SYSTEMATICS OF SOME LATE ORDOVICIAN ENCRINURINE TRILOBITES FROM LAURENTIAN NORTH AMERICA

DAVID K. MOSS[1] AND STEPHEN R. WESTROP[2]

[1]Department of Earth Sciences, Syracuse University, Syracuse, NY 13244, USA, <dkmoss@syr.edu>; and
[2]School of Geology and Geophysics, University of Oklahoma, Norman, OK 73072, USA, <swestrop@ou.edu>

ABSTRACT—Classification and relationships of the Ordovician encrinurines *Frencrinoides* Lespérance and Desbiens and *Walencrinoides* Lespérance and Desbiens are poorly understood, with little evidence for monophyly of either genus. We revise the type species of both genera, *F. capitonis* (Frederickson) and *W. rarus* (Walcott), using new and archival material. We explore their species composition and phylogenetic relationships with a parsimony analysis that includes 17 well-documented ingroup species that can be coded readily, and which is rooted with *Encrinuroides regularis* Parnaste, the oldest known encrinurine. The results support monophyly of *Frencrinuroides* and *Walencrinuroides*, albeit with more limited species membership than proposed by Lespérance and Desbiens. Previous suggestions that both *E. uncatus* Evitt and Tripp and *E. neuter* Evitt and Tripp should be assigned to *Erratencrinurus* Kruger are also supported by our analysis, as is monophyly of *Physemataspis* Evitt and Tripp. New species are *W. rolfi* and *W. tremblayi*.

INTRODUCTION

ENCRINURINES ARE persistent, albeit generally rare (e.g., Chatterton and Ludvigsen, 1976, table 1, fig. 4), elements of Middle and Upper Ordovician trilobite faunas of Laurentian North America. Traditionally, virtually all species were assigned to *Encrinuroides* Reed, 1931 (e.g., Tripp, 1962, 1967, 1979, 1980; Shaw, 1968, 1974; Chatterton and Ludvigsen, 1976; Evitt and Tripp, 1977; Ludvigsen, 1979; DeMott, 1987). However, over the last 15 years, it has become apparent that *Encrinuroides* is not monophyletic, although attempts to revise the genus, notably by Lespérance and Desbiens (1995), who established *Frencrinuroides* and *Walencrinuroides* to accommodate several species, have met with mixed success (Edgecombe et al., 1998; Parnaste, 2006). It is far from clear whether *Frencrinuroides* and *Walencrinuroides* are clades, and the availability of abundant material of the type species of the former, *Encrinuroides capitonis* Frederickson, 1964 from the Bromide Formation of Oklahoma, and undescribed sclerites from the Lebanon Limestone of Tennessee that we assign to the type species of the latter, *Ceraurus rarus* Walcott, 1877, prompted us to take a fresh look at both genera in the context of a new phylogenetic analysis (Fig. 1). This work includes restudy of relevant type material as well as new specimens from Oklahoma and Tennessee.

MATERIAL AND STRATIGRAPHIC SETTING

Eastern Tennessee.—New material of *Walencrinuroides rarus* (Walcott) was collected from the Lebanon Limestone near Lebanon, Tennessee, which lies in the Nashville Dome, a topographic feature located between the Cincinnati Arch and the Appalachian Foreland Basin that records the peripheral bulge of the Taconic Orogeny (Beaumont et al., 1988). The sclerites were collected from a small abandoned quarry and associated road cut (Nashville Speedway section; Moss, 2012) along TN 452 (Bill France Boulevard), 0.5 km west of its intersection with TN 231 (Murfreesboro Road) and about 4 km southeast of the Nashville Speedway, in southern Wilson County.

A middle "massive member" of fine grainstone permits an informal, tripartite division of the Lebanon Limestone (e.g., Holland and Patzkowsky, 1998, fig. 8; their Fall Creek section is 5.5 km east of the Nashville Speedway section). The Nashville Speedway section lies in the lower member and is composed of shallow subtidal, bioclastic pack-, grain-, and rudstone with interbeds of lenticular mudstone and packstone (Moss, 2012). The trilobites are part of a more diverse fauna that includes rhynchonelliform brachiopods and leperditicopid arthropods.

Graptolites indicate that the lower part of the upper informal member lies in the lower part of the *Diplograptus foliacious* Zone (Goldman et al., 2002). As such, the Lebanon can be assigned to the latter half of Sandbian Stage (stage slice Sa2 of Bergström et al., 2008). Holland and Patzkowsky (1997, 1998) assigned the entire Lebanon limestone to their M3 depositional sequence, and this is in accord with the age suggested by the graptolites. As such, *W. rarus* in Tennessee falls into the lower half of the range of the species in its type area in Wisconsin (M3–M4; see below) and overlaps in range with *Frencrinuroides capitonis* in Oklahoma (M3; see below).

Southern Oklahoma.—Much of the figured material of *Frencrinuroides capitonis* came from exposures of the Bromide Formation at a quarry in the Criner Hills, Carter County, southern Oklahoma, that has, as a result of changing ownership, been reported in the literature as the Dunn Quarry (Karim and Westrop, 2002), the Geological Enterprises Quarry (Amati and Westrop, 2004), and the Tyson Quarry (Carlucci et al., 2012); Shaw (1974, p. 49) erroneously referred to it as the Rudd Quarry. The private quarry is operated by a commercial fossil supply company, and is located about eight miles southwest of Ardmore (Carlucci et al., 2012, fig. 1). At this locality, trilobites are abundant in storm-influenced, bioclastic rudstone horizons (Karim and Westrop, 2002, fig. 5) in an approximately six-meter interval at the top of the Bromide (Carlucci et al., 2010, fig. 2). These strata have been assigned to the youngest Pooleville Member of the Bromide in most previous work (e.g., Shaw, 1974; Karim and Westrop, 2002; Carlucci et al., 2010), but analysis of the regional sequence stratigraphy (Carlucci, 2012) shows that the Pooleville Member becomes cut out down-ramp into the Southern Oklahoma Aulacogen, and exposures at the Dunn-Tyson Quarry belong to the underlying upper Mountain Lake Member. In terms of the depositional sequences defined for the Middle and Upper Ordovician succession of eastern Laurentia by Holland and Patzkowsky (1997, 1998), this interval is no younger than sequence M3 (Sandbian Stage). Other material, including the
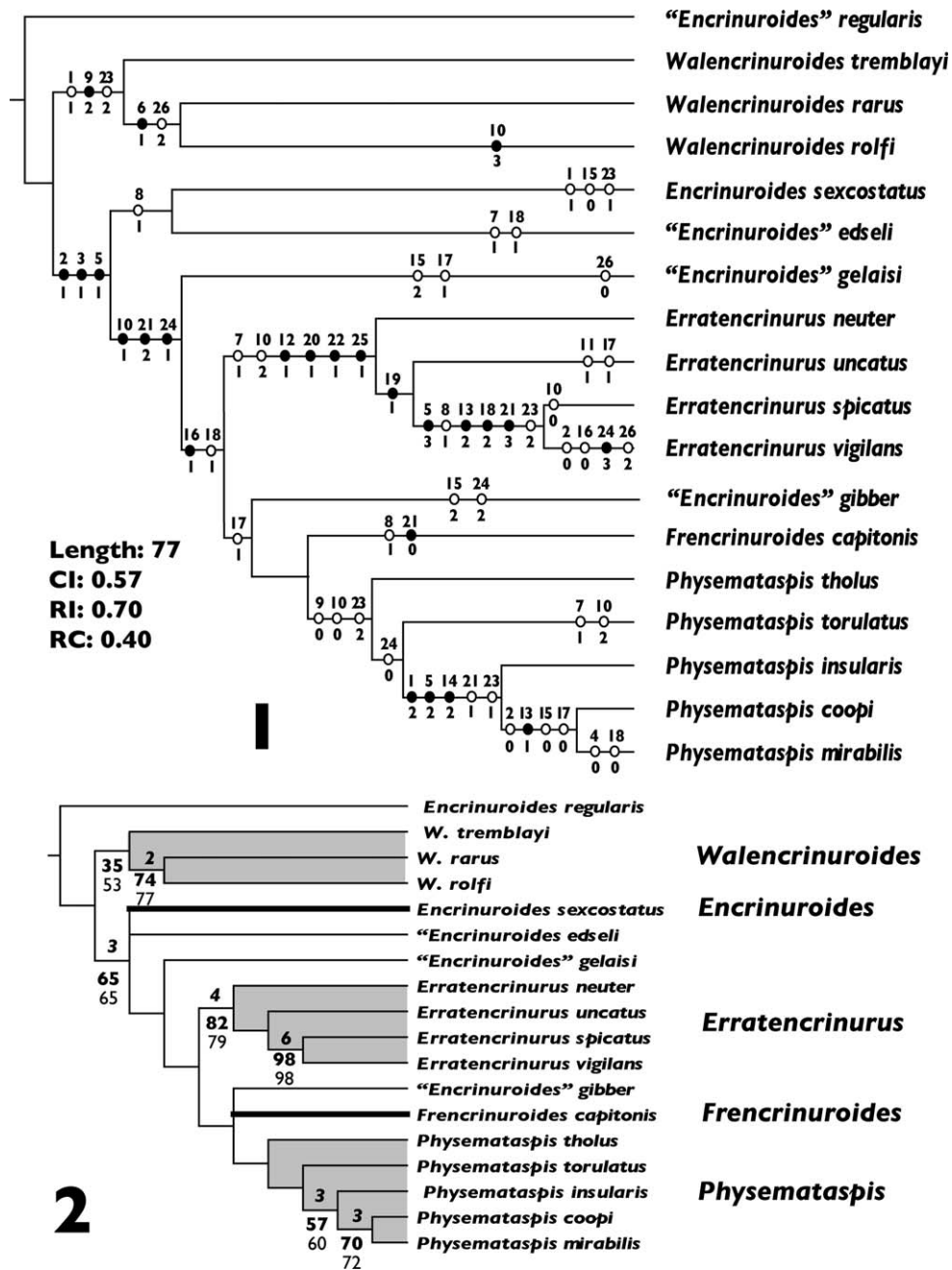
FIGURE *1*—Results of parsimony analysis of the matrix (Table 1) using a branch-and-bound search (implicit enumeration). *1*, optimized character distribution plotted on one of six equally parsimonious trees; upper numbers indicate characters, lower numbers indicate particular states (see Appendix); only unambiguous state changes (i.e., show the same transformations at the nodes under the assumptions of ACCTRAN and DELTRAN) are shown; filled circles show states that originate at a single node; open circles indicate those that show homoplasy; *2*, strict consensus of the eight trees; Bremer support >1 is indicated by the numbers in italics; bold face indicates GC support; other numbers indicate standard bootstrap support.

holotype of *F. capitonis* (Fig. 2.6–2.8), is from the upper Bromide at the well-known Rock Crossing section along Hickory Creek (Sutherland and Amsden, 1959), about 3.3 km southeast of the Dunn-Tyson Quarry. As at the latter locality, the upper Bromide was long believed to represent the Pooleville Member, but is now (Carlucci, 2012) assigned to the upper Mountain Lake Member.

Wisconsin.—The type species of *Walencrinuroides*, *W. rarus* (Walcott), is from the Plattin Subgroup of the Platteville Group (Templeton and Willman, 1963) of Wisconsin. According to DeMott (1987, p. 80), the holotype cranidium (Fig. 9.1) and associated pygidium (Fig. 9.10, 9.11; assigned originally to *Encrinurus varicostatus* Walcott, 1877) are from the Grand

Detour Formation, which lies in lower half of the subgroup (Templeton and Willman, 1963, fig. 17). Most of the other material figured by DeMott (1987, pl. 8, figs. 13–22; reillustrated here as Fig. 9.2–9.8) is from the basal Mifflin Formation of the Plattin, with one pygidium from the Quimby's Mill Formation at the top of the subgroup (DeMott 1987, pl. 11, figs. 23–25). DeMott (1987, p. 80) also records the species from the Pecatonica Formation, which underlies the Plattin, although this identification is unsupported by figured specimens. All of these occurrences are below the Deicke metabentonite, which lies at the base of the Castlewood Member of the Spechts Ferry Formation, the oldest unit of the overlying Decorah Subgroup of
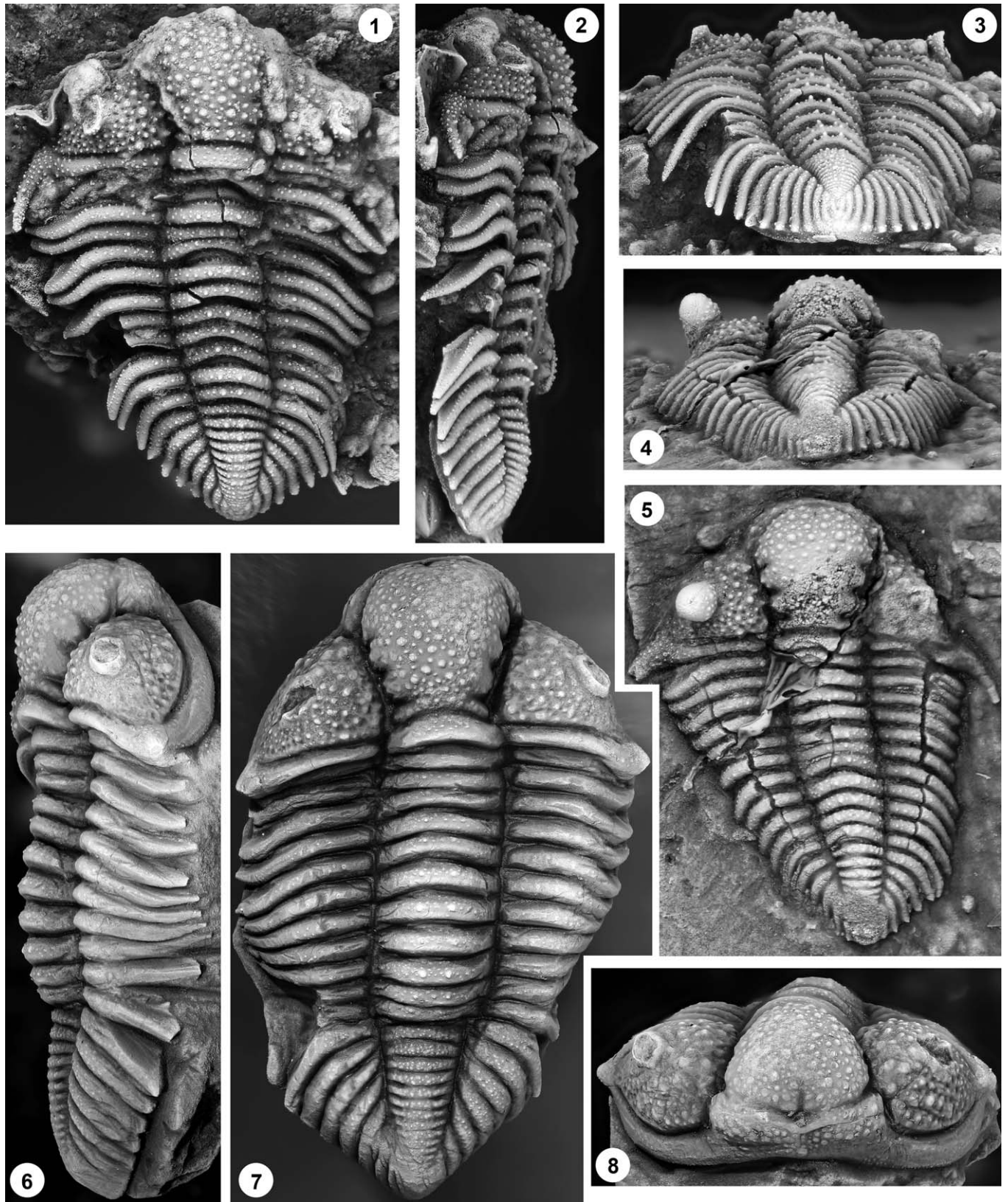
FIGURE *2—Frencrinuroides capitonis* (Frederickson, 1964), Mountain Lake Member, Bromide Formation, Criner Hills, southern Oklahoma. All exoskeletons, and all from the Dunn-Tyson Quarry except *6–8* (Rock Crossing). *1–3*, OU 221555, dorsal, lateral and posterior views, ×10; *4, 5*, OU 8066, posterior and dorsal views, ×10 (figured previously by Shaw, 1974, pl. 10, figs., 1, 2); *6–8*, OU 3412 (holotype), lateral, dorsal and anterior views, ×5.
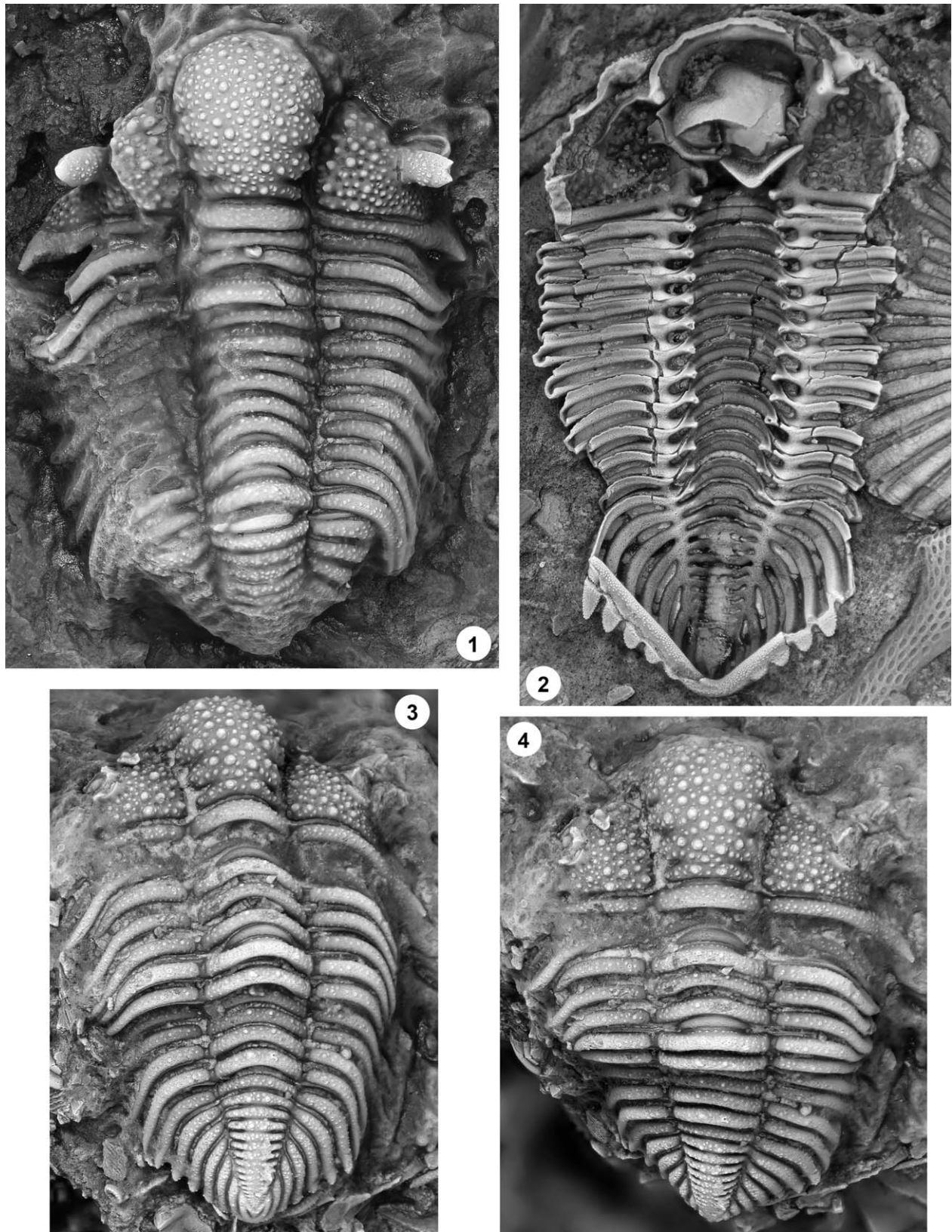
FIGURE 3—*Frencrinuroides capitonis* (Frederickson, 1964), Mountain Lake Member, Bromide Formation, Criner Hills, southern Oklahoma. All exoskeletons and all from the Dunn-Tyson Quarry. *1*, OU 12556, dorsal view, ×6; *2*, OU 12630, ventral view, including crushed and slightly displaced hypostome, ×6; *3*, *4*, OU 12631, pygidium and cranidium oriented in dorsal views, ×7.

