THE OTARIONINE TRILOBITE CYPHASPIS, WITH NEW SPECIES FROM THE SILURIAN OF NORTHWESTERN CANADA

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ABSTRACT—The genus Cyphaspis Burmeister, 1843, is first known from the northern Laurentian Sheinwoodian. By the late Homerian, the genus had appeared in England and Baltica, and from the Ludlow through the Lower and Middle Devonian it had an essentially cosmopolitan distribution. The Mississippian Dixiphogyge Brezinski, 1988, may represent a relict distribution of Cyphaspis, and if so should be considered a junior subjective synonym. Cyphaspis is considered the sister taxon of Otarion Zenger, 1833. The oldest, Sheinwoodian, species of either genus are very similar, but the clades evolved to the point of gross morphological disparity in the Devonian.

New species from the Wenlock and probably Ludlow of northwestern Canada are Cyphaspis lowei, C. muni, C. buchbergeri, and C. mactavishi. New ontogenetic material of the Zichovian C. dabrwni (Chatterton, 1971) further demonstrates the pervasiveness of the basic juvenile morphology of the tribe Otarionini.

INTRODUCTION

This paper is fourth in a series describing the aulacopleurid trilobites of the upper Whittaker Formation and Delorme Group of the central Mackenzie Mountains, Northwest Territories, Canada. Previous works have dealt with the genera Otarion (Adrain and Chatterton, 1994), Harpiddlella and Maurotarion (Adrain and Chatterton, 1995a), and Aulacopleura and Songkania (Adrain and Chatterton, 1995b). The aulacopleurids recovered from these units are silicified and rank among the best preserved species yet found. Representatives of most of the major clades are present, and several horizontal series have yielded excellent juvenile growth stages. As such, the ongoing descriptions have provided a great deal of new information relevant to studies of aulacopleurid ontogeny, phylogeny, and evolution.

In concert with descriptive paleontology, an attempt has been made to revise the family on a world-wide basis, and to organize its constituents into robustly defined monophyletic groups. Two subfamilial groupings have been recognized, in part by reference to comparative ontogenies. The less diverse Aulacopleurinae has been discussed by Adrain and Chatterton (1995b), while generic groupings within the Otarionini have been the subject of Adrain and Chatterton (1994, 1995a). The latter theme is continued in the present work, through treatment of Cyphaspis, one of the major otarionine genera.

Locality information follows Chatterton and Perry (1983, 1984), Over and Chatterton (1987), and Chatterton et al. (1990). The graptolite zonation referred to is that established for the Cape Phillips Basin of the central Canadian Arctic (Lenz, 1990; Lenz and Melchin, 1990, 1991). These zones are cited based upon correlation of the Mackenzie Mountains trilobite faunas with those of the Cape Phillips Basin, description and redescription of which has been begun by Adrain (1994) and Adrain and Edgecombe (1995). Figured specimens are in the palaeontological collections of the Department of Geology, University of Alberta, with prefix UA.

SYSTEMATIC PALEONTOLOGY

Family AULACOPLEURIDAE Angelin, 1854
Subfamily OTARIONINAE Richter and Richter, 1926
Tribe OTARIONINI Richter and Richter, 1926
Genus CYPHASPIS Burmeister, 1843

Type species. — Phacops ceratophthalmus Goldfuss, 1843, Eifelian, Gees, near Geloisheim, Germany.

Other species. — Information is given in the following order:
Diagnosis.—Otarionines with glabella inflated, overhanging preglabellar field when occipital ring is held in vertical plane; preglabellar field short; interocular fixigenae narrow; L1 small; librigenal field relatively broad and short (exsagittally); genital spine long and robust; 11 thoracic segments, with long axial spine on sixth; pygidium narrow and small even for subfamily, with transverse rows of tubercles on axial rings and posterior pleural plates; primitively three or four axial rings; pygidial doublure broad for family.

Discussion.—Adrain and Chatterton (1994) interpreted Cyphaspis and Otarion as sister taxa, and provided a differential diagnosis. Briefly, Cyphaspis is distinguished from Otarion in its shorter, more inflated glabella; smaller L1; shorter preglabellar field; broader, shorter (exsagittally) librigena with usually much longer genital spine; possession of 11 as opposed to 12 or more thoracic segments, with much longer axial spine on sixth; and relatively smaller, narrower pygidium, with more pronounced tubercle rows and broader doublure. More derived species of Cyphaspis, including the type (see Thomas and Owens, 1978, plate 7, figures 4, 8), display an inflated librigenal trunk, which interrupts the contact between the posterior and lateral border furrows at the genital angle. This morphology is seen elsewhere in some species of Harpidelia McCoy, 1849 (H. spinaprons Williams in Cooper and Williams, 1935, and related species; see Adrain and Chatterton, 1995a), but never in Otarion.

