Early Permian Carbonitidae (Ostracoda): ontogeny, affinity, environment and systematics

JULIE B. RETRUM[1] & ROGER L. KAESLER[1, 2]
[1] Department of Geology, University of Kansas, 1475 Jawhawk Blvd., Room 120, Lawrence KS 66045-7613, USA
[2] Paleontological Institute and Natural History Museum–Biodiversity Research Center, University of Kansas, Lawrence, KS 66045-7613, USA

ABSTRACT – An assemblage of four *Carbonita* species was deposited with charophytes, lungfishes and lysorophids in a lenticular mudstone from a Cisuralian freshwater pond deposit from the lowest Permian. Samples contained few adult *Carbonita*, indicating perhaps a stressed and unstable environment. Two species new to science, *C. ovata* n. sp. and *C. triangulata* n. sp., occur together with *C. evelinae* and *C. pungens*. Morphological characters of these *Carbonita* suggest an affinity with the Healdioidea, marine taxa that are probably ancestral to the Carbonitidae. The muscle-scar patterns of Carbonitidae, which comprise closely grouped circular bundles of secondary muscle scars, resemble closely those of Healdioidea and not those of Cypridoidea and Cytheroidea, whose muscle scars are fewer and spaced further apart. The muscle-scar pattern of *C. pungens*, described here for the first time, is a circular scar with an ascertainable pattern of secondary scars. *C. pungens* and species of *Darwinula* are morphologically similar, but study of additional specimens of *C. pungens* with better-preserved muscle scars is essential to determine their evolutionary affinity. *J. Micropalaeontol.* **24**(2): 179–190, October 2005.

KEYWORDS: *Ostracoda, Carbonita, Permian, freshwater, palaeoenvironments*

INTRODUCTION

The Family Carbonitidae Swain, 1976, was distributed widely in Pangaea during the Late Palaeozoic, but research has produced mixed results regarding its evolutionary relationships, ontogeny and palaeoenvironmental significance. Differences of opinion regarding these aspects of the Carbonitidae have been attributed to poorly preserved specimens (Bless & Pollard, 1973) and to inaccurate illustrations and imprecise descriptions (Anderson, 1970; Bless & Pollard, 1973). The purpose of this paper is to re-evaluate these aspects of Carbonitidae by studying a Permian fauna from Wolfcampian rocks of the Midcontinent of North America. The species that comprise the fauna lived in a freshwater pond. The ontogeny of four species is traced, two new species of the genus *Carbonita* Strand, 1928 are described and evidence for the affinity of *Carbonita* to the healdiid ostracodes is provided, suggesting that their invasion of the continental freshwater environment was a separate event from that of the Cypridoidea Baird, 1845, Cytheroidea Baird, 1850 and, very likely, the Darwinuloidea Brady & Norman, 1889.

The Speiser Shale (Cisuralian, Asselian) near Eskridge, Kansas, contains a lens of green, carbonate-rich mudstone and claystone with abundant *Carbonita* (Schultze, 1985; Hembree *et al.*, 2004). *C. evelinae* (Jones, 1870), *C. pungens* (Jones & Kirkby, 1867) and two new species, *C. ovata* n. sp. and *C. triangulata* n. sp., occur in the lens of mudstone (Pl. 1).

Some previous researchers regarded Carbonitidae as having close evolutionary relationships with modern freshwater Cypridoidea (Scott & Summerson, 1943; Swain, 1976). In contrast, Sohn (1985) suggested that *Carbonita* evolved from the Late Palaeozoic marine Healdioidea Harlton, 1933. More recently, Whatley *et al.* (1993) classified the family in the Order Podocopida Müller, 1894, suborder and superfamily uncertain.

THE LOCALITY

The Speiser Shale is the youngest stratigraphic unit in the Council Grove Group (Cisuralian, Asselian) (Fig. 1). It was deposited near the shoreline of a shallow epeiric sea. Early in the Permian, the North American Midcontinent was located in the tropics (Frazier & Schwimmer, 1987) and glaciers on Gondwana were retreating and advancing, causing glacioeustatic sea-level changes (Dickinson *et al.*, 1994; Olszewski & Patzkowsky, 2003). The Speiser Shale was deposited during a relative lowstand of sea-level (C. R. Cunningham, pers. comm., 1989), during which the North American Midcontinent did not receive monsoonal rains. As a result, conditions were more arid than during eustatic highs (Rankey, 1997; Olszewski & Patzkowsky, 2003).

The Speiser Shale overlies the Funston Limestone and is overlain by the Wreford Limestone. The Speiser Shale crops out across Kansas from Marshall and Nemaha Counties in the north to Cowley County in the south. It ranges in thickness from 10 m in the north to 39 m in the south (Hattin, 1957), but is much thinner in the area studied.

Approximately 3 km northwest of Eskridge, Kansas, on Kansas Highway 4 is a road cut about 100 m long that exposes 8 m of section, including the top of the Funston Limestone, the Speiser Shale and the base of the Wreford Limestone (Fig. 2). The Speiser Shale is 4.2 m thick at this locality and contains ten distinct lithofacies, including a green, carbonate-rich mudstone and claystone lens with abundant vertebrate and invertebrate fossils. (For further descriptions of the lithofacies see Hembree *et al.*, 2004.) This outcrop was chosen for study because of its well-studied flora and vertebrate and invertebrate fauna, including abundant Ostracoda (Schultze, 1985; Hembree *et al.*, 2004; Watabe & Kaesler, 2004).