the Galena Group (Templeton and Willman, 1963; DeMott, 1987; see Kolata et al., 1998, fig. 5 for an alternative interpretation that treats the Castlewood as the youngest unit of Plattin). This means that strata yielding *W. rarus* in Wisconsin are correlatives the M4 depositional sequence (Holland and Patzkowsky, 1997, 1998), and almost certainly extend down into M3. As such, the lower part of the range of *W. rarus* likely overlaps with the range of *F. capitonis* in Oklahoma (see above).

Eastern Canada.—For comparative purposes, we illustrate material from Quebec and Newfoundland. "*Encrinuroides*" *gelaisi* (Lespérance and Desbiens, 1995; Figs. 12, 13) is from Unit 1 of the Shipshaw Formation, Lac Saint-Jean, Quebec. This unit is a succession of shale and interbedded wackestone, packstone, and grainstone that is up to 15 m in thickness (Desbiens and Lespérance, 1989). Desbiens and Lespérance (1989, p. 1194) considered the lower Shipshaw to be of Edenian age, which translates into mid-Katian of the global stadial nomenclature (e.g., Bergström et al., 2008, fig. 1).

The type and other material (see Edgecombe and Chatterton, 1990, p. 823) of "*Encrinuroides*" *gibber* (Dean, 1979) was collected from the Lourdes Limestone (Long Point Group) along the southeast coast of Long Point, Port au Port Peninsula, western Newfoundland. The collecting locality (GSC locality 84824; Dean, 1979, p. 3) lies within the in the upper part of the middle (member II) of three informal members of the Lourdes Limestone established by Bergstrom et al. (1974), and which corresponds to the Black Duck Member of Stait and Barnes (1991). The upper Black Duck Member includes tabulate coral buildups and biostromes (Batten Hender and Dix, 2006) that form part of a highstand systems tract, and which overlies a transgressive systems track of oncoidal and skeletal carbonate sands (Batten Hender and Dix, 2008). Available biostratigraphic data (Fåhraeus, 1973; Bergström et al., 1974) indicate that the lower part of the Beach Point Member (informal member III of Bergström et al; 1974; unit E of Fåhraeus, 1973), which overlies the Black Duck Member, lies in the *Prioniodus gerdae* Subzone of the *Amorphognathus tvaerensis* Zone, suggesting that "*E.*" *gibber* is early to mid-Sandbian age, and is likely somewhat older than *F. capitonis* in Oklahoma.

PREVIOUS PHYLOGENETIC ANALYSES

Reed (1931) established *Encrinuroides*, as a subgenus of *Encrinurus*, with *E. sexcostatus* (Salter, in Phillips and Salter, 1848) as the type species; other species included were *E. varicostatus* (Walcott, 1877), *E. vannulus* (Clarke, 1894), *E. rarus* (Walcott, 1877), *E. contentus* (Reed, 1914), and *E. fallax* (Reed, 1899). Ultimately *E. varicostatus* and *E. vannulus* would be treated as junior synonyms of *E. rarus* by DeMott (1987), but the others remain valid species. Subsequent workers treated *Encrinuroides* as a distinct genus (e.g., Whittington, 1950; Shaw, 1968, 1974; Chatterton and Ludvigsen, 1976; Struz, 1980), but monophyly has been questioned for more than two decades (Edgecombe and Chatterton, 1990; Lespérance and Desbiens, 1995; Edgecombe et al., 1998; Parnaste, 2006). Reed (1931) did not provide a diagnosis for *Encrinuroides*. However, Whittington (1950) designated a complete exoskeleton as the neotype of *E. sexcostatus* and identified such characters as the presence of a preglabellar furrow and a longitudinal median furrow, an anteriorly expanded glabella with well-defined glabellar lobes, and relatively wide pygidium as diagnostic of the genus (see also Edgecombe and Chatterton, 1990, p. 821). From the 1960s to the early 1990s the number of species assigned to *Encrinuroides* increased significantly, with the description of, among others, *E. autochthon* Tripp, 1962, *E. capitonis* Fredrickson, 1964, *E. obesus* Tripp, 1965, *E. periops* Tripp, 1967, *E. polypleura* Tripp, 1967, *E. insularis* Shaw, 1968,

E. hornei Dean, 1973, *E. tholus* Evitt and Tripp, 1977, *E. torulatus* Evitt and Tripp, 1977, *E. uncatus* Evitt and Tripp, 1977, *E. neuter* Evitt and Tripp, 1977, *E. stincharensis* Reed, 1906, (see Tripp, 1979 for reillustration), *E. lapworthi* Tripp, 1980, and *Encrinurus gibber* Dean, 1979 (reassigned by Edgecombe and Chatterton, 1990).

Strusz (1980, p. 8) addressed the status of *Encrinuroides* in what was the last major, pre-cladistic assessment of Encrinurinae. He took a broad view of the genus, although his phylogenetic trees (e.g., Strusz, 1980, fig. 9) also showed that he regarded some species to be more closely related (and indeed ancestral to) to species of *Physemataspis* Evitt and Tripp, 1977 and *Erratencrinurus* Krueger, 1972. Strusz's work remains the most recent attempt at a comprehensive analysis of the subfamily, and his hypotheses of relationships were a starting point for subsequent work (e.g., Edgecombe and Chatterton, 1990).

Edgecombe and Chatterton (1990) conducted the first parsimony analysis of Encrinurinae, albeit focused on a small subset of species. With *E. torulatus* as an outgroup, they succeeded in diagnosing monophyletic *Curriella* and *Encrinurus* but their results indicated that *Encrinuroides* was paraphyletic. A subsequent analysis by Lespérance and Desbiens (1995) used some of Edgecombe and Chatterton's characters in an attempt to revise *Encrinuroides*. They (Lespérance and Desbiens, 1995, fig. 1, p. 4) transferred some species to two new genera, *Walencrinuroides*, and *Frencrinuroides*. *Encrinuroides rarus* (Walcott, 1877) (although the specimens figured by Chatterton and Ludvigsen, 1976, that were used as coding sources are interpreted here as a separate species; see below) and *E. capitonis* Fredrickson, 1964 were selected as the type species for *Walencrinuroides* and *Frencrinuroides* respectively. *Walencrinuroides* was diagnosed on the basis of pygidium whose length was roughly equal to width, and included *W. gelaisi* Lespérance and Desbiens, *W. stincharensis*, *W. lapworthi*, *W. rarus*, *W. autochthon*, and *W. polypleura*. *Frencrinuroides* was named for a group of species, including *F. gibber*, *F. tholus*, *F. capitonis*, and *F. torulatus*, that shared a glabella whose width exceeds its length, a round middle body of the hypostome, and "significant" genal spines.

Edgecombe et al. (1998) updated Lespérance and Desbiens' (1995) analysis by expanding the ingroup to include *Erratencrinurus spicatus* Tripp, 1974 and a new species of *Frencrinuroides*, by rectifying some apparent coding errors in the original matrix, and by adding three new characters. The results led to a dramatic loss of resolution in the strict consensus tree, which failed to support monophyly of both *Frencrinuroides* and *Walencrinuroides*.

More recently, Parnaste (2006) was strongly critical of Lespérance and Desbiens' (1995) analysis in a paper that described a new species, *Encrinuroides regularis*, which is apparently the oldest member of Encrinurinae. She presented a valuable analysis of the morphology of Ordovician encrinurines, including assessments of character polarity using the anatomy of *E. regularis* as a guide to plesiomorphic states. Her work has influenced our analysis, and we use *E. regularis* as the outgroup instead of *E. hornei* Dean, 1973 (e.g., see Lespérance and Desbiens, 1995; Edgecombe et al., 1998). In places, Parnaste (2006, p. 158, discussion of *Walencrinuroides* and *Frencrinuroides*) seems to imply that character states present in an outgroup are disqualified as potential synapomorphies, but here we disagree. It is common for character states to originate independently at two or more nodes in a cladogram, so that the utility of characters in supporting monophyly must be evaluated on a case-by-case basis in the context of a phylogenetic
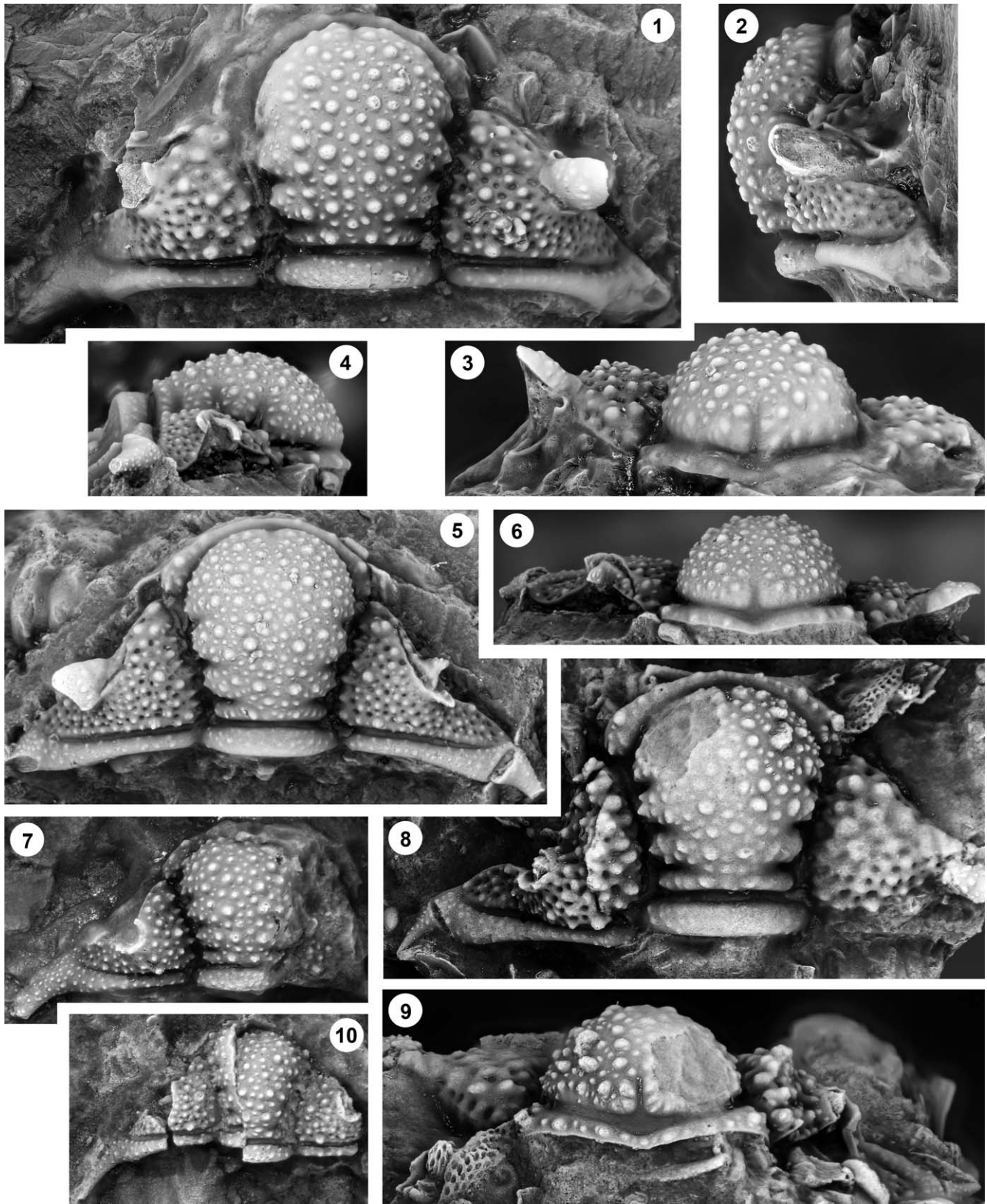
FIGURE *4*—*Frencrinuroides capitonis* (Frederickson, 1964), Mountain Lake Member, Bromide Formation, Criner Hills, southern Oklahoma. All cranidia and all from the Dunn-Tyson Quarry. *1–3*, OU 8067, dorsal, lateral and anterior views, ×9 (figured previously by Shaw, 1974, pl. 10, figs., 1, 2); *4–6*, OU 12632, lateral, dorsal and anterior views, ×10; *7*, OU 12570, dorsal view, ×12; *8, 9*, OU 12558 dorsal and anterior views, ×8.5; *10*, OU 12633, dorsal view, ×15.
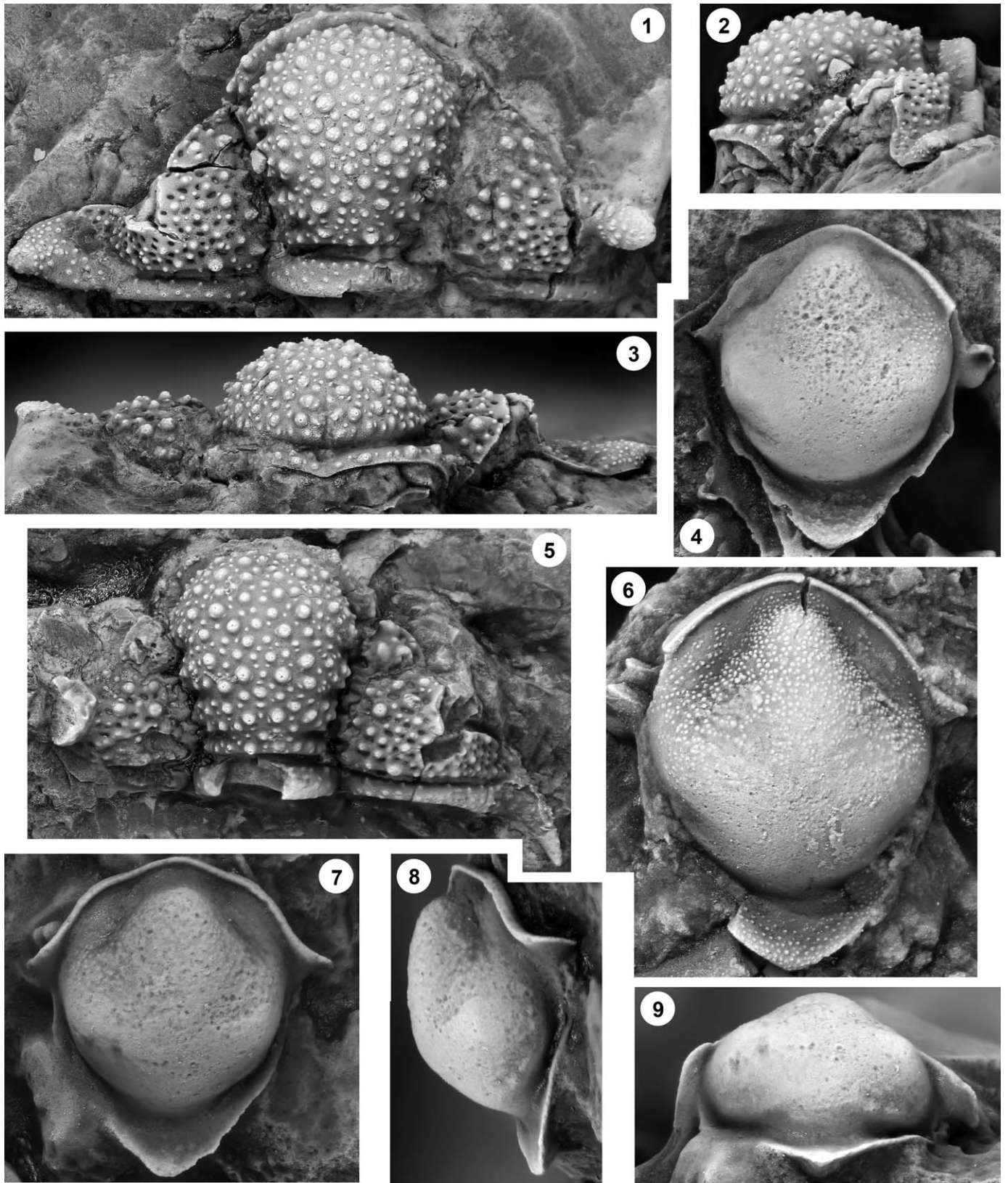
FIGURE *5—Frencrinuroides capitonis* (Frederickson, 1964), Mountain Lake Member, Bromide Formation, Dunn-Tyson Quarry, Criner Hills, southern Oklahoma. *1–3*, cranidium, OU 12634, dorsal, lateral and anterior views, ×10; *4*, hypostome, OU 8069, ventral view, ×20 (figured previously by Shaw, 1974, pl. 10, fig. 5); *5*, cranidium, OU 12635, dorsal view, ×10; *6*, hypostome, OU 12636, ventral view, ×18; *7–9*, hypostome, OU 8068, ventral, lateral and posterior views, ×20 (figured previously by Shaw, 1974, pl. 10, fig. 4).

hypothesis. In addition, her blanket dismissal of length-width relationships of sclerites as phylogenetically informative seems, to say the least, premature. This is based on a single study (Männil, 1986) that reported apparent environmentally related variation in pygidial outline. However, there is significant ontogenetic variation in pygidial outline in our material (e.g., Fig. 7.1, 7.6), and this could confound attempts to detect environmental patterns. Moreover, even if distributions do turn out to be environmentally related, they need not record ecophenotypic effects within single species. Alternative hypotheses involving geographically or environmentally arrayed groups of related species cannot be ruled out and, indeed, are supported by the growing data on phylogeography of modern animals (see Westrop and Adrain, 2007 for further discussion). At the current state of knowledge, we can see no reason to eliminate any characters from consideration in phylogenetic analyses.

