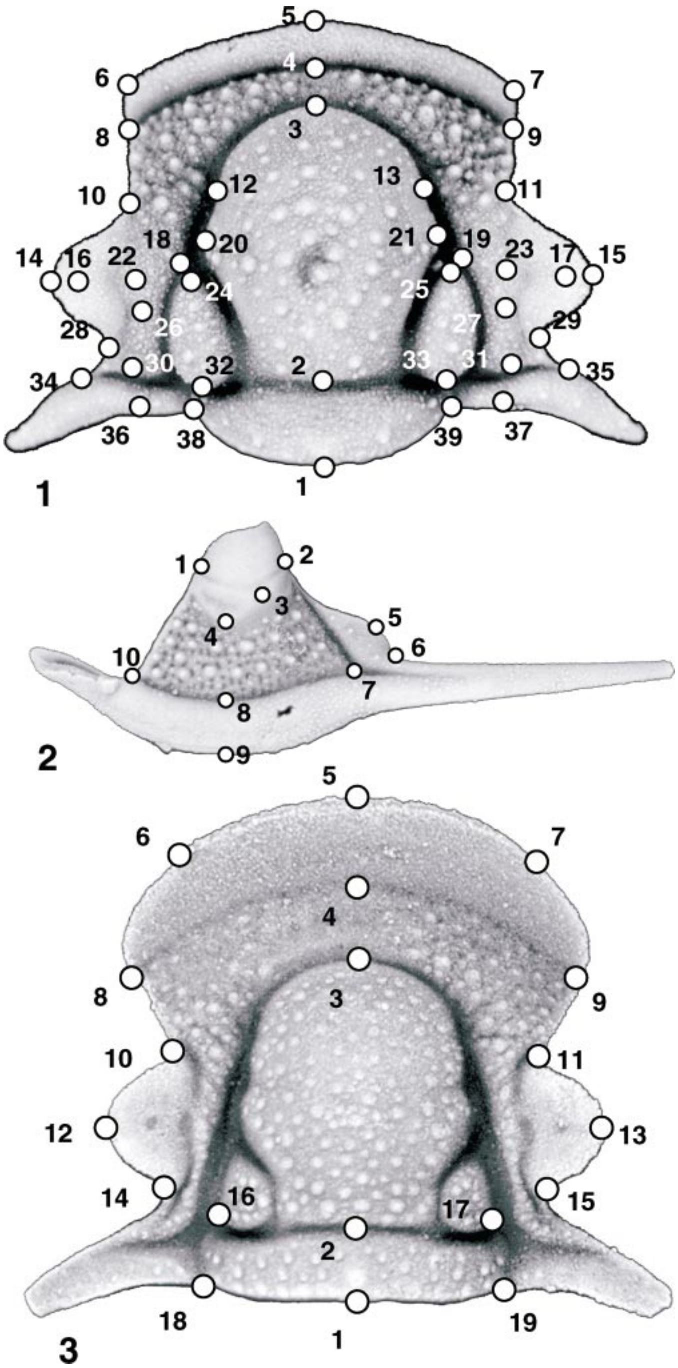

FIGURE *1*—*1*, Thirty-nine cranidial landmarks used in morphometric analysis of three species of *Harpidella* M'Coy, 1849 dealt with herein. Cranidium of *H. triloba* (Hu, 1975a) shown. *2*, Ten landmarks used in morphometric analysis of three species of *Harpidella* dealt with herein. Librigena of *H. triloba* shown. *3*, Nineteen landmarks used to illustrate intraspecific variation in *Strasburgaspis cona* (Hu, 1971).

to a single landmark after reflection. This technique has the advantage of allowing the use of less complete specimens in which a paired landmark is present on at least one side, but not necessarily both. In cases where the landmark was present on only one side or the other, this value represented the single landmark after reflection.

Ten librigenal landmarks were located (Fig. 1.2). Left librigenae were arbitrarily chosen for analysis, and right librigenae were scored by flipping the image horizontally prior to digitizing.

Landmarks.—

Cranidium—sagittal landmarks

1–Intersection of sagittal line and posterior edge of L0, excluding median occipital node if overhanging.
2–Intersection of sagittal line and posterior margin of main part of glabella.
3–Intersection of sagittal line and anterior margin of glabella.
4–Intersection of sagittal line and rear of anterior border furrow.
5–Intersection of sagittal line and anterior cranidial margin.

Cranidium—paired landmarks

6, 7–Intersection of anterior facial suture and anterior cranidial margin (α).
8, 9–Intersection of anterior facial suture and rear of anterior border furrow.
10, 11–Change in slope of anterior facial suture in front of palpebral lobe (γ).
12, 13–Lateralmost point of L3.
14, 15–Lateralmost point of margin of palpebral lobe (δ).
16, 17–Center of pit in palpebral lobe.
18, 19–Inflection in median edge of fixigena in front of L1.
20, 21–Lateralmost edge of L2.
22, 23–Center of Fx3.
24, 25–Anterior point of L1, at junction of axial furrow and S1.
26, 27–Center of Fx2.
28, 29–Medianmost point of posterior facial suture (ϵ).
30, 31–Center of Fx1.
32, 33–Break in slope of outline of L1 at posteromedian part.
34, 35–Intersection of posterior border furrow with posterior facial suture.
36, 37–Center of prominent tubercle on posterior border behind Fx1.
38, 39–Intersection of posterior margin of L0 with axial furrow.

Librigena

1–Contact of furrow beneath visual surface with anterior section of facial suture.
2–Contact of furrow beneath visual surface with posterior section of facial suture.
3–Middle of area between eye socle lobes (position of tubercle developed in *H. whittingtoni* n. sp. and *H. evitti* n. sp.).
4–Lateralmost part of margin of anterior eye socle lobe (and narrowest point of field).
5–Point at which posterior section of facial suture cuts across posterior margin of posterior border.
6–Angle between posterior border and genal spine.
7–Confluence of posterior border furrow and lateral border furrow.
8–Adaxial edge of lateral border transversely opposite landmark 4.
9–Abaxial edge of lateral border transversely opposite landmark 8.
10–Contact of lateral border furrow and anterior section of facial suture.

Results.—Seventeen cranidia of *Harpidella triloba* were digitized, nine belonging to *H. whittingtoni*, and 12 belonging to *H. evitti*. Following reflection across the plane of symmetry, a Procrustes GLS mean reference form was calculated using all 28 specimens. Partial warp scores were derived from thin-plate spline

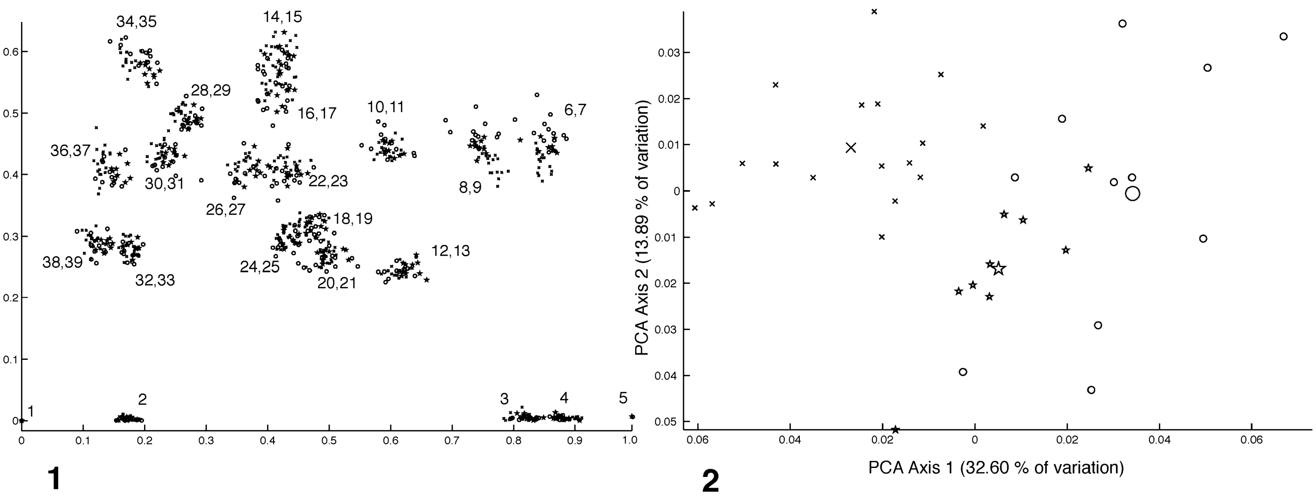

FIGURE 2—Morphometric analysis of *Harpidella* cranidial shape. *1*, Cranidial landmarks after reflection, shown in Bookstein Coordinates with baseline between landmarks 1 and 5 (i.e., rear and front of sagittal axis of cranidium; anterior to the right). *2*, First two principal components axes for cranidial partial warp scores. Crosses = *H. triloba*; stars = *H. whittingtoni* n. sp.; circles = *H. evitti* n. sp. Large symbols in *2* show position of means.

decomposition of the data, and principal components analysis was performed on these scores.

Cranidial landmarks of all three species are shown as Bookstein Coordinates (registered to a baseline from landmarks 1 to 5—i.e., the sagittal midlength of the cranidium) in Figure 2.1. It is apparent that much of the obvious shape difference between the species is related to differences in the width of the anterior part of the cranidium, reflected in the spread of specimens across landmarks 6/7 and 8/9. *Harpidella evitti* has the anteriorly widest cranidium, whereas *H. whittingtoni* is intermediate and partially overlaps the range of *H. evitti*. Anterior cranidial landmarks of *Harpidella triloba* are mostly grouped adaxially from those of the other species. This general pattern of cranidial shape contrast is borne out by principal components analysis of partial warp scores (Fig. 2.2), in which the first PCA axis (accounting for 32.60% of variation) separates *H. triloba* from the other species, and separates *H. whittingtoni* and *H. evitti* with some overlap.

Librigenal data tell a similar story. Ten librigenae of *Harpidella triloba* were digitized, eight belonging to *H. whittingtoni*, and 10 belonging to *H. evitti*. Principal components analysis was carried out in the same manner as for cranidia. Librigenal landmarks for all three species are shown as Bookstein Coordinates, with a baseline between landmarks 10 and 7, in Figure 3.1. There is an obvious pattern of scatter of the landmarks in the eye region, with *H. evitti* specimens nearer the top, *H. whittingtoni* intermediate, and *H. triloba* nearer the bottom. This is clearly related to the width of the librigenal field, and this is the main and most obvious shape difference separating librigenae of the species. For example, taking the ratio of the interlandmark distance between landmarks 4 and 8 versus that between landmarks 8 and 9 (essentially, the minimum width of the field divided by the width of the lateral border), *H. triloba* scores 1.560, *H. whittingtoni* scores 1.849, and *H. evitti* scores 2.152. That is, the width of the field in *H. evitti* is nearly 40% wider than in *H. triloba*, with *H. whittingtoni* intermediate. The distributions of these and other librigenal ratios, such as the ratio of the width of the cheek to the length of the cheek (4–8 vs. 10–7; 0.345, 0.425, 0.468 for *H. triloba*, *H. whittingtoni*, and *H. evitti*, respectively) show clear distinctions, with

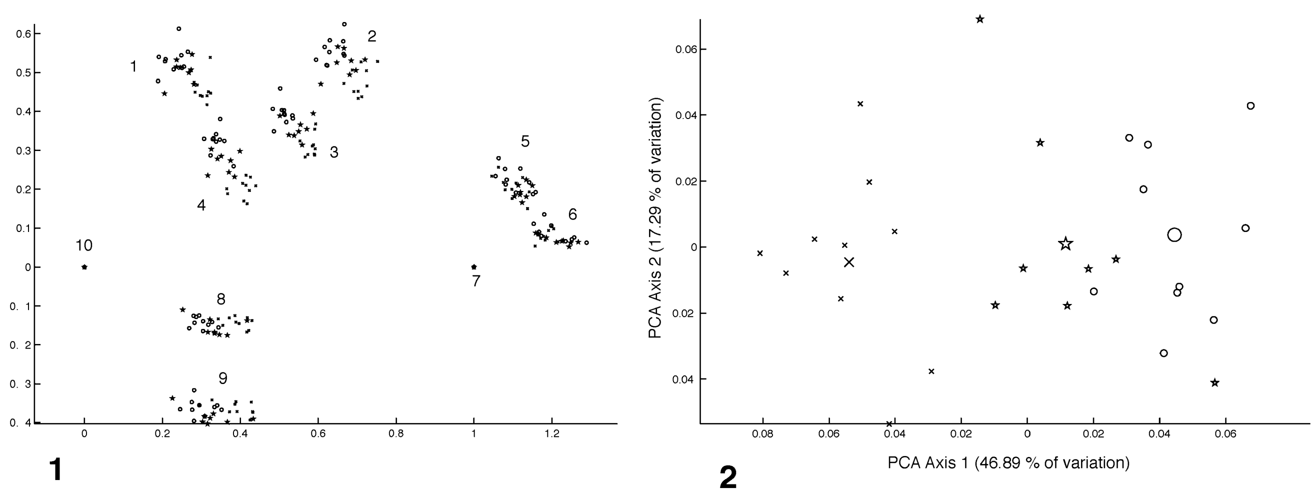

FIGURE 3—Morphometric analysis of *Harpidella* librigenal shape. *1*, Librigenal landmarks shown as Bookstein Coordinates with baseline between landmarks 10 and 7. *2*, First two principal components axes for cranidial partial warp scores. Crosses = *H. triloba*; stars = *H. whittingtoni* n. sp.; circles = *H. evitti* n. sp. Large symbols in *2* show position of means.

only minor overlap in ranges. The first two axes of the PCA (Fig. 3.2) show that *H. triloba* is unambiguously separate from the other species along the first axis (accounting for 46.89% of variation). *Harpidella whittingtoni* and *H. evitti* overlap only by one end-member specimen from either species.

