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Unravelling parallel conceptions of the Ordovician trilobite *Flexicalymene senaria* (Conrad, 1841) and description of *Flexicalymene trentonensis*, n. sp.

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ABSTRACT

Over the past 180 years, there has been occasional observation that museum collections of specimens identified as "*Calymene senaria*" or "*Flexicalymene senaria*" comprise more than one species. This was first recognized within a year after the species was named and has been remarked upon as recently as 2002. Perusal of compiled literature in concert with examination of new and historical collections at the American Museum of Natural History, the New York State Museum, Paleontological Research Institution, and Harvard Museum of Comparative Zoology, reveals that this history is due to the perpetuation of parallel conceptions of this species, in part because of the lack of an original type and relatively recent adoption of a neotype (Ross, 1967), as well as the application of the name to specimens from a wide range of localities. We review the taxonomic history of *Flexicalymene senaria* (Conrad, 1841) and provide a formal description of a second species, which we designate *Flexicalymene trentonensis*, n. sp. In addition we note that many specimens in museum collections of "*senaria*" also include specimens of the genus *Gravicalymene*. We correct taxonomic assignments for over 350 specimen lots housed in the above repositories, and describe how the clarification of this taxonomic history impacts our understanding of important faunal assemblages (Walcott-Rust Quarry, NY) and the reinterpretation of previously documented phyletic patterns.

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INTRODUCTION

Flexicalymene senaria (Conrad, 1841) was first named as "*Calymene senaria*" to describe specimen(s) found in the Trenton Limestone of New York State. Within a year, Vanuxem (1842: 48) had noted that "There are two species in [the Trenton limestone], which are blended together in description, but nevertheless require separation." This would not be the last time this conflation would be remarked on: Ross (1967: pl. 4, figs. 11–13) figured, as *Flexicalymene* sp., a specimen from Trenton Falls, commenting that it was "Clearly not the same species as *F. senaria* (Conrad)," and as recently as 1999, Brett et al. (1999: 301) noted the "figured specimen [MCZ 111710], from the Walcott-Rust Quarry, is clearly a different species than the neotype."

Brett et al. (1999) and Whiteley et al. (2002) offered the larger tuberculation on the exoskeleton and the presence of short genal spines as primary differences between specimens recovered from the Walcott-Rust Quarry of New York and the neotype of *F. senaria*. Additional morphological differences in the former include the shape of the anterior border, which is medially expanded and less sharply inflected dorsally, and the greater number of pygidial axial rings. These differences are relevant because they are often more ready observable compared to sculpture, which may be weathered away easily, and compared to the presence of short genal spines, which may be broken off or incompletely exposed. It is also sometimes possible to discern the shape of the border or number of axial rings from early descriptions in historical literature and illustrations. Bearing these differences in mind, an exhaustive review of the literature describing "*Flexicalymene senaria*" or "*Calymene senaria*" was undertaken (see the appendix for tabulation), and from which it has become clear that more than one conception of the species has persisted in the literature up to the present day. There are several possible reasons for this, including the fact that original illustration accompanying Conrad's 1841 report was not widely distributed and is rarely associated with the report in library collections at the present time (Bailey, 1990; M. Reitmeyer, personal commun., 2022). Nor did Conrad assign a type specimen and, despite subsequent papers referring to illustrated specimens as either "*C. senaria*" or "*F. senaria*," a neotype was not designated for over 100 years (Ross, 1967). These and other circumstances are elaborated below.

Institutional abbreviations: American Museum of Natural History (AMNH); Museum of Comparative Zoology, Harvard University (MCZ); Paleontological Research Institution (PRI); New York State Museum (NYSM); Philadelphia Academy of Natural Sciences (ANS).

Taxonomic History (1841–1936) of *Calymene senaria* Conrad, 1841

Conrad's (1841) description of *Calymene senaria* largely comprised a comparison with the previously named *Calymene blumenbachii* Brongniart in Desmarest, 1817, with which it was frequently confused.[3] Of particular note is the description of the anterior margin of the cra-

[3] The original description of *Flexicalymene senaria* (Conrad, 1841: 49) is as follows: "*Calymene senaria*. This name is proposed for the trilobite of the Trenton limestone, usually confounded with *C. Blumenbachii*; it differs in having no tubercle between the eye and the middle tubercle of the central lobe; the front, anterior

nidium, which Conrad described as "much smaller and the margin more acutely rounded." The description was included in a report on the geology of New York State and, while at least one plate apparently accompanied some copies of the report (Bailey, 1990),[4] neither AMNH Library staff nor NYSM staff have been able to locate any printed or digital copy of it nor are any available with digital versions of the report available in online repositories (e.g., Hathi Trust). Although a plate was reproduced by James Hall in 1862 after Ezekiel Billings (1861) accused him in writing of suppressing the distribution of the figures, presumably in favor of his own species conceptions (Bailey, 1990), the engraving did not include an illustration of *Calymene senaria*.

The first illustration purported to be of *Calymene senaria*, then, may be found in Emmons (1842: 390, fig. 100.2), published the year after Conrad's report. The illustrated specimen has a smoothly rounded anterior border and no genal spines. Emmons (1842) noted similar-looking specimens from the Midwest (Ohio, Indiana, Michigan) but confined the name *Calymene senaria* to the "Trenton Limestone" of New York and Vermont. The same illustration was reproduced in later publications (Emmons, 1855, 1860). In contrast, Hall's (1847) conception of *Calymene senaria* included specimens from New England, the Midwest, and Canada. He described the anterior margin as "regularly rounded in front, *or* slightly projecting in front of the glabella" (1847: 238; italics added). Hall (1847) figured two specimens from AMNH collection 843/1, which was acquired by the AMNH in 1875, along with the rest of the James Hall Collection (Landman and Winston, 1999). One of those specimens (1847: pl. 64, fig. 3b) would later be designated the neotype by Ross (1967, see below) and another (1847: pl. 64, fig. 3a) would be reidentified as *Gravicalymene* (Ross, 1967: pl. 3, figs. 22, 23).