TAXON SELECTION AND CODING SOURCES

Matrices used in previous phylogenetic analyses of Ordovician encrinurines (Edgecombe and Chatterton, 1990; Lespérance and Desbiens, 1995; Edgecombe et al., 1998) have been constructed largely from published images of ingroup and outgroup species. However, in many cases, species are known only from poorly illustrated, often indifferently preserved, sclerites; most have not been studied for half a century. These include virtually all of the species of "*Encrinuroides*" described by Tripp (1962, 1965, 1967, 1976, 1979) from the Ordovician terranes of the Southern Uplands of Scotland. In our view, none of these can be coded adequately from the published record. Our knowledge of many species of "*Encrinuroides*" from Laurentian North America is scarcely better, often comprising small, poorly focused or lit photographs (e.g., Shaw, 1974, pl. 9, figs. 15, 19–23, pl. 10, figs. 1–13; DeMott, 1987, pl. 11, figs. 13–25).

We maintain that progress in understanding Ordovician encrinurine phylogeny will be limited until species are documented by modern, high-resolution digital images. In this paper, we restudy species from Laurentian North America that have been included in recent analyses and, in addition to new collections, we have borrowed and refigured all type and other previously published material that can be loaned safely. These species are *Frencrinuroides capitonis*, *Walencrinuroides rarus*, "*Encrinuroides*" *gelaisi*, and "*Encrinuroides*" *gibber*, and they were coded from images in Figures 2–14. A number of other species are known only from silicified sclerites that are too fragile to be loaned but are well enough illustrated to be coded adequately from photographs in the original publications. These include sclerites assigned to *W. rarus* by Chatterton and Ludvigsen (1976) and Tremblay and Westrop (1991), which are interpreted here to record two distinct species (see below); "*Encrinuroides*" *torulatus*, "*E.*" *tholus*, "*E.*" *uncatus*, "*E.*" *neuter*, and *Physemataspis coopi* from Ordovician strata of Virginia (Evitt and Tripp, 1977); and "*E.*" *insularis* Shaw, 1968 from New York. The ingroup also includes two species of *Erratencrinurus*, *E. spicatus* (Tripp, 1974; coded from photographs accompanying the original description) and *E. vigilans* (Hall, 1847; coded from photographs in Ludvigsen, 1979, fig. 27). Although poorly known from mostly compacted and otherwise deformed material (Whittington, 1950, 1965; Price, 1974), we felt obliged to include *Encrinuroides sexcostatus*, the type species of the genus; removal of this species from the matrix has no impact on the topology of the strict consensus (Fig. 1.2), although the number of equally parsimonious trees is cut in half. Although known only from a single cranidium, we also added *P. mirabilis* Tripp, 1980 in an attempt to more fully

explore the relationship of *Physemataspis* with such species as "*E.*" *insularis*; again, omission of this species has little impact on the analysis, and the strict consensus is unchanged aside from "*E.*" *insularis* moving up-tree to become the sister of *P. coopi*. *Encrinurus regularis* Parnaste was selected as the outgroup in preference to *E. hornei* Dean, 1973 for various reasons outlined by Parnaste (2006).

CHARACTER SELECTION

Previous phylogenetic analyses by Edgecombe and Chatterton (1990), Lespérance and Desbiens (1995), and Edgecombe et al. (1998) were starting points for the compilation of characters. However, a number of the characters identified by these authors were either inapplicable to the ingroup (e.g., character 2 of Edgecombe and Chatterton, 1990, table 1) or were parsimony uninformative (e.g., character 15 of Edgecombe and Chatterton, 1990, table 1; character 16 of Lespérance and Desbiens, 1995, appendix). In other cases, we modified the original character to fit our ingroup. Finally, Parnaste's (2006) discussion of encrinurine morphology provided guidance on a number of characters that had not been used in previous analyses. A total of 26 characters were selected and are described in the Appendix.

RESULTS

The data matrix comprised 17 ingroup species, 14 binary, and 12 unordered multistate characters (Table 1). Autapomorphies of individual species were not included (except when parts of multistate characters; e.g., character 24 of Table 1) and therefore branch-collapsing rules were not enforced. Characters states that were inapplicable for some species were handled using reductive coding (Strong and Lipscomb, 1999). A branch-and-bound search (implicit enumeration), implemented with both with PAUP* (Swofford, 2001) and TNT (Golobloff et al., 2008), yielded six equally parsimonious trees (length, 77; CI, 0.57; RI, 0.70; RC, 0.40); the strict consensus tree is shown in Figure 1.2. Character optimization (Fig. 1.1) employed both PAUP* and Winclada (Nixon, 2002). About half (54%; six nodes) of the nodes of the strict consensus have Bremer support values of 2 or more, and 64% (seven nodes) of nodes also have GC and/or conventional bootstrap support values that exceed 50% (Fig. 1.2).

The results support monophyly of *Walcrinuroides*, albeit in a far more limited sense than as used by Lespérance and Desbiens (1995). In our analysis, the genus comprises the type species, *W. rarus* (Walcott) and two closely related, new species from the Mackenzie Mountains of northern Canada. Synapomorphies (Fig. 1.1) include a strongly expanded, "mushroom-shaped" glabella (character 1, state 1), strongly perforated, small tubercles in the 1L-1, 2L-1, and 3L-1 positions (character 9, state 2), and a relatively narrow pygidium whose length is greater than 90% of maximum width (character 23, state 2). A number of states, including a relatively flat glabellar crest (character 4, state 0), deep, slot-like lateral furrows (character 5, state 0), and minimum glabellar width at L2 (character 3, state 0) are shared with *E. regularis*. Choice of *E. regularis* as the outgroup places *Walcrinuroides* as a basal encrinurine clade that retains several plesiomorphic states. However, selection of the outgroup is somewhat arbitrary in this case as it is based solely on stratigraphic age. As should be apparent from the topology of the strict consensus tree (Fig. 1.1), rerooting on, for example, *E. sexcostatus*, places *E. regularis* as a basal member of *Walcrinuroides*, with character states 3(0), 4(0), and 5(0) acting as synapomorphies.

Frencrinuroides as defined by Lespérance and Desbiens (1995, fig. 1) is not monophyletic. However, it is conceivable that a clade
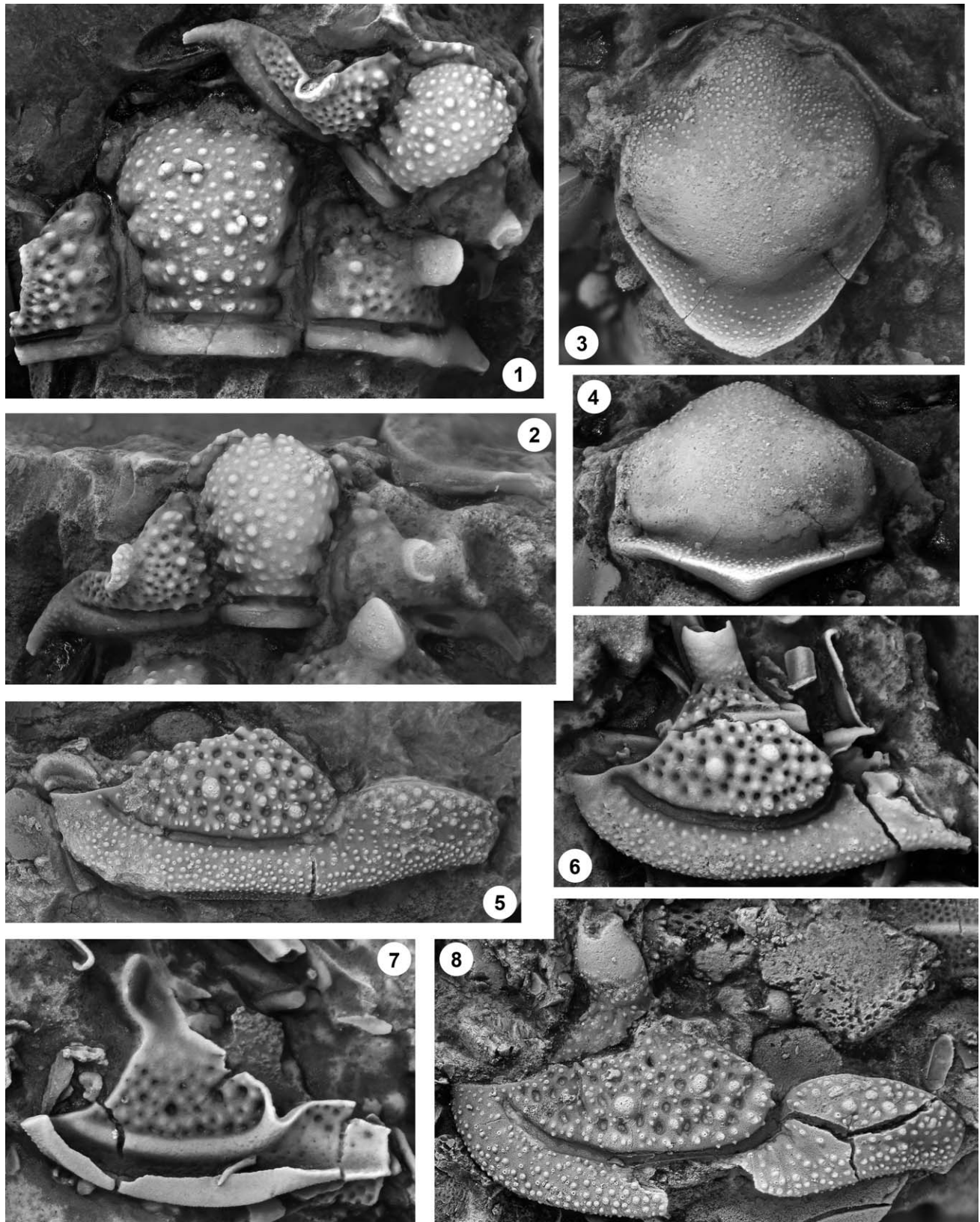
FIGURE 6—*Frencrinuroides capitonis* (Frederickson, 1964), Mountain Lake Member, Bromide Formation, Dunn-Tyson Quarry, Criner Hills, southern Oklahoma. *1*, cranidium, OU 8604, dorsal view, ×10 (illustrated previously by Shaw, 1974, pl. 9, fig. 15); *2*, cranidium, OU 8604, dorsal view, ×10 (illustrated previously by Shaw, 1974, pl. 9, fig. 15); *3*, *4*, hypostome, OU 12637, ventral and posterior views, ×20; *5*, librigena, OU 12638, lateral view, ×9; *6*, librigena, OU 8075, lateral view, ×12 (figured previously by Shaw, 1974, pl. 10, fig. 11); *7*, librigena, OU 12639, ventral view, ×12 (previously unfigured, associated with OU 8075); *8*, librigena, OU 12640, lateral view, ×9.

FIGURE *7*—*Frencrinuroides capitonis* (Frederickson, 1964), Mountain Lake Member, Bromide Formation, Criner Hills, southern Oklahoma. All pygidia and all from the Dunn-Tyson Quarry. *1–3*, OU 12641, dorsal, posterior and lateral views, ×9; *4*, OU 12584, dorsal view, ×16; *5*, OU 12642, dorsal view, ×10; *6*, OU 8074, dorsal view, ×15 (figured previously by Shaw, 1974, pl. 10, fig. 10); *7, 8*, OU 12643, dorsal and lateral views, ×10; *9*, OU 12644, dorsal view, ×10.