Species of Otarion (O. huddyi Adrain and Chatterton, 1994) and of Cyphaspis (C. muniti n. sp.) occurring at section Avalanche Lake Four, 126 m above base, are of mid-Shenwoodian age, and are apparently the oldest known members of their respective genera. They also appear to be the most primitive examples of each group, and comparison, particularly of cranial features, shows close similarity. Were it not for the subsequent separate history of each clade, showing considerable diversification until at least the Middle Devonian, the Wenlock members of either group might be classified together in a single genus. Nevertheless, both O. huddyi and C. muniti possess the synapomorphies of their respective clades, and given the morphological disparity between the groups achieved in the Devonian, there is every reason to treat the sister taxa as separate genera, rather than subgenera or species-groups.

Adrain and Chatterton (1994) described well-preserved ontogenetic material of their new Otarion huddyi, and considered developmental morphology, particularly of the cephalic spine array, to be of critical importance in adding phylogenetic relationships within the subfamily. The tribe Otarionini was diagnosed on the basis of its derived juvenile spine morphology. Its presence in Cyphaspis is demonstrated herein. Comparison of the juvenile cranidia of Cyphaspis lower n. sp. (Figures 1.40, 1.47, 2.1–2.4) with those of O. huddyi (Adrain and Chatterton, 1994, figures 5.25, 5.29, 7.1–7.3) reveals essential correspondence in all features of the spine array (spines labelled following Adrain and Chatterton (1994, p. 305–306, figure 1)). Diagnostic of the tribe, C. lower has G2 and G3 crowded near the front of the glabella, Fx2 and Fx3 suppressed, palpebral spines reduced to a single P1, and a double row of anterior border spines. This morphology is seen in every species of Otarion and Cyphaspis for which any ontogenetic information is available. As outlined by Adrain and Chatterton (1994, page 310, figure 4), the spine array is hypertrophied and retained in the holaspids of members of Namuropyge.

While the respective juvenile cranidia and pygidia of species referred to Otarion and Cyphaspis are very similar, they can nevertheless be differentiated. As far as is known, early-degree meraspis sclerites of Otarion have an essentially smooth sculpture on areas between spines (Adrain and Chatterton, 1994, figures 7, 9). Those known for Cyphaspis (the Wenlock C. lowei and the Zlichovian C. dabrowni; see Figure 2) have a distinct granular sculpture on the dorsal areas of both cranidia and transitory pygidia.

Adrian and Chatterton (1994) emphasized the role of heterochrony in the evolution of the Otarionini. There is some evidence that Cyphaspis may itself have had a paedomorphic origin: 1. The holaspid segment count of 11 is the fewest known for an otarionine. The sister group of Cyphaspis, Otarion, has a primitive segment count of 12. 2. The oldest known species of Cyphaspis, C. muniti n. sp., retains a short median occipital spine in mature holaspids. It is now well established that this feature is very long in the earliest ontogeny of members of Otarionini (see Adrain and Chatterton, 1994, figures 5, 7, for Otarion huddyi; see Adrian and Chatterton, 1994, figure 9 for O. brauni Perry and Chatterton, 1979; see below for O. lowei n. sp.; see Chatterton, 1971 and below for C. dabrowni. The spine becomes progressively shorter through ontogeny, and in virtually all members of the clade, is reduced to a small node in mature holaspides. Retention in the oldest known species of Cyphaspis of a short spine is consistent with the idea that the species reflects development from an arrested degree 11 meraspis of an ancestor with 12 segments. 3. Species of Cyphaspis have mature pygidia that are commonly (and primitively) highly tuberculate. Smaller Otarion pygidia are similarly tuberculate (cf. O. huddy, Adrian and Chatterton, 1994, figures 6.25, 7.8; O. brauni, Adrian and Chatterton, 1994, figure 8.30–8.32), but the tubercules become progressively effaced in larger specimens. Hence, the Cyphaspis condition is consistent with derivation from a juvenile Otarion morphotype.

New discoveries of Telychian and earliest Shenwoodian diversity will be required for a full understanding of the origin of Otarionini and the identification of the tribe's thus far unknown sister taxon. These observations, however, allow at least the plausible suggestion that Cyphaspis evolved through arrested development of a very late-degree meraspis of an older species.