Clarke (1897, a reprint of 1894) was the first to attribute (and illustrate) a specimen with an extended anterior margin and clear genal spines to *Calymene senaria*, and Clarke's drawing was reproduced by Grabau and Shimer (1910). Ruedemann (1901) similarly described *Calymene senaria* as having a "long shovel-shaped anterior expansion." Foerste (1910: pl. 2, fig. 14) assigned to this species a specimen with an elongated anterior margin and incipient genal spines. As Foerste (1910: 82–83) describes, "the most striking feature of this specimen is the nasute [= having a long snout] outline of the anterior part of the cephalon. This nasute border extends fully 4 mm forward from the anterior border of the glabella. Viewed from the side, it does not appear strongly retrorse as in [specimens from Ohio]."

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to the first tubercle, is much smaller and the margin more acutely rounded; there is also no tubercle on the margin of the middle lobe, between the second and third large tubercles; these latter are oblique, which is not the case in *C. Blumenbachii*; the granules of the surface are more minute and less unequal in size than those of the latter species. Its geological position is widely different. The specific name has allusion to the six tubercles of the buckler."

[4] Bailey (1990) noted that Hall reprinted Conrad's plate as "Plate II" [i.e., as Roman numeral 2] but inspection of Hall (1862) reveals that it is in fact plate 11 [i.e., Arabic number 11], which follows the numbering of the other plates in Hall's publication. The plate does not show illustrations of all taxa described in Conrad's 1841 report, with the implication that there was only one plate to begin with. That said, we cannot be sure of this at this point because Hall's preoccupation was with the bivalve species illustrated in the republished plate.

Taxonomic History (1936–present) of *Flexicalymene senaria* (Conrad, 1841)

Shirley (1936) proposed the name "*Flexicalymene*" for Ordovician calymenids that differ from Silurian genera, including *Calymene*, in having a cone-shaped glabella without papillate second glabellar lobes (see also Systematic Paleontology).

In 1941, Whittington described silicified trilobites, including ontogenetic material, from the Martinsburg Formation of Spring Hill, Virginia. Holaspid cranidia assigned to *Flexicalymene senaria* show a narrow margin and lack genal spines at the lateral edge of the posterior border. In 1953, Evitt and Whittington published a detailed description of the exoskeleton of *Flexicalymene*, based on silicified material they assigned to *F. senaria* from Virginia and Chazy, New York, and *F. meeki* material from Ohio. This report focused on the ventral morphology, the exoskeleton when enrolled, and the structure of the granulation. The only dorsal view of a cranidium assigned to *F. senaria* was a silicified specimen from Chazy. This specimen has a somewhat nasute cranidial margin and is 11.6 mm in length.

Stumm and Kauffman (1958) assigned several calymenid specimens from the Chandler Falls limestone (Michigan) with narrow, smoothly curved anterior borders and no genal spines to *F. senaria* based on comparisons with Hall's (1847: pl. 64, fig. 3a, 3b-c) illustrations of *F. senaria* from AMNH collection 843/1. Ross (1967) selected a neotype for *F. senaria* from the same collection,[5] noting that it "fills the generally accepted concept of *F. senaria*," and that not all specimens assigned to *F. senaria* in AMNH and Smithsonian collections are the same species. Based on references to "topotype material" from Trenton Falls (Ross, 1967: 1, 8), it appears that Ross considered Trenton Falls to be the type locality, although it is not clear what this was based on nor why he then selected a neotype from Middleville, New York. Ludvigsen (1979) figured specimens assigned to *F. senaria* from the Verulam Formation (Ontario), which is in the *Corynoides americanus* graptolite zone (latest Sandbian–early Katian), making it coeval with the Denley Formation of New York (Paton and Brett, 2020). The cranidium has a narrow, smoothly curved anterior border and no genal spines; the pygidium has six axial rings with an incipient seventh.

More recently, Brett et al. (1999) called into question the assignment of some *Flexicalymene* specimens from the Walcott-Rust Quarry to *F. senaria* because they do not adhere to the conception of the species represented by Ross's neotype. A later compilation of New York State trilobites by some of the same authors identified Walcott-Rust Quarry specimens as "*Flexicalymene* cf. *F. senaria*" (Whiteley et al., 2002: pl. 69).

Summary of Taxonomic History

Based on this history, it is apparent that two conceptions of *Flexicalymene senaria* (Conrad, 1841) have been maintained for specimens of eastern North America since the first descrip-

[5] Note that Ross (1967) erroneously reported the collection number as 834/1 in the main text but correctly reports it as 843/1 in the caption for plate 4. Note also that the locality information is incorrect in the text (p. 14) but correct in the plate caption.

tions of the species were published, one with a smoothly curved anterior border and no genal spines and one with an elongate, almost shovel-shaped ("nasute") anterior margin and short genal spines. The former was followed by Emmons (1842, 1855), Hall (1847), Whittington (1941, 1968), Stumm and Kaufman (1958), Ross (1967), and Ludvigsen (1979). The latter was followed by Clarke (1897), Ruedemann (1901), and Foerste (1910, 1919). Several researchers (Vanuxem, 1842; Ruedemann, 1926: 135; Ross, 1967; Brett et al., 1999) noted outright that there were multiple forms or species in collections of specimens referred to as *senaria*.