Hence, in addition to qualitative characters on the cranidia and the librigena, and contrasts also in pygidia, there are clearly discriminated differences in both cranidial and librigenal shape separating the Edinburg, Oranda, and Martinsburg species of *Harpidella*. Clearly discriminated yet closely similar species are typical of other trilobite groups occurring in the faunas, including for example the odontopleurid *Diacanthaspis* Whittington, 1941 (see Whittington, 1956) and the dimeropygid *Dimeropyge* Öpik, 1937 (see Whittington and Evitt, 1954; Tripp and Evitt, 1983; Chatterton, 1994).

HARPIDELLA TRILOBA (Hu, 1975a)
Figures 4, 5

Otarion trilobus HU, 1975a, p. 115, pl. 1, figs. 3–16, 18–20 [*non* fig. 1 = encrinurid protaspid; *non* fig. 2 = cheiruroidean meraspid cranidium; *non* fig. 17 = proetoidean thoracic segments; *non* figs. 21–26 = *Panarchaeogonus acris* (HU, 1976)], text-fig. 1c-i [*non* text-fig. 1a, b, j, k].

''*Proetus*'' *strasburgensis* COOPER, 1953; HU, 1975a, *partim*, p. 122, pl. 2, fig. 16 [*only*].

Mesotaphraspis acris HU, 1976, *partim*, p. 251, pl. 27, figs. 16, 22?, 27–20, 30?, text-fig. 2n [*only*].

Harpidella triloba (HU, 1975a); ADRAIN AND CHATTERTON, 1995a, p. 310, fig. 2.1–2.28.

Diagnosis.—Anterior sections of facial suture typically anteriorly convergent; cranidial anterior border lacking dorsal tubercles; palpebral lobes with at most a single tiny tubercle; librigenal field with minimum width 156% width of border and 34.5% length of field; librigenal lateral border with only uniform granulose sculpture; eye socle with well-expressed figure-eight shape; pygidium with dorsal sculpture of crowded granules, with only faint trace of subdued transverse tubercle rows on some specimens.

Description.—Cranidial ratios are based upon measurements of 14 nearly complete specimens. Cranidium with width across anterior border 83.6% (77.9–88.5) sagittal length and width across midlength of palpebral lobes 120.6% (115.4–126.3) sagittal length; glabella with length (including L0) 81.1% (78.7–83.5) cranidial sagittal length; width across anterior edge of palpebral lobes 105.2% (96.7–114.5) width across anterior border; anterior border short (sag.; exsag.), of similar length sagittally and exsagittally, sagittally convex and tubelike, lacking sculpture, anterior margin describing even, shallow, anterior arc; anterior border furrow deeply incised and short, describing arc subparallel with that of anterior margin; anterior sections of facial sutures typically slightly anteriorly convergent, subparallel to slightly anteriorly divergent in some specimens; frontal area and preglabellar field with sculpture of fine, densely spaced caecal pits and small to medium, densely spaced tubercles; preglabellar field with sagittal length similar to that of anterior border; interocular fixigena with Fx2 and Fx3 discernible in almost all specimens, with smaller scattered tubercles ranging from very sparse (Fig. 4.17, 4.28) to moderately dense (Fig. 4.2, 4.39); interocular fixigena slightly narrower than L1; palpebral lobe inclined at about 45 degrees to horizontal in anterior view, lacking sculpture except for prominent central pit, lateral margin not describing even curve, more convex at lateral extremity; palpebral furrow ranging from shallow (Fig. 4.39) to essentially effaced, discernible only as a break in slope (Fig. 4.3); posterior fixigenae with Fx4 clearly expressed in all specimens; glabella with L1 large, laterally displaced, and completely isolated from median lobe by S1 (with the exception of one unusual specimen; see below); L3 expressed as subtle lateral swelling; S2 expressed as gentle notch; L2 with slight lateral inflation; preglabellar furrow with contact with axial furrow ranging from gradational (Fig. 4.18) to more typically forming an obvious angle (Fig. 4.1), anterior curvature ranging from nearly even (Fig. 4.3, 4.29) to a slight median angle (Fig. 4.1, 4.2, 4.17); axial furrow quite wide from contact with posterior border furrow anteriorly to L3, at which point much narrower posterior to contact with preglabellar field; S1 deepest and widest abaxially at contact with axial furrow, becoming slightly narrower and shallower posteriorly; median glabellar lobe with moderate dorsal inflation in sagittal profile, sculpture of typically quite dense small and medium-sized tubercles, similar to those on frontal area and preglabellar field; L1 with similar sculpture as median lobe; S0 ranging from transversely straight (Fig. 4.2, 4.18) to slightly posteriorly bowed (Fig. 4.1, 4.3), long (sag.; exsag.) and shallow, anterior margin at rear of median lobe steeper and more sharply defined than posterior margin at front of L0; L0 with small median node situated on rear half of sagittal length, in rare specimens overhanging posterior margin, sculpture ranging from two lateral pairs of tubercles (Fig. 4.28, 4.36) to a single transverse row of tubercles (Fig. 4.17), to fairly dense and scattered tubercles (Fig. 4.1, 4.2, 4.14); L0 quite long, slightly shorter than combined length of preglabellar field and anterior border; posterior border furrow shorter and more deeply incised than S0, bowed posteriorly behind posterior fixigena; posterior border forming lateral projections of cranidium, turned back at fulcrum, with typical dorsal sculpture of a single row of transverse tubercles, serial homologue of Fx4 always discernible; cranidial doublure restricted to very small inturned section beneath extremity of posterior border and long articulating section under L0, with fine transverse lines; very small fossular pits present just in front of L3; small apodeme present at ventral junction of posterior border and L0 doublure.

Librigena with minimum width of field 34.5% (29.5–37.3) exsagittal length and 156.0% (133.1–179.0) width of border; length of course of anterior section of facial suture (between landmarks 1 and 10, Fig. 1.2) 55.0% (52.3–62.8) length of field; eye set off from socle by narrow, shallow but firmly inscribed furrow; socle of two lobes, each with depression in middle, anterior lobe larger than posterior lobe; socle lacking sculpture; field with

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FIGURE 4—*Harpidella triloba* (Hu, 1975a), from the Edinburg Formation, Locality 3. All magnifications are ×12. *1, 7, 11, 12,* Cranidium, USNM 521881, dorsal, right lateral, anterior, and ventral views (Evitt 70). *2, 8, 9,* Cranidium, USNM 521882, dorsal, right lateral, and anterior views (600p). *3–5,* Cranidium, USNM 521883, dorsal, right lateral, and anterior views (600p). *6, 10, 16, 24,* Cranidium, USNM 521884, dorsal, anterior, oblique, and right lateral views (Evitt 70). *13–15,* Cranidium, USNM 521885, right lateral, dorsal, and anterior views (Evitt 70). *17, 20, 25,* Cranidium, USNM 521886, dorsal, anterior, and right lateral views (Evitt 70). *18, 19, 23,* Cranidium, USNM 521887, dorsal, anterior, and left lateral views (600p). *21, 22, 26,* Cranidium, USNM 521888, dorsal, anterior, and right lateral views (600p). *27, 28, 33,* Cranidium, USNM 521889, anterior, dorsal, and right lateral views (600p). *29, 34, 40,* Cranidium, USNM 521890, dorsal, anterior, and right lateral views (Evitt 70). *30, 31, 35, 42,* Cranidium, USNM 521891, dorsal, anterior, right lateral, and ventral views (Evitt 70). *32, 37, 39,* Cranidium, USNM 521892, right lateral, anterior, and dorsal views (600p). *36, 38, 43,* Cranidium, USNM 521893, dorsal, anterior, and right lateral views (Evitt 70). *41, 44, 45,* Cranidium, USNM 521894, right lateral, dorsal, and anterior views (Evitt 70).


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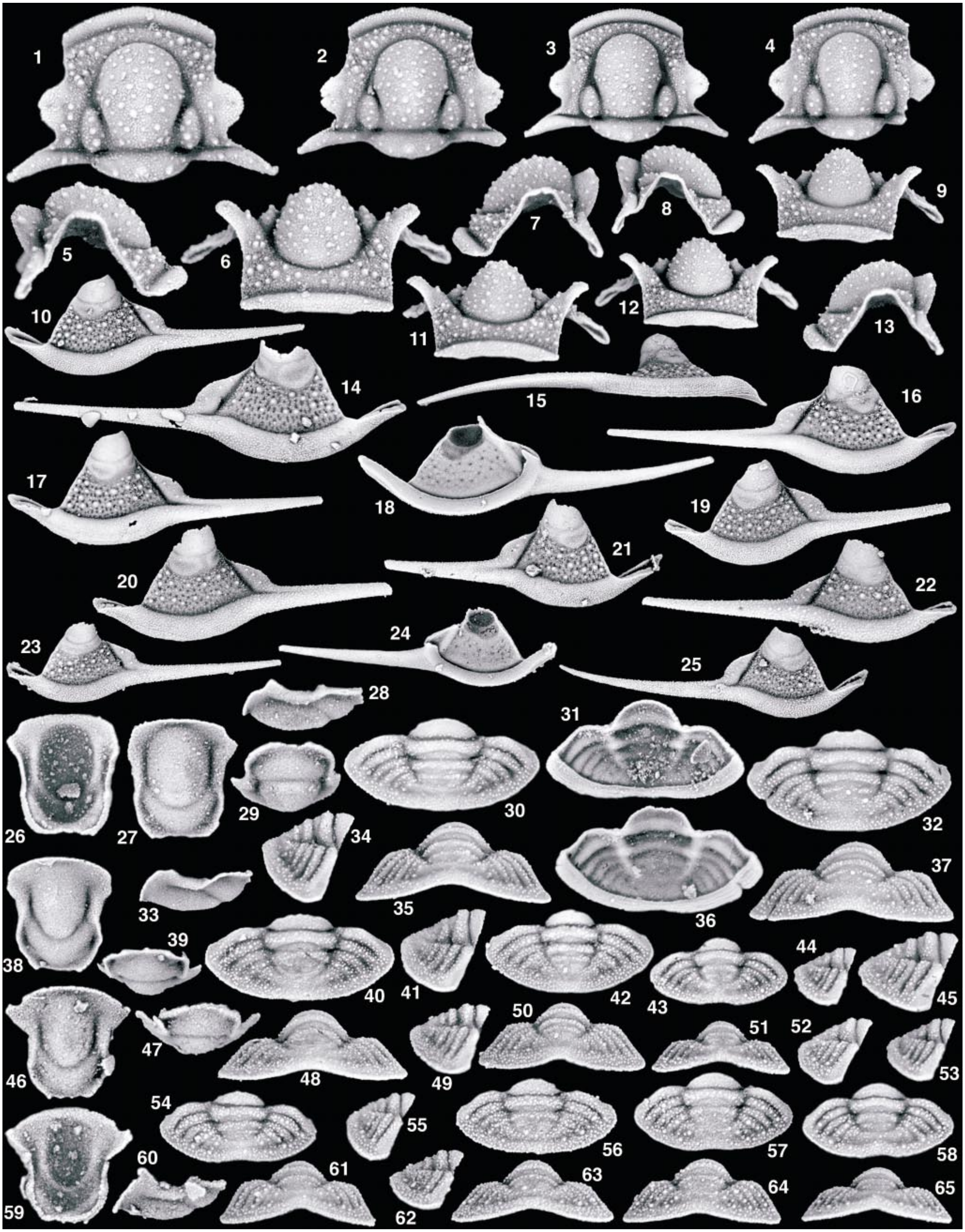
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prominent caecal pitting and scattered medium-sized tubercles, tending to be more dense on anterior and adaxial areas; posterior and lateral border furrows deep and of similar width, meeting at acute angle behind field to form a single furrow extended along the dorsal aspect of the proximal part of the genal spine; genal spine slightly shorter to slightly longer than the remainder of the librigena, including the anterior projection, tapering gently to sharp tip, ranging from slightly (Fig. 5.16) to moderately (Fig. 5.25) curved, with granular dorsal sculpture similar to that of lateral border and faint row of proximal tubercles in some specimens continued from a row on the posterior border (Fig. 5.17) or lateral border (Fig. 5.22); lateral border of similar width anteriorly and posteriorly, most specimens lacking sculpture except for dense granules; length of anterior projection between half and two-thirds length of field; doublure forms relatively sharp edge with lateral margin of border, with inner edge underlying border furrow, posteriorly cutting across posterior border furrow (suggestion of a Panderian opening on Fig. 5.18 is artifactual), with sculpture of very fine and subdued raised lines subparallel with margin.