The initial, Shenwoodian, distribution of Cyphaspis seems to be limited to northern Laurentia, where the genus is very common in both the Mackenzie Mountains and the Cape Phillips Basin of the Canadian Arctic. The genus appears elsewhere for the first time in the Homian, in the form of C. elachopos in the Coalbrookdale Formation and Much Wenlock Limestone Formation of England, together with undescribed material from Gotland, Sweden (L. Ramsköld, personal commun.). From the Ludlow onward until at least the Givetian, Cyphaspis is widely distributed, although it is absent the Malvinokaffric Realm. An exception is the Devonian of North America, from which until recently the genus was unknown. A very primitive species has recently been discovered in the Lochkovian Haragan Formation of Oklahoma (G. J. Kloe, personal commun.).

Brezinski (1988) erected the monotypic Dixiphopyge for Bacichthyetopus armatus Vogdes, 1891, from the Mississippian Chouteau Limestone of Missouri, comparing the taxon to Cyphaspis and Namuropyge Richter and Richter, 1939. Adrian and Chatterton (1994) argued that Namuropyge was a paedomorphic member of Otarionini, with a possible origin in Otarion. They included Dixiphopyge with question in Otarionini.

The pygidium of Dixiphopyge resembles that of Namuropyge in its many segments and pleural spines, and indicates a similar potential origin from an arrested transitory pygidium of an earlier species. As noted by Brezinski (1988), the inflated glabella does resemble that of Cyphaspis.

A cranidium illustrated by Přibyl and Vaněk (1981, plate 3,
figure 7) as Otarion (Cyphaspis) hydrocephalum cornigerum (Hawle and Chatterton, 1847), from the Pragian of the Czech Republic, shows the juvenile glabellar and occipital spines of a species of Cyphaspis retained as robust structures in a mature holaspis. This, as outlined by Adrain and Chatterton (1994), is the process by which the spinose adult morphology of Namurophyge was achieved. It does little, however, to explain the origin of Dixiphopyge. Dixiphopyge lacks either prominent glabellar or median occipital spines. While its hypertrophied palpebral spines are consistent with the Otarionini morphology, its long paired occipital spines are unknown elsewhere in Aulacopleuroidea and, as noted by Adrain and Chatterton (1994); also Brezinski, 1988), the very large L1 of Dixiphopyge do not agree with those of most species of Cyphaspis (although the cranidium figured by Přibyl and Vaněk does have an unusually large L1). Nevertheless, Brezinski’s (1988) assignment of the taxon to Aulacopleuroidea remains the most plausible hypothesis, based mainly on the structure of the pygidium and its similarity to that of Namurophyge. If the inflated glabella is ultimately shown through new discoveries to reflect origin in Cyphaspis, Dixiphopyge should be considered a subjective junior synonym, as it would create pointless paraphyly based on autopomorphies. In the present state of knowledge, it seems best to continue to assign Dixiphopyge with question to Otarionini.

**Cyphaspis lowei** new species

**Figures 1, 2.1–2.8**

**Diagnosis.**—Cyphaspis with glabella moderately inflated and with dense, even sculpture of small tubercles; anterior border tubercles suppressed in holaspis; occipital node prominent in holaspis, but not extended into spine; librigenal field with sculpture of dense, fine tubercles, thinning out along lateral border furrow; genital spine long, but relatively narrow for genus, with very faint dorsal tubercle row in holaspis; pygidium with three axial rings, incipient fourth sometimes indistinguishable from terminal piece; each pygidial segment with prominent transverse row of 10–14 tubercles.

**Description.**—Cranial anterior border slightly longer (sagittally, exsagittally) than occipital rim, with prominent, even dorsal convexity, lacking sculpture in mature holaspides; anterior border of similar length sagittally and exsagittally; anterior border furrow evenly arcuate to very slightly anteriorly directed “V” shape, deep; preglabellar field of similar length (sag.) to anterior border, with prominent dorsal convexity, bearing sculpture of fine caecal pits largely obscured by densely scattered small tubercles; glabella large, inflated, with dense, even tuberculation, slightly larger than those on preglabellar field; preglabellar furrow strongly arcuate, describing semicircle in dorsal view; axial furrows bowed out around L1, then parallel for short distance to smooth grade into preglabellar furrow; L1 small, with densely scattered tubercles similar in size to those of preglabellar field; S1 deep; S2 and anterior furrows obscure; interocular fixigena very narrow, dorsally convex, separated from pealpebral lobe by shallow but distinct palpebral furrow, with tuberculate sculpture similar to preglabellar field; preglabellar lobe narrow, short (exsag.), with prominent PI retained in holaspis and very distinct laterally-placed pit; S0 and posterior border furrow very deep; occipital ring with prominent median node and 4–8 moderately large tubercles more or less transversely aligned; posterior border narrow (transversely), lacking dorsal sculpture.