It remains unclear which of these forms Conrad was studying when he proposed the name "*Calymene senaria*." Furthermore many workers, particularly more recently, have adopted the name "*Flexicalymene senaria*" to refer to the former form. Thus we have uncovered no reason to consider the designation of AMNH 29474 as the neotype to be invalid. We propose the name *Flexicalymene trentonensis*, n. sp., for the latter form.

On the Name "*Calymene callicephala*"

As described above, the neotype designated by Ross (1967) was sourced from specimens figured by Hall (1847), which were part of AMNH 843/1. The figured specimens as well as additional specimens cataloged as AMNH 843/1 were labeled as "*Calymene callicephala*" when they entered the AMNH collections (fig. 1A). "*Calymene callicephala*" was a name proposed by Green (1832) and represented by cast no. 2 accompanying his manuscript (fig. 1B). Green's description noted that the "buckler [= cephalon] is subtriangular; on the front there is a figure of high relief, somewhat resembling a fleur de lis" (1832: 30), the latter of which we believe to be a reference to the shape of the glabella with its relatively prominent L1 lobes. Hall (1847) included the type specimen of *C. callicephala* in his description of "*Calymene senaria*," effectively synonymizing them, but subsequent workers disagreed with this (e.g., Salter, 1864) even though Green's (1832) conception of "*C. callicephala*" and Hall's (1847) conception of *C. senaria* were so broad that both included Ohio specimens now recognized as *Flexicalymene meeki* (Foerste, 1910, 1924).

Importantly, Green (1832: 31) stated that "*C. callicephala*" had never been found at Trenton Falls, "which yields the true *C. blumenbachii* [= *C. senaria*]."[6] Green (1832) reported that the specimen he used as a model for his plaster cast (cast no. 2) was from Hampshire, Virginia, but Foerste (1924) noted that there is no town of Hampshire in Virginia nor are there rocks of the right age outcropping in Hampshire County of West Virginia, leaving the provenance of the specimen in doubt. The type specimen was reported as lost by Bassler (1915: 166). This was confirmed several decades later (Whittington, 1963), and recent investigation suggests that the type may have been lost in a fire (John Sime, personal commun., 2022). The name "*Calymene callicephala*" was used in faunal lists (for non-New York State areas) published in the early 20th century (e.g., Bassler, 1909; Cumings, 1908; Cumings and Galloway, 1912; Foerste, 1916; Watson and Powell, 1911), but by 1926 it had been abandoned[7] (Ruedemann, 1926). Interestingly,

[6] Green's "*C. blumenbachii*" (cast no. 1) was reidentified as *C. senaria* by Hall (1847).

[7] Ruedemann (1926: 133–134) noted that "[*Calymene callicephala*] was, as pointed out by Clarke (1897, republished from 1894: 699), undoubtedly intended for the *Calymene* of the Cincinnatian beds, but since the type specimen is labeled as coming from a district in West Virginia which is not known to contain any

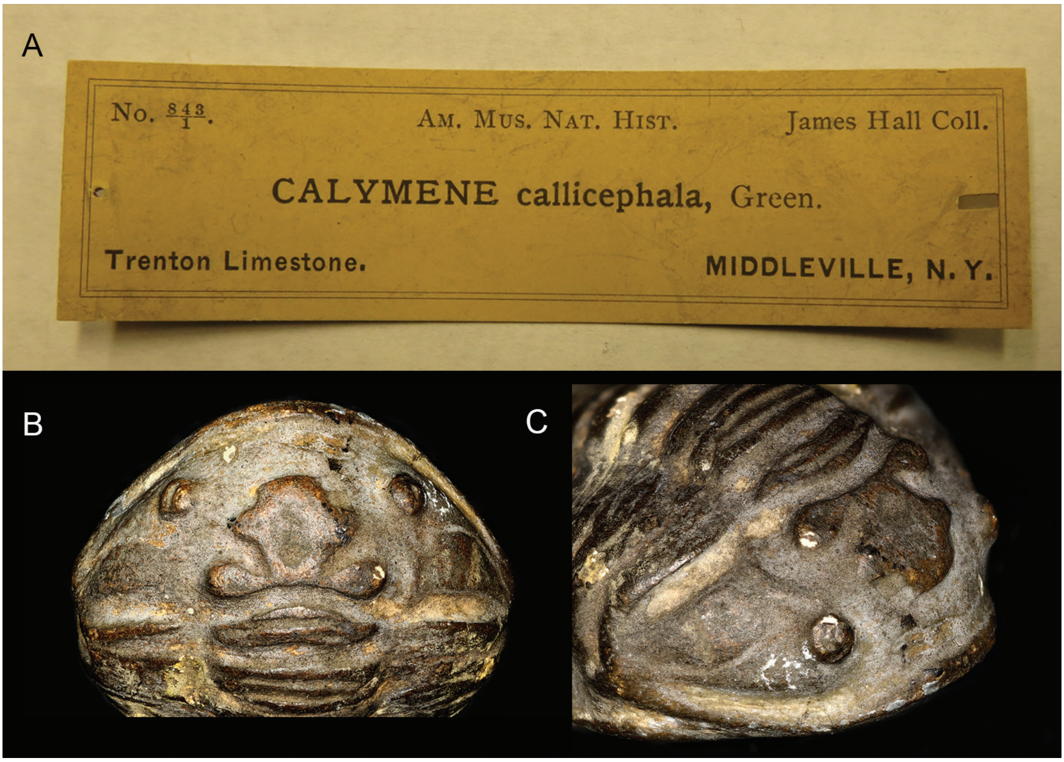

FIGURE 1. Materials related to the name "*Calymene callicephala*." **A.** Historic label from collection 843/1 from the James Hall Collection at the AMNH. **B.** Dorsal view of cephalon of cast no. 2 from Green (1932), ANS. **C.** Oblique view of cephalon from cast no. 2 from Green (1932), ANS.