centered on *F. capitonis*, the type species, might emerge from a more comprehensive analysis, with characters of the librigena acting as synapomorphies. Parnaste (2006, p. 160) commented on the ill-defined precranidial lobes on librigenae of *E. capitonis*, *E. obesus* Tripp, and *E. periops* Tripp (character 21, state 0; Appendix). Inadequate illustrations prevent the latter two species from being coded for analysis, but they could prove to be closely related to *E. capitonis*. Parnaste (2006) also noted that the precranidial lobe is weakly expressed in *E. regularis*, although her material (2006, fig. 5J) is poorly preserved and we cannot be sure whether it records state 0 or state 1 of our character 21 (Appendix). Accordingly, we coded this character as missing in *E. regularis*, but an alternate run in which this species was coded as state 0 retrieved the same set of six trees; both ACCTRAN and
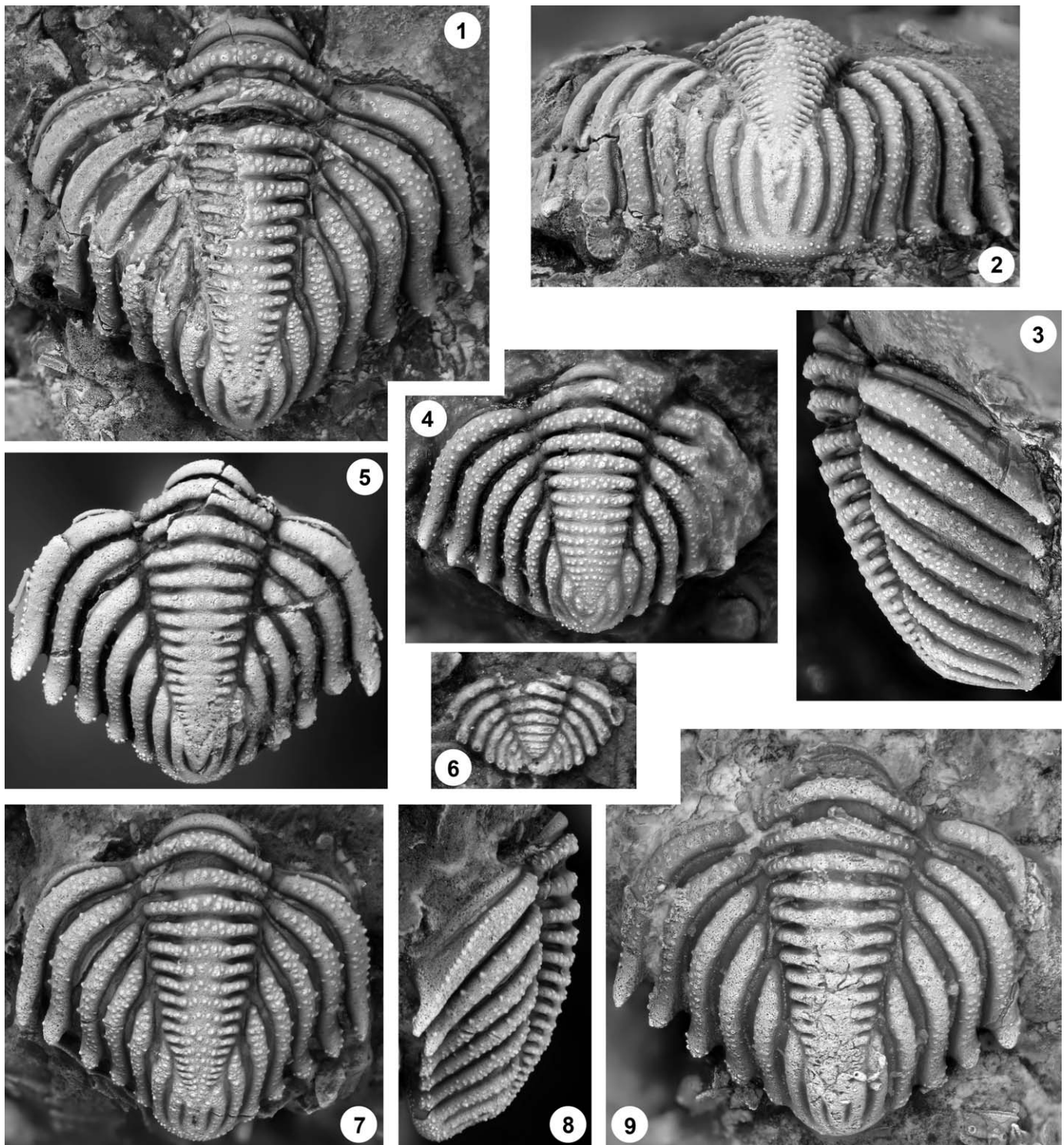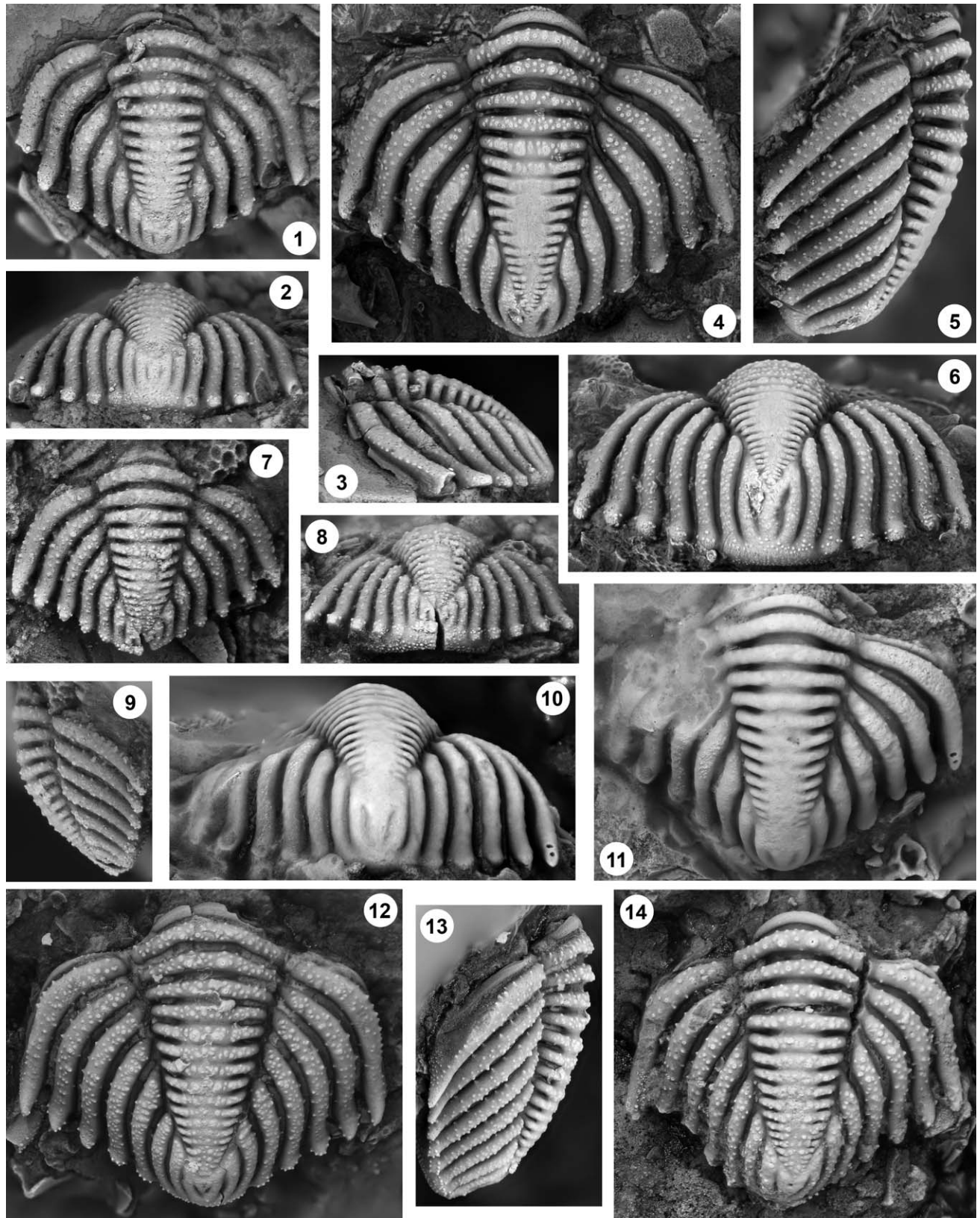
FIGURE 8—*Frencrinuroides capitonis* (Frederickson, 1964), Mountain Lake Member, Bromide Formation, Criner Hills, southern Oklahoma. All pygidia and all from the Dunn-Tyson Quarry. *1–3*, OU 12645, dorsal, posterior and lateral views, ×15; *4–6*, OU 12646, dorsal, lateral and posterior views, ×10; *7–9*, OU 12647, dorsal, posterior and lateral views, ×16; *10*, *11*, OU 8065, posterior and dorsal views, ×12 (figured previously by Shaw, 1974, pl. 9, figs. 19, 20); *12*, *13*, OU 12648, dorsal and lateral views, ×10; *14*, OU 12649, dorsal view, ×14.
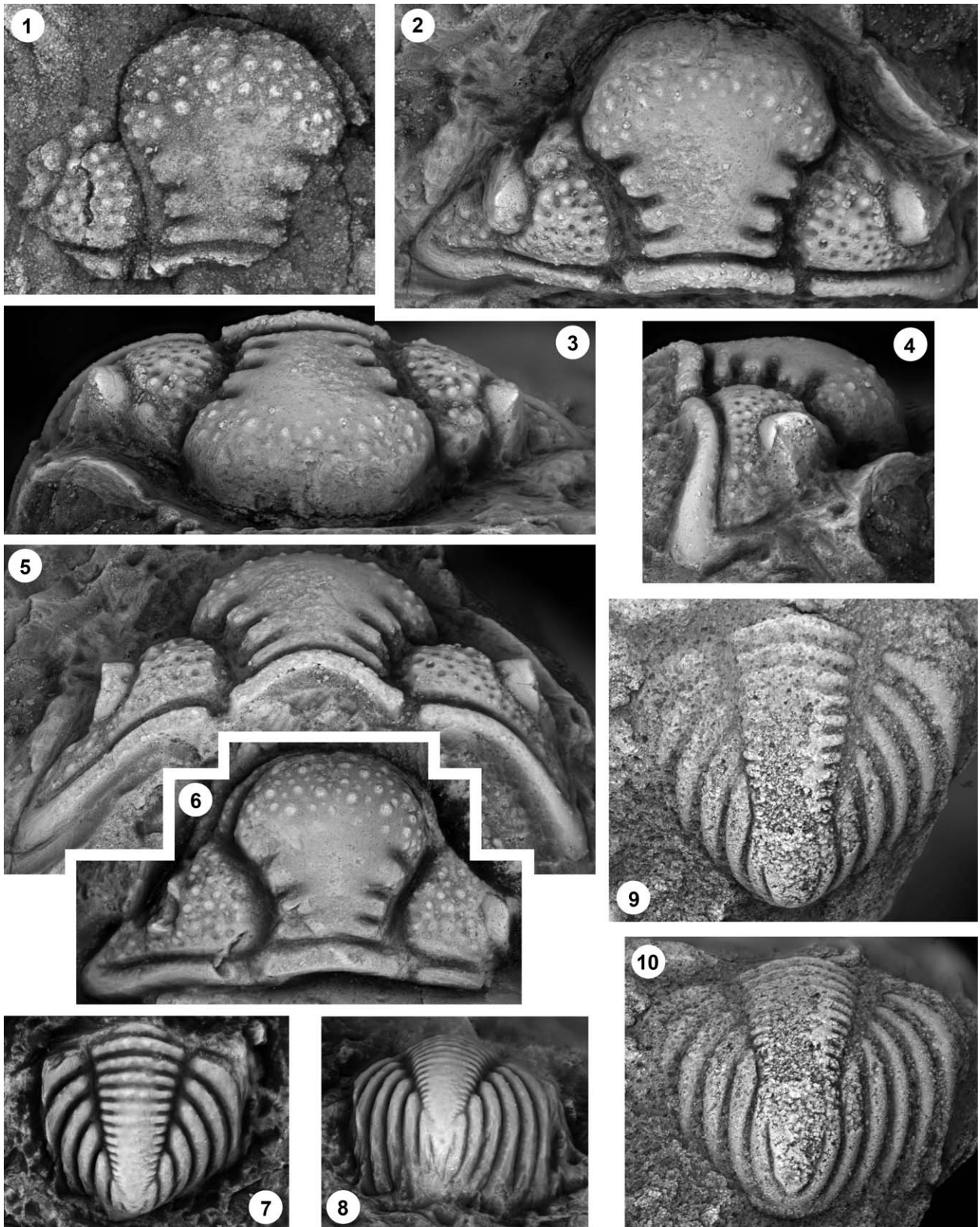
FIGURE *9—Walencrinuroides rarus* (Walcott, 1877), Plattin Subgroup, Platteville Group, Wisconsin. *1*, *9*, *10* from the Grand Detour Formation, Beloit. *1*, cranidium, UC 12322 (holotype), dorsal view, ×15; *9*, *10*, pygidium, UC 12323, dorsal and posterior views, ×9 (assigned originally to *Encrinurus varicostatus* by Walcott, 1877); *2–8*, from the Mifflin Formation, and all from the Mount Ida East roadcut, Grant County, except *7*, *8* (Dixon North Quarry, Lee County; see DeMott, 1987, table 10.1 for details of localities); *2–5* cranidium MCZ 107677, dorsal, anterior, lateral and posterior views, ×10; *6*, cranidium, MCZ 107678, dorsal view, ×10; *7*, *8*, pygidium, MCZ 107697, dorsal and posterior views, ×10.

DELTRAN optimization indicated independent acquisition of state 0 in *E. capitonis*. Thus, the current state of knowledge does not preclude configuration of the precranidial lobe and anterior furrow acting as a potential apomorphy of *Frencrinuroides*. Further progress must await restudy of "*Encrinuroides*" from the terranes of the Southern Uplands of Scotland.

All previous workers (e.g., Edgecombe and Chatterton, 1990; Lespérance and Desbiens, 1995; Edgecombe et al., 1998; Parnaste, 2006) have recognized *Physemataspis* Evitt and Tripp as a distinct monophyletic group that is defined by the architecture of the glabella and the palpebral lobe. In our analysis, the genus includes at minimum *P. coopi*, *P. mirabilis* and *P. insularis*. A case can perhaps be made for inclusion of *P. torulatus* and *P. tholus* (Fig. 1.1), although support is ambiguous. Like *P. coopi*, *P. mirabilis*, and *P. insularis*, *P. tholus* lacks ii0 and iii0 glabellar tubercles, although *P. torulatus* possesses both of these tubercles. *Physemataspis coopi* and *P. torulatus* share distinctive, inflated, paired axial tubercles on thoracic segments (Evitt and Tripp, 1977, pl. 13, fig. 16a, 16b, and pl. 3, figs. 2a, 3d), but thoracic segments are unknown in *P. tholus*, *P mirabilis*, and *P. insularis*.

Four species, *E. vigilans*, *E. spicatus*, *E. neuter*, and *E. uncatus*, are assigned to *Erratencrinurus*. Several characters support monophyly in our analysis, although we recognize that some of these (e.g., configuration of the tubercles of the pygidial axis; character 25, state 1 of Appendix) could prove to be synapomorphies of broader groupings that include post-Ordovician taxa. Characters shared by all four species include large, closely-packed glabellar tubercles (character 7, state 1), nine tubercles along the anterior cranidial border (character 12, state 1), a row of large tubercles on the librigenal border (character 20, state 1), an axial spine on some thoracic segments (character 22, state 1) and median tubercles on the pygidial axis (character 25, state 1). This grouping of species is comparable to results of an analysis reported by Edgecombe et al. (1998, fig. 5), and corroborates Parnaste's (2006, p. 159) suggestion that both *E. neuter* and *E. uncatus* should be assigned to *Erratencrinurus*.

Placement of some species, including "*E.*" *gibber*, "*E.*" *gelaisi*, and "*E.*" *edseli*, is poorly constrained. We label these as "*Encrinuroides*" without implying that any of them is necessarily closely related.

SYSTEMATIC PALEONTOLOGY

Repositories of specimens are indicated by the following abbreviations: UA, Department of Earth and Atmospheric Sciences, University of Alberta; GSC, Geological Survey of Canada, Ottawa; MCZ, Museum of Comparative Zoology, Harvard University; OU, Oklahoma Museum of Natural History; ROM, Royal Ontario Museum; UC, Field Museum of Natural History. To maximize depth of field, all digital images were rendered from stacks of images focused at 100–500 micron intervals using Helicon Focus 4.0 for the Macintosh, <http://www.heliconsoft.com>. Proportions expressed in percentages in descriptions and diagnoses are means, with numbers in parentheses indicating the range of values. All measurements were made on digital images to the nearest tenth of a millimeter using the Measure Tool of Adobe Photoshop.™

Family ENCRINURIDAE Angelin, 1854
Subfamily ENCRINURINAE Angelin, 1854
Genus FRENCRINUROIDES LESPÉRANCE and DESBIENS, 1995

Type species.—*Encrinuroides capitonis* Fredrickson, 1964, from the Bromide Formation, south-central Oklahoma (by original designation).

Diagnosis.—Librigena with precranidial lobe barely differentiated from anterior cephalic border, and with mostly granulose sculpture; anterior furrow obsolete (Fig. 6.8) or expressed only as reduction in density of sculpture (Fig. 6.5).

Remarks.—In the analysis (Fig. 1), *Frencrinuroides* is monotypic. However, once species from the Southern Uplands (Tripp, 1962, 1965, 1967, 1979) are documented properly with large, high-resolution images, we think it likely that some of them will prove to be close relatives of *F. capitonis*. As discussed above, librigenal characters are candidates for synapomorphies of *Frencrinuroides*. The librigena of *F. capitonis* (Fig. 6.5–6.8) is characterized by a weakly expressed precranidial lobe (see also Parnaste, 2006), with mostly granulose sculpture and an anterior furrow (Evitt and Tripp, 1977, fig. 1) that is identifiable at best only by a reduction in the density of granules. Other encrinurines have shallow anterior furrows, but these are readily recognizable by the absence of sculpture, and by a sharp contrast in the sculptural style of the border and precranidial lobe (e.g., Fig. 12.10).

"*Encrinuroides*" *obesus* Tripp, 1965 (pl. 82 figs. 18–28) appears to be the closest to *F. capitonis* in that the photograph of the librigena (Tripp, 1965, pl. 82, fig. 20) shows no trace of a border furrow, and Tripp (1965, p. 593) describes the precranidial lobe and anterior cephalic border as "fused." As far as can be determined from the other miniscule, harshly lit photographs, there are broad similarities in hypostomal morphology (compare Tripp, 1965, pl. 82, fig. 22 and Fig. 6.3), and in the proportions of the cranidium. The apparent transglabellar S1 of the smaller cranidium of "*E.*" *obesus* (Tripp, 1965, pl. 82, fig. 19a) is almost certainly exaggerated by the lighting, but similar furrows can be seen in some cranidia of *E. capitonis* (e.g., Fig. 6.1). As discussed earlier in the text (see also Parnaste, 2006, p. 160), other poorly known species of "*Encrinuroides*" may share the librigenal morphology of *F. capitonis* and could conceivably belong to *Frencrinuroides*. We conclude that there is sufficient support for monophyly to provisionally retain *Frencrinuroides*, albeit with a different species composition that originally envisaged by Lespérance and Desbiens (1995).

FRENCRINUROIDES CAPITONIS Frederickson, 1964
Figures 2–8

1964 *Encrinuroides capitonis* FREDRICKSON, p. 71, pl. 1, figs. 1–5.
1974 *Encrinuroides capitonis*; SHAW, p. 37, pl. 9, figs. 15, 19–23, p. 38, pl. 10, figs. 1–13.
1995a *Frencrinuroides capitonis*; LESPÉRANCE and DEBIENS, p. 11.

Diagnosis.—In addition to librigenal characters in the genus diagnosis, glabellar tubercles imperforate; paired 1L-1, 2L-1, and 3L-2 usually evident. Palpebral lobe raised on tall, narrow stalk. Pygidium with seven pairs of pleural ribs, five of which carry free spines.