Librigenal field with sculpture of very fine, dense caetal pits and fine tubercles; tubercles slightly larger on anterior and adaxial area of field, becoming smaller and less dense toward lateral border furrow and on glabellar tooth; external view, showing slightly around shoulder and sometimes broadening into shallow area posteriorly; middle furrow running strongly posteriorly from point anterior to shoulder, sagittal midpoint about 20 percent distance posteriorly on middle body; middle body smooth and unsculptured; anterior wings flared laterally and subtriangular, with tiny pit near extreme lateral extent; shoulder extended laterally to about half width of anterior wing; lateral border with one or two subparallel terrace lines sometimes visible; posterior border transversely straight; two small, posteromedially directed spines set at posterolateral corners of hypostome.

Thoracic segments narrow, with fulcrum set near to axial furrow than lateral margin; fulcrum articulatory boss only weakly developed; pleural furrow deep, shallowing abruptly near tip and near contact with axial furrow; anterior and posterior pleural bands of similar length (exsag.), length remaining essentially even along pleural width; pleural tip with small articulating facet.

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**Figure 1**—Cyphaspis lowei new species, from section Avalanche Lake Five, 58–60 m above base, Delorme Group, Wenlock (Homarner, correlated with the Cyrtograptus longigrani-Monograptus testis Zone of the Cape Phillips Basin, central Canadian Arctic), central Mackenzie Mountains, Northwest Territories, Canada. Magnifications are ×10, except where otherwise noted: 1, 6, cranidium, UA 10384, dorsal and lateral views; 2, 7, 15, holotype, cranidium, UA 10385, dorsal, left lateral, and anterior views; 3, 8, cranidium, UA 10386, dorsal and left lateral views; 4, 9, cranidium, UA 10387, dorsal and lateral views; 5, 10, cranidium, UA 10388, dorsal and lateral views; 11, 13, 17, cranidium, UA 10389, dorsal, left lateral, and anterior views; 12, 21, right librigena, UA 10390, dorsal and external views; 14, 22, thoracic segment, UA 10391, lateral and dorsal views; 15, left librigena, UA 10392, external view; 16, right librigena, UA 10393, external view; 18, right librigena, UA 10394, external view; 20, right librigena, UA 10395, external view; 23, thoracic segment, UA 10396, dorsal view; 24, left librigena, UA 10397, external view; 25, left librigena, UA 10398, ventral view; 26, hypostome, UA 10399, ventral view; 27, hypostome, UA 10400, ventral view; 28, 31, hypostome, UA 10401, dorsal and ventral views; 29, left librigena, UA 10402, internal view; 30, left librigena, UA 10403, external view; 32, thoracic segment, UA 10404, ventral view; 33, thoracic segment, UA 10405, dorsal view; 15, 34, thoracic segment, UA 10406, dorsal view; 15, 35, right librigena, UA 10407, external view; 36, pygidium, UA 10408, ventral view; 37, 39, 46, 48, pygidium, UA 10409, ventral, dorsal, posterior, and left lateral views; 38, 45, pygidium, UA 10410, dorsal and posterior views; 40, 41, cranidium, UA 10411, dorsal, anterior, and left lateral views; 42, pygidium, UA 10412, dorsal view; 43, pygidium, UA 10413, dorsal view; 47, 49, cranidium, UA 10414, dorsal and left lateral views; 20, 22, cranidium, UA 10415, dorsal and lateral views; 2ug.
on anterior band, lateral to and behind which are developed 5–6 short spines; axial furrow shallow; ring furrow deep; articulating half ring only slightly shorter (sag.) than axial ring; axial ring lacking dorsal sculpture; thoracic axial spine very long, extending posteriorly past pygidium of articulated exoskeleton.