Rafinesque (1832) had assigned *Calymene callicephala* to *Orimops*, but this name appears to have been used rarely (e.g., Fisher, 1957, figured a specimen under the name "*Orimops (Flexicalymene) senaria*") and would later be considered either a junior synonym of *Flexicalymene* (Whittington in Harrington et al., 1959: 452) or unrecognizable (Henningmoen in Harrington et al., 1959: 525) and ultimately a nomen dubium (Dean, 1962; Whittington, 1963). The only other mention of "*C. callicephala*" that we are aware of comes from the taxonomic history of *Flexicalymene granulosa* (Foerste, 1909: 294), which was originally described as a subspecies ("*Calymene callicephala granulosa*").

Foerste (1924: 247) describes the type of *C. callicephala* as characterized by the "protrusion of the border anterior to the glabella, giving it a triangular outline as in *C. senaria,* rather than the upturned rostral border found in *C. meeki.*" Since Foerste's conception was allied with the form described herein as *F. trentonensis*, n. sp. (see above), one could argue the name *C. callicephala* takes precedence. However, Clarke (1897) previously and correctly noted that the glabella on Green's cast no. 2 is abraded, making the glabella appear shorter (sag.) and further from the anterior border than it likely was. Further, he noted how different Green's cast no. 2

Cincinnatian rocks (see Foerste, 1910: 83) and since that specimen does not represent the common trilobite of the Cincinnati region, Green's name has been abandoned."

was from Trenton Falls specimens in "decided genal spinules and the long shovel-shaped, not abruptly concave, anterior extension," of which he included a line drawing (his fig. 3). Our own examination of examples of Green's cast no. 2 (fig. 1B) from the Philadelphia Academy of Sciences reveals them to be more consistent with Ross's (1967) neotype of *F. senaria*, calling into doubt Foerste's description of the type specimen of *C. callicephala*. Given the ambiguity resulting from (1) the lost type specimen associated with Green's cast no. 2 of *Calymene callicephala*; (2) the lack of extended nasute anterior border or genal spines on casts no. 2 that were available for examination; (3) the inconsistency around the provenance of the type for *C. callicephala* (not to mention the fact that Green stated that the form associated with the name was never found at Trenton Falls), and (4) common abandonment of the name *C. callicephala* by most workers by the mid-1920s; we consider that the most conservative and least confusing approach is to avoid resurrecting the name *callicephala* for the species described herein.

SYSTEMATIC PALEONTOLOGY

Class Trilobita Walch, 1771

Order Phacopida Salter, 1864

Family Calymenidae Burmeister, 1843

Flexicalymene Shirley, 1936

Type species: *Flexicalymene caractaci* (Salter, 1865).

Discussion: Relationships of genera within Calymenidae have long been debated. The basis for Shirley's (1936) "Group A" vs. "Group B" distinction was the presence of "papillate second glabellar lobes" or "buttresses," terms that refer to contact of the fixigenal area with, at minimum, glabellar lobe L2, giving the appearance of constriction of the axial furrow at this point (see also Whittington, 1971). The absence of buttresses was also used to unite *Gravicalymene* with *Flexicalymene*, *Platycalymene*, *Metacalymene*, *Thelecalymene*, and *Sthenarocalymene* into the subfamily Flexicalymeninae (Siveter, 1976), but the monophyly of the subfamily has recently been called into question (Adrain et al., 2020; Holloway et al., 2020; Smith and Ebach, 2020).

Many museum collections identified as "*Flexicalymene senaria*" include specimens of *Gravicalymene*. This has been previously remarked on both implicitly (Ruedemann, 1901) and explicitly (Ross, 1967). In the supplementary material (available online: https://doi.org/10.5531/sd.sp.71), we have noted specimens that are better assigned to *Gravicalymene*. Diagnostic differences between *Flexicalymene* and *Gravicalymene* include the cone shaped vs. bell shaped glabella, respectively. We also observe differences in the shape of the pygidium, at least among North American species. Shirley (1936: 410) referred to the *Gravicalymene* pygidium as "with a tendency to a 'butterfly wing' outline" because the pleural fields extended in way that is reminiscent of some open butterfly wings. In contrast, the *Flexicalymene* pygidium could be comparatively described as "moth shaped" after the more triangular or kite-like shape of some moth wings.

More explicitly, the pygidium in *Gravicalymene* has a greater width:length ratio with the widest point more anterior than in *Flexicalymene*. A revision of eastern North American *Gravicalymene* species is in preparation and will be published in a subsequent paper.