Description.—Cephalon wider than long and roughly triangular in outline. Genal spines long on smallest specimens, equal to nearly half of glabellar length (Figs. 2.1, 4.10), but reduced substantially in size during holaspid ontogeny, becoming roughly equal to length of SO (Fig. 4.8). Glabella nearly parallel sided between LO and L2, then expands forward without overhanging anterior cranidial border, becoming well rounded anteriorly; width at narrowest point across L1 equal to 66% (59–75) of maximum width at base of frontal lobe; glabellar length and maximum width approximately equal. Lateral profile of glabella (Figs. 4.2, 4.4, 5.2) rises from SO to reach maximum inflation near S3, then curves steeply forward and downward to well incised preglabellar furrow. Longitudinal median furrow well defined, merging with preglabellar furrow, and short (sag.), evident in dorsal view only as weak notch in glabellar outline. SO firmly impressed and transverse; LO forms narrow

FIGURE *10—Walencrinuroides rarus* (Walcott, 1877), lower informal member, Lebanon Limestone, Wilson County, Tennessee. All cranidia ×12, and all from the Nashville Speedway Section along HW 452. *1*, OU 12650, dorsal view; *2*, *3*, OU 12591, dorsal and posterior views; *4*, OU 12651, dorsal view; *5*, OU 12590, dorsal view; *6*, *7*, OU 12586, anterior and dorsal views; *8–10*, OU 12588, lateral, dorsal and anterior views.
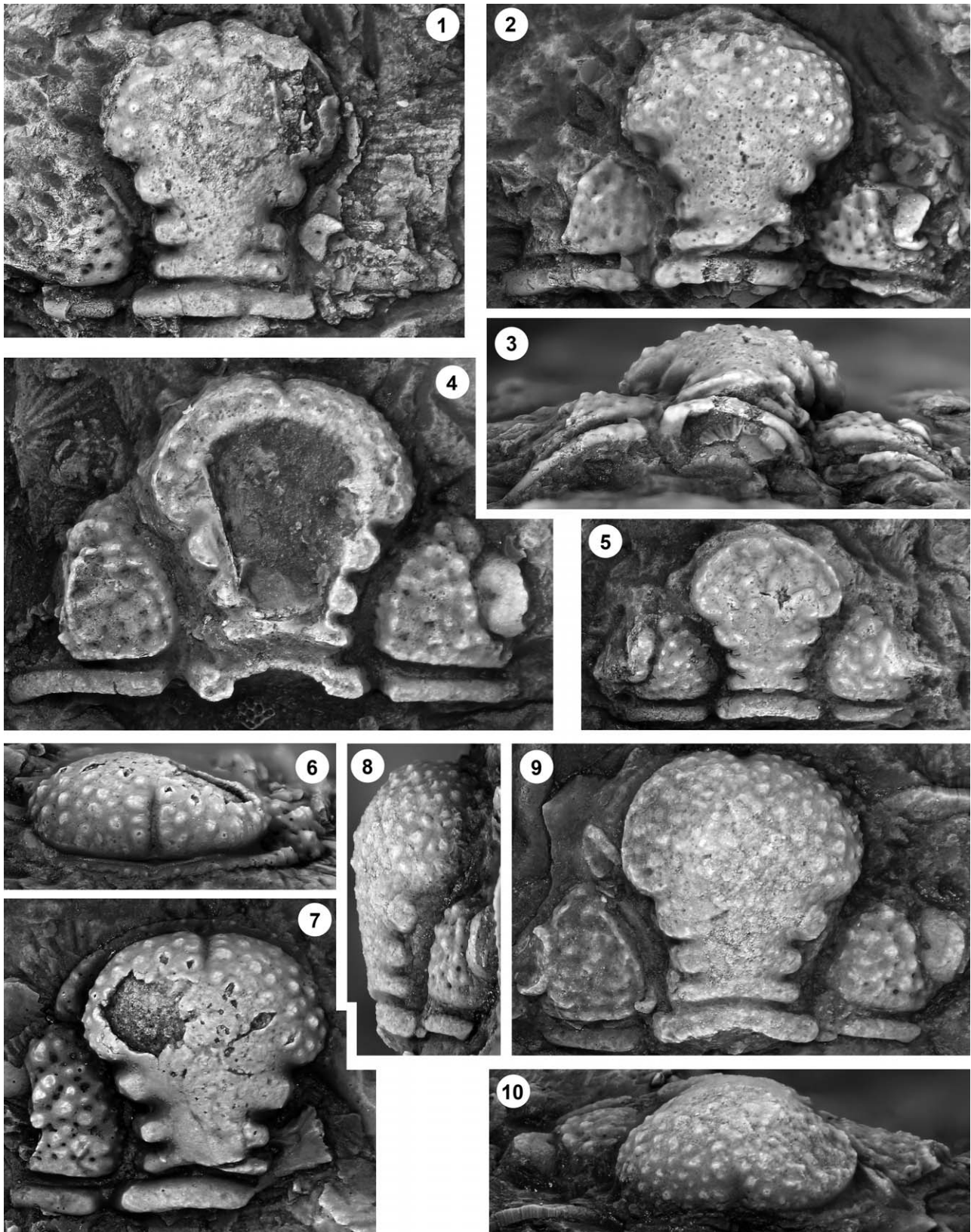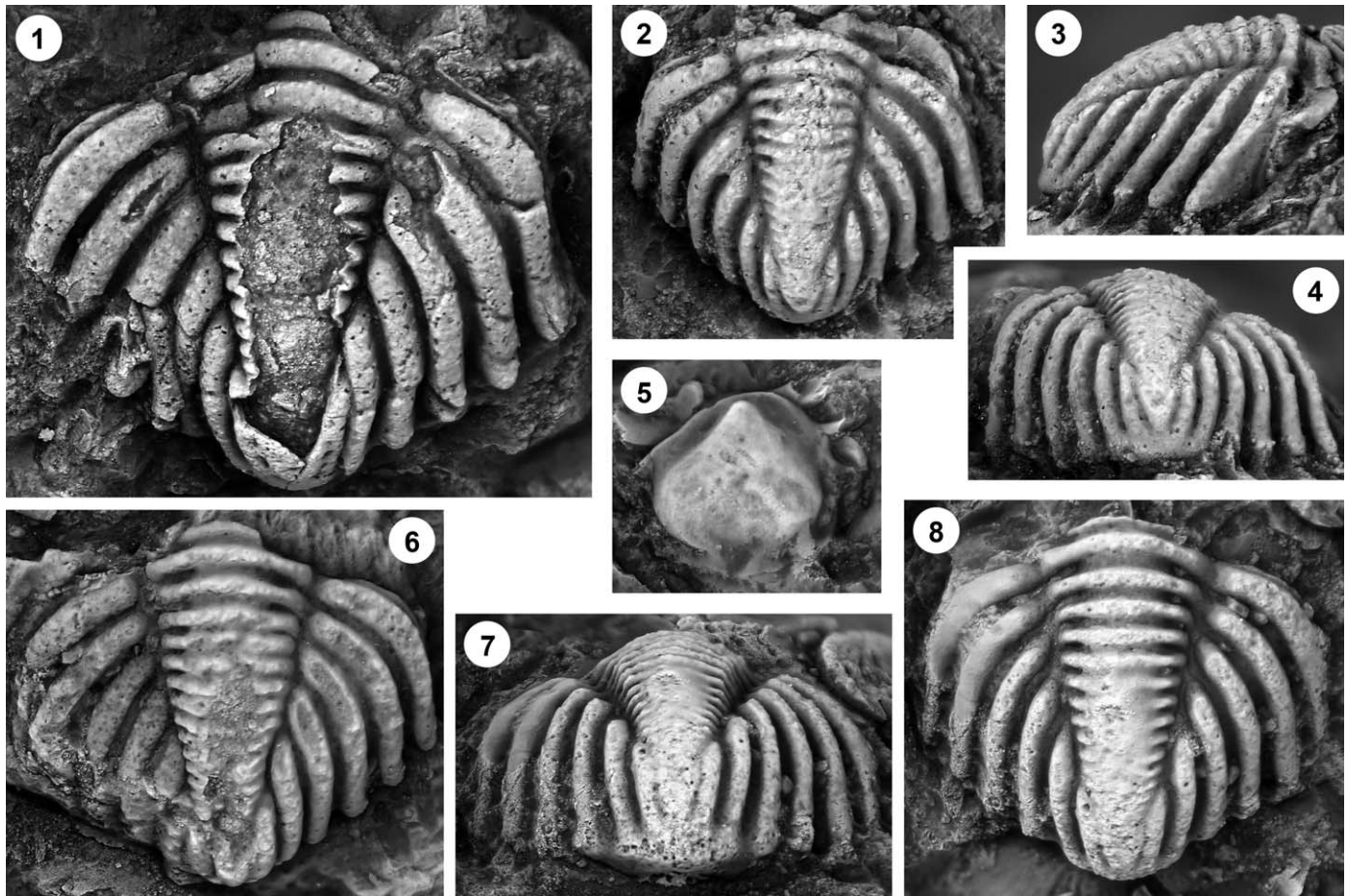
FIGURE *11*—*Walencrinuroides rarus* (Walcott, 1877), lower informal member, Lebanon Limestone, Wilson County, Tennessee. All pygidia except *5* (incomplete hypostome), and all from the Nashville Speedway Section along HW 452. *1*, OU 12596, dorsal view, ×12; *2–4*, OU 12593, dorsal, lateral and posterior views, ×15; *5*, OU 12652, ventral view, ×12; *6*, OU 12594, dorsal view, ×12; *7*, *8*, OU 12595, posterior and dorsal views, ×12.

band of even width (sag. exsag.), occupying 14% (14–15) of glabellar length. S1–S3 expressed abaxially as short (exsag.) notches that become progressively narrower (tr.) and somewhat shallower; S1 is transglabellar on some specimens (e.g., Figs. 4.8, 5.1), with faint transverse furrow connecting deeper notches. L1 is short (sag.;exsag.) band, about half of length of LO. L2 and L3 subequal in length (exsag.), about twice as long as L1. Frontal lobe accounts for approximately 43% (38–46) of length of glabella. Anterior cranidial border short (sag.), equal to 5% (4–5) of glabellar length medially but expands abaxially (Fig. 4.8); nearly flat. Palpebral lobe mounted on tall, narrow stalk and differentiated only by reduction in, or absence of, granulose sculpture (Fig. 4.1); base of stalk extends from rear of L2 to middle of L3. Eye ridge with independent convexity, located close to, and parallel with, sutural margin, and intersecting axial furrow just in front of level of S3. Anterior branches of facial suture run inward and downward along nearly straight path (Fig. 4.3) before curving inward along edge of anterior cranidial border; posterior branches diverge sharply backward and downward to intersect lateral cephalic margin opposite S1. Preocular area of fixigena reduced to barely expressed vestige in front of palpebral ridge; palpebral and posterior areas inflated and roughly triangular in outline. Posterior border furrow narrow and firmly impressed for most of width, but shallows and curves gently forward near cephalic margin; bounded anteriorly in some specimens (Fig. 4.5) by weak ridge that marks rear edge of posterior field. Posterior border convex, nearly transverse and shorter than SO near glabella but expands towards genal spine. Occipital ring and posterior border granulose (Fig.

2.1). Preoccipital glabella with bimodal distribution of imperforate tubercles, with spacing of larger ones greater than their diameter; spaces between tubercles include coarse granules; some large tubercles paired, with 1L-1, 2L-1, and 3L-2 usually evident. SO, posterior border and genal spine with coarse granules (Figs. 2.1, 4.5). Anterior cranidial border with eight large tubercles and numerous course granules to very fine tubercles. Palpebral area and posterior field of fixigena with conspicuous pits and coarse granules. Coarser tubercles present on palpebral ridge, palpebral area and postocular area, but pairing is obscure aside from possible CT-0, CT-1 (torular), and FT tubercles (Fig. 4.1, 4.5; see Parnaste, 2006, fig. 3 for tubercle nomenclature) on some specimens.

Librigena with conspicuous eye stalk. Librigenal field subtriangular in outline and separated from convex lateral border by deep lateral border furrow. Precranidial lobe very weakly convex, subrectangular, with anterior furrow barely recognizable only as narrow band in which density of glabellar sculpture somewhat reduced. Anterior cephalic border little different in convexity from precranidial lobe and ill-defined. Librigenal field with conspicuous pits and scattered tubercles and coarse granules; two conspicuous tubercles likely part of circumocular ring. Lateral border, anterior border and precranidial lobe with granulose sculpture, becoming coarser near sutural margin of precranidial lobe.

Hypostome roughly elliptical in outline, maximum width equal to length; anterior margin rounded and posterior margin bluntly pointed. Middle body strongly inflated, subcircular in outline. Maculae weak, ill-defined smooth patches (Figs. 5.4, 6.4).

FIGURE *12*—"*Encrinuroides*" *gelaisi* Lespérance and Desbiens, 1995, Unit 1, Shipshaw Formation, Lac Saint-Jean region, Quebec. All from a quarry 1.5 km north of the Ouiatchouaniche River, Roberval, and all ×9. *1–4*, cranidium, GSC 110321 (paratype), anterior, dorsal, posterior and lateral views; *5–7*, cranidium (paratype), GSC 110322, lateral, dorsal and anterior views; *8, 9*, enrolled exoskeleton, GSC 110326 (holotype), dorsal views centered on pygidium and cranidium; *10, 11*, librigena, GSC 110323 (paratype), lateral and dorsal views.
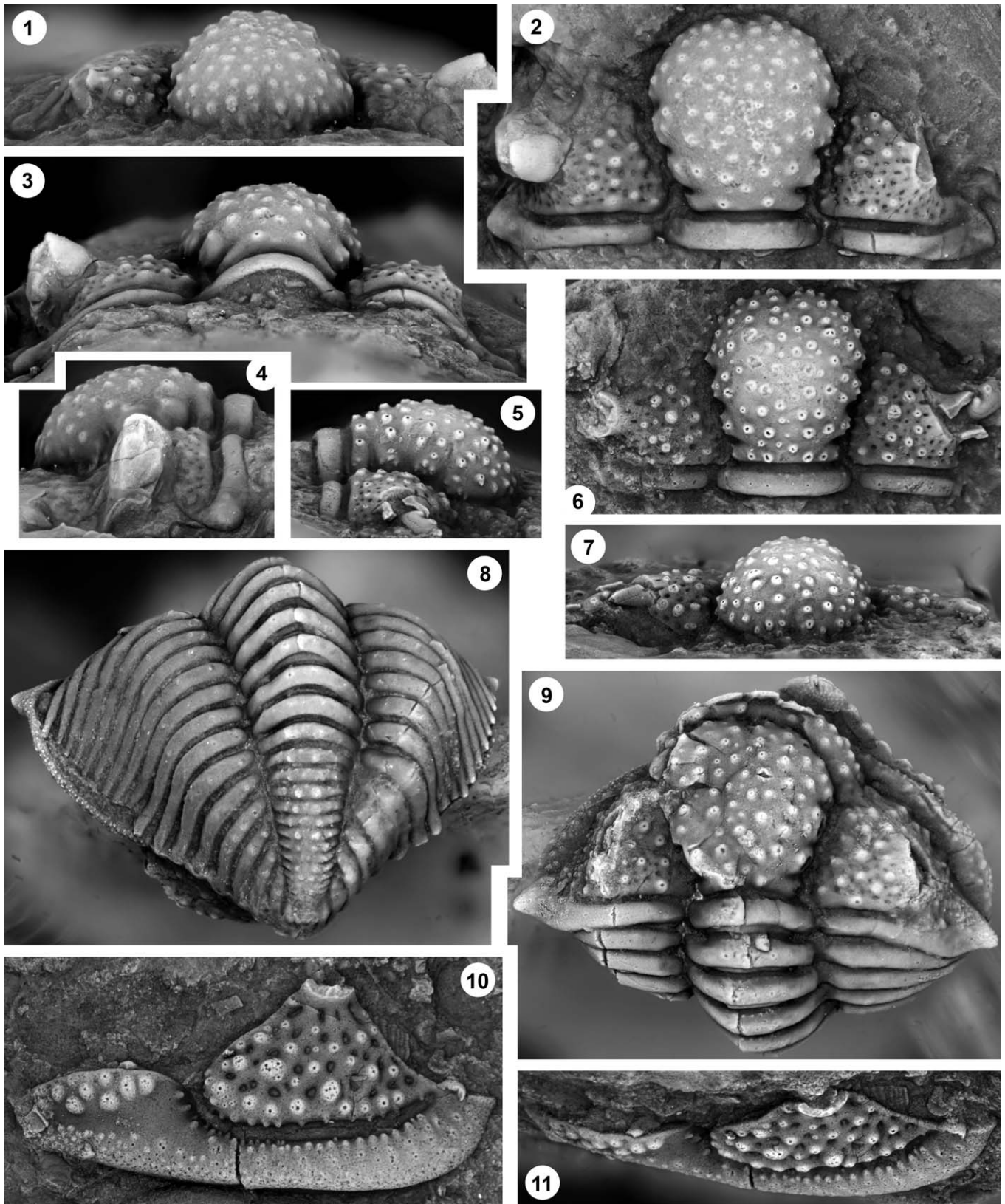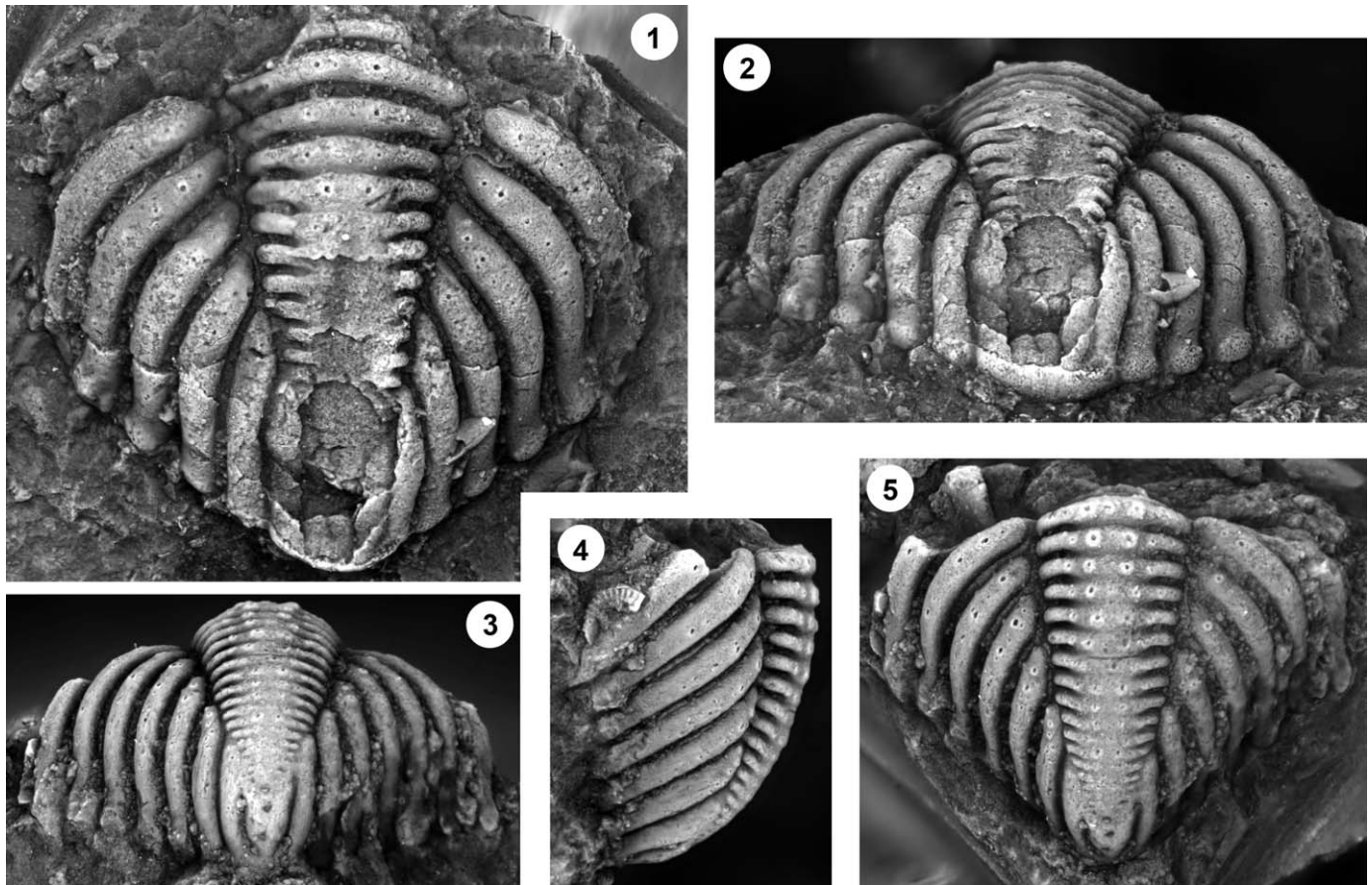
FIGURE 13—"*Encrinuroides*" *gelaisi* Lespérance and Desbiens, 1995, Unit 1, Shipshaw Formation, Lac Saint-Jean region, Quebec. All pygidia ×10 and all from a quarry 1.5 km north of the Ouiatchouaniche River, Roberval. *1, 2*, GSC 110325, dorsal and posterior view; *3–5*, GSC 110324, posterior, lateral and dorsal views.