THE SAMPLES

Samples were collected from intervals 5 cm thick from the western and eastern parts of the mudstone lens; a total of eight samples, each about 2.5 kg in weight, were collected. The samples were dried, crushed coarsely and treated with Amosol (Stoddard's solvent) to disaggregate the mudstone. The residues were wet sieved through 20-mesh (833 μm), 100-mesh (149 μm)
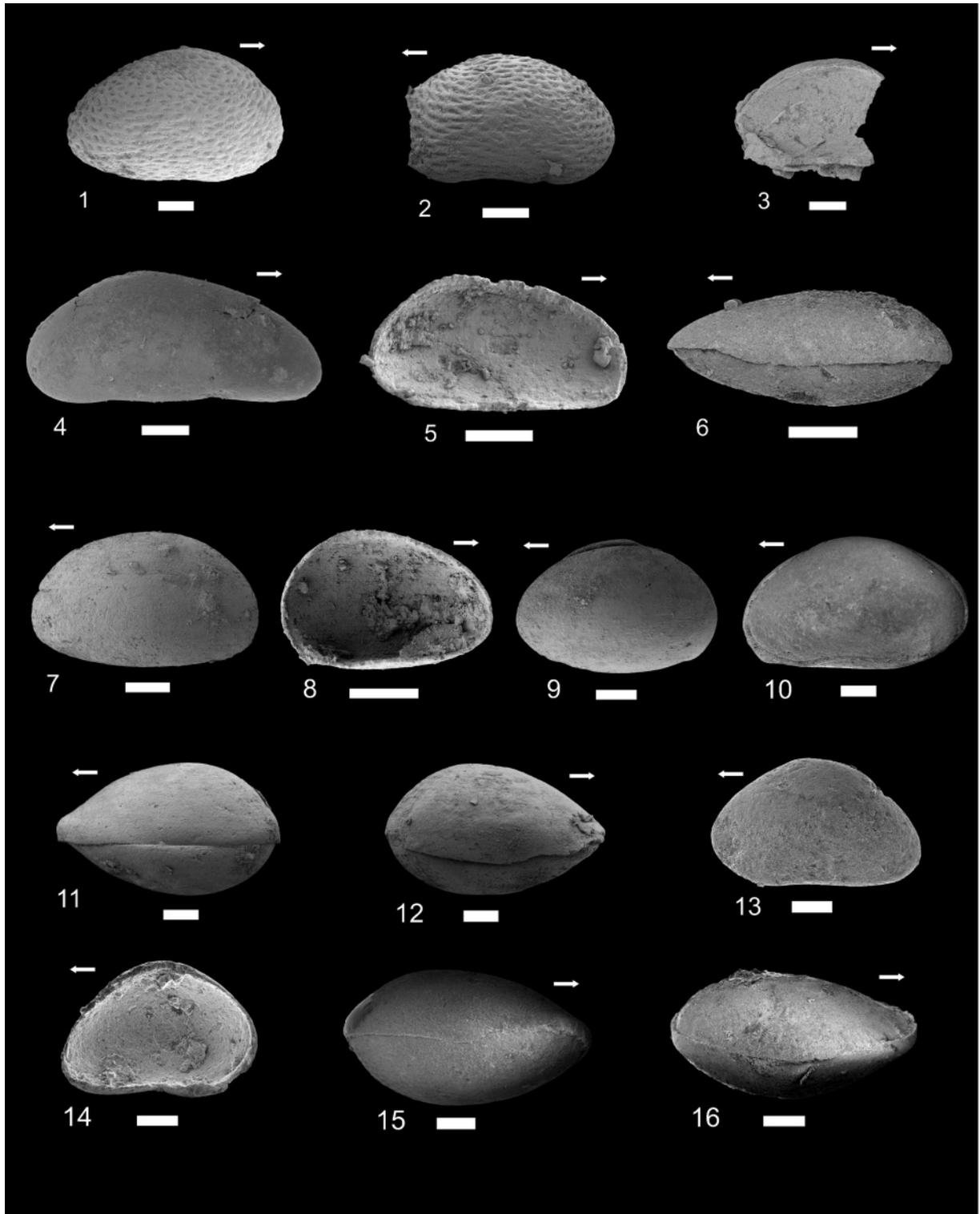
Explanation of Plate 1.

SEM photomicrographs of *Carbonita* species from the Speiser Shale, Eskridge, Kansas, depicting morphological features of instars and adults. All scale bars are 100 µm. **figs 1–3.** *Carbonita evelinae* (Jones, 1870): **1,** right valve, exterior, A-1, KUMIP 1,136,686; **2,** left valve, exterior, A-2, KUMIP 1,136,687; **3,** left valve, interior, KUMIP 1,136,688. **figs 4–6.** *C. pungens* (Jones & Kirkby, 1867): **4,** right valve, exterior, Adult, KUMIP 1,136,690; **5,** left valve, interior, A-1, KUMIP 1,136,691; **6,** ventral view, steinkern, KUMIP 1,136,692. **figs 7–12.** *C. ovata* n. sp.: **7,** left valve, exterior, A-1, holotype KUMIP 1,136,671; **8,** left valve, interior, A-3, paratype KUMIP 1,136,672; **9,** left valve, steinkern, note the overlap of the right valve along the dorsal margin, paratype KUMIP 1,136,673; **10,** right valve, steinkern, paratype KUMIP 1,136,674; **11,** dorsal view, steinkern, paratype KUMIP 1,136,675; **12,** ventral view, steinkern, paratype KUMIP 1,136,676. **figs 13–16.** *C. triangulata* n. sp.: **13,** left valve, exterior, A-1, paratype KUMIP 1,136,681; **14,** right valve, interior, A-1, note the circular muscle-scar, holotype KUMIP 1,136,680; **15,** ventral view, steinkern, paratype KUMIP 1,136,682; **16,** dorsal view, steinkern, paratype KUMIP 1,136,683.
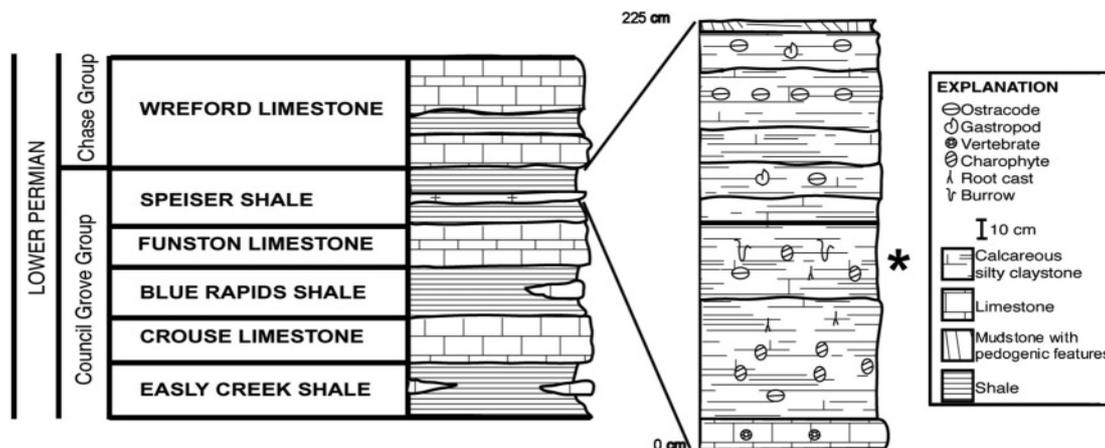
Fig. 1. Stratigraphy of the Speiser Shale at the Eskridge outcrop showing associated formations (Zeller, 1968). *Carbonita* specimens were collected from a green mudstone layer indicated by the asterisk (modified from Watabe & Kaesler, 2004).

and 200-mesh (74 μm) sieves to remove mud and clay particles. *Carbonita* is rare in all samples except for one in which *C. ovata* n. sp. and *C. triangulata* n. sp. were abundant. Lengths and heights of all specimens of *Carbonita* were measured and the ontological growth series of each species were plotted. Adult valves of *C. ovata* n. sp. and *C. triangulata* n. sp. were also measured for width to determine if sexual dimorphism occurs in these species. Scanning electron microscopy (SEM) photomicrographs show shell ornamentation, a few poorly preserved muscle scars, hinges and other internal features.

HISTORY OF CARBONITIDAE
Jones (1870) was the first to describe and classify Carbonitidae ostracodes. He distinguished the Family Carbonitidae from other known ostracodes by its circular muscle-scar pattern with secondary muscle-scar bundles and vascular impressions on reticulated valves (Anderson, 1970).
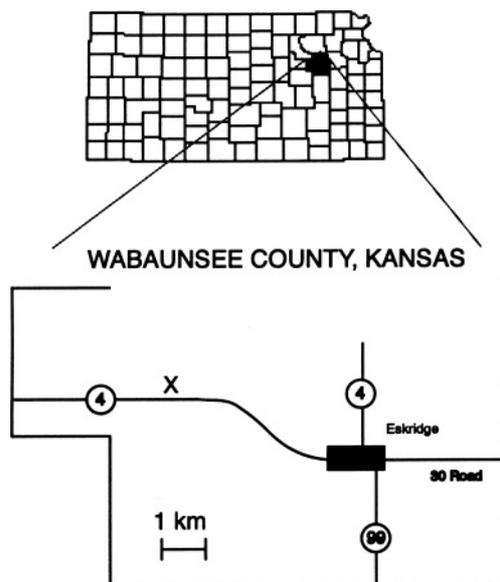
Fig. 2. Location of the outcrop, X (lat. 39° 6.3′N, long 96° 8.8′W) approximately 3 km northwest of Eskridge, Kansas, in Wabaunsee County.