Rostral plate not identified.

Hypostome with sagittal length about 90% maximum width across anterior wings and 130% width across shoulders; anterior margin slightly flared into downturned rim; anterior wings triangular, with granular sculpture; lateral border confluent with anterior wing, forming a raised ridge from opposite middle furrow to rear of hypostome; lateral border furrow cut off anteriorly by lateral border running into middle body, deep opposite rear lobe of middle body, confluent with much shallower posterior border which forms gentle posterior arc; pair of very short, nearly cylindrical spines developed at posterior termination of lateral borders; both anterior and posterior lobes of middle body with weak ventral inflation and lacking sculpture, anterior lobe about 75% maximum width of posterior lobe; middle furrow fairly deep and incised medially, evenly arcuate in some specimens (Fig. 5.27), with more convex median part in others (Fig. 5.38); posterior lobe forming broad U-shape; doublure forming narrow rim around lateral and posterior borders.

Thorax not identified, but see Adrain and Chatterton (1995a, fig. 2.16) for illustration of a single segment from the posterior part of the thorax.

Pygidium with sagittal length (including articulating half-ring) 45%–50% width; axis with anterior width about 40% that of pygidium; articulating half-ring subelliptical, with slight median anterior bow, lacking sculpture except for transverse row of very fine tubercles along posterior margin; ring furrow firmly inscribed, either transverse (Fig. 5.32, 5.54) or slightly bowed (Fig. 5.30); axial furrows posteriorly convergent, shallow, in some specimens shallowed but definitely meeting posteriorly to fully circumscribe axis (Fig. 5.30, 5.58), more typically effaced at posteriormost part (Fig. 5.32, 5.42); three axial rings, all with dorsal sculpture of fine granules, first two fully expressed, third varying from transversely complete (Fig. 5.30) to discernible only abaxially (Fig. 5.56, 5.57); pseudoarticulating half-ring well developed in front of second axial ring, very short pseudoarticulating half-ring variably developed in front of third ring; ring furrows deeper laterally than medially; axis weakly inflated, forming slightly dorsally bowed slope to posterior margin in sagittal view; first two interpleural furrows and first three pleural furrows impressed on most specimens, third interpleural furrow usually absent, very weakly expressed on some specimens; pleurae with sculpture of granules on both anterior and posterior bands, very fine transverse tubercle row in some specimens on posterior pleural band of first (Fig. 5.42) or first and second (Fig. 5.57, 5.58) segments; anterior and posterior pleural bands subequal in length, of similar length medially and laterally; area behind axis smooth; pygidial border well developed, about as wide or slightly wider than pleural bands of first segment, very slightly dorsally concave, with sculpture of granules similar to those on pleural bands, slightly wider at lateral extremity and slightly narrower medially; posterior margin with distinct median flexure in posterior view; doublure with width similar to border, broader laterally, with sculpture of fine contiguous lines subparallel with margin.

Material examined.—The holotype (Hu, 1975a, pl. 1, fig. 10) is UCGM 40429, from the Edinburg Formation (Turinian), near Strasburg, Shenandoah County, Virginia. Material illustrated herein is USNM 521881–521920, from the lower Edinburg Formation, Locality 3.

Intraspecific variation.—Minor variation is listed in the description above, but more substantial variation is discussed here. All of the specimens occur together in the same collections, there seems to be no disjunct patterns of variation, nor does variation in some features seem to be coordinated with that in others, and there is hence little reason to suspect that more than one species is involved. *Harpidella triloba* exhibits little shape variation in cranidial outline, the exception being the course of the anterior sections of the facial sutures, which are typically slightly anteriorly convergent (Fig. 4.1, 4.14, 4.17, 4.30), but subparallel in some specimens (Fig. 4.39), and in rare instances slightly anteriorly divergent (Fig. 4.3). The most obvious variation in cranidia is in the size and density of tuberculate sculpture. Most specimens have fairly densely spaced tubercles (Fig. 4.2). In rare instances, the sculpture on the median glabellar lobe has fewer tubercles developed (Fig. 4.17 and especially 4.28). The position of the median occipital node is somewhat variable. In most specimens it is clearly set forward from the posterior margin of L0, but in some it contacts the margin (Fig. 4.3, 4.39) and in rare cases actually overhangs the margin (Fig. 4.28).

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FIGURE 5—*Harpidella triloba* (Hu, 1975a), from the Edinburg Formation, Locality 3. Magnifications are ×12 and from collection Evitt 70 except where noted. *1, 5, 6,* Cranidium, USNM 521895, dorsal, right lateral, and anterior views, ×20. *2, 7, 11,* Cranidium, USNM 521896, dorsal, left lateral, and anterior views, ×20. *3, 8, 12*, Cranidium, USNM 521897, dorsal, right lateral, and anterior views, ×15. *4, 9, 13*, Cranidium, USNM 521898, dorsal, anterior, and left lateral views, ×20. *10,* Left librigena, USNM 521899, external view. *14,* Right librigena, USNM 521900, external view. *15, 16, 18,* Right librigena, USNM 521901, ventrolateral, external, and internal views. *17,* Left librigena, USNM 521902, external view. *19,* Left librigena, USNM 521903, external view (600p). *20,* Left librigena, USNM 521904, external view (600p). *21,* Right librigena, USNM 521905, external view. *22,* Right librigena, USNM 521906, external view, ×15. *23, 24,* Left librigena, USNM 521907, external and internal views. *25,* Right librigena, USNM 521908, external view. *26–29,* Hypostome, USNM 521909, dorsal, ventral, left lateral, and posterior views, ×20. *30, 31, 34, 35,* Pygidium, USNM 521910, dorsal, ventral, right lateral, and posterior views, ×20. *32, 36, 37, 45,* Pygidium, USNM 521911, dorsal, ventral, posterior, and right lateral views, ×20. *33, 38, 39,* Hypostome, USNM 521912, left lateral, ventral, and posterior views, ×20. *40, 41, 48,* Pygidium, USNM 521913, dorsal, right lateral, and posterior views, ×20. *42, 49, 50,* Pygidium, USNM 521914, dorsal, right lateral, and posterior views, ×20. *43, 44, 51,* Pygidium, USNM 521915, dorsal, right lateral, and posterior views, ×20. *46, 47, 59, 60,* Hypostome, USNM 521916, ventral, posterior, dorsal, and left lateral views, ×20. *52, 57, 64,* Pygidium, USNM 521917, right lateral, dorsal, and posterior views, ×20. *53, 58, 65,* Pygidium, USNM 521918, right lateral, dorsal, and posterior views, ×20. *54, 55, 61,* Pygidium, USNM 521919, dorsal, right lateral, and posterior views, ×20. *56, 62, 63,* Pygidium, USNM 521920, dorsal, right lateral, and posterior views, ×20.

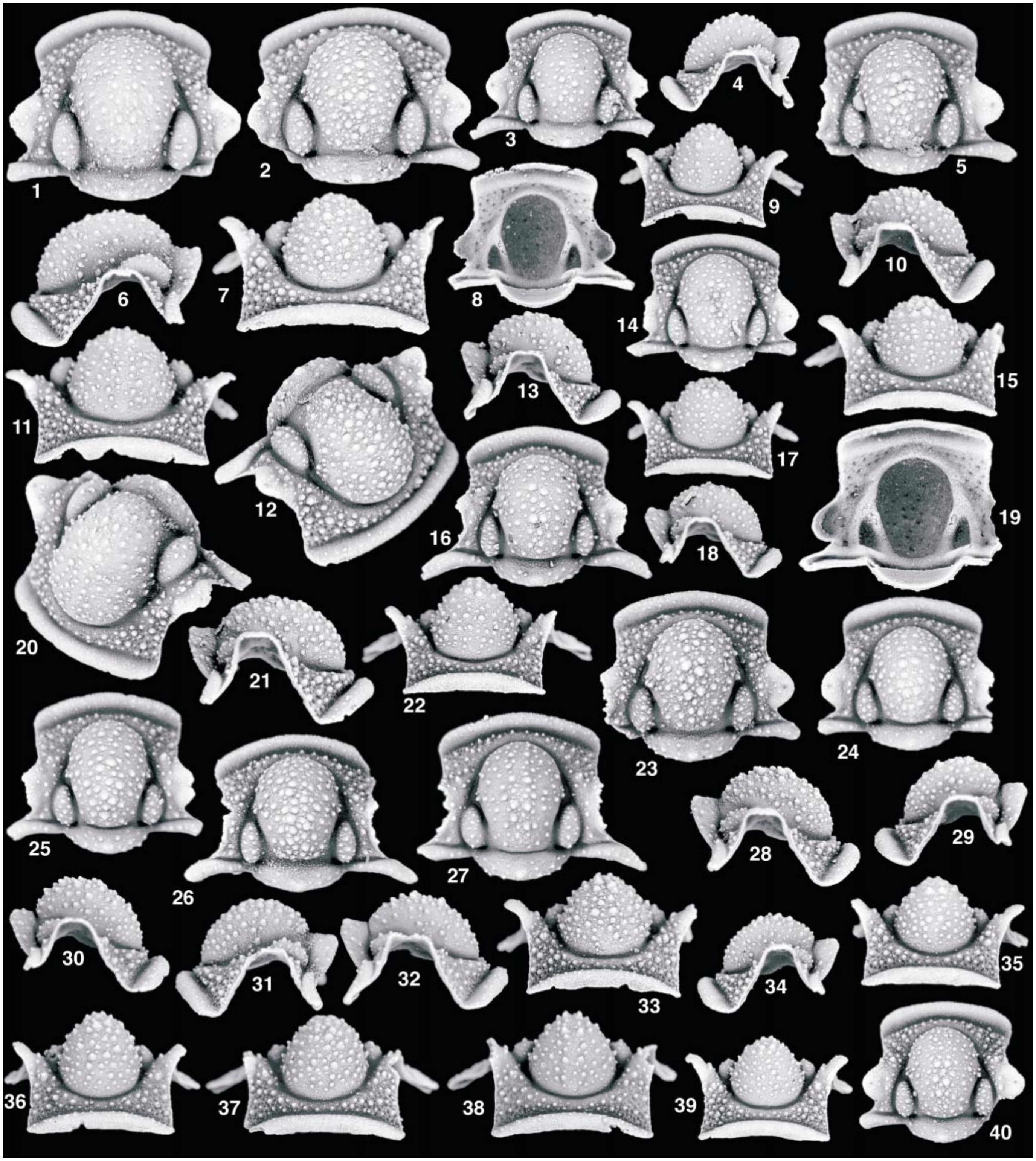

FIGURE 6—*Harpidella whittingtoni* n. sp., from the Oranda Formation, Locality 8. Magnifications are ×12 except where noted and all specimens are from collection 600k. *1, 6, 11, 20,* Cranidium, holotype, USNM 521921, dorsal, left lateral, anterior, and oblique views. *2, 7, 12, 21,* Cranidium, USNM 521922, dorsal, anterior, oblique, and right lateral views. *3, 4, 8, 9,* Cranidium, USNM 521923, dorsal, left lateral, ventral, and anterior views. *5, 10, 15, 19,* Cranidium, USNM 521924, dorsal, right lateral, anterior, and ventral views. *13, 16, 22,* Cranidium, USNM 521925, right lateral, dorsal, and anterior views. *14, 17, 18,* Cranidium, USNM 521926, dorsal, anterior, and right lateral views. *23, 28, 33,* Cranidium, USNM 521927, dorsal, right lateral, and anterior views. *24, 29, 35,* Cranidium, USNM 521928, dorsal, left lateral, and anterior views, ×15. *25, 30, 36,* Cranidium, USNM 521929, dorsal, right lateral, and anterior views, ×15. *26, 31, 37,* Cranidium, USNM 521930, dorsal, left lateral, and anterior views, ×15. *27, 32, 38,* Cranidium, USNM 521931, dorsal, right lateral, and anterior views, ×15. *34, 39, 40,* Cranidium, USNM 521932, left lateral, anterior, and dorsal views.