Rhynchos defined largely by increase in inflation of middle body and without bounding furrows; broadly based and tapered forward to rounded terminus, so that outline is subtriangular; terminates short of anterior border. Anterior border is narrow (sag, exsag.) raised rim. Anterior wings incompletely preserved but apparently broad. Posterior border long, accounting for 19% (17–20) of hypostomal length (sag.), and with gently concave surface; crescentic in outline, tapering to bluntly pointed posterior tip. Posterior border furrow deep medially but shallows towards lateral margins. Well-preserved specimens (Figs. 5.6, 6.3) show sculpture of coarse granules over at least anterior half of middle body, including rhynchos, anterior wings and posterior border; furrows, maculae and anterior border apparently smooth.

Thorax with 11 segments. Axial furrows shallow. Axial ring convex, occupying 31% (29–32) of thoracic width at anterior; articulating furrow firmly impressed transverse groove and articulating half-ring curved gently forward, length equal to about half of axial ring length. Ventrally (Fig. 3.2), conspicuous apodemes present at ends of articulating furrow. Pleura flexed down steeply at fulcrum located about one third of pleural width from axis; tips bluntly pointed (Fig. 2.2, 2.6). Short (exsag.) anterior (Fig. 3.4) and very short posterior (Fig. 2.3) articulating flanges present; articulating facet broad, with row of coarse granules running along upper and lower margins. Well-preserved specimens (Figs. 2.1, 3.1, 3.4); with granulose sculpture over entire surface except for articulating facet and articulating half-ring. Pair of small median tubercles on at least rings 6–11 (Fig. 2.1).

Pygidium subtriangular in outline, length equal to 80% (72–87) of maximum width in large sclerites, although small specimens (Fig. 7.6) are proportionately wider, with length only 30% of width; strongly arched. Articulating flange runs along anterior-most pleura, which also carries well-defined articulating facet. Axial furrows deep grooves. Axis convex, strongly so anteriorly but barely raised above pleural field near posterior tip, and tapered backward, so that width at adaxial tip of fifth pleural rib is 56% (51–62; lower values in smaller sclerites) of width at first axial ring; width at first axial ring equal to 38% (35–42) of maximum pygidial width. Seventeen to 18 axial rings present; first three rings congruent with pleural ribs, with intercalated, non-congruent rings appearing posteriorly; articulating furrow firmly impressed and articulating half-ring bowed forward, length (sag.) slightly shorter than adjacent axial ring. First five or six ring furrows transverse and deep, extending across axis; remainder well-incised only abaxially, and shallow abruptly over medial part of axis, where rings become ill-defined and flat topped (Fig. 7.1–7.3, 7.8, 7.9). Pleural field flexed steeply downward and traversed by seven pairs of convex pleural ribs (excluding terminal piece) separated by deeply incised pleural furrows. First five ribs with free tips, bluntly spinose on the two anteriormost ribs but rounded posteriorly, overhanging border, with extent of overhang decreasing posteriorly (Fig. 3.2); remaining ribs with tips fused with border. In some specimens (e.g., Fig, 7.1, 7.2, 7.7), terminal piece clearly composed of a pair of partly fused ribs separated by an incomplete median furrow; in others, the ribs are completely fused (Fig. 8.6). Border narrow,
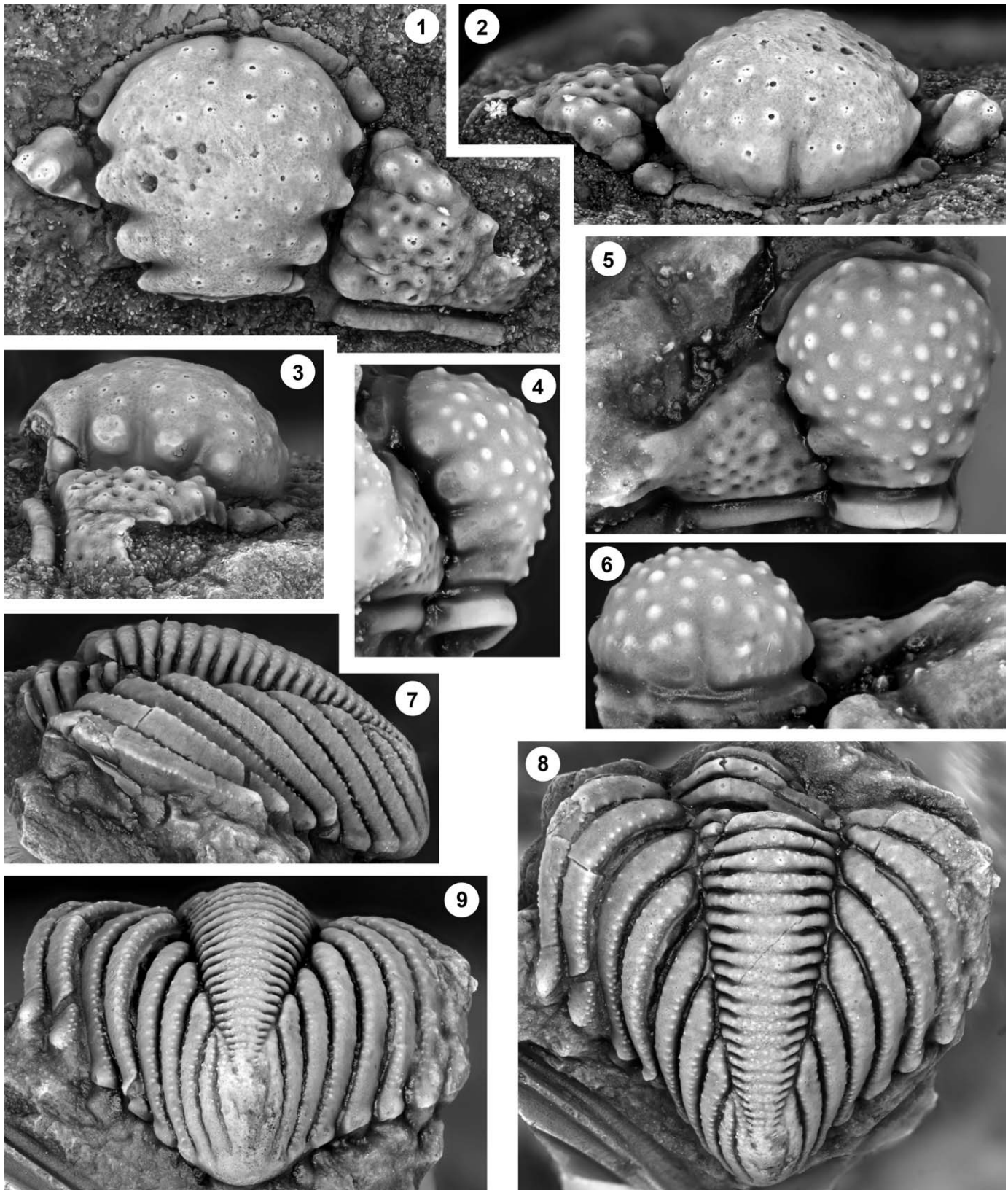
FIGURE *14*—"*Encrinuroides*" *gibber* (Dean, 1979) from the upper Black Duck Member, Lourdes Limestone, GSC loc. 84824, western end of Salmon Cove, Port au Port Peninsula, western Newfoundland. *1–3*, cranidium, GSC 38644, dorsal, anterior and lateral views, ×7 (figured previously as *Ceraurus* sp. by Dean, 1979, pl. 4, figs. 3–9); *4–6*, cranidium, GSC 38645, lateral, dorsal and anterior views, ×12 (figured previously as *Ceraurus* sp. by Dean, 1979, pl. 2, fig. 6); *7–9*, pygidium, GSC 38650 (holotype), lateral, dorsal and posterior views, ×6.5.

TABLE 1—Data matrix used in the phylogenetic analysis (Fig. 1).

	Character																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
En. regularis	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	?	?	0	0	0	0
En. sexcostatus	1	1	1	1	1	0	0	1	?	0	0	?	0	0	1	0	?	0	0	0	1	0	1	0	0	1
"En" gelaisi	0	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	2	0	0	1	0	0	0
W. rarus	1	0	0	0	0	1	0	0	?	0	0	0	0	0	1	0	0	0	0	0	?	?	?	2	0	2
"En." gibber	0	1	1	1	1	0	0	0	0	1	0	0	0	1	2	?	1	?	0	?	?	?	?	2	0	1
P. tholus	0	1	1	1	1	0	0	0	1	0	0	0	0	1	1	1	1	1	0	?	?	?	2	1	0	1
F. capitonis	0	1	1	1	1	0	0	1	0	1	1	0	0	1	1	1	1	0	0	0	0	0	1	0	1	1
P. torulatus	0	1	1	1	1	0	1	0	1	2	1	0	0	1	1	1	1	0	0	0	0	2	2	2	0	1
"En." edseli	0	1	1	1	1	0	1	1	?	0	1	0	0	0	1	0	0	1	0	0	1	?	0	0	1	1
W. tremblayi	1	0	0	1	0	0	0	0	2	0	0	0	0	0	1	0	0	?	0	0	?	?	2	0	0	1
W. rolfi	1	0	0	0	0	1	0	0	2	3	0	0	0	0	1	0	0	0	0	0	1	0	2	0	0	2
P. insularis	2	1	1	1	2	0	0	0	?	0	1	0	0	2	1	1	1	1	0	0	1	?	1	0	0	1
P. coopi	2	0	1	1	2	0	0	0	3	0	1	0	1	2	0	1	0	1	0	0	1	2	1	0	0	1
Er. neuter	0	1	1	1	1	0	1	0	1	2	0	1	0	1	1	1	0	1	0	1	2	1	0	1	1	1
Er. uncatus	0	1	1	1	1	0	1	0	0	2	1	1	0	1	1	1	0	1	1	1	2	1	0	1	1	1
Er. spicatus	0	1	1	1	3	0	1	0	1	0	0	1	2	1	?	1	0	2	1	1	3	?	2	1	1	1
Er. vigilans	0	0	1	1	3	0	1	1	0	2	0	1	2	1	2	0	0	2	1	1	3	1	2	3	1	2
P. mirabilis	2	0	1	0	2	0	0	0	3	?	?	0	1	2	0	?	0	0	0	0	?	?	?	?	?	?

vertically directed, and aside from at the posterior end of the pygidium, visible clearly only in lateral and ventral views. Apart from furrows, articulating half-ring, articulating flange and articulating facet, external surface carries coarse granules to fine tubercles, some of which are perforate.

Holotype.—Complete exoskeleton (OU 3412), Mountain Lake Member, Bromide Formation, Criner Hills, Oklahoma (Fig. 2.6–2.8).

Occurrence.—Mountain Lake Member, Bromide Formation, south-central Oklahoma.

Material.—Figured specimens include six articulated exoskeletons, eight cranidia, three hypostomata, four librigenae, and twelve pygidia.

Remarks.—The material illustrated here (Figs. 2–8) includes specimens figured by Fredrickson (1964) and Shaw (1974), as well as new material from the Dunn-Tyson Quarry near Ardmore, Oklahoma. Some previously illustrated specimens (e.g., Figs. 2.7, 5.7, 8.11) preserve very little of the original sculpture, either due to natural weathering or by excessive use of air abrasive preparation techniques. Our new specimens allow sculpture to be documented fully for the first time.

As noted earlier in the text, *Frencrinuroides capitonis* is most likely related to a set of poorly known species from the Southern Uplands of Scotland. Of these, *"Encrinuroides" obesus* Tripp is most like *F. capitonis*. As far as can be determined from published images, *"E." obesus* has a noticeably narrower lateral border on the librigena (compare Fig. 6.5–6.8 with Tripp, 1975, pl. 82, fig. 20), and the pygidium is relatively shorter and wider (compare Figs. 7, 8, with Tripp, 1965, pl. 82, figs. 25, 26). *"Encrinuroides" periops* Tripp (1967, pl. 5, figs. 9–16) and *E. polypleura* (Tripp, 1967, figs. 1–8) are based on flattened and somewhat distorted material, so that comparisons with *F. capitonis* are difficult. At minimum, the former species differs from *F. capitonis* in having a very long eye stalk, whereas *E. polypleura* apparently has a pygidium with eight to nine, rather than seven pairs of pleural ribs, and only four of these have free spines, whereas *F. capitonis* has spines on five pairs of ribs. Sclerites of *"E." autochthon* (Tripp, 1962, pl. 3, figs. 18–25) are also deformed to varying extents and cannot be assessed with any confidence. The librigenal field is short (tr.) with no trace of an eyestalk, and there are only four pairs of pleural ribs with free spines (Tripp, 1962, p. 24). Finally *"E." stincharensis* (Reed; Tripp, 1979, pl. 39, figs. 1–17) also lacks an eyestalk, and the lateral border of the librigena is shorter (tr.); the pygidium has nine pairs of pleural ribs, but only four of these carry free spines.

The phylogenetic analysis (Fig. 1) showed that *F. capitonis* is closely related to species that are assigned to *Physemataspis*. Similarities are closest with the basal members of this clade, *P. tholus* (Evitt and Tripp) and *P. torulatus* (Evitt and Tripp). *Physemataspis tholus* is differentiated from *F. capitonis* by its relatively longer and wider pygidium (Evitt and Tripp, 1977, pl. 4, fig. 4), with a length–width ratio that exceeds 0.9, vs. 0.8 in the relatively wider pygidium of the latter. *Physemataspis torulatus* has a distinct anterior furrow and dense tuberculate sculpture on the precranidial lobe of the librigena (Evitt and Tripp, 1977, pl. 1, figs. 2b, 2c, pl. 2, fig. 5a), glabellar sculpture of densely packed tubercles (Evitt and Tripp, 1977, pl. 1, figs. 1a, 2a) that are larger than those of *F. capitonis*, pairs of large, inflated tubercles on at least some thoracic segments (Evitt and Tripp, 1977, pl. 3, figs. 2a, 3b, 3d), and a pygidium with six pairs of pleural ribs, only four of which have free spines (Evitt and Tripp, 1977, pl. 3, fig, 4a, 4e). More derived species of *Physemataspis*, including *P. coopi* Evitt and Tripp (1977, pls. 12–14), *P. insularis* (Shaw, 1968, pl. 10, figs. 9–21), are differentiated from *F. capitonis* on the basis of, among other features, their strongly inflated glabellae and relatively wider pygida with free spines on only the first four pairs of pleural ribs.

The phylogenetic analysis also suggests that *"Encrinuroides" gibber* (Dean, 1979; Fig. 14) is also closely related to *F. capitonis* and, indeed, Lespérance and Desbiens (1995, fig. 1) assigned this species to *Frencrinuroides*. It clearly differs from *F. capitonis* in pygidial morphology. The holotype (Fig. 14.7–14.9) is crushed anteriorly but has eight pairs of pleural ribs, six of which have free spines; in contrast, *F. capitonis* has seven pairs of ribs, with free spines on five of them. In addition, *"E." gibber* has a more posteriorly positioned palpebral lobe and conspicuous CT-1 and FT tubercles on the fixigena.

In their original description, Edgecombe et al. (1998) assigned *Frencrinuroides edseli* to the genus with some reservation. Our analysis suggests that this species is misplaced in *Frencrinuroides*, and it occupies a basal position within a broader grouping that includes both *Physemataspis* and *Erratencrinurus* (Fig. 1.2); we assign it to *"Encrinuroides."* Edgecombe et al. (1998, p. 691) listed several differences between *F. capitonis* and *"E." edseli*. Our new material of the former allows further elaboration of distinguishing characteristics. Compared to *F. capitonis*, *"E." edseli* has a far more densely tuberculate glabella, to the extent that paired tubercles cannot be identified with any confidence in large holaspids (e.g., Edgecombe et al., 1998, fig. 6.2, 6.8). In addition, the hypostome of *"E." edseli* has a proportionately

shorter middle body with short marginal spines on the posterior border, which has a truncate, rather than a bluntly pointed, terminus (Edgecombe et al., 1998, figs. 6.18–6.22, 7.1–4; compare with Fig. 6.3, 6.4); the rhynchos is smaller and less clearly defined than in *F. capitonis*. The librigena (e.g., Edgecombe et al., 1998, fig, 6.2, 6.8) has a distinct anterior furrow and coarser sculpture on the precranidial lobe. Pygidial differences include the presence of six pairs of pleural ribs in front of the terminal piece, rather than seven, and spines on the first four pairs of ribs, the most posterior of which are barely expressed (e.g., Edgecombe et al, 1998, fig. 7.11, 7.12, 7.18–7.20).