The first known Carbonitidae evolved during the Mississippian, while the youngest are known from the Cisuralian or Guadalupian in the Permian (Cooper, 1942; Kellett, 1943). During this time, Carbonitidae had a wide distribution throughout Europe and North America in continental freshwater deposits (Scott & Summerson, 1943) and other presumably low-salinity deposits with marine to estuarine affinities (Jones & Kirkby, 1879; Knight, 1928; Anderson, 1970; Tibert & Scott, 1999). Carbonitids are most common in deposits of freshwater swamps, slow streams and lagoons, all of which received freshwater (Scott & Summerson, 1943). The presence of Carbonitidae in marine and estuarine deposits indicates that some species may have tolerated oligohaline conditions or were transported from nearby freshwater habitats (Pollard, 1966).

The classification of genera now grouped into the Family Carbonitidae was debated widely during the twentieth century. Knight (1928) placed *Carbonita* into the Superfamily Cytheroidea because of the presence of a single species in marine deposits. Scott & Summerson (1943) compared *Carbonita fabulina* (Jones & Kirkby, 1867) to the modern freshwater species *Cypridopsis vidua* (Müller, 1776) and placed carbonitids into the Family Cyprididae Baird, 1845, having found no significant differences in the carapaces that would justify their being classified elsewhere. Swain (1976) placed the carbonitids into a separate family, Carbonitidae, which he erected based on their elongate-elliptical outline that is uncommon in species of *Cypridopsis* Brady, 1867. More recently, Sohn (1985) determined that the muscle scars of Carbonitidae resemble closely those of the marine Healdioidea and not of the Cypridoidea. He erected the Superfamily Carbonitoidea and, again, the Family Carbonitidae. Other researchers have found no conclusive evidence for classification of the carbonitids and placed them into an uncertain suborder and superfamily of the Order Podocopida (Whatley *et al.*, 1993).

ONTOGENY AND SEXUAL DIMORPHISM
Four species of *Carbonita* occur in the Eskridge samples, including two previously undescribed species: *C. evelinae, C. pungens, C. ovata* n. sp. and *C. triangulata* n. sp. All specimens were preserved either as finely recrystallized valves or as steinkerns.
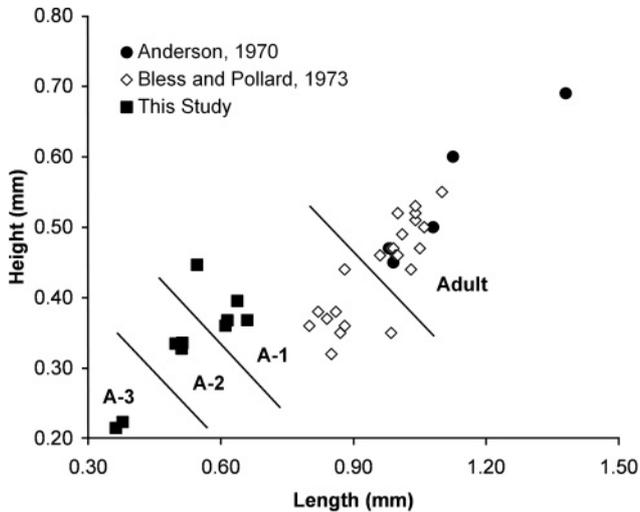
Fig. 3. Plot of length versus height of *Carbonita evelinae* specimens from Eskridge samples, Anderson (1970) and Bless & Pollard (1973) showing groupings of adults and instars A-1 to A-3.

Fig. 4. Plot of length versus height of *Carbonita pungens* specimens from Eskridge samples, Anderson (1970) and Bless & Pollard (1973) showing groupings of adults and instar A-1.

Graphs of ontogenetic series can show instar and adult stages where specimens are clustered. Stages can be difficult or impossible to distinguish, especially in the fossil record. This blurring of growth stages may result from time-averaging of specimens from different environments or seasons (Whatley & Stephens, 1977). Conspecific ostracodes tend to be smaller in the spring than in the fall (Whatley & Stephens, 1977). Brooks' rule suggests that crustaceans double their volume and increase linear dimensions by approximately the cube root of two (1.26) with each moult (Brooks, 1886). The rule is a general observation of crustacean growth but is not necessarily true of all ostracode ontogenies. Brooks' rule is useful for recognizing instars and adults of ostracodes and may provide insight into heterochrony in the evolution of the Ostracoda or into the timing of such ontogenetic changes as addition of appendages and development of sexual maturity.

Ten complete valves of *C. evelinae* were collected, representing three distinct instars (Fig. 3; Pl. 1, figs 1–3). Bless & Pollard (1973) constructed a growth series of specimens of *C. evelinae* from the Westphalian of Great Britain and the Netherlands. Their data demonstrate two clusters of data points with mean height and length of approximately 0.37 mm and 0.87 mm and approximately 0.49 mm and 1.02 mm, respectively. Bless & Pollard (1973) inferred these two clusters to be the A-1 instar and the adult. If so, then the three instars in the Eskridge samples are probably the A-1 to A-3 instars, suggesting that no adults were collected. The largest specimens here have a mean height of 0.39 mm, similar to that of Bless & Pollard's A-1. While the mean height of instar A-1 of their specimens is similar to those in the Eskridge samples, the mean length differs: Eskridge specimens average 0.61 mm in length compared with 0.87 mm for Bless & Pollard's (1973). Their specimens range in height: length ratio from 0.36 to 0.52, while the Eskridge specimens range from 0.56 to 0.82. Such differences could stem from the very small sample size of the current study, be the result of environmental differences or be due to taxonomic differences. Specifically, the *C. evelinae* here may be, instead, *C. humilis* Jones & Kirkby, 1879, as this species has also a punctate surface
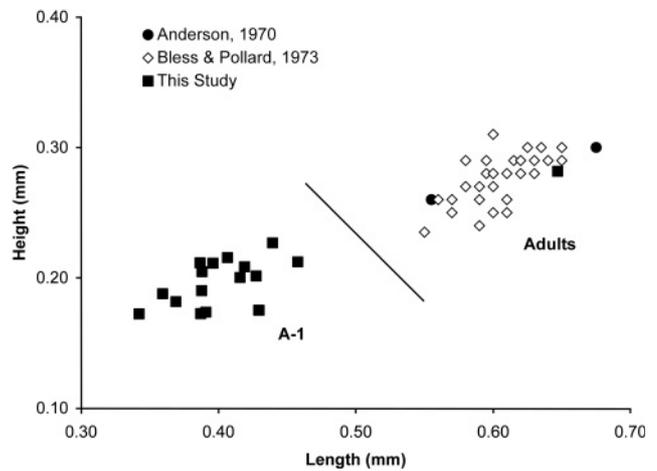
ornamentation and a height: length ratio of 0.60 to 0.70 (Pollard, 1966). *C. humilis*, however, has rounded, not elongated punctae as is characteristic of *C. evelinae* and its anterior end is pointed more acutely than that of *C. evelinae*. The dearth of specimens of *C. evelinae* in the current samples makes it difficult to determine whether these specimens of *C. evelinae* follow Brooks' rule (Fig. 3).