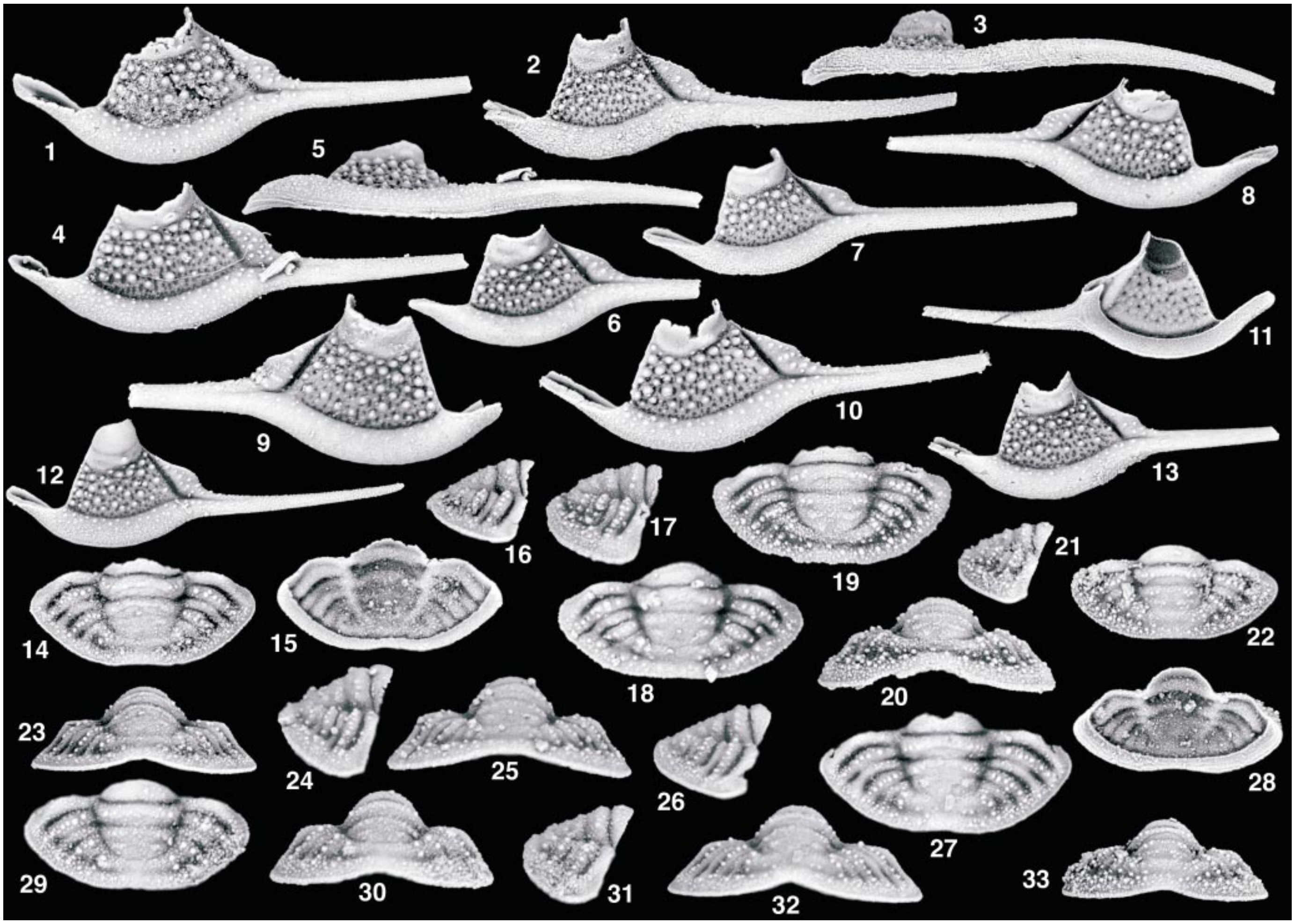

FIGURE 7—*Harpidella whittingtoni* n. sp., from the Oranda Formation, Locality 8. Magnifications are ×12 except where noted and all specimens are from collection 600k. *1,* Left librigena, USNM 521933, external view. *2, 3,* Left librigena, USNM 521934, external and ventrolateral views. *4, 5,* Left librigena, USNM 521935, external and ventrolateral views. *6,* Left librigena, USNM 521936, external view. *7,* Left librigena, USNM 521937, external view. *8,* Right librigena, USNM 521938, external view. *9,* Right librigena, USNM 521939, external view. *10,* Left librigena, USNM 521940, external view. *11, 13,* Left librigena, USNM 521941, internal and external views. *12,* Left librigena, USNM 521942, external view. *14–16, 23,* Pygidium, USNM 521943, dorsal, ventral, right lateral, and posterior views, ×15. *17, 19, 20,* Pygidium, USNM 521944, right lateral, dorsal, and posterior views, ×15. *18, 24, 25,* Pygidium, USNM 521945, dorsal, right lateral, and posterior views, ×20. *21, 22, 28, 33,* Pygidium, USNM 521946, right lateral, dorsal, ventral, and posterior views, ×15. *26, 27, 32,* Pygidium, USNM 521947, right lateral, dorsal, and posterior views, ×20. *29–31,* Pygidium, USNM 521948, dorsal, posterior, and right lateral views, ×20.

In librigenal features, there is variation in the density of tubercles on the field and in the prominence of the caecal pitting. The eye socle is commonly broad and ''figure-eight'' shaped, but in rare cases is narrower and compressed (Fig. 5.23).

In pygidial features, the expression of the third axial ring is variable, ranging from distinctly expressed and complete medially (Fig. 5.30, 5.42), to nearly so (Fig. 5.32), to expressed only laterally and effaced medially (Fig. 5.58), to nearly completely effaced (Fig. 5.56).

Unusual specimens.—One cranidium (Fig. 4.44) has S1 completely terminated anteriorly, about halfway down the length of L1, a nearly obsolete S0, with the median glabellar lobe more or less grading into L0, and a pair of strange ridges running forward obliquely across the posterior fixigenae to about the midlength of L1 (there is a fracture running obliquely forward from the right of the median occipital node which is a postmortem break in the specimen—all other features were apparently part of the animal while alive). In all other respects the specimen is a typical *H. triloba* cranidium. It is possible that the unusual morphology represents a healed injury which impacted the rear of the cranidium.

One pygidium (Fig. 5.32, 5.36) appears to have the first pygidial segment partially separated on the left side. The doublure is cut across ventrally opposite the first interpleural furrow. This is not a retained thoracic segment, as the pygidium is otherwise typically three-segmented. It appears that an incipient suture formed at the termination of the meraspid period as if the first pygidial segment were to be shed. This type of incipient suturing has also been documented in the Silurian *Aulacopleura konincki* (Barrande, 1846) by Hughes and Chapman (1995, fig. 1k, 1l).

Discussion.—*Harpidella triloba* differs from *H. whittingtoni* n. sp. and *H. evitti* n. sp. in the following features:

1. The anterior sections of the facial sutures range from slightly anteriorly divergent to anteriorly convergent, but most specimens are convergent. All known specimens of the younger species have anteriorly divergent facial sutures. Associated

with this difference, *H. triloba* is relatively narrower across the anterior border than the younger species.

2. The anterior border of *H. triloba* is smooth and entirely lacking in tubercles. That of *H. whittingtoni* ranges from nearly smooth (e.g., Fig. 6.3) to typically bearing multiple very fine scattered tubercles (e.g., Fig. 6.12, 6.27). That of *H. evitti* invariably bears fine tubercles.
3. The dorsal cranidial sculpture of *H. triloba* features tubercles with smaller average size and less dense spacing, particularly on the median glabellar lobe, than is typical for the younger species.
4. The palpebral lobe of *H. triloba* lacks tubercles in most specimens. Rarely, a single minute tubercle occurs (e.g., Fig. 4.21). Large cranidia of both *H. whittingtoni* and *H. evitti* invariably have several small tubercles on the palpebral lobe, adaxial to the pit.
5. The posterior margin of the posterior border of most specimens of *H. triloba* features a distinct break in course at the fulcrum in palpebral view (e.g., Fig. 4.1, 4.17, 4.30). This break in slope is much less evident on cranidia of *H. whittingtoni*, and absent entirely on those of *H. evitti*, in which the posterior margin describes a shallow, smooth arc.
6. The librigenal field of *H. triloba* is narrower than that of the younger species.
7. The eye socle of *H. triloba* never has a tubercle developed between the main lobes. There is a tubercle in this position in all specimens of *H. whittingtoni* and most of *H. evitti*.
8. The librigenal field of *H. triloba* has finer and less dense tubercles than that of *H. whittingtoni*, and similar-sized but slightly more dense tubercles than that of *H. evitti*.
9. The librigenal lateral border of *H. triloba* has a uniform granular sculpture, with at most a faint line of tubercles posteriorly carried forward from the genal spine (Fig. 5.22). That of *H. whittingtoni* and *H. evitti* typically has many small tubercles along its length, especially on the adaxial part along the lateral border furrow.
10. The eye socle of *H. triloba* features two large lobes, each with a distinct depression in their center, creating a ''figure of eight'' outline (e.g., Fig. 5.14, 5.17, 5.19, 5.20). The socle in *H. whittingtoni* is narrower, and the depression is much more linear. The socle in *H. evitti* is narrower still, with the posterior lobe merged into a single narrow band, and the anterior lobe ranging from retention of a narrow depression (e.g., Fig. 9.11) to nearly completely merged (e.g., Fig. 9.8).
11. The pygidium of *H. triloba* features a dorsal sculpture of mainly densely spaced granules on the anterior and posterior pleural bands, with transverse tubercle rows at most weakly expressed (e.g., Fig. 5.42), but absent in most specimens. All pygidia of *H. whittingtoni* and *H. evitti* bear well-developed transverse tubercle rows on the posterior pleural bands of the first two segments.

Few other Ordovician species of *Harpidella* are well known. The latest Ordovician species *H. kurrii* Adrain and Chatterton, 1995a, from the Mackenzie Mountains of northwestern Canada, differs from *H. triloba* in its anteriorly more divergent anterior facial sutures, less laterally protruded palpebral lobes, relatively smaller L1, and wider librigenal field almost entirely lacking in tubercles.

HARPIDELLA WHITTINGTONI new species
Figures 6, 7

Diagnosis.—Anterior facial sutures moderately anteriorly divergent; cranidial dorsal sculpture of dense tubercles, with largest tubercles along median part of glabella; librigena with field with minimum width on average 42.5% exsagittal length and 185% width of lateral border; librigenal field with prominent tubercles; pygidia with well-expressed rows of distinct, small tubercles on axial rings and posterior pleural bands.

Etymology.—After H.B. Whittington.

Types.—Holotype, cranidium, USNM 521921 (Fig. 6.1, 6.6, 6.11, 6.20), and paratypes USNM 521922–521948.

Occurrence.—All from the Oranda Formation, Locality 8.

Discussion.—*Harpidella whittingtoni* was compared with *H. triloba* above. It differs from *H. evitti* n. sp. in its somewhat more widely divergent anterior sections of the facial suture, more incised and shorter anterior border furrow, more robustly tuberculate frontal area, narrower librigenal field, much coarser tubercles on the librigenal field, retention of discernibly figure-eight-shaped eye socle in most specimens versus collapsed into band in many specimens, and pygidium with less prominent transverse rows of tubercles on the posterior pleural bands and axial rings, with tubercles smaller but slightly more numerous.

Although *H. whittingtoni* and *H. evitti* are more similar to each other on the basis of cranidial and librigenal shape than either is to *H. triloba* (Figs. 2, 3), *H. whittingtoni* retains a robust tuberculate sculpture on its librigenal field and cranidial frontal area that compares more closely with *H. triloba*. Its pygidial tuberculation, though less robust, is closer in its development to that of *H. evitti*. Among known species, the Virginia species appear to have sister-group relationships concordant with their stratigraphic order. That is, *H. whittingtoni* and *H. evitti* are sister species, and *H. triloba* is sister to this pair. Various characters show a stratigraphically consistent morphocline between the three species. These include divergence of the anterior sections of the facial suture that is narrowest in the stratigraphically lowest *H. triloba*, intermediate in *H. whittingtoni*, and greatest in *H. evitti*, increasing average width of the librigenal field, increasing compaction of the eye socle, decreasing prominence of the tuberculate sculpture on the librigenal field and frontal area, and increasing prominence of the tuberculate sculpture on the pygidium.

HARPIDELLA EVITTI new species
Figures 8, 9

Otarion sp. WHITTINGTON, 1941, p. 512, pl. 72, figs. 28–30, 35–37, 41.