Pygidium with length (sag., excluding articulating half ring) 40–45 percent of width; axial furrows shallow but meeting posteriorly to fully define axis; three axial rings defined, faint fourth often merged with terminal piece; only first ring furrow well defined, with small pseudoarticulating half ring; axial rings with two to four prominent transversely aligned tubercles; first three pleural segments defined, becoming increasingly faint posteriorly, fourth sometimes weakly defined; first intrapleural furrow well expressed; first interpleural furrow less so, and successive furrows progressively shallower; posterior pleural bands with four or five transversely aligned tubercles of similar size to those of respective axial rings; all furrows terminating at very narrow but distinct border; doublure broadest anteriorly, extending sag-
Itally almost to rear of axis, with several subparallel terrace lines aligned with posterior margin; pygidium with considerable transverse flexure, describing shallow inverted “V” shape in posterior view.

Discussion. — Comparisons with other new species are given below. In addition to these taxa, the lower Homerian Cyphaspis lowei is also similar to the English Wenlock C. elachopos, and to the Australian Ludlow C. horani. Most of the C. elachopos specimens (Thomas, 1978, plate 7, figures 5, 8–13) are to some degree flattened. The species has a maximum possible stratigraphic range from mid-Sheinwoodian to lower Ludlow. This has to some extent been maximized to account for poorly localized museum collections (Thomas et al., 1984), and is unlike anything observed in well-controlled northern Laurentian collections. Nevertheless, on the basis of the published sample, there is no reason to suspect more than one taxon is involved. Cyphaspis lowei appears to be distinguished from C. elachopos in the possession of a sagittally shorter glabella, smaller L1, more slender genal spine, and seemingly more tuberculate pygidium. In addition, the thoracic axial rings of C. elachopos often have fairly prominent transversely aligned tubercles (Thomas, 1978, plate 7, figures 5, 11, 12), while those of C. lowei are smooth (Figure 1.2, 1.23, 1.33, 1.34). Some of these differences might be due to the poorer preservation of the English material. On balance, however, the species, while similar, seem distinct.

Cyphaspis horani (see Chatterton, 1971, plate 24, figures 1–6; Chatterton and Campbell, 1980, plate 11, figures 13, 14) is known mainly from ventral morphology, but the lectotype is an external mold of an articulated dorsal exoskeleton. Again, comparison with C. lowei is hampered by different styles and quality of preservation. Cyphaspis horani, however, appears to be distinguished in the possession of a longer, less tuberculate librigenal field, more slender genal spine, and relatively wider pygidium.

Etymology. — After Kevin Lowe.

Material. — Holotype cranidium UA 10385 (Figure 1.2, 1.7, 1.16); paratypes UA 10384, 10386–10422. All from section Avalanche Lake Five, 58–60 m above base, Delorme Group, Wenlock (lower Homerian, correlated with Cyrtograpthus lundgreni-Monograptus testis Zone of Cape Phillips Basin, central Canadian Arctic), central Mackenzie Mountains, Northwest Territories, Canada.

**Cyphaspis dabbrowi** (Chatterton, 1971)

Figure 2.9–2.18

*Otarion* (Otarion) dabbrowi Chatterton, 1971, p. 67, pl. 17, figs. 1–37, pl. 18, figs. 13–32; CHATTERTON, JOHNSTON, AND CAMPBELL, 1979, p. 810.


Diagnosis. — Emended from Chatterton (1971, p. 67). Preglabellar field very short; glabella strongly inflated, with narrow smooth band around anterior base, directly above preglabellar furrow; L1 very small; librigenal field small in area; eye tall; genal trunk swollen and inflated; faint furrow and tubercle row on dorsal aspect of long genal spine; pygidium with typical three segments bearing transverse tubercle rows, often partially effaced posteriorly.

Discussion. — Chatterton (1971) has discussed this species, but so much new information about the group is now available that an updated assessment is possible. We illustrate additional new material to emphasize the stability and pervasiveness of the basic Otarionini meraspid anatomy (see Adrain and Chatterton, 1994, figure 1.3).

**Cyphaspis muni** new species

Figure 3

Diagnosis. — L1 large (for genus); glabella only moderately inflated and elongate; occipital node retained as very short spine in holaspis; librigenal field relatively narrow, lateral border broad, broadening anteriorly, wider than posterior border; genal spine stout; pygidium with three axial rings, indistinct fourth; transverse tubercle rows on axial rings and on both posterior and anterior pleural bands.

Discussion. — This species is so similar to Cyphaspis lowei that description is best accomplished through differential diagnosis, listing all perceived contrasts.

Intercocular fixigenae slightly broader; glabella slightly longer and less inflated, with slightly coarser tuberculate sculpture; L1 larger; occipital node retained as short spine versus more subdual tubercle; librigenal field narrower, with slightly sparser and coarser tuberculate sculpture; lateral border broader; genal spine stouter and less curved; transverse tubercle rows present on anterior pleural bands of pygidium, versus at most one or two abaxially set tubercles.