The specimens of *C. pungens* are a single valve of an adult and 17 A-1 instars (Fig. 4; Pl. 1, figs 4–6). The adult specimen is similar in size to Bless & Pollard's (1973) adults, which have a mean height and length of 0.28 mm and 0.60 mm, respectively (Fig. 4). Specimens measured and illustrated by Anderson (1970) are 0.30 mm by 0.68 mm and 0.26 mm by 0.56 mm, both comparable in size to the adult specimen here (Fig. 4).

The samples yielded specimens of *C. ovata* n. sp. from adults to the A-3 instar (Fig. 5a; Pl. 1, figs 7–8). Adults and A-3 instars are easily identifiable, with gaps separating them from other instars. Instars A-1 and A-2, however, have a broad distribution, with no appreciable gap between them. The dotted line in Figure 5a, separating the A-1 and A-2 instars, is based on Brooks' rule. This divided the collection into 16 adults, 38 A-1 instars, 39 A-2 instars and 8 A-3 instars. Adult height: length ratios range from 0.52 to 0.68. The width of adult valves was also measured to show variation in the posterior end and to assess sexual dimorphism. Widths of adults seem to be distributed bimodally, with four adults having a width less than 0.18 mm and nine adults having a width greater (Fig. 6a), suggestive of sexual dimorphism, although further investigation with a larger sample size is needed.

The samples yielded 53 specimens of *C. triangulata* n. sp.: 13 adults, 19 A-1 instars, 29 A-2 instars, and 2 A-3 instars (Fig. 5b; Pl. 1, figs 13–14). Adult and all instars are easily identifiable, with gaps separating them from one another. Adult height: length ratios range from 0.58 to 0.69. The widths of adults may be distributed bimodally, with seven adults having a width less than 0.19 mm and six adults having a greater width (Fig. 6b), again suggestive of sexual dimorphism.

Variation in size and height: length ratios of adults of both *C. ovata* n. sp. and *C. triangulata* n. sp. could result from sexual

(a)

(b)
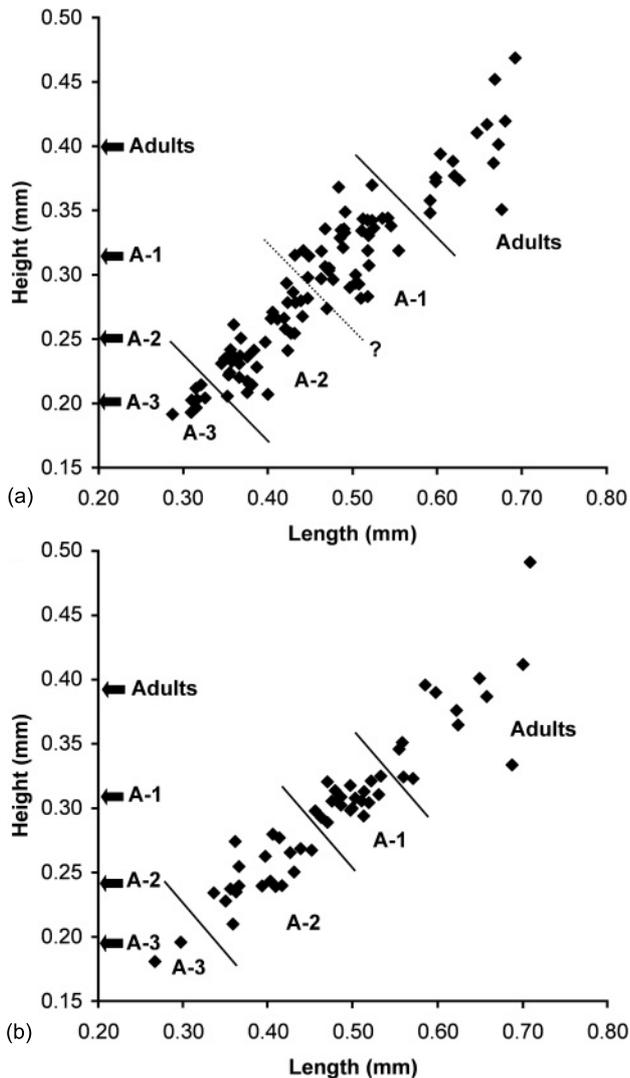
Fig. 5. Plot of length versus height of (**a**) *Carbonita ovata* n. sp. and (**b**) *C. triangulata* n. sp. specimens from Eskridge samples, showing groupings of adults and instars A-3. Instar heights as predicted by Brooks' rule are marked on the ordinate with arrows, beginning with the mean height of instar A-3 stage, each subsequent arrow being located 1.26 times the previous height. The dotted line separating the A-1 and A-2 instars in (a) was calculated based on Brooks' rule.

(a)

(b)

Fig. 6. Distribution of posterior widths of valves of adult specimens. The bimodal distribution suggests the two species are sexually dimorphic, presuming the males have the narrower posterior widths and the females are wider. (**a**) *Carbonita ovata* n. sp.; (**b**) *C. triangulata* n. sp.

dimorphism, which has been postulated for *C. humilis* (Jones & Kirkby, 1879) (Pollard, 1966; Bless & Pollard, 1973, 1975) and *C. inflata* (Jones & Kirkby, 1879) (Anderson, 1970), based on differences in the swelling of the posterior end. Bless & Pollard (1973, 1975) found also noticeable differences in height: length ratios, degree of arching of the dorsum and relative positions of maximum height of *C. humilis* among ostracodes from separate localities. Bless & Pollard (1975) recognized that the variation among localities could result also from conditions other than sexual dimorphism: parthenogenetic reproduction in an unstable environment or a combination of syngamic reproduction during unstable environmental times and parthenogenetic reproduction during stable environmental times.

Height: length ratios of adults of both *C. ovata* n. sp. and *C. triangulata* n. sp. are quite variable, but their distribution is not bimodal and the amount of variation is similar to that of the A-1 and A-2 instars. The widths of the valves are distributed bimodally (Fig. 6). This may indicate that the variation in adult specimens is sexual dimorphism, or it may stem from life in an unstable environment and time-averaging of the fossils. It is unfeasible to speculate on sexual dimorphism and the nature of the variability in *C. ovata* n. sp. and *C. triangulata* n. sp. until further information is available from study of larger collections that include other localities.