Diagnosis.—Anterior facial sutures more anteriorly divergent

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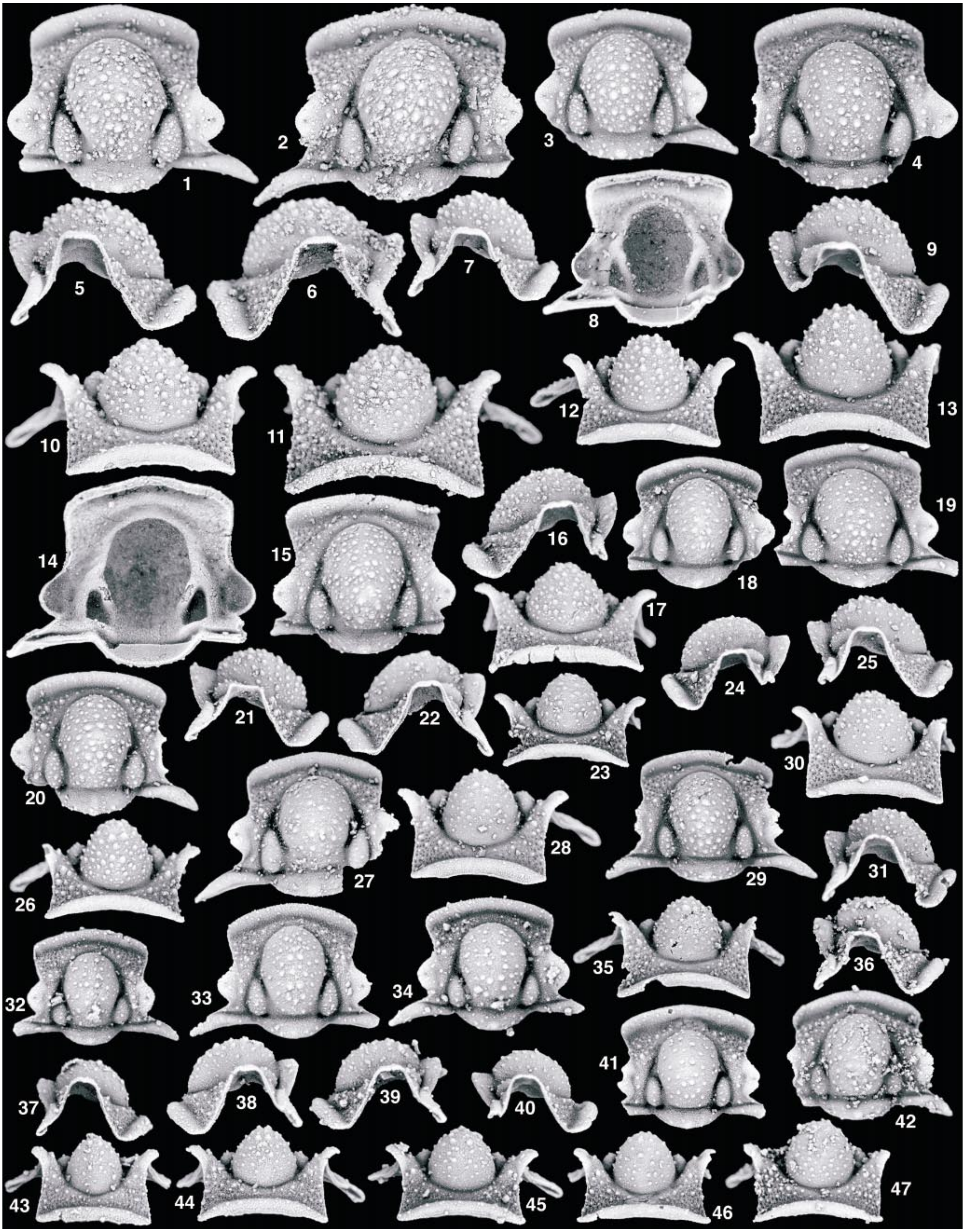
FIGURE 8—*Harpidella evitti* n. sp., from the Martinsburg Formation, Locality 10. Magnifications are ×12 and specimens are from collection Evitt 153a except where noted. *1, 5, 10, 14,* Cranidium, holotype, USNM 521949, dorsal, right lateral, anterior, and ventral views. *2, 6, 11,* Cranidium, USNM 521950, dorsal, left lateral, and anterior views. *3, 7, 8, 12,* Cranidium, USNM 521951, dorsal, right lateral, ventral, and anterior views. *4, 9, 13,* Cranidium, USNM 521952, dorsal, right lateral, and anterior views. *15–17,* Cranidium, USNM 521953, dorsal, left lateral, and anterior views. *18, 23, 24,* Cranidium, USNM 521954, dorsal, anterior, and left lateral views (153). *19, 25, 30,* Cranidium, USNM 521955, dorsal, right lateral, and anterior views. *20, 21, 26,* Cranidium, USNM 521956, dorsal, right lateral, and anterior views (153). *22, 27, 28,* Cranidium, USNM 521957, left lateral, dorsal, and anterior views. *29, 31, 35,* Cranidium, USNM 521958, dorsal, right lateral, and anterior views. *32, 37, 43,* Cranidium, USNM 521959, dorsal, right lateral, and anterior views, ×15. *33, 38, 44,* Cranidium, USNM 521960, dorsal, left lateral, and anterior views, ×15. *34, 39, 45,* Cranidium, USNM 521961, dorsal, left lateral, and anterior views, ×15. *36, 42, 47,* Cranidium, USNM 521962, right lateral, dorsal, and anterior views (153). *40, 41, 46,* Cranidium, USNM 521963, right lateral, dorsal, and anterior views 153).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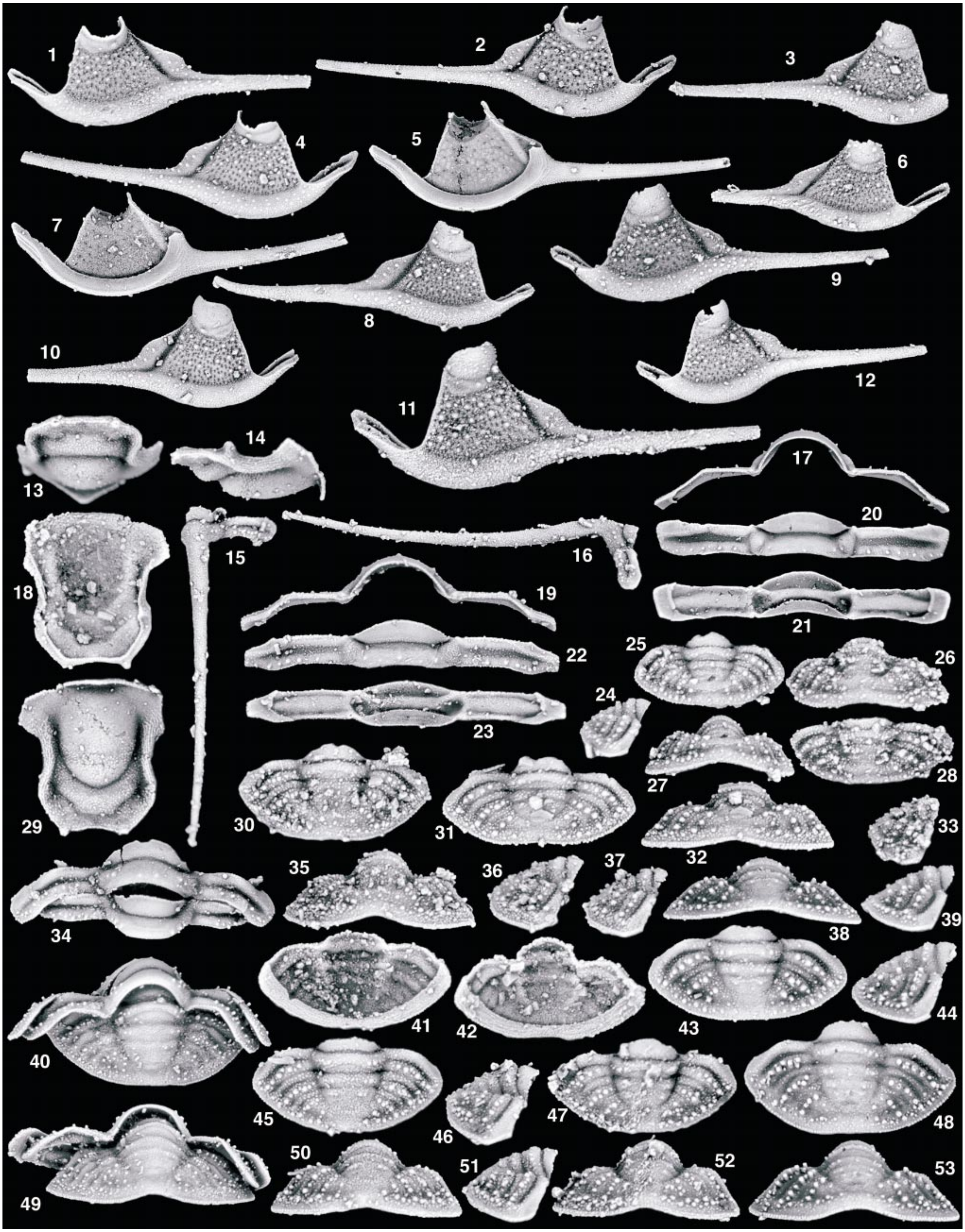
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than either *H. triloba* or *H. evitti*; tuberculate sculpture sparse on anterolateral part of frontal area; librigena with field with minimum width on average 46.8% exsagittal length and 215% width of lateral border; librigenal field sparsely tuberculate, tubercles small and more common on adaxial two-thirds of field; eye socle with posterior lobe compressed into single band on most specimens, anterior lobe compressed but usually retaining central depression; pygidia with rows of moderate to large tubercles on posterior pleural bands and more subdued tubercles on axial rings.

Etymology.—After W.R. Evitt III.

Types.—Holotype, cranidium, USNM 521949 (Fig. 8.1, 8.5, 8.10, 8.14), and paratypes USNM 521950–521986.

Occurrence.—All from the lower Martinsburg Formation, Locality 10.

Discussion.—*Harpidella evitti* was compared with both *H. triloba* and *H. whittingtoni* n. sp. above.

Subfamily Uncertain

STRASBURGASPIS new genus

Type species.—*Phaseolops conus* Hu, 1971, from the Edinburg Formation.

Other species.—*Otarion kielanae* Petrunina *in* Repina et al., 1975; *Strasburgaspis*? n. sp. A (see below); *Phaseolops* cf. *cona* of Fortey (1997).

Diagnosis.—Although the genus is not monotypic, only *Strasburgaspis cona* is known from more than a single cranidium; hence, the diagnosis corresponds to that species: Anterior sections of facial sutures moderately to strongly divergent; anterior border long and flat; palpebral lobes large; L1 relatively small and not protruding laterally, glabella thimble-shaped; librigena with eye socle lobes extremely large but subdued, covering most of area of field; thoracic axial seemingly absent; pygidium with strongly raised axis and prominent median axial tubercles/spines on first three axial rings.

Etymology.—After Strasburg County, Virginia, and the Greek noun *aspis*, a shield.

Discussion.—Hu (1971) misassociated cranidia of *Strasburgaspis* with librigenae and pygidia belonging to one or more tropidocoryphid proetoideans. He assigned his new species to *Phaseolops* Whittington, 1963, the type species of which, *P. sepositus*, was described by Whittington (1963) from the early Whiterockian of the Shallow Bay Formation, western Newfoundland, Canada. Opinions on the affinities of *Phaseolops* have varied. Most authors (e.g., Pillet, 1969; Owens, 1973; Lütke, 1980) have considered it a proetoidean. Fortey and Owens (1975, p. 230) regarded it as possibly a ''specialised, reef-dwelling offshoot'' of their ''Proetidae B'' group, which in essence is now the family Tropidocoryphidae Přibyl, 1946. Owens *in* Owens and Hammann (1990) assigned the genus to his new family Rorringtoniidae. Adrain and Fortey (1997), however, argued that it represented a basal tropidocoryphid group. In any event, no subsequent authors have accepted Hu's assignment of *conus* to *Phaseolops*, and the species has been nearly universally regarded as an aulacopleurid (e.g., Fortey and Owens, 1975; Přibyl and Vaněk, 1981; Adrain and Chatterton, 1995a; Adrain and Fortey, 1997). An exception is Fortey (1997, p. 425), who assigned his *Phaseolops* cf. *conus* to Rorringtoniidae but did not explain the basis for this decision (''Here I place the species in Rorringtoniidae, and simply compare it with Hu's species.'').