Finally "*Encrinuroides*" *gelaisi* (Lespérance and Desbiens, 1995; Figs. 12, 13) is differentiated from *F. capitonis* by a number of characters. The glabella has a lower density of tubercles, and these are perforate rather than imperforate as in *F. capitonis*. Encrinurine trilobites commonly show ontogenetic reduction in the size of the genal spines (Edgecombe and Chatterton, 1987), but the rate of reduction apparently differs between *F. capitonis* and "*E.*" *gelaisi*. In "*E.*"*gelaisi*, the spine is reduced to a mere nub that is barely expressed in the largest specimen (Fig. 12.2–12.4, 12.9), whereas the spine remains short but well defined in similarly sized cranidia of *F. capitonis*. Librigenae of "*E.*" *gelaisi* (Fig. 12.10, 12.11) have a shallow, smooth anterior furrow and a precranidial lobe that carries sculpture of close-packed, large but low tubercles that contrast with the granular sculpture of the anterior border. The pygidia differ in sculpture. "*Encrinuroides*" *gelaisi* lacks the abundant granules evident on *F. capitonis* (e.g., Fig. 7.7, 8.12) and has low, perforate tubercles that are paired both on most axial rings and between opposing left and right pleural ribs (Fig. 13.1, 13.5). The free tips of pleural ribs of "*E.*" *gelaisi* appear to be uniformly rounded, whereas the tips of at least the first two pairs of ribs of *F. capitonis* are distinctly spinose (Figs. 7, 8).

Genus WALENCRINUROIDES Lespérance and Desbiens, 1995

Type species.—*Ceraurus rarus* Walcott, 1877, from the Platteville Group, Wisconsin (by original designation).

Diagnosis.—Strongly expanded, "mushroom-shaped" glabella (character 1, state 1), strongly perforated, small tubercles in the 1L-1, 2L-1, and 3L-1 positions (character 9, state 2), and a relatively narrow pygidium whose length is greater than 90% of maximum width (character 23, state 2).

Remarks.—Raymond and Barton (1913) transferred *C. rarus* Walcott, 1877 to *Encrinurus*, and it was later assigned to *Encrinuroides* by Reed (1931). More recently, Lespérance and Desbiens (1995) designated *E. rarus* as the type species of *Walencrinuroides*. As discussed elsewhere in the text, *Walencrinuroides* has generally been viewed as problematic, and recent work has found little support for monophyly (Edgecombe et al., 1998; Parnaste, 2006). In our revision of *W. rarus*, we conclude that sclerites attributed to this species from various parts of Laurentian North America actually record three distinct species, and that material conspecific with Walcott's holotype occurs only in Wisconsin and central Tennessee. We agree with Lespérance and Desbiens (1995, p. 9) that *W. rarus* sensu Tremblay and Westrop (1991), from the Sunblood Formation, northern Canada, represents a new species, and it is formally named later in the text as *W. tremblayi*. Further, sclerites from the overlying Esbataottine Formation, attributed to *W. rarus* by Chatterton and Ludvigsen (1976), also represent a distinct, diagnosable species that is named below as *W. rolfi*. Together, these three species emerge as a monophyletic group in the phylogenetic analysis (Fig. 1) defined by their strongly expanded glabellae (e.g., Fig. 9.1–9.7), strongly perforated, typically small 1L-1–3L-1 glabellar tubercles, and a comparatively long and narrow pygidium with a length–width ratio that

exceeds 0.9. *Encrinuroides sexcostatus* also has a strongly expanded glabella, and we gave it the same coding in the matrix with the result that this state originates independently in this species. However, as material of *E. sexcostatus* is variably deformed, the coding is conservative, and it is conceivable that this species has an alternative, bulb-shaped glabellar outline that is more strongly and evenly rounded anteriorly (e.g., Whittington, 1950, pl. 68, fig. 9). As discussed above, removal of *E. sexcostatus* from the matrix does not influence the remaining topology of the six trees retrieved from the analysis, but this of course makes glabellar outline an unambiguous synapomorphy of *Walencrinuroides*.

As noted earlier, in the discussion of the results of the phylogenetic analysis, *W. rarus* shares several characters with *E. regularis*, including a flattened glabellar crest, although these states are constrained by outgroup selection to optimize as conserved symplesiomorphies of *Walencrinuroides*. In addition, the glabellar outline of *E. regularis* (Parnaste, 2006, fig. 5A) can be viewed as a muted version of the strongly expanded glabellae of species of *Walencrinuroides*. These various characters suggest a relationship between *E. regularis* and *Walencrinuroides*, and it would be unsurprising if a broader phylogenetic analysis rooted with a different outgroup indicated that the former was a basal member of the latter.

WALENCRINUROIDES RARUS (Walcott, 1877)
Figures 9–11

?1869	*Encrinurus excedrinus* SAFFORD, p. 290 [appears in faunal list only and is a *nomen nudum*].
1877	*Ceraurus rarus* WALCOTT, p. 68.
1877	*Encrinurus varicostatus* WALCOTT, p. 69.
1894	*Encrinurus vannulus* CLARKE, p. 739, figs. 56, 57.
1894	*Encrinurus raricostatus* [sic]; CLARKE, p. 740.
?1889	*Encrinurus varicostatus*; SAFFORD and VODGES, p. 167.
1913	*Encrinurus rarus*; RAYMOND and BARTON, p. 541, pl. 2, fig. 3.
non1928	*Encrinurus rarus*; TROEDSSON, p. 59, pl. 16, figs. 4–10.
non1975	*Encrinuroides* c.f. *rarus*; LUDVIGSEN, pl. 3, figs. 22, 23 [=*W. rolfi* n. sp.].
1976	*Encrinuroides rarus*; CHATTERTON and LUDVIGSEN, pl. 15, figs. 1–43 [=*W. rolfi* n. sp.]
non1978	*Encrinuroides raru*s; LUDVIGSEN, pl. 2, fig. 22 [=*W. rolfi* n. sp.].
non1979	*Encrinuroides rarus*; LUDVIGSEN, p. 21, figs. 42–48 [=*W. rolfi* n. sp.].
1987	*Encrinuroides rarus*; DEMOTT, pl. 11, figs. 13–25.
non1991	*Encrinuroides rarus*; TREMBLAY and WESTROP, fig. 17.27–17.36 [=*W. tremblayi* n. sp.; see Lésperence and Debiens 1995, p. 9].
1995	*Walencrinuroides rarus*; LESPÉRANCE and DESBIENS, p. 9.

Diagnosis.—Glabella does not overhang the anterior cranidial border medially, which expands appreciably abaxially, Glabellar crest strongly flattened. Coarse glabellar tuberculate sculpture restricted to the frontal lobe. Rhynchos of hypostome small, strongly tapered and bluntly pointed anteriorly.

Description.—Cephalon wider than long and roughly triangular in outline; genal angle with bluntly pointed vestige of spine. Axial furrows firmly impressed grooves; preglabellar furrow shallower but still well incised. Glabella strongly expanded anteriorly, mushroom-shaped in outline, with minimum width at L2 equal to 54% (51–55) of maximum width at frontal lobe. Crest of glabella flattened between SO and S3, but lateral profile of frontal lobe curved steeply downward towards preglabellar furrow. SO narrow (sag., exsag.) groove, curved gently forward. S1–S3 deep notches; S3, slightly narrower (tr.) and shallower that S1 and S2; S1 may be

connected across glabella by faint, nearly transverse furrow (Figs. 9.1, 10.2, 10.9). Longitudinal median furrow well incised and clearly visible in dorsal view, extending across anterior 25% of frontal lobe; produces distinctly bilobate anterior glabellar margin (e.g., Fig. 10.7). LO wider (tr.) than L1, and accounts for 11% (9–12) of glabellar length; strongly arched in posterior view (Fig. 9.5). L1 forms low ridge across the glabella, equal to about two-thirds length (sag.) of LO. L2 and L3 roughly equal in length (exsag.). Frontal lobe long, accounts for 56% (52–62) of length of glabella. Anterior border of cranidium short, flat but not overhung by glabella (Fig. 10.7); expands abaxially. Palpebral lobe low flap, wider than high, length equal to 27% (26–30) of glabellar length, and centered opposite anterior tip of L2. Anterior branches of facial sutures converge forward and downward along nearly straight course, then curve inward along anterior cranidial margin; posterior branches diverge abruptly along faintly curved path to reach lateral cephalic margin opposite S2. Palpebral area of fixigena weakly inflated; posterior area of fixigena flexed strongly downward. Posterior border furrow deep groove, nearly transverse near glabella but curved gently forward abaxially. Posterior border convex band, nearly transverse from axial furrow to point immediately behind palpebral lobe, with length (exsag.) equal to 8% (6–9) of glabella length; then curves gently forward towards genal angle, expanding slightly. Material with variably weathered surfaces, so that sculpture poorly preserved. On glabella, large tubercles present only on frontal lobe; holotype (Fig. 9.1) preserves smaller, strongly perforate tubercles on L1, L2, and L3; all cranidia lack any trace of sculpture on SO or posterior border. Fixigena with pits and scattered tubercles; circum-ocular tubercles not recognizable.

Incomplete hypostome shows inflated, suboval middle body with tapered, bluntly pointed rhynchos. Anterior border furrows shallow grooves; anterior border incomplete but apparently raised rim.

Pygidium subtriangular in outline, slightly wider than long, length equal to 90% (87–93) of width, and strongly convex; pleural field flexed strongly downwards. Axial furrows are firmly impressed grooves. Axis narrow, width at anterior equal to 41% (39–46) of maximum pygidial width, and tapers backward, with width opposite fifth pair of pleural ribs equal to 54% (51–55) of width at anterior. Articulating furrow well incised, curved forward; articulating half-ring also curved forward and slightly shorter than anteriormost axial ring. At least sixteen axial rings present; first three are congruent with pleural ribs (Fig. 11.8), with intercalated rings appearing in remainder of axis. Rings 1–3 curved forward, curvature decreasing in successive rings; remaining rings transverse. At least first eight ring furrows trans-axial, but remainder apparently not connected across axis. Six pairs of pleural ribs separated by deep pleural furrows, plus terminal piece. First four pairs of ribs with free spines that have slightly expanded, rounded tips; remaining ribs with tips fused into border. Surfaces of available specimens variably weathered but apparently relatively smooth with no evidence of coarse tuberculate sculpture.

Holotype.—A cranidium (UC 12322; by monotypy) from the Grand Detour Formation, Plattin Subgroup, Platteville Group, Beloit, Wisconsin (Fig. 9.1).

Occurrence.—Pecatonica, Grand Detour, Mifflin, and Quimby's Mill formations, Platteville Group, Wisconsin. Lebanon Limestone, central Tennessee.

Material.—Three cranidia and three pygidia from Wisconsin. Seven crandia and 12 pygidia from Tennessee.

Remarks.—The only previous photographic illustration of the holotype cranidium of *W. rarus* was published a century ago by Raymond and Barton (1913). Our new image of this sclerite demonstrates that, unlike the majority of cranidia available to us (e.g., Fig. 9.2) the anterior cranidial border is preserved medially and on the right side. It is not overhung by the glabella. The surface is somewhat weathered, but demonstrates that coarse

tuberculate glabellar sculpture is confined to the frontal lobe. There remain traces of strongly perforated tubercles on L1, L2, and L3, similar to those on *W. rolfi* n. sp. (e.g., Chatterton and Ludvigsen, 1976, pl. 15, figs. 1, 2), that have been by obliterated by weathering on most of our material. Additional sclerites from Wisconsin illustrated previously by DeMott (1987) provide further information on cranidial morphology (Fig. 9.1–9.7). We also illustrate (Fig. 9.10, 9.11) the best preserved of the two type pygidia of *Encrinurus varicostatus* Walcott, which were transferred to *W. rarus* by DeMott, (1987). This specimen shows that there are six pairs of pleural ribs plus a terminal piece, and that the posterior two pairs have their tips fused into the border.

Although also weathered, it is evident that cranidia from the Lebanon Limestone (Fig. 10) also have borders that are not overhung medially by the glabellae (e.g., Fig. 10.6, 10.7), and coarse glabellar tubercles are confined to the frontal lobe. This combination of characters supports an assignment to *W. rarus*. Associated pygidia (Fig. 11) are similar to those from Wisconsin.

As diagnosed here, *W. rarus* occurs only in Wisconsin and Tennessee. Material from the northern Canada (Chatteron and Ludvigsen, 1976; Tremblay and Westrop, 1991) represent new species that are compared to *W. rarus* later in the text. Sclerites illustrated by Troedsson (1928) from the Cape Calhoun Formation, Greenland, are misidentified (see also Chatterton and Ludvigsen, 1976). As they possess coarse tubercles on the entire glabella, subparallel axial furrows, and a weakly expanded glabella, they are not only distinct from *W. rarus*, but also from all other species of *Walencrinuroides*.

<div align="center">W<small>ALENCRINUROIDES</small> <small>TREMBLAYI</small> new species</div>

1991 *Encrinuroides rarus*; T<small>REMBLAY</small> and W<small>ESTROP</small>, fig. 17.27–17.36.
1995 *Walencrinuroides* n. sp. 1 L<small>ESPÉRENCE</small> and D<small>EBIENS</small>, p. 9.

Diagnosis.—Cranidium with short border that does not expand abaxially. Coarse tuberculate sculpture extends over entire preoccipital glabella. Glabellar crest arched in anterior view.

Description.—See remarks below.

Holotype.—A cranidium (ROM 47792) from the Sunblood Formation, Mackenzie Mountains illustrated by Tremblay and Westrop (1991, fig. 17.27–17.30). The remaining sclerites illustrated by Tremblay and Westrop are paratypes.

Etymology.—For James Tremblay.

Occurrence.—Sunblood Formation, Section Z, Sunblood Range, South Nahanni River area, Mackenzie Mountains, northern Canada, collection Z208, *Bathyurus granulosus* Zone.

Remarks.—Lespérance and Desbiens (1995) were the first to recognize that the sclerites illustrated by Tremblay and Westrop (1991) under the name *Encrinuroides rarus* in fact represented the distinct species that we name *Walencrinuroides tremblayi*. They identified the uniform distribution of coarse sculpture over the preoccipital glabella as a diagnostic character. To this we add a short anterior cranidial border that does not expand appreciably abaxially and a glabellar crest that is strongly arched in anterior view. These features also separate *W. rolfi* n. sp., to which it is so similar that a description is unnecessary.

<div align="center">W<small>ALENCRINUROIDES</small> <small>ROLFI</small> new species</div>

1975 *Encrinuroides* cf. *rarus* (Walcott); L<small>UDVIGSEN</small>, pl. 3, figs. 22, 23.
1976 *Encrinuroides rarus*; C<small>HATTERTON</small> and L<small>UDVIGSEN</small>, p. 74, pl. 15, figs. 1–43.
1978 *Encrinuroides rarus*; L<small>UDVIGSEN</small>, pl. 2, fig. 22.
1979 *Encrinuroides rarus*; L<small>UDVIGSEN</small>, p. 21, figs. 42–48.

Diagnosis.—Glabella overhangs anterior cranidial border medially, which emerges abaxially as narrow (exsag.) band. Glabella

crest weakly flattened, gently arched in dorsal view. Coarse glabellar tubercles confined to anterior lobe. Rhynchos of hypostome broad (tr.), gently tapered and well rounded anteriorly.

Description.—Chatterton and Ludvigsen (1976, p. 74–76) presented an exhaustive description of this species under the name, *Encrinuroides rarus*.

Holotype.—A cranidium (UA 1372) from the Esbataottine Formation, Mackenzie Mountains, illustrated by Chatterton and Ludvigsen (1976, pl. 15, fig. 1). The remaining sclerites illustrated by Chatterton and Ludvigsen are paratypes.

Etymology.—For Rolf Ludvigsen.

Occurrence.—Esbattaotine Formation, Sections A and P, Sunblood Range, South Nahanni River area, Mackenzie Mountains, northern Canada, collections A125, P1497, *Ceraurinella nahanniensis* Zone. A few, younger sclerites from the *Gabriceraurus gabrielsi* Zone (collection A385) and *C. longispina* Zone (collection A615) illustrated by Ludvigsen (1979) seem also to represent this species.

Remarks.—Although clearly a close relative of *Walencrinuroides rarus*, *W. rolfi* n. sp. differs in a few distinctive features. The anterior cranidial border of *W. rolfi* is obscured medially by an overhanging glabella and is only evident in dorsal view abaxially (compare Chatterton and Ludvigsen, 1976, pl. 15, figs. 1, 2, 20 with Figs. 9.1, 10.7). Also, although the crest of the glabella is weakly arched, it does not approach the degree of dorsal flattening of the glabella of *W. rarus*. Finally, the rhynchos of *W. rolfi* is well developed, broad, gently tapered and rounded anteriorly (Chatterton and Ludvigsen, 1976, pl. 15, figs. 10, 25, 28), whereas the rhynchos of *W. rarus* is ill-defined except anteriorly, where it tapers strongly to a bluntly pointed terminus (Fig. 11.5).

Genus ENCRINUROIDES Reed, 1931

Type species.—*Cybele sexcostata* Salter, in Phillips and Salter, 1848 from the Sholeshook Limestone, South Wales (by original designation).

Remarks.—"*Encrinuroides*" is used here as a label of convenience for species whose relationships were poorly resolved in the phylogenetic analysis. It is not meant to indicate that any of them are closely related to *E. sexcostatus* or, for that matter, are closely related to each other.

"ENCRINUROIDES" GELAISI Lespérance and Debiens, 1995
Figures 12, 13

1989   *Encrinuroides* n. sp. DESBIENS and LESPÉRANCE, p. 1191
1995   *Walencrinuroides gelaisi* LESPÉRANCE and DESBIENS, p. 9, fig. 3.6–3.13.

Diagnosis.—Gently expanded glabella with minimum width at L2; scattered perforate glabellar tubercles with pairing on L1 and L2, but obscure anteriorly. Genal spine reduced to bluntly pointed nub. Palpebral lobe strongly elevated on narrow stalk centered opposite anterior half of L2. Librigena with shallow anterior furrow defined largely by absence of scupture; closely spaced, large tubercles on precranidial lobe. Pygidium with low, paired perforate tubercles on axial rings; paired tubercles on opposing right and left pleural ribs mostly effaced and expressed largely by perforations. Seven pairs of pleural ribs, with tips of two posteriormost pairs fused into border; free tips of anterior pairs rounded rather than spinose.