EVOLUTIONARY AFFINITY
Muscle-scar pattern, overlap of the hinges and free margins, ornamentation and shapes of species of *Carbonita,* along with their environment of deposition, have been used to establish their evolutionary affinities to other known ostracodes. Evolutionary affinities with the Superfamilies Cytheroidea (Knight, 1928), Cypridoidea (Scott & Summerson, 1943; Swain, 1961, 1976) and Healdioidea (Sohn, 1985) have been suggested. Species of the Superfamily Darwinuloidea and the Late Palaeozoic genera *Whipplella* Holland, 1934, and *Gutschickia* Scott, 1944a, also have superficial similarities to some species of Carbonitidae (see Table 1). Although these taxa have not been suggested as ancestral to the carbonitids, Anderson (1970) and Bless & Pollard (1973) suggested that the genera *Whipplella* and *Gutschickia* are synonymous with *Carbonita.*

Superfamily	Range	Overlap ventral margin	Muscle-scar pattern
Carbonitidae	Carboniferous–Permian	RV over LV	Circular outline with secondary scars
Cypridoidea	Triassic–Holocene	Both	Non-linear and non-radial pattern of secondary scars
Cytheroidea	Ordovician–Holocene	Both	Vertical rows of secondary scars
Darwinuloidea	Carboniferous–Holocene	RV over LV	Circular outline with elongated secondary scars
Healdioidea	Devonian–Cretaceous	LV over RV	Circular outline with secondary scars
Uncertain Superfamily *Gutschickia*	Carboniferous–Permian	RV over LV	Circular outline with secondary scars
Uncertain Superfamily *Whipplella*	Carboniferous–Permian	LV over RV	Circular outline with elongated secondary scars

Table 1. Summary of ranges and morphological characteristics of Carbonitidae, Cypridoidea, Cytheroidea, Darwinuloidea, Healdioidea, *Gutschickia* sp., *Whipplella* sp.

The value of muscle scars in the systematics of these Ostracoda has been debated. Scott (1944b) argued that muscle scars, when present, vary insignificantly within genera, whereas Gramm *et al.* (1972) found healdiid's muscle scars to be monotypic at the family level. Kristan-Tollmann (1977) judged that because fossil ostracodes have few characteristics, the muscle-scar pattern is of primary importance in taxonomic determination. Muscle-scar patterns of *Bairdia* McCoy, 1844, have changed little since the Carboniferous (Sylvester-Bradley, 1950). Alternatively, Smith (1964) found considerable variation in muscle scars among specimens of *Cypridopsis vidua* and *Chlamydotheca arcuata* Sars, 1901, and judged that they should not be used in classification.

Muscle scars of a few specimens of *Carbonita pungens* (Pl. 1, fig. 5) and *C. triangulata* n. sp. (Pl. 1, fig. 14) were observed and used to evaluate tentatively the evolutionary affinities. The muscle-scar pattern has an almost circular outline containing smaller secondary muscle scars within it (Figs 7a, c). Poor preservation of the muscle scar made it difficult to determine the number and shape of the secondary muscle scars, but they appear to be rounded to elongated (Figs 7b, d). Anderson's (1970) illustration of the muscle-scar pattern of *Carbonita* shows peripheral scars surrounding a few central scars (Fig. 8a).

Sohn (1985) suggested that *Carbonita*'s muscle-scar pattern resembles those of the Healdioidea. Pre-Carboniferous healdiid muscle-scar patterns are known only from a single Early Devonian species (Gramm, 1987). This species has a circular muscle-scar pattern with convex rows of 7–9 secondary muscle scars (Fig. 8b). Carboniferous and Permian healdiids have a circular muscle scar with many secondary muscle scars (Gramm *et al.*, 1972; Kristan-Tollmann, 1977) (Fig. 8c). The secondary muscle scars can be divided into two groups: a central group of 6–8 secondary scars that vary in arrangement and a peripheral group that varies in arrangement and also in number (Gramm *et al.*, 1972). The muscle scar of healdiids, as is true of *Carbonita* and many other kinds of ostracodes, is located slightly anterior of the median (Scott, 1944b).

The Superfamilies Cytheroidea and Cypridoidea both contain freshwater species and have been suggested as having evolutionary relationships to carbonitids (Knight, 1928; Scott & Summerson, 1943; Swain, 1961, 1976). The muscle scars of both superfamilies differ from carbonitids in being not arranged
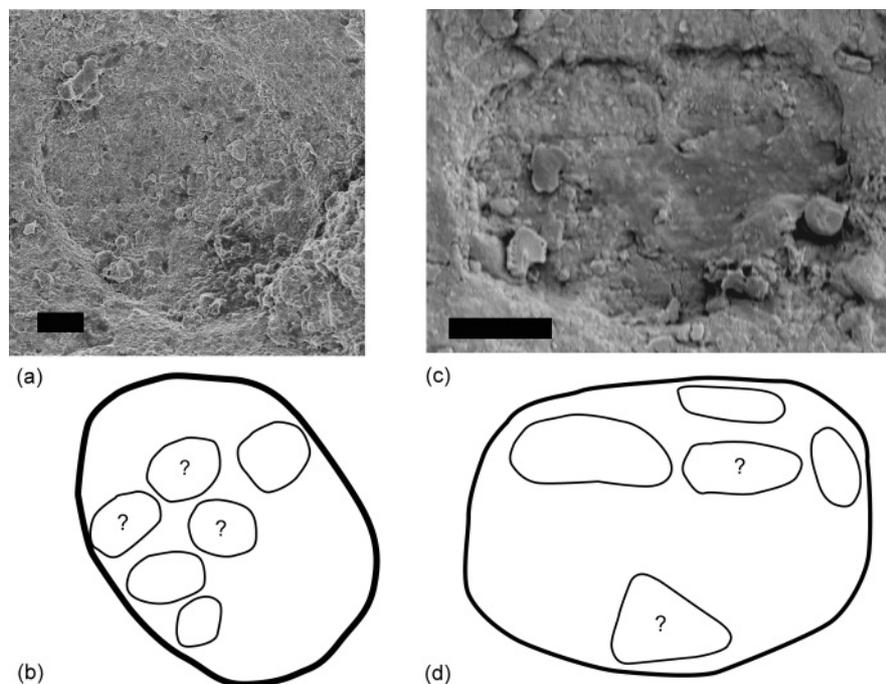
Fig. 7. Muscle-scar patterns and suggested secondary muscle scars. Scale bars represent 10 μm. (**a**, **b**) *Carbonita triangulata* n. sp.; (**c**, **d**) *C. pungens*.
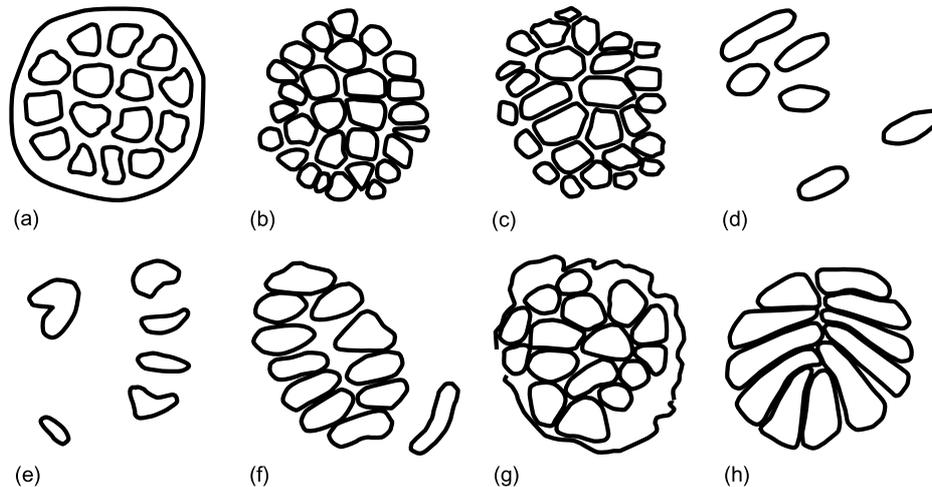
Fig. 8. Muscle-scar patterns of *Carbonita* and genera that have been considered to have evolutionary affinities with *Carbonita*. (**a**) *Carbonita* sp., redrawn from Anderson (1970, fig. 1g). (**b**) *Healdia?* *obtusa* (Abushik, 1971), Lower Devonian, redrawn from Gramm (1987, fig. 1). (**c**) *Bythocyproidea* sp., Mississippian, redrawn from Gramm *et al.* (1972, fig. 1). (**d**) *Cypridopsis vidua* (Müller, 1776), Holocene, redrawn from Moore (1961, fig. 21). (**e**) *Cythere lutea* (Brady & Norman, 1889), Holocene, redrawn from Moore (1961, fig. 185). (**f**) *Whipplella* sp., Permian, redrawn from Sohn (1977, fig. 1). (**g**) *Gutschickia* sp., Pennsylvanian, redrawn from Sohn (1977, fig. 1). (**h**) *Darwinula stevensoni* (Brady & Robertson, 1870), Holocene, redrawn from Sohn (1976, pl. 3).