**Cyphaspis muni** is the oldest known member of the genus. It occurs together with *Otarion huddyi* Adrain and Chatterton, 1994. Given the close similarity of these species (see above and Adrain and Chatterton, 1994), the basis for association of sclerites must be outlined. 1. The most straightforward means of associating Cyphaspis sclerites is reference to the morphology of species that do not occur with close relatives with which they may be confused. The species *C. lowei* and *C. mactavishi* each occurs as the only aulacopleurid at its respective horizon. 2. *Cyphaspis muni* is of rare occurrence, while *Otarion huddyi* is very common. Similarly, *C. buchergeri* is very rare, while *O. brauni*, with which it occurs, is very common. 3. While these factors leave little doubt about assignment of most sclerites, there is very little variation in morphology of the hypostome (cf. those of *Cyphaspis lowei*, Figure 1.26, 1.27, 1.31, with those assigned to *Otarion huddyi* Adrain and Chatterton, 1994, figure 6.18, 6.19). It does not seem possible to assign hypostomes with confidence when species of either genus occur together. Those assigned to *O. huddyi* by Adrain and Chatterton were done so on the basis of the much more common occurrence of that species, but they could conceivably belong to *C. muni*.

**Cyphaspis buchergeri** new species

Figure 4

Diagnosis. — Cranidium and glabella narrow and elongate; anterior sections of facial suture nearly parallel, only gently anteriorly divergent; glabellar tuberculation coarse; L1 very low; S0 very long (sagittally, exsagittally), especially above L1, where it becomes a long, subtriangular smooth area; librigenal field
Figure 3—Cyphaspis munii new species, from section Avalanche Lake Four, 126 m above base except 5 (AV 4 128 m), Delorme Group, Wenlock (mid-Sheinwoodian, correlated with the Monograptus instrenus-Cyrtograptus ka/lbus Zone of the Cape Phillips Basin, central Canadian Arctic), central Mackenzie Mountains, Northwest Territories, Canada. Magnifications: 1-14 are ×10, 15-26 are ×15. 1, 6, 11, holotype, cranidium, UA 10432, dorsal, left lateral, and anterior views; 2, 7, cranidium, UA 10433, dorsal and right lateral view; 3, 8, cranidium, UA 10434, dorsal and right lateral view; 4, 9, 10, cranidium, UA 10435, dorsal, left lateral, and anterior view; 5, cranidium, UA 10436, dorsal view; 12, 14, right librigena, UA 10437, external and ventrolateral views; 13, right librigena, UA 10438, external view; 15, pygidium, UA 10439, dorsal view; 16, pygidium, UA 10440, dorsal view; 17, 18, 21, 22, cranidium and right librigena, UA 10441, dorsal (palpebral), right lateral, anterior, and occipital views; 19, pygidium, UA 10442, dorsal view; 20, pygidium, UA 10443, dorsal view; 23, pygidium, UA 10444, dorsal view; 24, 26, pygidium, UA 10445, dorsal view with articulating half-ring held in vertical plane, and standard dorsal view; 25, pygidium, UA 10446, ventral view.

broad, with sparse tuberculation and prominent genal trunk; eye tall; pygidium broad with very strong transverse tubercle rows on axial rings and posterior pleural bands.

Description.—Description is accomplished through differential diagnosis with C. lowei.

Anterior sections of facial sutures gently, versus strongly, anteriorly divergent in front of eye; glabella with similar inflation but longer relative to width; glabellar tuberculation much coarser, but less dense; L1 of similar size, but less inflated; SO much longer (sag., exsag.); eye taller; librigenal field broader; librigenal
tubercles larger but much more sparsely distributed; genal trunk prominent on external surface, versus obscure; genal spine less curved, pygidium broader, with much stronger transverse tuberculation; 9–10 axial ring tubercles versus 2–5.

**Discussion.** — *Cyphaspis buchbergeri* occurs together with *Otario braunii* Perry and Chatterton, 1979 (see Adrain and Chatterton, 1994). The basis for sclerite associations was given under discussion of *C. muni* above.