Flexicalymene senaria (Conrad, 1841)

Figure 2

Calymene senaria Conrad, 1841: 38.
Calymene senaria Conrad, 1841: Emmons, 1842: 390, fig. 2.
Calymene senaria Conrad, 1841: Hall, 1847: 238, pl. 64, figs. 3b, c; non figs. 3a, d–g; ? figs. 3h, k–n.
Calymene senaria Conrad, 1841: Emmons, 1855: p. 15, fig. 16 [refigured from Emmons, 1842]; ? 251, fig. 72e–h.
Calymene senaria Conrad, 1841: Billings, 1856: 45, fig. 10.
Calymene senaria Conrad, 1841: Emmons, 1860: 98, fig. 87 [reproduced from Emmons, 1842].
?*Calymene senaria* Conrad, 1841: Hitchcock, 1861: 300, fig. 213 [possibly copied from Hall, 1847].
Calymene senaria: Salter, 1865: non pl. 9, figs. 6–8, fig. 11; ?98, fig. 21, pl. 9, figs. 9, 10.
?*Calymene senaria* Conrad, 1841: Etheridge, 1878: 591.
?*Calymene senaria* Conrad, 1841: Walcott, 1879: pl. 1, figs. 1, 2, 5.
non *Calymene senaria* Conrad, 1841: Walcott, 1881: pl. 4, fig. 7, pl. 5, figs. 1–4 [= *F. trentonensis*]; ? pl. 5, fig. 5.
Calymene senaria Conrad, 1841: Lesley, 1889: 110, fig. 11b; non 11a, c.
?*Calymene senaria*: Keyes, 1894: 230.
non *Calymene senaria* Conrad, 1841: Bernard, 1894: 427, fig. 13, 15, 17 [= *F. trentonensis*; reproduced from Walcott, 1881].
non *Calymene senaria* Conrad, 1841: Clarke, 1897: 700, fig. 3 [= *F. trentonensis*].
non *Calymene senaria* Conrad, 1841: Ruedemann, 1901: 67 [= *F. trentonensis*].
?*Calymene senaria* Conrad, 1841: Weller, 1903: 203, pl. 15, fig. 23.
non *Calymene senaria* Conrad, 1841: Grabau and Shimer, 1910: 315, fig. 1624c, d [= *F. trentonensis*; reproduced from Clarke, 1897].
non *Calymene senaria* Conrad, 1841: Foerste, 1910: 82, pl. 11, fig. 14 [= *F. trentonensis*].
non *Calymene senaria* Conrad, 1841: Ruedemann, 1912: 120, pl. 9, fig. 6-10 [= *Gravicalymene magnotuberculata*].
non *Calymene senaria* Conrad, 1841: Walcott, 1918: 147, pl. 28, figs. 7-8 [= *F. trentonensis*; reproduced from Walcott, 1881]; ?pl. 26, figs. 1–7, 9–13, pl. 27, figs. 4–14, pl. 33.
Flexicalymene senaria (Conrad, 1841): Whittington, 1941: 493, pl. 72, figs. 1–27, 31–34, 38–40, 42–47, text fig. 1.
Flexicalymene senaria (Conrad, 1841): Shimer and Shrock, 1944: 645, pl. 272, figs. 3–5 [reproduced from Whittington, 1941].
Flexicalymene senaria (Conrad, 1841): Wilson, 1947: 48, pl. 10, figs. 11a, 11b, 12.
Flexicalymene senaria (Conrad, 1841): Evitt and Whittington, 1953: 49, pl. 9, figs. 1–16, pl. 10, fig. 1.
Flexicalymene senaria (Conrad, 1841): Stumm and Kaufmann, 1958: 949, pl. 123, figs. 1–11.
Flexicalymene senaria (Conrad, 1841): Ross, 1967: B14, pl. 4, figs. 1–6.
non *Flexicalymene* cf. *F. senaria* (Conrad, 1841): Ross, 1967: pl. 3, figs. 24–28 [= *F. trentonensis*].
Flexicalymene senaria (Conrad, 1841): Ludvigsen, 1979: 46, fig. 29.

Flexicalymene senaria (Conrad, 1841): Chatterton et al., 1990: 266, fig. 1.1–1.15, 2.1, 2.2, 5.1–5.18, 6.1–6.21.
Flexicalymene senaria (Conrad, 1841): Brett et al., 1999: 301, fig. 9.2; non fig. 9.1 [= *F. trentonensis*]; ?fig. 9.11.
Flexicalymene senaria (Conrad, 1841): Whiteley et al., 2002: 133, pl. 67, 70; ?pl. 68.
non *Flexicalymene cf. F. senaria* (Conrad, 1841): Whiteley et al., 2002: pl. 69 [= *F. trentonensis*].
non *Flexicalymene senaria* (Conrad, 1841): Losso et al., 2023a: fig. 1a, 1e [= *F. trentonensis*]; ?figs. 2c, 3a.
non *Flexicalymene senaria* (Conrad, 1841): Losso et al., 2023b: fig. 4c [= *F. trentonensis*].

Neotype: AMNH-FI-29474, articulated specimen (fig. 2A; see also fig. 7E–H).

Type locality: Ross (1967) selected the neotype from specimens figured by James Hall (1847) from his collection 843/1.[8] The original labels for specimens from collection 843/1 indicate that they were collected from the Trenton Limestone, Middleville, NY (fig. 1A).[9] The New York State Museum has collections made by James Hall from five localities near Middleville (L. Amati, personal commun., 2022), and it is possible that collection 843/1 is a mix from more than one of these.

Other geographic occurrences: UNITED STATES: Black River and Mohawk valleys, NY; Champlain Valley, NY, VT; Spring Hill, Augusta County, VA; Chandler Falls, Delta County, MI. CANADA: south-central Ontario; Montmorency Falls, Quebec.