Strasburgaspis (Figs. 10, 11, 13) is interpreted here as an aulacopleurid, but its phylogenetic relationships are not obvious. The hypostome differs from the generalized aulacopleurid type represented by the species of *Harpidella* described herein, and known in most other aulacopleurid genera (e.g., *Aulacopleura*: Hughes and Chapman, 1995, fig. 1g, 1h; *Cyphaspis*: Adrain and Chatterton, 1996, figs. 1.26, 1.27, 1.31, 2.12, 5.12; *Maurotarion*: Adrain and Chatterton, 1995a, fig. 9.22, 9.23, 9.32; *Otarion*: Adrain and Chatterton, 1994, figs. 6.18, 6. 19, 7.6, 9.8, 9.9). In particular, it is narrower relative to its length, has less laterally protruding anterior wings, has more anteriorly set shoulders, and has posterior spines that are flat and triangular versus narrow and tubelike. In cephalic features, *S. cona* is broadly similar to the upper Wenlock or lower Ludlow *Maurotarion instita* (Whittington and Campbell, 1967) from Maine, but this is likely convergence due to similarly broad cephalic borders. *Maurotarion instita* has the *Maurotarion* condition of a very subdued eye socle, but a normally sized anterior lobe is visible in Whittington and Campbell's photographs (1967, pl. 6, figs. 4, 5), very unlike the extremely broad lobes of *Strasburgaspis*. Although Whittington and Campbell (1967) were unable to definitively assign pygidia to the aulacopleurid species in their collections, none of their illustrated specimens has prominent median axial tubercles like those of *Strasburgaspis*. The librigenal morphology of *Strasburgaspis* is also different from that of most other aulacopleurids. The posterior and lateral borders run smoothly into a flattened genal spine, such that the lateral margin of the librigena describes a smooth and unbroken arc along the lateral border and down the spine. Similarly, although some specimens show a faint angulation (e.g., Fig. 11.25), in most cases the margin of posterior border also grades gently into that of the adaxial edge of the genal spine. In contrast, the common condition in aulacopleurids is a tubelike, not flattened, genal spine, the base of which forms a distinct angle with both the margins of the lateral and posterior borders. Exceptions to this are restricted to what seems clearly to be derived inflation of the lateral borders in taxa such as the Devonian Malvinokaffric *Maurotarion* group (see Adrain and Edgecombe, 1996). Older species of *Maurotarion* show the conventional tubelike aulacopleurid morphology.

An alternative hypothesis is that *Strasburgaspis* represents a

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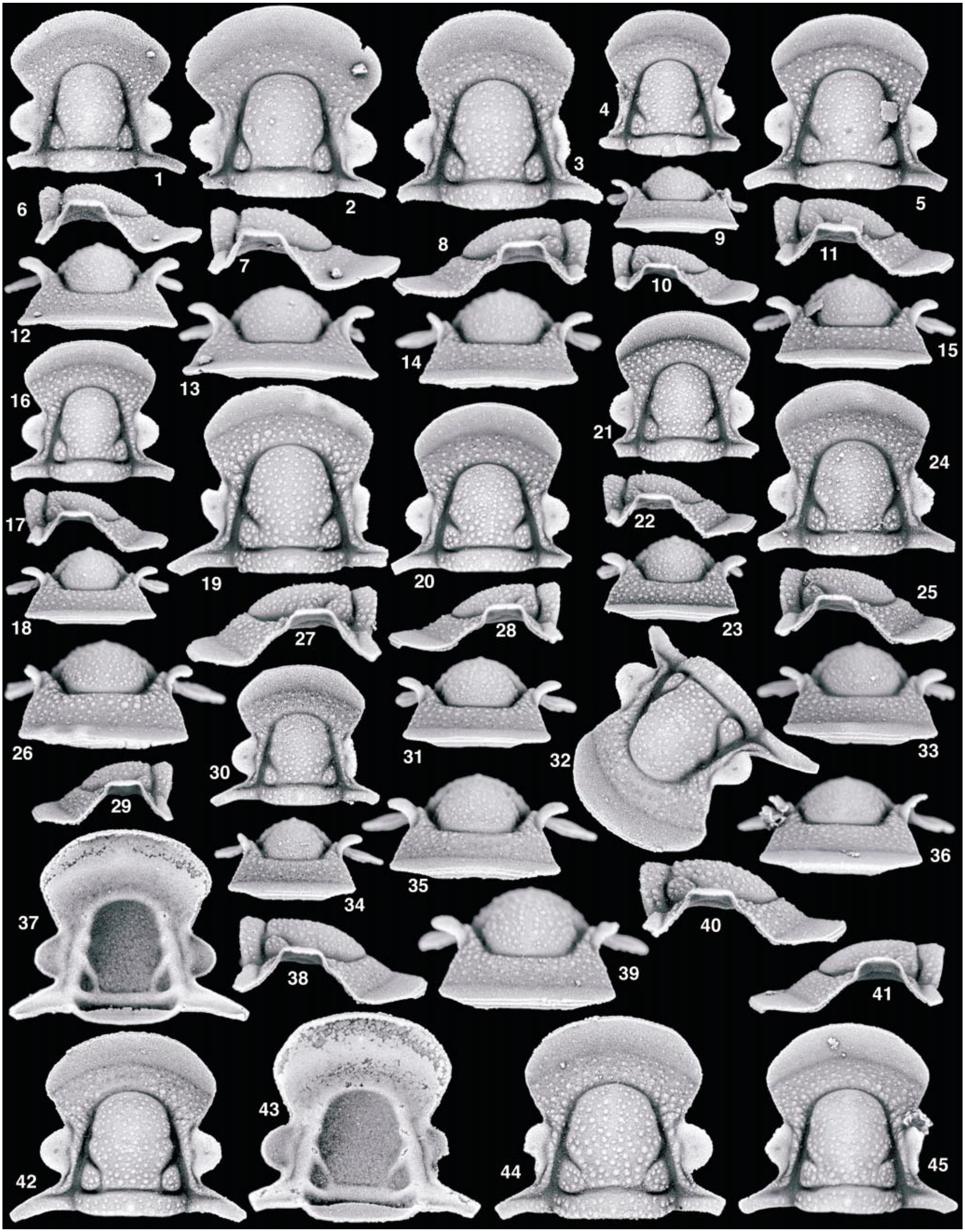
FIGURE 9—*Harpidella evitti* n. sp., from the Martinsburg Formation, Locality 10. Specimens are from collection Evitt 153a except where noted. *1*, Left librigena, USNM 521964, external view, ×15. *2, 5*, Right librigena, USNM 521965, external and internal views, ×12. *3*, Right librigena, USNM 521966, external view, ×15. *4, 7*, Right librigena, USNM 521967, external and internal views, ×12. *6*, Right librigena, USNM 521968, external view, ×15. *8*, Right librigena, USNM 521969, external view, ×15. *9*, Left librigena, USNM 521970, external view, ×15. *10*, Right librigena, USNM 521971, external view, ×12. *11*, Left librigena, USNM 521972, external view, ×15. *12*, Left librigena, USNM 521973, external view, ×12. *13, 14, 18, 29*, Hypostome, USNM 521974, posterior, right lateral, dorsal, and ventral views, ×20. *15, 16*, Thoracic segment, USNM 521975 dorsal and right lateral views, ×15. *17, 20, 21*, Thoracic segment, USNM 521976, anterior, dorsal, and ventral views, ×12. *19, 22, 23*, Thoracic segment, USNM 521977, anterior, dorsal, and ventral views, ×15. *24, 25, 27*, Pygidium, USNM 521978, right lateral, dorsal, and posterior views, ×20. *26, 28, 33*, Pygidium, USNM 521979, posterior, dorsal, and right lateral views, ×20. *30, 35, 36*, Pygidium, USNM 521980, dorsal, posterior, and right lateral views, ×20. *31, 32, 37*, Pygidium, USNM 521981, dorsal, posterior, and right lateral views, ×20. *34, 40, 49*, Pygidium and thoracic segments, USNM 521982, dorsal thoracic, dorsal pygidial, and posterior views, ×15 (153). *38, 39, 43*, Pygidium, USNM 521983, posterior, right lateral, and dorsal views, ×20 (153). *41, 45, 50, 51*, Pygidium, USNM 521984, ventral, dorsal, posterior, and right lateral views, ×20. *42, 46, 47, 52*, Pygidium, USNM 521985, ventral, right lateral, dorsal, and posterior views, ×20. *44, 48, 53*, Pygidium, USNM 521986, right lateral, dorsal, and posterior views, ×20 (153).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plesiomorphic member of Brachymetopidae Prantl and Přibyl, 1951. The sister group and origins of brachymetopids are unknown, though many authors (e.g., Campbell, 1977) have considered them closely related to aulacopleurids and they are clearly ingroup Aulacopleuroidea. Adrain and Kloc (1997, p. 707–709) reviewed the diverse and conflicting opinions on the content and affinity of the family. Features potentially linking *Strasburgaspis* with Brachymetopidae include the general cranidial dimensions. In particular, specimens of *S. cona* at the extreme range of variation in the divergence of the anterior sections of the facial suture (e.g., Fig. 10.2) are a very close match for the anterior cranidial morphology of such Silurian species as *Radnoria triquetra* Owens and Thomas, 1975. In addition to the wide anterior region, such specimens have a very effaced anterior border furrow and long anterior border. All specimens of *S. cona* have a thimble-shaped glabella with small L1 which does not protrude laterally, very similar again to *R. triquetra*. The cranidial sculpture of *R. triquetra* is poorly preserved on the available specimens, but the scattering of subdued tubercles on the preglabellar field and frontal area of *S. cona* is quite similar to that observed in *R. syrphetodes* Owens and Thomas, 1975 (pl. 95, fig. 1a, 1b). The librigenal doublure and lateral border of *S. cona* are broad for an aulacopleurid, and flattened as in brachymetopids, as opposed to the inflated and nearly tubular cross section typical of aulacopleurids. The lateral librigenal margin describes a smooth curve, as in brachymetopids but as noted above dissimilar to most aulacopleurids. The elongate hypostome of *S. cona* is unlike that of most aulacopleurids (see above), but very similar to a specimen illustrated by Hammann (1992, pl. 20, fig. 9) which is probably that of *Radnoria carlsi* Owens and Hammann, 1990 (compare to Fig. 11.5 herein). *Strasburgaspis cona* lacks a thoracic axial spine (based on the block collected by M. Kay, in which the species is very common but which did not yield any segments with an axial spine). This is consistent with brachymetopids, which universally lack such a spine, but many aulacopleurids also lack one. Finally, the pygidium of *S. cona* has median axial tubercles or short spines. When not effaced, the axial rings of all brachymetopid pygidia bear median tubercles (e.g., *Radnoria triquetra* Owens and Thomas, 1975, pl. 96, fig. 5a). In contrast, median tubercles are very rare in aulacopleurids, which tend to have either transverse tubercle rows with no obviously prominent median tubercle (e.g., *Harpidella* herein; *Otarion* in Adrain and Chatterton, 1994; *Cyphaspis* in Adrain and Chatterton, 1996), or else to be dorsally effaced, but with no sign of a median tubercle earlier in ontogeny (e.g., *Maurotarion* in Adrain and Chatterton, 1995a). Median tubercles do, however, occur rarely in aulacopleurid thoracopygidia, for example in Devonian species of *Maurotarion* such as *M. struszi* (Chatterton, 1971; see the transitory pygidia illustrated by Adrain and Chatterton, 1995a, fig. 10.8, 10.18, 10.19) and *M. isaacsoni* Adrain and Edgecombe, 1996.

Though known only from a single cranidium, the morphology of *Strasburgaspis* n. sp. A (Fig. 13) is even more strikingly *Radnoria*-like. It is effaced to a similar degree as most species of *Radnoria*, has a very elongate anterior border, and the glabella is more elongate and more nearly parallel-sided than that of *S. cona*. Nevertheless, the specimen differs only in effacement and minor dimensions from cranidia of *S. cona*, and seems almost certainly related with its nearly identical palpebral lobes, palpebral furrow, glabellar furrows, and overall shape.

The most obvious problem with the hypothesis that *Strasburgaspis* is a plesiomorphic brachymetopid is radical differences in pygidial morphology. All known brachymetopids have a large pygidium, approaching the isopygous condition, with typically more than 10 segments. That of *S. cona* is small and micropygous, with only four segments, and in almost all respects is typically aulacopleurid. It is unfortunate that *S.* n. sp. A is known from a single specimen; if its pygidium was found to be in any way transitional in morphology between that of *S. cona* and those of *Radnoria*, one would not hesitate to infer that *S.* n. sp. A and *S. cona* are successive sister taxa to *Radnoria*. In the present state of knowledge, *Strasburgaspis* is assigned to Aulacopleuridae.

STRASBURGASPIS CONA (Hu, 1971)
Figures 10, 11

Phaseolops conus HU, 1971, p. 111, pl. 23, figs. 1–9?, 10–21, 22? (*non* figs. 23–31 = Proetoidea), text-fig. 53a–d?, e–g, j (*non* text-fig. 53 i, h, k, l–Proetoidea).
Phaseolaspis canus HU; HU, 1974b, p. 353 [misspelling of *Phaseolops conus*].
Phaseolupis canus HU; HU, 1974b, p. 354 [misspelling of *Phaseolops conus*].
Mesotaphraspis acris HU, 1976, *partim*, p. 251, pl. 27, figs. 34–36 [*only*], text-fig. 2o, p.
Harpidella (*Harpidella*?) *conus* (HU, 1971); PŘIBYL AND VANĚK, 1981, p. 170.
Phaseolops? *conus* HU, 1971; FORTEY, 1997, p. 425.

Diagnosis.—See genus diagnosis.