Adrain and Chatterton (1994, page 316) regarded the Irish species *Conoparia hollandi* Siveter, 1989, as a possible junior subjective synonym of *Otario braunii*, drawing attention to the fact that of the two librigenae assigned to the former (Siveter, 1989, plate 17, figures 11, 14) only one was similar to those of *Otario braunii*. In light of the additional material of *O. braunii* figured by Adrain and Chatterton (1994), one of the few remaining contrasts between the species is the morphology of the second librigena assigned to *hollandi* (Siveter, 1989, page 124, plate 17, figure 14). Adrain and Chatterton (1994) questioned whether this sclerite was actually conspecific with the remainder of the Irish material assigned to *hollandi*. It may well be, and if so *Otario hollandi* should likely be retained as a separate species (Siveter [personal commun.] points out also that the preglabellar field of specimens of *O. hollandi* is more steeply inclined than that of *O. braunii*). Nevertheless, comparison of the librigena in question with those of *Cyphaspis buchbergeri*, with which *O. braunii* occurs in northern Canada, reveals striking similarity (see, in particular, Figure 4.17). These specimens have a smaller, more tuberculate librigenal field and more robust genal spine than is typical of species of *Otario*. It is possible that a rare species of *Cyphaspis* occurs in the Irish fauna, similar to the situation in many northwestern and Arctic Canadian faunas, to which the librigena illustrated by Siveter (1989, plate 17, figure 14) belongs. A much greater sample of the Irish material, particularly of librigenae, would be required to resolve the problem.

*Cyphaspis buchbergeri* is distinguished from *C. muni* in its narrower glabella, less anteriorly divergent anterior sections of the facial suture; smaller, less inflated L1; coarser glabellar tuberculation; much longer S0; taller eye; broader and more tuberculate librigenal field with prominent, versus obscure, genal trunk; slightly narrower genal spine; and broader pygidium with more prominent transverse tubercule row, but with some development of tubercles on the anterior pleural bands. The species is contrasted with *C. mactavishi* below.

*Cyphaspis buchbergeri* is similar in age (late Homerian) to Much Wenlock Limestone material of *Echacophos* Thomas. Nevertheless, the early Homerian *C. lowei* is much more similar to the English taxon.

**Etymology.** — After Kelly Buchberger.

**Material.** — Holotype craniidium UA 10449 (Figure 4.3, 4.7); paratypes UA 10447, 10448, 10450–10456, from section DR, 114.3–126.5 m above base, Delorme Group, Wenlock (upper Homerian, correlated with *Priistigraptus ludensis* Zone of the Cape Phillips Basin, central Canadian Arctic), central Mackenzie Mountains, Northwest Territories, Canada.

**Cyphaspis mactavishi** new species

**Figure 5**

**Diagnosis.** — Anterior sections of facial suture subparallel to slightly anteriorly convergent immediately in front of eye; interocular fixigenae very broad for genus; eye short; librigenal field narrow, tuberculation very sparse; genal trunk visible near genal angle, but very weakly expressed.

**Description.** — Description is accomplished through differential diagnosis with *Cyphaspis lowei*.

Anterior sections of facial suture nearly anteriorly convergent immediately in front of eye, in general subparallel and anteriorly divergent only opposite anterior border, versus strongly anteriorly divergent; librigenal field slightly longer; interocular fixigena much broader; L1 slightly larger; glabellar tuberculation slightly coarser and less dense; librigenal field narrower; many fewer, coarser tubercles on librigenal field; genal trunk visible versus obscured; tubercle row on at least proximal dorsal aspect of genal spine much more robust.

**Discussion.** — *Cyphaspis mactavishi* is most similar among described species to *C. lowei*. While the contrasts noted above leave little doubt that the species are separate and distinct, the pygidia are virtually indistinguishable, although the transverse tuberculation of those assigned to *C. mactavishi* is somewhat more robust. *Cyphaspis mactavishi* is distinguished from *C. muni* in the possession of subparallel, versus strongly anteriorly divergent, anterior sections of the facia sutures; smaller L1; wider interocular fixigena; median occipital structure a small node versus a short spine; slightly narrower librigenal field with much sparser tuberculation; genal trunk visible versus obscure; slightly narrower lateral border; prominent, versus tiny, dorsal tubercles on proximal part of genal spine; pygidium with much less well-developed tuberculation on anterior pleural bands.

*Cyphaspis mactavishi* is similar to *C. buchbergeri* in its more or less subparallel anterior sections of the facial sutures and its relatively sparse librigenal field tuberculation, with the genal trunk visible. It is distinguished from *C. buchbergeri* in its wider interocular fixigena; broader glabella; much shorter S0; shorter eye; narrower librigenal field; possession of prominent dorsal tubercles on the proximal part of the genal spine versus their apparent absence in large holaspid specimens (faint tubercles are visible on the smaller cheek of Figure 4.17, but not on those of Figure 4.14, 4.15, 4.19); and much narrower pygidium.