circularly. Cyprid muscle-scar patterns contain a cluster of scars that is not radially or linearly arranged (Swain, 1961) (Fig. 8d), while cytherids have typically a nearly vertical row of four scars with a few anterior scars (Howe & Sylvester-Bradley, 1961) (Fig. 8e). Scars of both these superfamilies are less complex than the scars of healdiids and carbonitids.

Freshwater species of Carbonitidae, *Whipplella*, *Gutschickia* and Darwinuloidea all evolved during the Late Palaeozoic and have broadly similar muscle-scar patterns. The muscle-scar pattern of *Whipplella* comprises radially arranged, elongated secondary muscle scars (Fig. 8f) and resembles that of *Suchonella* Spizharsky, 1937 (Sohn, 1977). The muscle-scar pattern of *Gutschickia* is an almost circular outline containing smaller secondary muscle scars (Sohn, 1977) (Fig. 8g). The muscle-scar pattern of *Darwinula* Brady & Robertson, 1885, consists of up to 12 palmate scars that are unequal in shape (Sohn, 1976) (Fig. 8h).

The muscle-scar pattern of carbonitids resembles closely those of Healdioidea and not those of Cytheroidea and Cypridoidea, thus suggesting that healdiids are closer evolutionary ancestors of carbonitids. The similarities in muscle-scar pattern of all the Late Palaeozoic freshwater genera, even those that have not been regarded as Carbonitidae, suggest also a close evolutionary affinity.

Another feature of Late Palaeozoic freshwater ostracodes to be used in classification is the valve overlap. Holland (1934) used valve overlap to distinguish species of *Whipplella* from *Carbonita*. Differences of valve overlap, however, may not be a good taxonomic indicator. Reversals are known to occur in Cytheroidea, Cypridoidea and Bairdioidea Sars, 1888, both among genera and within species (R. C. Whatley, pers. comm., 2004) and in *Carbonita* (Bless & Pollard, 1973).

Valves of carbonitids have generally the right valve overlapping the left valve along the venter (Jones & Kirkby, 1879; Anderson, 1970; Bless & Pollard, 1973), with the exception of most specimens of *C. pungens*, which have the opposite pattern

(Bless & Pollard, 1973). Darwinulids (Swain, 1961) and *Gutschickia* (Scott, 1944a) have the same overlap pattern as carbonitids, while in healdiids (Shaver, 1961) and *Whipplella* (Holland, 1934) the left valve overlaps the right. Cyprids and cytherids have both patterns of overlap. In the dorsum along the hinge, the left valve of *Carbonita* overlaps the right valve (Kellett, 1935; Anderson, 1970; Bless & Pollard, 1973). The same pattern of dorsal overlap occurs in *Gutschickia* (Scott, 1944a), but *Whipplella* has the reverse overlap pattern, right valve over left valve (Holland, 1934).

Whether *C. pungens* belongs to the genus *Carbonita* or *Darwinula* has been debated. The general left over right valve overlap is the reverse of most *Carbonita* and *Darwinula* species, and it lacks also a dorsal overlap at the hinge, characteristic of *Carbonita*. The muscle-scar pattern of *C. pungens* has not been observed previously. Cooper (1946) reclassified *C. pungens* as *Darwinula pungens* after reviewing Pennsylvanian specimens from Illinois. His reclassification was based on the maximum valve overlap being around the ends, not around the ventral margin, and lack of a dorsal overlap at the hinge – both characteristics of carbonitids. His specimens' heights and lengths are larger than those of other *C. pungens*. Anderson (1970) retained *C. pungens* in the genus *Carbonita* but regarded Cooper's *D. pungens* to be not synonymous with *C. pungens* because the right valve overlapped the left valve along all free margins. Pollard (1966) and Bless & Pollard (1973) disagreed with Anderson and regarded Cooper's specimens of *D. pungens* as *Carbonita pungens*, citing that the variance was the result of the structural simplicity of a small, thinly shelled species. Other Late Palaeozoic *Darwinula* species have been recognized from West Virginia (Sohn, 1976, 1985) and Virginia (Sohn, 1985) and have a typical darwinulid muscle-scar pattern. Some *Darwinula* species from Virginia are larger than *C. pungens*. Without being able to observe the muscle-scar pattern of *C. pungens*, its difference, if any, from *Darwinula* could not be assessed.

PALAEOENVIRONMENTAL INDICATIONS

The presence of *Carbonita* species, charophytes [*Stomochara moreyi* (Peck, 1934)], lungfishes (*Gnathorhiza* sp.) and lysorophid amphibians (*Brachydectes elongates* Wellstead, 1991) and the absence of marine fossils in the green mudstone lens in the Speiser Shale indicate a freshwater environment, not a tidally influenced marine mudflat, as suggested previously (Schultze, 1985). Laterally adjacent to the mudstone lens is a red palaeosol (Hembree *et al.*, 2004) that suggests it developed on a floodplain or coastal plain near a lake or pond (Picard & High, 1972). The mudstone lens has been interpreted as a pond deposit that filled a topographic low, possibly the result of eolian deflation or a shallow temporary stream cut (Hembree *et al.*, 2004). The pond's source of freshwater is likely to have been from rainwater or overland flow as a result of local flooding (Hembree *et al.*, 2004).

The distribution of carbonitids is variable both laterally and vertically within the Eskridge pond. There is no evidence of pooling of specimens in the lysorophid burrows or of the accumulation of specimens at desiccation surfaces. The variable distribution is probably the result of abiotic factors of wind or water, predation, a combination of both, or poor preservation.

Many of the specimens are nested, with small instars inside larger instars or adults. Often only two specimens are nested, but in some instances three or four specimens are nested. Commonly the same species are nested with each other, but occasionally two species are nested together. Lane (1964) noticed similar nesting of carbonitid valves in other Lower Permian rock units in Kansas. The nesting could be the result of water or wind influences or such biotic factors as stacking within the digestive tract of a predator.