Holotype.—An enrolled exoskeleton (GSC 110326) from Unit 1, Shipshaw Formation in a quarry 1.5 km north of the Ouiatchouaniche River, Roberval, Lac Saint-Jean region, Quebec (Fig. 12.8, 12.9).

Occurrence.—Shipshaw Formation, Lac Saint-Jean region, Quebec.

Material.—One enrolled, nearly complete individual, two cephala, one librigena, and two pygidia.

Remarks.—Although this species was described not quite two decades ago, it is poorly documented. Lespérance and Desbiens (1995, fig. 3.6–3.13) illustrated it with small photographs that were limited to dorsal views aside from one oblique-lateral view of a paratype cranidium. Here we provide larger images of each specimen in multiple views (Figs. 12, 13) so that convexity, elevation of the palpebral lobes, depth of axial furrows, among other features, can be assessed fully for the first time. The depths of the axial furrows on the cranidium (Fig. 12.2, 12.6) and of the lateral border furrow of the librigena (Fig. 12.10) are exaggerated by shadows in original photographs; shadows also obscure the faint longitudinal median glabellar furrow, which is visible in anterior view (Fig. 12.1, 12.7). The palpebral lobe is strongly elevated, rising almost as high as the strongly arched crest of the glabella. The pygidial axis carries low, paired perforate tubercles (Fig. 13); tubercles on the pleural ribs are virtually effaced, expressed largely by the perforations, and are paired between opposing left and right ribs. Similar effaced tubercles are present on glabellar SO and the posterior border, and also appear to be paired (Fig. 12.6). Circumocular tubercles are difficult to identify, but a conspicuous tubercle between the palpebral lobe and axial furrow is a candidate for CT-1, and a second tubercle near the posterior border furrow may represent FT (Fig. 12.6).

"*Encrinuroides*" *gelasi* was originally assigned to *Walencrinuroides* by Lespérance and Desbiens (1995), but it lacks all of the synapomorphies of this clade. In particular, the glabella of "*E.*" *gelaisi* is gently, rather than strongly, expanded, reaching minimum width at L1, rather than at L2 (Fig. 12.6). The pygidium (Fig. 13) is relatively narrower than in species assigned to *Walencrinuroides*, with a mean length–width ratio that is less than 0.85, rather than greater than 0.9. The only character state shared with *W. rarus* and *W. rolfi* n. sp. is reduction of the genal spine to a bluntly pointed nub (e.g., compare Fig. 9.2 with Fig. 12.2).

Cranidially, "*E.*" *gelaisi* is most like "*E.*" *gibber* (Dean, 1979; Fig. 14) in having a gently expanded glabella with scattered perforate tubercles on the preoccipital glabella, and a conspicuous anterior cranidial border that broadens (exsag.) slightly abaxially. "*Encrinuroides*" *gibber* differs primarily in having a less strongly elevated palpebral lobe that is located farther back on the cranidium. The pygidium of "*E.*" *gibber* (Fig. 14.7–14.8) carries paired perforated tubercles on at least the anterior pairs of axial rings that resemble those of "*E.*" *gelaisi*; the pleural sculpture is, however, in the form of coarse tubercles along the edges of the ribs. In addition, "*E.*" *gibber* has eight pairs of pleural ribs, rather than seven, and six of these terminate as free tips.

"ENCRINUROIDES" GIBBER (Dean, 1979)
Figure 14

1979   *Encrinurus gibber* DEAN, pl. 2, figs. 6, 7, pl. 4, figs. 3, 6, 9, 10, pl. 5, figs., 8, 11, 12, pl. 6, figs. 2, 3.
1979   *Ceraurus* sp. DEAN, p. 8, pl. 2, figs. 6, 7, pl. 4, figs. 3, 6, 7 [only; pl. 4, figs. 2, 5, 7, 8, pl. 5, figs. 1, 2=*Ceraurus* sp.].
1990   *Encrinuroides gibber*; EDGECOMBE and CHATTERTON, p. 823.
1995   *Frencrinuroides gibber*; LESPÉRANCE and DESBIENS, p. 11.

Diagnosis.—Palpebral lobes on narrow stalks and posteriorly positioned, opposite S1. Conspicuous CT-1 (torular) and FT tubercles on fixigena. (Fig. 14.5). Eight pairs of pygidial ribs in front of terminal piece, six of which have free spines.

Holotype.—A pygidium (GSC 38650) from the upper Black Duck Member, Lourdes Limestone, western end of Salmon Cove (GSC loc. 84824), Port au Port Peninsula (Fig. 14.8–14.10).

Occurrence.—Black Duck Member, Lourdes Limestone, Long Point Group, Port-au-Port Peninsula, southwestern Newfoundland

Material.—Two cranidia, one free cheek, two pygidia.

Remarks.—We follow Edgecombe and Chatterton (1990) in considering cranidia of *Ceraurus* sp. of Dean (1979) to represent "*E.*" *gibber*. The best preserved of these sclerites are refigured at larger magnifications and with multiple views (Fig. 14.1–14.6), as is the holotype pygidium (Fig. 14.7–14.9). The latter is partly crushed and too poorly preserved to be measured accurately so the pygidial length–width ratio could not be coded for the analysis. The pygidium does seem to be relatively long and narrow, and has more pairs of pygidial ribs with free spines than most of the ingroup. We count a total of eight pairs of ribs in front of the terminal piece, six of which have free spines; Dean (1979, p. 10) stated that nine pairs were present, and presumably included the fused ribs of the terminal piece. These pygidial characters might indicate a relationship with *Erratencrinurus*, although the low density of cranidial tubercles, and the presence of multiple, rather than single, tubercles on the pygidial axis suggest otherwise.

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APPENDIX I

Characters used in the phylogenetic analysis

1. Shape of glabella; 0, gently expanded (e.g., *Frencrinuroides capitonis*, Fig. 5.1); 1, strongly expanded, mushroom-shaped (e.g., *Walencrinuroides rarus*, Fig. 9.2); 2, subcircular (e.g., *Physemataspis coopi*, Evitt and Tripp, 1977, pl. 12, fig. 1a). Modified from Lespérance and Desbiens (1995) and Edgecombe et al. (1998) to cover a broader range of glabellar outlines.

2. Maximum width of glabella; 0, well beyond S3 (e.g., *Walencrinuroides rarus*, Fig. 9.2); 1, immediately in front of S3 (e.g., *Frencrinuroides capitonis*, Fig. 3.1). This corresponds to character 3 of Lespérance and Desbiens (1995), with the polarity of states switched to reflect choice of *Encrinuroides regularis* Parnaste as the outgroup.

3. Narrowest part of glabella; 0, at L2 (e.g., *Walencrinuroides rarus*, Fig. 9.2); 1, at L1 (e.g., *Frecrinuroides capitonis*, Fig. 4). New character that accounts for variation in the point of minimum width in species whose glabellae expand forward (character 1, state 0). The pleisomorphic state is retained in *Walencrinuroides* as defined here. Parnaste (2006, p. 165) noted that state 0 is present in juveniles of a variety of other species.

4. Crest of glabella; 0, flat to very weakly convex (e.g., *Walencrinuroides rarus*, Fig. 9.4); 1, strongly arched (e.g., *Frencrinuroides capitionis*, Fig. 4.4). New character. Parnaste (2006, p. 165) also drew attention to the flattened crests of glabellae of *W. rarus* and *E. regularis*.

5. Condition of lateral lobes; 0, wide notches (e.g., *Walencrinuroides rarus*, Fig. 9.2); 1, narrow (tr.) and with furrows becoming less well defined anteriorly (e.g., *Frencrinuroides capitonis*, Fig. 5.1, 5.5); 2, indistinct due to high convexity of glabella (e.g., *Physemataspis coopi*, Evitt and Tripp, 1977, pl. 12); 3, obscured by large tubercles (e.g., *Erratencrinurus vigilans*, Ludvigsen, 1979, fig. 27a). New character. The pleisomorphic state is retained in *Walencrinuroides* as defined here.

6. Glabellar tubercle distribution; 0, present on entire glabella (e.g., *Frencrinuroides capitonis*, Fig. 3.4); 1, concentrated on the frontal lobe (e.g., *Walencrinuroides rarus*, Fig. 9.2). This is corresponds to Lespérance and Desbiens' (1995) character 15.

7. Density of glabellar tubercles; 0, Larger tubercles widely spaced with inter-tubercle distance generally at least equal to diameter of largest tubercles and with smaller intercalated tubercles and coarse granules usually present (e.g., *Frencrinuroides capitonis*, Fig. 4.1); 1, tubercles closely packed with inter-tubercle distance less than diameter of largest tubercles (e.g., *Erratencrinurus vigilans*, Ludvigsen, 1979, fig. 27a). New character.

8. Glabellar tubercle type; 0, perforated (e.g., *Walencrinuroides rolfi*, Chatterton and Ludvigsen, 1976, pl. 15, figs. 1, 2); 1, imperforate (e.g, *Frencrinuroides capitonis*, Fig. 4). New character.

9. Paired glabellar tubercles; 0, at least 1L-1, 2L-1, and 3L-2 (e.g., *Frencrinuroides capitonis*, Fig. 4), and may include 4L pairs (e.g., *Encrinuroides regularis*, Parnaste 2006, fig. 5A.); 1, clearly defined on L1 and L2, but obscured anteriorly (e.g., "*Encrinuroides*" *gelaisi*, Lespérance and Desbiens 1995, Fig. 12.2, 12.6); 2, strongly perforated, small tubercles in 1L-1–3L-1 positions (e.g., *Walencrinuroides rolfi*, Chatterton and Ludvigsen, 1976, pl. 15, figs. 1, 2); 3, 1L-1 and 2L-1 and at anterior end of glabella (e.g., *Physemataspis coopi*, Evitt and Tripp, 1977, pl. 12, fig. 1a); species with dense tuberculation that obscures pairing entirely (e.g., *Frencrinuroides edseli*, Edgecombe et al., 1998, fig. 6.3) were coded as missing data.

10. ii0 and iii0 tubercles; 0, absent (e.g., *Walencrinuroides rolfi*, Chatterton and Ludvigsen, 1976, pl. 15, figs. 1, 2); 1, only ii0 expressed consistently (*Frencrinuroides capitonis*, Fig. 4); 2, ii0 and iii0 (e.g., *Erratencrinurus neuter*, Evitt and Tripp, 1977, fig. 10a, pl. 8, fig. 1a). This character is adapted from Evitt and Tripp (1977).

11. Sculpture of LO; 0, smooth (e.g., *Walencrinuroides rolfi*, Chatterton and Ludvigsen, 1976, pl. 15, figs. 1, 2); 1, tubercles or granules (e.g., *Frencrinuroides capitonis*, Fig. 4.7). This is modified from Lespérance and Desbiens' (1995) character 10.

12. Number of tubercles on anterior border of cranidium; 0, fewer than nine (e.g., *Frencrinuroides capitonis*, Fig. 4); 1, nine (e.g., *Erratencrinurus uncatus*, Evitt and Tripp, 1977, pl. 5, fig. 1c). Inclusion of this character was prompted by Parnaste's (2006, p. 159) suggestion that border tubercle number might ally *E. neuter* and *E. uncatus* with *Erratencrinurus*.

13. Pitting on fixigena; 0, present (e.g., *Frencrinuroides capitonis*, Fig. 4); 1, absent on surfaces with coarse granules to fine tubercles (e.g., *Physemataspis coopi*, Evitt and Tripp, 1977, pl. 12, fig. 4a); 2, obscured by very large tubercles (e.g., *Erratencrinurus vigilans*, Ludvigsen, 1979, fig. 27a). New character.

14. Palpebral lobe type; 0, low flap, wider than high (e.g., *Walencrinuroides rarus*, Fig. 9.2); 1, narrow stalk (e.g., *Frencrinuroides capitonis*, Figs. 3.1, 4.1); 2, large, strongly elevated flap (e.g., *Physemataspis insularis*, Shaw, 1968, pl. 10, fig. 10). New character.

15. Palpebral lobe position; 0, midpoint opposite L3 (e.g., *Encrinuroides regularis*, Parnaste, 2006, fig. 5a); 1, midpoint opposite L2 or S2 (e.g., *Walencrinuroides rarus*, Figs. 9.2, 10.4, 10.9); 2, midpoint opposite L1or S1 (e.g., "*Encrinuroides*" *gibber*, Fig. 14.5). This is a modification of Edgecombe and Chatterton's (1990) character 9 by addition of state 2.

16. Sculpture on palpebral lobe; 0, tubercles or coarse granules absent (e.g., *Walencrinuroides rarus*, Figs. 9.2, 10.4, 10.9); 1, tubercles or coarse granules present (e.g., *Frencrinuroides capitonis*, Fig. 3.1). New character.

17. Eye ridge; 0, absent or weak and marked only by line of tubercles (e.g., *Walencrinuroides rolfi*, Chatterton and Ludvigsen, 1976, pl. 15, figs. 1, 2); 1, distinct with independent convexity (e.g., *Frencrinuroides capitonis*, Fig. 4.1, 4.3). This corresponds to character 1 of Edgecombe and Chatterton (1990).

18. Nature of genal spine; 0, very short (e.g., *Walencrinuroides rarus*, Fig. 9.2); 1, longer than LO (e.g., *Frencrinuroides capitonis*, Fig. 4.1); 2, longer than the glabella (e.g., *Erratencrinurus spicatus*, Tripp, 1974), fig. 1.1a). This is modified from character 8 of Lespérance and Desbiens (1995).

19. Large tubercles on base of genal spine; 0, absent; 1, present. Parnaste (2006, p. 159) noted that the apomorphic state served to link *E. neuter* and *E. uncatus* with *Erratencrinurus*.

20. Row of large tubercles on librigenal lateral border; 0, absent (e.g., *Frencrinuroides capitonis*, Fig. 6.5, 6.8); 1, present (e.g., *Erratencrinurus uncatus* Evitt and Tripp 1977, pl. 5, fig. 1b). Parnaste (2006, p. 159) noted that the apomorphic state is shared between *E. neuter*, *E. uncatus* and *Erratencrinurus*.

21. Sculpture of precranidial lobe of librigena; 0, fine to coarse granules over entire surface, anterior furrow (Evitt and Tripp, 1977, fig. 1) undifferentiated (e.g., *Frencrinuroides capitonis*, Fig. 6.5, 6.8); 1, coarse granules to fine tubercles, with smooth anterior furrow (e.g., *Walencrinuroides rolfi*, Chatterton and Ludvigsen, 1976, pl. 15, figs. 11, 21); 2, coarsely spaced tubercles in more than one row (e.g., *Erratencrinurus torulatus*, Evitt and Tripp, 1977, pl. 1, fig. 2c); 3, single row of closely spaced tubercles (e.g., *Erratencrinurus spicatus*, Tripp, 1974, pl. 1, fig. 5). Morphology of the outgroup (*E. regularis*) is unclear due to poor preservation (Parnaste, 2006, fig. 5J), and could represent either states 0 or 1. In the matrix, *E. regularis* is coded as missing data (?), but coding it as both 0 and 1 retrieves the same set of six trees, and results in parallel acquisition of either states 0 or 1 at higher levels in the trees.

22. Axial spine or large tubercles on at least one thoracic segment; 0, absent (e.g., *Walencrinruoides gelaisi*, Fig. 12.8, 12.9); 1, single spine (e.g., *Erratencrinurus uncatus*, Evitt and Tripp, 1977, pl. 7, fig. 4d); 2, large, inflated, paired tubercles (e.g., *Frencrinuroides torulatus*, Evitt and Tripp,

1977, pl. 3, figs. 3a, 2a). New character. Selection of state 0 is arbitrary, as condition is unknown in outgroup.

23. Pygidial outline; 0, length:width=0.8–0.85 (e.g., *Frencrinuroides capitonis*, Figs. 7, 8); 1, length:width <0.8 (e.g., *Physemataspis coopi*, Evitt and Tripp, 1977, pl. 14, fig. 1a); 2, length:width >0.9 (e.g., *Walencrinuroides rolfi*, Chatterton and Ludvigsen, 1976, pl. 15, figs. 13, 31). This is modified from Lespérance and Desbiens' (1995) character 17. Our measurements fell into three "bins", none of which corresponded to their state 2 ("longer than broad"). As there is significant ontogenetic variation in outline in some species (e.g., Fig. 7), we used large holaspids to define length:width ratios.

24. Number of pairs pleural ribs with free spines; 0, 4 (e.g., *Walencrinuroides rolfi*, Chatterton and Ludvigsen, 1976, pl. 15, figs. 13, 14); 1, 5 (e.g., *Frencrinuroides capitonis*, Fig. 7.1–7.5), 2, 6 (e.g., "*Encrinuroides*" *gibber*, Fig. 14.7–14.9), 3, 7 (e.g., *Erratencrinurus vigilans*, Ludvigsen, 1979, fig. 27c). Modified from Lespérance and Desbiens' (1995) character 7.

25. Sculpture on pygidial axis; 0, granules and/or variably expressed paired tubercles (e.g., *Frencrinuroides capitonis*, Fig. 7.7; *Walencrinuroides rolfi*, Chatterton and Ludvigsen 1976, pl. 15, fig. 13); 1, single median tubercles skipping every 2–3 rings (e.g., *Erratencrinurus vigilans*, Ludvigsen, 1979, fig. 27c). Modified from Lespérance and Desbiens' (1995) character 12.

26. Sculpture on pleural ribs; 0, paired tubercles present on opposite ribs (e.g., *Encrinuroides regularis*, Parnaste, 2006, fig. 6B); 1, scattered coarse granules to fine tubercles (e.g., *Frencrinuroides capitonis*, Fig. 7); 2, mostly smooth (may have scattered granules on distal tips of ribs) (*Walencrinuroides rolfi*, Chatterton and Ludvigsen 1976, pl. 15, fig. 13). New character.