The age of the type stratum of *C. mactavishi*, section AV 7, 312 m, is poorly constrained (see discussion in Edgecombe and Chatterton, 1993, p. 3). Horizon AV 7 70 m contains trilobites which correlate exactly with those of section AV 5 58–60 m. These strata, by correlation with the trilobites of the Cape Phillips Basin, central Canadian Arctic, are lower Homerian (*Cyrtograptus ludenri*- *Monograptus tessellatus* Zone of Lenz and Melchin, 1990, 1991). The upper constraint is a conodont sample from AV 7, 430 m, which indicates a Ludlow–Pridoli assignment (Over and Chatterton, 1987; see Edgecombe and Chatterton, 1993). Hence, AV 7, 312 m is maximally lower Homerian, but more likely upper Homerian or Ludlow. All trilobite species recovered are unique to the interval AV 7, 255.6–312.0 m. Definitely dated upper Homerian trilobites are known from the Cape Phillips Basin, and correlate well with those from sections DR 114.3–147.8 m (including *Otario braunii* Perry and Chatterton, 1979, and *Cyphaspis buchbergeri* n. sp.), and section AV 4, 165–248.5 m. In addition, lowermost Ludlow (*Lobograptus progenitor* Zone) faunas have been recovered from the Arctic which correlate with section DR 182.9 m. Hence, if the assumption is made that the Arctic sequence of trilobite faunas is more or less complete and accurate, the age of section AV 7, 312 m would be, by exclusion, Ludlow (and younger than earliest Ludlow) to possibly early Pridoli. It should be stressed however, that while the Arctic faunas are by far the most numerous and most highly resolved from this interval from anywhere in the world (Adrain, 1994), whether or not they are complete can never be known. In the absence of further data, it remains conceivable that the horizon could ultimately prove to be upper Wenlock or lowermost Ludlow.

**Etymology.** — After Craig MacTavish.

**Material.** — Holotype craniidium UA 10458 (Figure 5.2, 5.3, 5.7); paratypes UA 10457, 10459–10475. All from section AV-
Figure 4—Cyphaspis buchbergeri new species, from section Delorme Range, 114.3–126.5 m above base, Delorme Group, Wenlock (upper Homerian, correlated with the Pristiograptus ludensis Zone of the Cape Phillips Basin, central Canadian Arctic), central Mackenzie Mountains, Northwest Territories, Canada. Magnifications are x10 except where otherwise noted. 1, 5, 9, 13, cranidium, UA 10447, dorsal, ventral, right lateral, and anterior views (DR 114.3 m); 2, 6, cranidium, UA 10448, dorsal and right lateral views (DR 114.3 m); 3, 4, 7, holotype, cranidium, UA 10449, dorsal, anterior, and right lateral views (DR 114.3 m); 8, 12, cranidium, UA 10450, dorsal and right lateral views (DR 126.5 m); 10, 11, cranidium, UA 10451, dorsal and left lateral views (DR 114.3 m); 14, 16, right librigena, UA 10452, external and internal views (DR
Cyphaspis mactavishi new species, from section Avalanche Lake Seven, 312 m above base, probably Ludlow, Delorme Group, central Mackenzie Mountains, northwest Territories, Canada. Magnifications are ×10 except where noted otherwise. 1, cranidium, UA 10457, dorsal view; 2, 3, 7, holotype, cranidium, UA 10458, dorsal, left lateral, and ventral views; 4, 9, cranidium, UA 10459, dorsal and right lateral views; 5, 10, cranidium, UA 10460, anterior and dorsal views; 6, 11, cranidium, UA 10461, dorsal and right lateral views, ×15; 8, 3, cranidium, UA 10462, dorsal and left lateral views, ×15; 12, hypostome, UA 10463, ventral view, ×15; 14, 15, cranidium, UA 10464, dorsal and left lateral view; 16, 19, right librigena, UA 10465, external and internal views; 17, left librigena, UA 10466, external view; 18, left librigena, UA 10467, external view; 20, left librigena, UA 10468, external view, ×15; 21, left librigena, UA 10469, external view; 22, right librigena, UA 10470, external view; 23, 25, pygidium, UA 10471, dorsal and ventral views, ×15; 24, thoracic segment, UA 10472, dorsal view; 26, thoracic segment, UA 10473, dorsal view, ×15; 27, pygidium, UA 10474, dorsal view, ×15; 28, right librigena, UA 10475, external view, ×15.
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