The Eskridge samples produced few adult specimens and no specimens of instars before A-3. This could be the result of poor preservation or of their being too rare to occur in the samples. The dearth of adult specimens could also be the result of an unstable environment. The small size and isolation of the pond would have made it sensitive to local fluctuations in seasonal climate (Picard & High, 1972), producing an unstable environment for the carbonitids. Hembree *et al.* (2004) observed three subaerial exposure surfaces with desiccation features and lysorophid aestivation burrows within the pond lens, suggesting that these surfaces formed during drying episodes of the pond during dry seasons. Drying of the pond would have affected water quality and chemistry, including ionic strength, temperature, reduction–oxidation potential and pH. Some modern freshwater ostracods species can be sensitive to temperature changes (Echols *et al.*, 1975; Delorme, 1990, 1991) and specific conductivity and redox potential of the solution (J. L. Castle, pers. comm., 2004). A stressful and unstable environment may have caused the Eskridge carbonitids to have high juvenile mortality rates, dwarfism, or, less likely, early sexual maturity (Bless & Pollard, 1975).

A few other assemblages of carbonitids have been described from the Cisuralian of Kansas (Lane, 1964; Peterson & Kaesler, 1980). Lane (1964) found *Carbonita* associated commonly with darwinulids, fish teeth and scales, and *Geisina* Johnson, 1936, a brackish-water ostracode genus. They occurred also less commonly with *Gutschickia* and with charophytes. Lane (1964) interpreted the assemblages with darwinulids, charophytes and

fish teeth and scales as occurring in freshwater deposits. The assemblages with *Geisina* were interpreted as being from freshwater to slightly brackish-water environments. He observed also that the assemblages of carbonitids were associated more commonly with green shales than red ones, suggesting that they were deposited in environments characterized by reduction of mud in a semi-permanent pond of freshwater or brackish water.

Peterson & Kaesler (1980) collected an assemblage of six species of *Carbonita* from Upper Pennsylvanian deposits. They inferred the lagoon and tidal-mudflat sediments in which the assemblage was deposited to have been influenced strongly by influx of freshwater. One species, *C. inflata,* was abundant in the freshwater deposits but occurred commonly also in nearshore environments, indicating either tolerance of saline conditions and the ability to live in a variety of environments or that their carapaces were transported into these environments. Re-examination of specimens they identified as *C. inflata* show them to be conspecific with *C. ovata* n. sp.

CONCLUSIONS

The collection of four species of *Carbonita* from a Cisuralian pond deposit provides new and supporting information to the solution of problems associated with ontogeny, systematics, evolutionary affinities and palaeoenvironment indicators.

1. The assemblage of carbonitids, lungfish, lysorophids and charophytes in a mudstone lens indicates a freshwater pond environment, which agrees with the environmental interpretations of Hembree *et al.* (2004).
2. The dearth of adult specimens of *Carbonita* suggests a stressful and unstable environment. Stressful environmental conditions may have favoured either dwarfism or a high juvenile mortality rate.
3. The circular muscle-scar pattern of *Carbonita* with secondary muscle scars and its location anterior of the median suggest a close affinity to the healdiids, as Sohn (1985) proposed.
4. Differences in muscle-scar pattern and geological ranges indicate no close affinity to either cytherids or cyprids as proposed by Knight (1928) and Scott & Summerson (1943), respectively.
5. The circular muscle-scar patterns of *C. pungens* are the first to be described for the species, but the arrangement of the secondary muscles could not be ascertained. The carapace of *C. pungens* is similar in shape to that of the darwinulids, but additional study of specimens with better-preserved muscle scars is essential to determining their affinity.
6. The posterior widths of adult specimens of *C. ovata* n. sp. and *C. triangulata* n. sp. indicate a bimodal distribution, suggestive of sexual dimorphism in these species.

SYSTEMATIC PALAEONTOLOGY

Repository. Types, figured specimens and other specimens studied are housed in the Division of Invertebrate Paleontology of the University of Kansas Natural History Museum and Biodiversity Research Center as specimens KUMIP 1,136,671 to 1,137,077. Specimens with the prefix NHM are in the Natural History Museum, London.

Phylum **Arthropoda** Siebold & Stannius, 1845
Class **Crustacea** Pennant, 1777
Subclass **Ostracoda** Latreille, 1806
Order **Podocopida** Müller, 1894
Suborder **Metacopina** Sylvester-Bradley, 1961
Superfamily **Healdioidea** Harlton, 1933
Family **Carbonitidae** Swain, 1976
Genus *Carbonita* Strand, 1928

Type species. *Carbonia agnes* Jones, 1870; designated subsequently by Bassler & Kellett, 1934, p. 237.

Diagnosis. Anderson (1970, p. 74) emended the diagnosis of *Carbonita* as follows:

Subovate, ovate, or elongate-ovate carapace narrowest and lowest at anterior end. Right valve larger (*vice versa* in inverse forms) overlapping the left ventrally and to a less extent anteriorly and posteriorly. Both valves swollen dorsally and extending above the hinge-line; smaller valve extending higher than the larger. Hinge-line straight and occupying the middle third of valve. Adductor muscle attachment a number of small translucent areas situated in a circular pit. Carapace frequently showing a narrow, sinuous internal thickening running vertically across behind the pit, sometimes also in front. The outer surface of the carapace may be smooth, finely punctate, striated, or reticulate, but sometimes only the inner surface is punctate. Hinge consisting of a shallow groove in the smaller valve accommodating a simple adont ridge in the larger valve.

Carbonita evelinae (Jones, 1870)
(Pl. 1, figs 1–3)

1870 *Carbonia evelinae* Jones: 220, pl. 9, fig. 4.
1870 *Carbonia agnes rugulosa* Jones: 220, pl. 9, fig. 8.
1870 *Carbonia agnes subrugulosa* Jones: 220, pl. 9, fig. 10.
1934 *Carbonita evelinae* (Jones); Bassler & Kellett: 237.
1943 *Hilboldtina evelinae* (Jones); Scott & Summerson: 670.
1943 *Hilboldtina multiplicata* Scott & Summerson: 670, pl. 1, figs 22–25.
1957 *Hilboldtina evelinae* (Jones); Copeland: 28, pl. 1, figs 5–7.
1966 *Carbonita evelinae* (Jones); Pollard: 686, fig. 7.
1970 *Carbonita evelinae* (Jones); Anderson: 78, pl. 7, figs 6–12.
1973 *Carbonita evelinae* (Jones); Bless & Pollard: 32, fig. 6, pl. 1, figs 1–9.

Diagnosis. A species of *Carbonita* characterized by an ovate carapace covered externally with fine longitudinal striae formed by rows of closely set elongated punctae.

Lectotype. Adams Collections No. 8, NHM. In. 56370, specimen marked 9. Selected by Anderson (1966, p. 693).

Material. Ten unbroken valves including five A-1 instars, three A-2 instars and two A-3 instars from eight samples. KUMIP 1,136,686 to 1,136,689 and 1,136,694 to 1,136,716.

Locality. Road cut 2 km east of Eskridge, Kansas, from the Cisurialian Speiser Shale, samples from a green, carbonate-rich mudstone and claystone lens, approximately 10 m above the base.

Description. Carapace ovate to elongate. Dorsal margin slightly arched; ventral margin slightly concave to convex. Left valve slightly overlapping of right valve at hinge; right valve strongly overlapping left valve along free margin, especially ventrally. Anterior end rounded; posterior end pointed more acutely. Dorsal view ovate, greatest width medial to posterior. Anterior view rounded. Surface ornamentation elongated punctae.

Dimensions. A-1 instars, mean height 0.39 mm, standard deviation 0.04 mm; mean length 0.61 mm, standard deviation 0.04 mm. A-2 instars, mean height 0.33 mm, standard deviation 0.00 mm, mean length 0.51 mm, standard deviation 0.01 mm. A-3 instars, mean height 0.22 mm, standard deviation 0.01 mm; mean length 0.37 mm, standard deviation 0.01 mm.