Description.—Cranidium with width across anterior sections of facial suture 90.2% (79.3–103.1, 14 specimens) sagittal length; length from rear of L0 to front of glabella 66.2% (63.8–68.6, 14 specimens) sagittal length; width across midlength of palpebral lobes 108.0% (95.7–116.1, 12 specimens) width across anterior sections of facial suture; glabella (excluding L0) with maximum width across L1 104.5% (100.5–109.5, 14 specimens) sagittal length; anterior border with anterior margin describing moderate (Fig. 10.16) to strong (Fig. 10.2) anterior arc, in most specimens somewhat less arcuate medially, long and flat, ranging from almost lacking dorsal sculpture (Fig. 10.1, 10.2) through extremely subdued and faint small tubercles (Fig. 10.3) to clear but sparse scattering of small tubercles over most of surface (Fig. 10.19, 10.20), anterior rim with single raised dorsal line immediately behind and subparallel with margin; anterior border furrow variable in expression, ranging from shallow but fairly short, inscribed line (Fig. 10.21) to almost effaced (Fig. 10.2); preglabellar field subequal to slightly greater in length than border, field and frontal area with sculpture of very fine caecal pits and fairly dense

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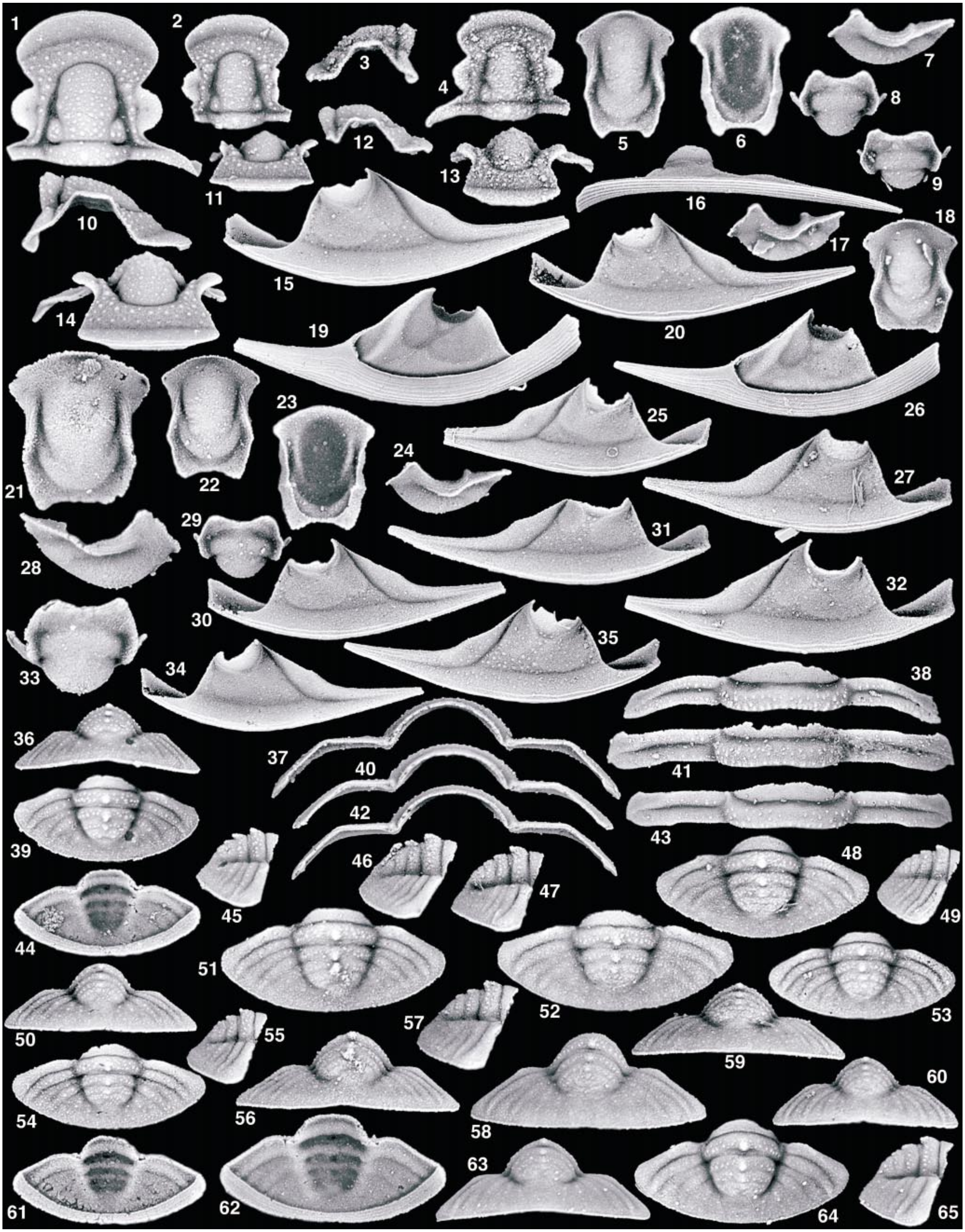
FIGURE *10*—*Strasburgaspis cona* (Hu, 1971), from the Edinburg Formation, Locality 3. Magnifications are ×15. *1, 6, 12,* Cranidium, USNM 521987, dorsal, right lateral, and anterior views (600o). *2, 7, 13,* Cranidium, USNM 521988, dorsal, right lateral, and anterior views (600o). *3, 8, 14,* Cranidium, USNM 521989, dorsal, left lateral, and anterior views (600o). *4, 9, 10,* Cranidium, USNM 521990, dorsal, anterior, and right lateral views (600p). *5, 11, 15,* Cranidium, USNM 521991, dorsal, right lateral, and anterior views (600p). *16–18,* Cranidium, USNM 521992, dorsal, right lateral, and anterior views (600o). *19, 26, 27,* Cranidium, USNM 521993, dorsal, anterior, and left lateral views (W6). *20, 28, 31,* Cranidium, USNM 521994, dorsal, left lateral, and anterior views (600p). *21–23,* Cranidium, USNM 521995, dorsal, right lateral, and anterior views (600o). *24, 25, 33,* Cranidium, USNM 521996, dorsal, right lateral, and anterior views (W7). *29, 30, 34,* Cranidium, USNM 521997, left lateral, dorsal, and anterior views (600p). *32, 35, 37, 38, 42,* Cranidium, USNM 521998, oblique, anterior, ventral, right lateral, and dorsal views (W7). *36, 41, 45,* Cranidium, USNM 521999, anterior, left lateral, and dorsal views (W7). *39, 40, 43, 44,* Cranidium, USNM 522000, anterior, right lateral, ventral, and dorsal views (600p).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small to medium-sized tubercles; anterior sections of facial suture extremely variable in degree of anterior divergence, with end-members represented by Figure 10.2 and 10.3; interocular fixigena very narrow, with sculpture of single row of densely spaced tubercles; palpebral furrow variable in depth, but firmly impressed in most specimens (Fig. 10.16, 10.19, 10.20), shallowed at midlength in some (Fig. 10.2) and very shallow to nearly effaced in some specimens (Fig. 10.1); palpebral lobe large and subsemicircular, held nearly in horizontal plane in anterior view, lacking sculpture, with very prominent median pit; glabella thimble-shaped in outline, with L1 not markedly protruded laterally from the main outline of the glabella; entire dorsal glabellar surface with sculpture of fairly densely spaced medium tubercles, usually more dense than on frontal area and preglabellar field; L1 quite small and roughly teardrop- shaped; S1 contacting axial furrow opposite midlength of palpebral lobe, deep abaxially, narrowing and shallowing adaxially, ranging from complete and in contact with S0 (Fig. 10.2) to terminated half to two-thirds distance posteriorly, with L1 posteromedially confluent with main part of glabella (Fig. 10.4, 10.45); S2 visible as distinct but very shallow notch; S3 visible in most specimens as very faint indentation of glabellar margin; glabella with weak dorsal inflation, entire cranidium low in sagittal profile; preglabellar furrow anteriorly arcuate; junction between axial and preglabellar furrow with quite distinct break in course in most specimens, but more or less a confluent arc in some; axial furrows straight, evenly anteriorly convergent, narrowing anteriorly; S0 with very slight anterior curvature, short and deeply incised over entire course, very slightly longer medially in some specimens; L0 with very slight W-shape, quite long both sagittally and exsagittally, shorter but still substantial behind L1, with sculpture of densely scattered medium tubercles similar to that of glabella, prominent median tubercle set slightly behind midlength of L0; posterior border furrow similar in length and depth adaxially to S0, tapering out rapidly to contact with posterior facial suture; posterior border forming a very short strip, turned slightly posteriorly, with sculpture of one or two subtransverse rows of fine tubercles; doublure extremely short beneath posterior border, forming standard articulating surface with parallel raised lines beneath L0; small apodemal swellings present ventrally at junctions of S1 and S2 and axial furrows; very prominent fossular pit located just behind and slightly lateral to junction of axial and preglabellar furrows.

Librigena with width of field at midlength of eye 26.5% (21.8–32.0, based on nine illustrated specimens) exsagittal length; eye relatively narrow and long; eye socle with single very narrow band beneath eye, separated from eye by very narrow shallow furrow, band interrupted and effaced at midlength of eye, anterior and posterior lobes of eye socle very large, spread over most of the area of the field, flat and uninflated, anterior lobe with lateral margin nearly reaching lateral border and anterior margin nearly reaching anterior facial suture, about double the area of posterior lobe, posterior lobe contacting posterior border furrow on about adaxial one half of that furrow's course, anterior and posterior lobes typically merged at contact (Fig. 11.25, 11.27, 11.30, 11.34) but clearly separate in some specimens (Fig. 11.20, 11.31); anterior facial suture set steeply, posterior suture with much shallower inclination, field with sculpture of very fine caecal pits and small to moderate, subdued and scattered tubercles; tubercles visible but even more subdued on those parts of of the field occupied by the eye socle lobes; lateral border furrow shallow but narrow and distinct, in some specimens with slightly deeper caecal pitting aligned with it (Fig. 11.15, 11.27, 11.31), with very gentle lateral convexity; posterior border furrow considerably deeper than lateral border furrow, describing shallow ''S'' shape; lateral and posterior border furrows meeting posteriorly to form single furrow which runs posteriorly along dorsal aspect of genal spine; posterior border slightly shorter (exsag.) than lateral border is wide (tr.), with sculpture of faint tubercles mostly near genal spine, flattened in section; lateral border nearly flat, with faint tubercles on adaxial part and one or two prominent raised lines near lateral margin, linear in some specimens (Fig. 11.27, 11.30), slightly irregular in course in others (Fig. 11.15, 11.32); lateral aspect of lateral border with sharp break in slope to dorsal aspect, forming lateral margin, with closely spaced subparallel raised lines (Fig. 11.16); anterior projection about 80% exsagittal length of field; genal spine flattened in section, tapering rapidly to a point and more subtriangular than tubelike, with dorsal sculpture of raised lines and furrow expressed nearly to tip, shallower distally; doublure quite broad, broader anteriorly on anterior projection, doublure and ventral aspect of genal spine with strong sculpture of raised subparallel lines.

Rostral plate not identified.

Hypostome with maximum width across anterior wings 84.2% (78.3–87.8, measurement based on three most complete illustrated specimens) sagittal length; anterior margin with strong anterior convexity, flared ventrally, forming slight furrow with middle body medially; anterior wings triangular, with blunt lateral terminations, wing process forming very fine pit in wing and small protrusion dorsally; lateral border flat anteriorly, developed into robust ridge near shoulder, with fine obliquely set raised lines anteriorly; shoulder forming very sharp and distinct lateral angle, lateral border ridge terminates at shoulder, with border flattened posteriorly; broad posterior lateral border with ventral sculpture of granules confluent with short posterior border; pair of flattened, triangular posterior spines confluent with surface of lateral/posterior border; posterior margin medially transverse; anterior part