Stratigraphic range: *Corynoides americanus* to *Orthograptus ruedemanni* graptolite biozones (latest Sandbian to early Katian; see Brett and Baird, 2002) of the Sugar River, Denley, and Rust formations (Black River and Mohawk valleys, NY), Martinsburg Formation (VA), Chandler Falls limestone (MI), Verulam and Lindsay Formations (Ontario; see Paton and Brett, 2020, for updated stratigraphy), and Deschambault and/or Neuville formations (Quebec).

Diagnosis: *Flexicalymene* species with L2 lobes that are 45% the size (area) as L1 lobes, strongly upturned anterior border that curves smoothly, bimodally sized granulation across dorsal surface and doublure, and pygidium with five distinct axial rings.

Description: Detailed descriptions of the exoskeleton and ontogeny of *F. senaria* were given in Whittington (1941), Evitt and Whittington (1953) and Chatterton et al. (1990), but none provided a diagnosis, which is rectified here.

Discussion: Most work on *F. senaria* has focused on specimens recovered from U.S. localities. Comparison to available material from Canada indicates that there is some subtle geographic variation across the specimens currently assigned *F. senaria*. For example, the anterior glabellar lobe is narrower in specimens known from the Verulum Formation in Ontario (fig.

[8] The specimens illustrated by Hall (1847) as "*C. senaria*" are not the only calymenid specimens in collection 843/1, nor are they the only specimens originally identified as "*Calymene callicephala*" or "*Calymene senaria*" in the Hall Collection (fig. 1). Specimens of "*Calymene senaria/callicephala*" from other collections in the James Hall Collection were sourced from other areas of upstate New York and may or may not belong to any of the species described herein. In the online supplement (https://doi.org/10.5531/sd.sp.71), we provide both confirmed and tentative species assignments for "*senaria*" or "*callicephala*" specimens in the AMNH collections and select NYSM, PRI, and MCZ collections.

[9] In the caption for plate 123, Stumm and Kauffman (1958) reported that the specimens were found near Watertown, New York, which is incorrect. Ross (1967) noted this error. Collection 843/6 is from Watertown and comprises one specimen of *Flexicalymene senaria* (see online supplement).