Distribution. Cisuralian, Kansas; Upper Westphalian A, Netherlands (Bless & Pollard, 1973); Westphalian C, Britain (Bless & Pollard, 1973; Anderson, 1970); Westphalian D, Britain (Anderson, 1970); Westphalian A, Nova Scotia (Copeland, 1957); and Pennsylvanian of eastern USA (Scott & Summerson, 1943).

Remarks. The largest specimens from the Speiser Shale are smaller than Bless & Pollard's (1973) adults, perhaps for reasons discussed earlier.

Carbonita pungens (Jones & Kirkby, 1867)
(Pl. 1, figs 4–6)

1867 *Cythere pungens* Jones & Kirkby: 222.
1879 *Carbonia pungens* (Jones & Kirkby): 37, pl. 3, figs 21–23.
1934 *Carbonita pungens* (Jones & Kirkby); Bassler & Kellet: 239.
1957 *Carbonita pungens* (Jones & Kirkby); Copeland: 26.
1966 *Carbonita pungens* (Jones & Kirkby); Pollard: 689.
1970 *Carbonita pungens* (Jones & Kirkby); Anderson: 98, pl. 18, figs 81–86.
1973 *Carbonita pungens* (Jones & Kirkby); Bless & Pollard: 29, fig. 4.

Diagnosis. A species of *Carbonita* characterized by a small, smooth elongated carapace. Anterior margin acutely pointed. Dorsal margin arched to convex.

Lectotype. NHM I. 1731. T. R. Jones Coll. Selected by Anderson (1966, p. 694).

Material. 18 unbroken valves including 1 adult and 17 A-1 instars from 8 samples. KUMIP 1,136,690 to 1,136,693 and 1,136,717 to 1,136,744.

Locality. Same as for *C. evelinae*.

Description. Carapace elongate. Dorsal margin arched; ventral margin straight. Left valve slightly overlapping of right valve along free margin. Anterior end rounded to pointed; posterior end rounded. Dorsal view ovate, greatest width medial to posterior. Anterior view rounded. Surface ornamentation smooth. Muscle-scar pattern circular, arrangement of secondary muscle scars not ascertained.

Dimensions. Adult, height 0.28 mm; length 0.65 mm. A-1 instars, mean height 0.20 mm, standard deviation 0.02 mm, mean length 0.40 mm, standard deviation 0.03 mm.

Distribution. Cisuralian, Kansas; Upper Westphalian A, Netherlands; Lower Westphalian C, Britain (Bless & Pollard, 1973); Visean and Namurian of Scotland; Westphalian A-D, Britain (Pollard, 1966; Anderson, 1970); Limburg (Bless, 1967); Westphalian A and B, Nova Scotia (Copeland, 1957); and France (Pruvost, 1911).

Remarks. The left valve over right valve overlap is the reverse of typical *Carbonita*. The elongated carapace shape and valve overlap resemble closely those of the Permian *Darwinula hollandi* Scott, 1944a. Scott (1944a), however, found no muscle scars of *D. hollandi*.

Carbonita ovata n. sp.
(Pl. 1, figs 7–12)

1980 *Carbonita inflata* (Jones & Kirkby, 1879): Peterson & Kaesler

Derivation of name. From the characteristic ovate shape in lateral view.

Diagnosis. A species of *Carbonita* characterized by a smooth ovate carapace.

Holotype. KUMIP 1,136,671.

Paratypes. KUMIP 1,136,672 to 1,136,678 and 1,136,745 to 1,136,977.

Material. 101 unbroken valves including 16 adults, 38 A-1 instars, 39 A-2 instars and 8 A-3 instar from 8 samples.

Locality. Same as for *C. evelinae*.

Description. Carapace ovate. Dorsal margin convex to slightly arched; ventral margin convex. Left valve slightly overlapping of right valve at hinge; right valve strongly overlapping left valve along free margin, especially ventrally. Anterior end rounded; posterior end more broadly rounded. Dorsal view ovate, greatest width posterior of median. Anterior view rounded. Relative shape of adults and A-1 similar. Possible sexual dimorphism in adults with presumed female having greater posterior width. Surface smooth.

Dimensions. Adults, mean height 0.39 mm, standard deviation 0.03 mm; mean length 0.64 mm, standard deviation 0.04 mm. A-1 instars, mean height 0.32 mm, standard deviation 0.02 mm; mean length 0.50 mm, standard deviation 0.03 mm. A-2 instars, mean height 0.25 mm, standard deviation 0.02 mm, mean length 0.39 mm, standard deviation 0.03 mm. A-3 instar, mean height 0.20 mm, standard deviation 0.01 mm; mean length 0.31 mm, standard deviation 0.01 mm.

Distribution. Upper Pennsylvanian to Cisuralian of Kansas.

Remarks. The carapace of *C. ovata* n. sp. is shaped similarly to *C. inflata* (Jones & Kirkby, 1879) but lacks the punctae ornamentation and the specimens from the current study are smaller. Widths of the posterior portions of adult specimens are distributed bimodally, suggesting sexual dimorphism. All specimens identified by Peterson & Kaesler (1980), which were from Upper Pennsylvanian rocks of Kansas, belong to this new species.

Carbonita triangulata n. sp.
(Pl. 1, figs 13–16)

Derivation of name. From the characteristic triangular shape.

Diagnosis. A species of *Carbonita* characterized by a smooth triangular carapace.

Holotype. KUMIP 1,136,680.

Paratypes. KUMIP 1,136,681 to 1,136,685 and 1,136,978 to 1,137,077.

Material. 53 unbroken valves including 13 adults, 19 A-1 instars, 19 A-2 instars, and 2 A-3 instar from 8 samples.

Locality. Same as for *C. evelinae*.

Description. Carapace triangular. Dorsal margin arched; ventral margin concave. Left valve slight overlap of right valve at hinge; right valve strongly overlapping left valve along free margin, especially ventrally. Anterior end rounded; posterior end more acutely pointed. Dorsal view ovate, greatest width median to posterior. Anterior view rounded. Relative shape of adults and A-1 similar. Possible sexual dimorphism in adults with presumed female having greater posterior width. Surface ornamentation smooth. Muscle-scar pattern circular, arrangement of secondary muscle scars not ascertained.

Dimensions. Adults, mean height 0.38 mm, standard deviation 0.05 mm; mean length 0.62 mm, standard deviation 0.06 mm. A-1 instars, mean height 0.31 mm, standard deviation 0.01 mm; mean length 0.50 mm, standard deviation 0.02 mm. A-2 instars, mean height 0.25 mm, standard deviation 0.02 mm, mean length 0.39 mm, standard deviation 0.03 mm. A-3 instar, mean height 0.19 mm, standard deviation 0.01 mm; mean length 0.28 mm, standard deviation 0.02 mm.

Distribution. Cisuralian of Kansas.

Remarks. The carapace is shaped similarly to *C. subangulata* (Jones & Kirkby, 1879). *C. subangulata*, however, is known only from Mississippian rocks and the specimens from the current study are appreciably smaller than *C. subangulata* described in the literature (Anderson, 1970), suggesting that the two are not conspecific. Widths of the posterior portions of adult specimens are distributed bimodally, indicating sexual dimorphism.

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