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FIGURE *11*—*Strasburgaspis cona* (Hu, 1971), from the Edinburg Formation, Locality 3. Magnifications are ×15 except where noted. *1, 10, 14,* Cranidium, USNM 522001, dorsal, right lateral, and anterior views, ×20 (W7). *2, 11, 12,* Cranidium, USNM 522002, dorsal, anterior, and right lateral views, ×20 (W7). *3, 4, 13,* Cranidium, USNM 522003, left lateral, dorsal, and anterior views, ×20 (600p). *5–8,* Hypostome, USNM 522004, ventral, dorsal, left lateral, and posterior views, ×20 (Evitt 70). *9, 17, 18,* Hypostome, USNM 522005, posterior, left lateral, and ventral views, ×20 (Evitt 70). *15, 16, 19,* Left librigena, USNM 522006, external, ventrolateral, and internal views (W6). *20, 26,* Left librigena, USNM 522007, external and internal views (600p). *21, 28, 33,* Hypostome, USNM 522008, ventral, right lateral, and posterior views, ×20 (Evitt 70). *22–24, 29,* Hypostome, USNM 522009, ventral, dorsal, left lateral, and posterior views, ×20 (Evitt 70). *25,* Right librigena, USNM 522010, external view (600p). *27,* Right librigena, USNM 522011, external view (W7). *30,* Left librigena, USNM 522012, external view (Evitt 70). *31,* Right librigena, USNM 522013, external view (Evitt 70). *32,* Right librigena, USNM 522014, external view (Evitt 70). *34,* Left librigena, USNM 522015, external view (Evitt 70). *35,* Right librigena, USNM 522106, external view (Evitt 70). *36, 39, 44, 45,* Pygidium, USNM 522017, posterior, dorsal, ventral, and right lateral view, ×20 (600o). *37, 41,* Thoracic segment, USNM 522018, anterior and dorsal views (M. Kay Block). *38, 40,* Thoracic segment, USNM 522019, dorsal and anterior views (M. Kay Block). *42, 43,* Thoracic segment, USNM 522020, anterior and dorsal views (M. Kay Block). *46, 51, 56, 62,* Pygidium, USNM 522021, right lateral, dorsal, posterior, and ventral views, ×20 (600o). *47, 48, 59,* Pygidium, USNM 522022, right lateral, dorsal, and posterior views, ×20 (W6). *49, 53, 60,* Pygidium, USNM 522023, right lateral, dorsal, and posterior views, ×20 (600p). *50, 54, 55, 61,* Pygidium, USNM 522024, posterior, dorsal, right lateral, and ventral views, ×20 (600p). *52, 57, 58,* Pygidium, USNM 522025, dorsal, right lateral, and posterior views, ×20 (W6). *63–65,* Pygidium, USNM 522026, posterior, dorsal, and right lateral views, ×20 (W7).

of lateral border furrow deep, slightly posteriorly convergent, runs without break into middle furrow; middle furrow U-shaped, effaced (Fig. 11.5, 11.21) or complete but shallow (Fig. 11.18, 11.22) medially; anterior lobe of middle body with strong ventral inflation, forming ventral ''hump'' in some specimens (Fig. 11.17, 11.28), faint maculae present on posterior part in some specimens (Fig. 11.18, 11.22), but not obvious in others (Fig. 11.5, 11.21); posterior lobe of middle body short and U-shaped; middle body lacking ventral sculpture except for very fine granules; lateral aspect of anterior part of lateral border with subparallel raised lines; small posterior wing beneath shoulder; doublure broadest posteriorly, narrow behind anterior wing.

Thoracic segments with axis about 40% total width of segment; pleural region proximal to fulcrum slightly wider than that distal to fulcrum; articulating half-ring broadly crescent-shaped, lacking sculpture; ring furrow with very shallow ''W'' shape, deep and similarly incised along its width; ring also describing shallow ''W,'' with sculpture of fairly densely scattered medium to fine tubercles; axial furrow shallow and with slight ''V'' shape (directed laterally); pleural furrow deeply inscribed, transverse to fulcrum, where it is turned posteriorly to a greater or lesser extent depending on the position of the segment in the thorax; anterior and posterior pleural bands of similar exsagittal length, each typically with single very faint transverse row of fine tubercles; anterior band terminates in forward-facing, triangular, articulating facet, posterior part of which forms very small, triangular spine; posterior band with sharp but small posterior deflection at fulcrum, terminating along facet.

Pygidium: Measurements made on the seven illustrated specimens. Sagittal length (including articulating half-ring) 45.7% (42.7–48.1) maximum width; anterior width of axis 36.1% (32.9–38.1) maximum width; articulating half-ring crescent-shaped, lacking sculpture; ring furrow slightly bowed posteriorly; proximal pleural region narrow, fulcrum close to axis; axial furrows moderately inscribed and narrow, typically entirely effaced at posteromedian junction (Fig. 11.51, 11.52), rear of axis either somewhat gradational with posterior area or in some specimens quite well defined as break in slope (Fig. 11.53); four axial rings, fourth very subdued, short, and nearly obsolete, rings with sculpture of fine tubercles; first three rings with prominent median tubercle, tubercle faintly developed on fourth ring in some specimens (Fig. 11.60, 11.63); very short pseudoarticulating half-ring present in front of second ring; ring furrows shallow, with slightly irregular versus perfectly transverse course, deepest laterally at contact with axial furrow; axis with moderate inflation, rear of axis with distinctly different slope than posterior area in sagittal view; pleural furrow of first segment well impressed, those of posterior segments increasingly effaced, but faint third furrow discernible in almost all specimens; first interpleural furrow impressed but shallower than first pleural furrow, second interpleural furrow visible in all specimens but substantially effaced, third furrow extremely weak and almost totally effaced; anterior and posterior pleural bands of similar exsagittal length; tuberculate sculpture either absent (Fig. 11.52), restricted to faint transverse row on posterior pleural band (Fig. 11.53, 11.64) or faint rows on both anterior and posterior bands (Fig. 11.39, 11.54); border weakly developed, pleural furrow cuts nearly across border in many specimens (Fig. 11.54), distal part of posterior pleural band turned posteriorly and slightly swollen, also cutting across border; swollen distal part of posterior band usually visible on second (Fig. 11.51, 11.52) and rarely third (Fig. 11.53) segments; first and usually second interpleural furrows cut across border to margin in all specimens; posterior margin with weak median flexure in posterior view; doublure short medially, lengthening slightly abaxially, with very fine raised lines subparallel with margin.

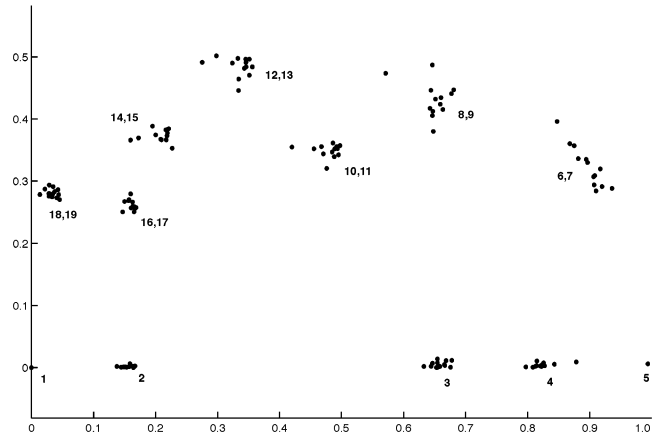

FIGURE *12*—Cranidial landmark data for *Strasburgaspis cona*, shown after reflection across axis of symmetry, in Bookstein Coordinates with baseline between landmarks 1 and 5 (i.e., rear and front of sagittal axis of cranidium; anterior to the right). Landmark numbers correspond to Figure 1.3.

Material examined.—The holotype (Hu, 1971, p. 112, pl. 23, fig. 21) is UCM 38742.

Occurrence.—From the Edinburg Formation, ''1.5 mile, southeastern Strasburg Junction [*sic*]''; figured material USNM 521987–522026 from Locality 3.

Intraspecific variation.—There is an obvious and unusually large (for an aulacopleurid) range of variation in the anterior region of the cranidium of *Strasburgaspis cona*. Typical specimens have moderately divergent anterior sections of the facial sutures (Fig. 10.5, 10.19, 10.20, 10.21, 10.24), but some (Fig. 10.1, 10.2) are considerably more divergent than the norm and others (Fig. 10.3) slightly less so. In order to document this variation, morphometric analysis of the cranidium was carried out using a subset of the landmarks employed in the *Harpidella* study. Five sagittal and 14 paired landmarks were located (Fig. 1.3), and 13 cranidia were digitized. The landmarks are shown as Bookstein Coordinates (registered to a baseline from landmarks 1 to 5—i.e., the sagittal midlength of the cranidium) in Figure 12. Note the extreme spread of landmarks 8/9 (the intersection of the anterior border furrow with the anterior section of the facial suture) and 6/7 (the intersection of the connective sutures with the margin of the anterior border).

Further variation is in the distinctness of the anterior border furrow. It more typically has a sharp posterior edge, forming a distinct line abruptly terminating the frontal area and preglabellar field (Figs. 10.5, 10.16, 10.19, 10.20, 10.21, 10.24, 10.30, 10.42, 10.45, 11.1). In some specimens, however, it is very shallow and the contact between the frontal area and anterior border is almost gradational (Fig. 10.11–10.3, 10.44). This variation does not seem to be tied to variation in the anterior width of the cranidium. There is variation in the depth and expression of the palpebral furrow. The furrow is typically firmly impressed (Fig. 10.16, 10.19), but in some specimens is partially (Fig. 10.2) or largely (Fig. 10.1) effaced. Finally, there is variation in the course of S1 and the degree of isolation of L1 from the median glabellar lobe. In some specimens S1 is clearly complete, though shallower posteriorly, and completely isolates L1 (Fig. 10.2). The typical condition is with S1 greatly shallowed but distinguishable posteriorly (Fig. 10.3, 10.24). On some specimens, S1 is clearly obsolete posteriorly, and the rear of L1 is confluent with the median lobe, with uninterrupted tubercles (Fig. 10.19, 10.20).

Discussion.—The only other named species, *S. kielanae* (Petrunina *in* Repina et al., 1975), is known from a single incomplete

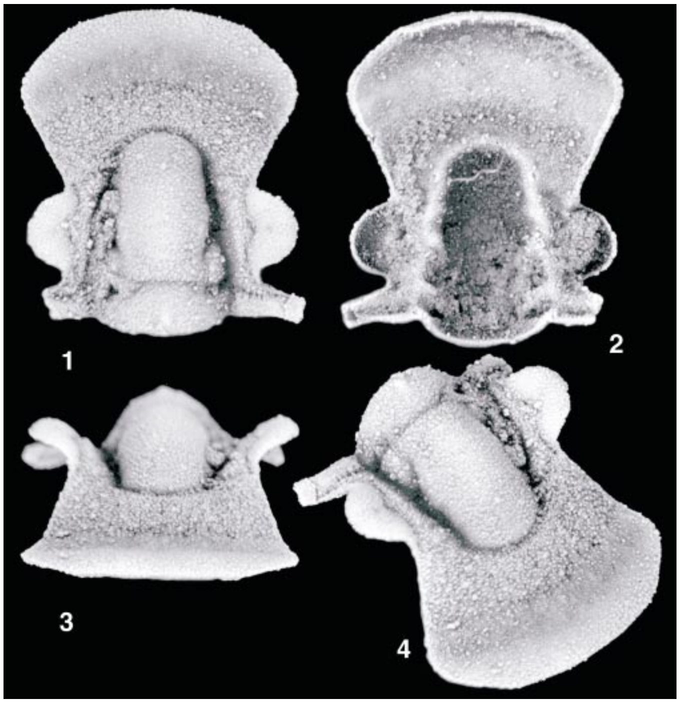

FIGURE 13—*Strasburgaspis* n. sp. A, from the Edinburg Formation, Locality 6. *1–4*, Cranidium, USNM 522027, dorsal, anterior, ventral, and oblique views, ×20 (600a).

cranidium from the Ashgill of Turkestan. Characters supporting its close relationship with *S. cona* include the long and flat anterior border, scattering of subdued tubercles on the frontal area, similarly thimble-shaped glabella with triangular S1 and clearly notched S2, and similar palpebral furrow. It differs in that the anterior border is apparently somewhat shorter than that of *S. cona*, the glabella is slightly more elongate, and L1 is relatively larger.

Vaněk and Vokáč (1997) referred a specimen from the Ashgill Králův Dvůr Formation of the Czech Republic to ''*Harpidella* (*H.*) cf. *kielanae* (Petrunina).'' The fragmentary specimen is so poorly preserved it is difficult to interpret meaningfully, but it shows no evidence of the small L1, glabellar shape, and tuberculate sculpture on the glabella and preglabellar field seen in *S. kielanae*. There is no reason to suspect it is related to Petrunina's species or that it represents *Strasburgaspis*. It is yet another scarcely interpretable Upper Ordovician aulacopleurid specimen.

Fortey's (1997) cf. *cona* specimen, from the lower part of the Caradoc Pa Kae Formation of southern Thailand, is also an incomplete cranidium, though actually more complete and better preserved than the unique specimen of *S. kielanae*. It differs from *S. cona* in its shorter anterior border, relatively longer preglabellar field, apparently smaller palpebral lobes, less well-expressed S2, and shallower S1.

Dean (1966) erected *Otarion insolitum* on the basis of a single poorly preserved internal mold from the mid-Arenig of southwestern France. It is at least broadly comparable in dimensions to cranidia of *Strasburgaspis*, but detailed comparison is impossible. It could represent a scharyiid like *Panarchaeogonus* Öpik, 1937, or a rorringtoniid like *Madygenia* Petrunina in Repina et al., 1975. If it is an aulacopleurid, it is more similar to *Strasburgaspis* than to otarionines such as *Harpidella*.

STRASBURGASPIS new species A
Figure 13

Material examined.—Assigned specimen USNM 522027.

Occurrence.—From the Edinburg Formation, Locality 6.

Discussion.—*Strasburgaspis* n. sp. A was compared with *S. cona* in the genus discussion above.

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