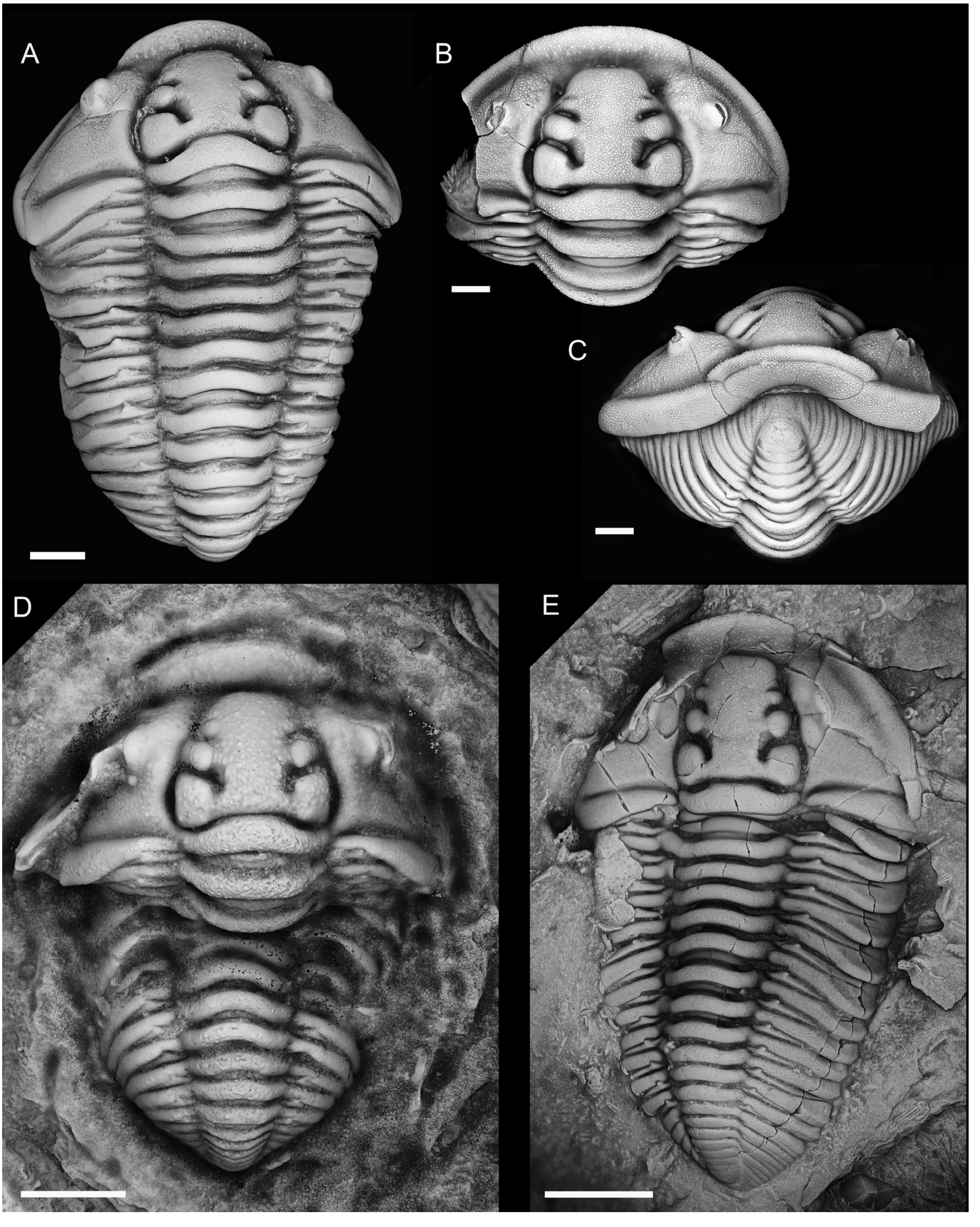

FIGURE 2. Geographically distributed examples of *Flexicalymene senaria* (Conrad, 1841), including the neotype from the Middleville area, NY. **A.** Dorsal view of neotype of *Flexicalymene senaria*, AMNH-FI-29474, scale bar = 2 mm. See also figure 7. **B, C.** *F. senaria* from the Verulam Formation near Gamebridge, Ontario, AMNH-FI-140958 scale bar = 2 mm. **D.** *F. senaria* from the Rust Formation, Walcott-Rust Quarry, MCZ 201040, scale bar = 3 mm. **E.** *F. senaria* from the Sugar River Formation, Ives Quarry, near Watertown, NY, AMNH-FI-139624, scale bar = 3 mm.

2B; Ludvigsen, 1979: fig. 29A). Whittington (1968) reported *F. senaria* occurring at Montmorency Falls, just north of Quebec City. This occurrence is confirmed by MCZ 111065, which was recovered above the falls and thus consistent with specimens recovered from the Deschambault or Neuville formations (Riva and Pickerill, 1987) within the *Corynoides americanus* to *Orthograptus ruedemanni* graptolite biozones (Goldman et al., 1994). *F. trentonensis* has also been recovered from Beaufort north of Quebec city (in addition to the type locality which is just south of Quebec city, see below), but its stratigraphic relationship to *F. senaria* is unknown.

Flexicalymene trentonensis, n. sp.

Figures 3–6A, 6B?, 6C?, 7

?*Calymene senaria* Conrad, 1841: Walcott, 1879: pl. 1, figs. 1, 2, 5.
Calymene senaria Conrad, 1841: Walcott, 1881: pl. 4, fig. 7, pl. 5, figs. 1–4; non pl. 5, fig. 5.
Calymene senaria Conrad, 1841: Bernard, 1894: 427, figs. 13, 15, 17 [reproduced from Walcott, 1881].
Calymene senaria Conrad, 1841: Clarke, 1897: 700, fig. 3.
Calymene senaria Conrad, 1841: Ruedemann, 1901: 67.
Calymene senaria Conrad, 1841: Grabau and Shimer, 1910: 315, fig. 1624c, d [reproduced from Clarke, 1897].
Calymene senaria Conrad, 1841: Foerste, 1910: 82, pl. 11, fig. 14.
Calymene senaria Conrad, 1841: Walcott, 1918: 147, pl. 28, figs. 7-8 [reproduced from Walcott, 1881]; ?pl. 26, figs. 1–7, 9–13, pl. 27, figs. 4–14, pl. 33.
Flexicalymene cf. *F. senaria* (Conrad, 1841): Ross, 1967: pl. 3, figs. 24–28.
Flexicalymene sp.: Ross, 1967: pl. 4, figs. 11–13.
Flexicalymene senaria (Conrad, 1841): Brett et al., 1999: 301, fig. 9.1 [image of paratype]; ?fig. 9.11.
Flexicalymene cf. *F. senaria* (Conrad, 1841): Whiteley et al., 2002: pl. 69 [image of paratype].
Flexicalymene senaria (Conrad, 1841): Losso et al., 2023a: fig. 1a [image of paratype], 1e; ?figs. 2c, 3a.
Flexicalymene senaria (Conrad, 1841): Losso et al., 2023b: fig. 4c [reproduced from Losso et al., 2023a].

Type material: Holotype: articulated exoskeleton, AMNH-FI-140954 (fig. 3). Paratypes: articulated enrolled exoskeleton from the type locality, AMNH-FI-140955 (fig. 6A); articulated exoskeleton from the Walcott-Rust Quarry, NY, MCZ 111710 (fig. 4A).

Type locality: Frontenac Quarry, Neuville, Quebec.[10]

Other geographic occurrences: UNITED STATES: Mohawk Valley, most notably the Walcott-Rust Quarry, near Rome, NY. CANADA: Beaufort, Quebec.

Stratigraphic range: *Flexicalymene trentonensis* is restricted to the *Orthograptus ruedemanni* graptolite biozone (early Katian; see Goldman et al., 1994; Brett and Baird, 2002). In New York, it is found in the Spillway Member of the Rust Formation and lateral equivalents, such as the Wintergreen Flat beds found within the Flat Creek Formation to the east. In Quebec, it is found in the Neuville Formation in the Quebec city area. In both areas, these formations are assigned to the Trenton Group.

[10] This quarry is currently under operation by Construction and Pavage Portneuf Inc.

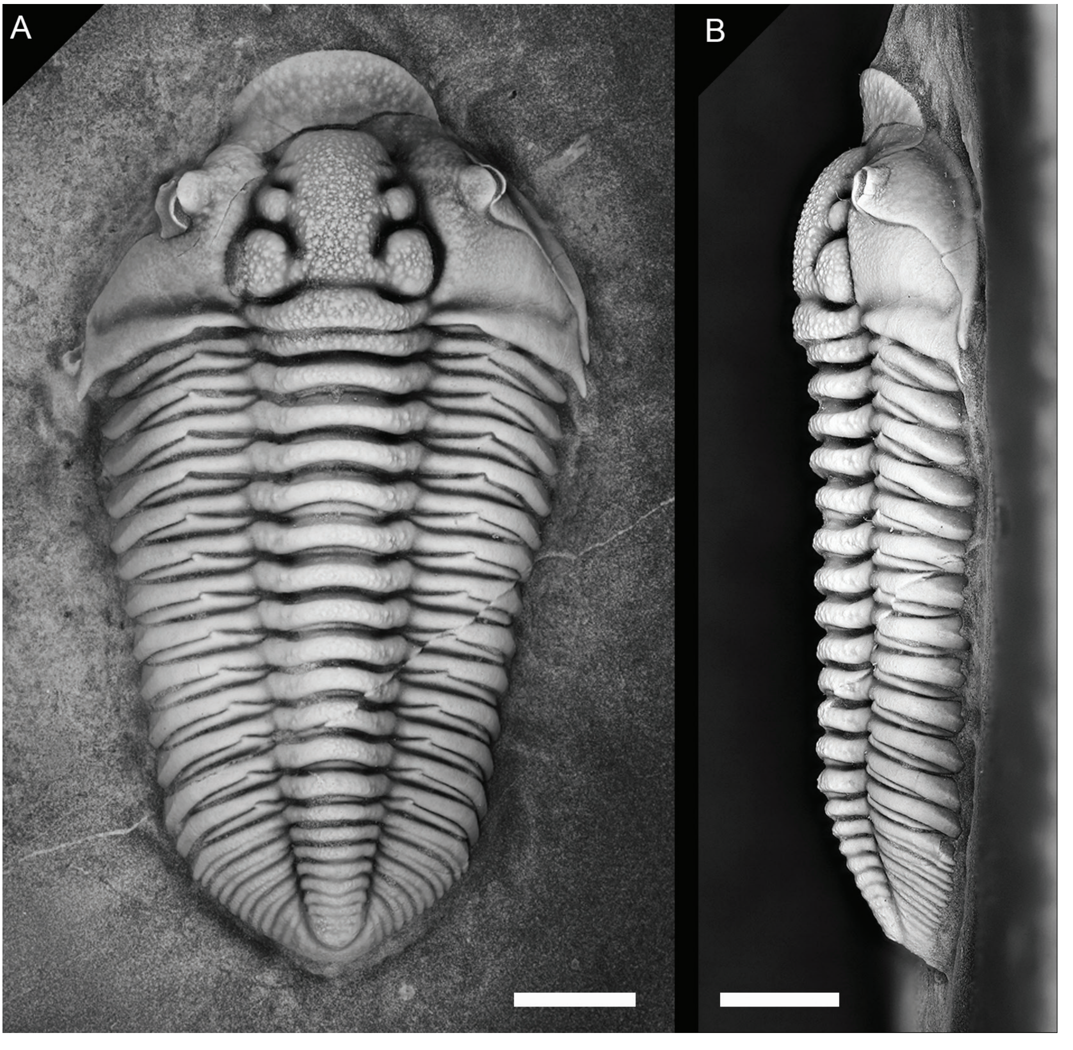

FIGURE 3. *Flexicalymene trentonensis*, n. sp., from Quebec city area, Quebec. **A.** Dorsal view of holotype, AMNH-FI-140954, scale bar = 5 mm. **B.** Lateral view of holotype, AMNH-FI-140954. Holotype is from the Neuville Formation, near Quebec city, Canada.

Diagnosis: *Flexicalymene* species with L2 lobes that are 33% the size (area) as L1 lobes, gently upturned anterior border that is wider medially than laterally, short genal spines, bimodally size granulation primarily on the axial lobe, and pygidium with six to seven distinct axial rings.

Description: Holotype is 37.9 mm long (sag.); length (sag.) of cephalon:thorax:pygidium is 11.5:19.6:6.9 (fig. 3A). Cephalon semitriangular in shape with length:width ratio of 0.55. Anterior margin strongly but smoothly curved laterally and weakly curved ("upturned") dorsally. Anterior border furrow shallow and weakly curved, so that anterior border is wider medially than laterally; length (sag.) of frontal area at sagittal axis is 30% the length of the cephalon. Lateral margin curves posteriorly gently and smoothly until angular curve of 19°

abaxial to the middle of L1, then directed posteriorly with no further inflection to base of genal spine. Posterior margin extends laterally with posterior angular inflection of 24° at fulcrum; additional inflection of 44° at base of genal spine. Posterior border furrow extends laterally, so that posterior border widens abaxially.

Glabella cone shaped with length:width ratio of 0.93; maximum glabellar width at midpoint of L1. Length (sag.) ratio of glabella:cephalon is 0.71; maximum width ratio of glabella:cephalon is 0.42. Axial furrow consistently strongly impressed. L1 elliptical in shape; L2 circular in shape; L2 is 33% the size (area) of L1; L3 is 28% the size (area) of L2. S1 strongly impressed, extends weakly posteriorly from axial furrow with posteriorly directed angular inflection of 51° about 1/3 of the way across glabella; does not reach S0. S2 strongly impressed, extends weakly posteriorly from axial furrow to same transverse position as S1 inflection point. S3 expressed as short transversely directed indent from axial furrow. Occipital ring has transverse posterior margin medially, curving anteriorly abaxially, ratio of occipital ring width (tr.) to maximal glabellar width is 0.89. S0 moderately convex forward so that ring is wider (sag.) medially than abaxially; strongly impressed laterally, becoming notably weaker at same exsagittal position as S1 inflection point. Preglabellar furrow shallower than remainder of axial furrow; smoothly curved anteriorly, converges with anterior border furrow.

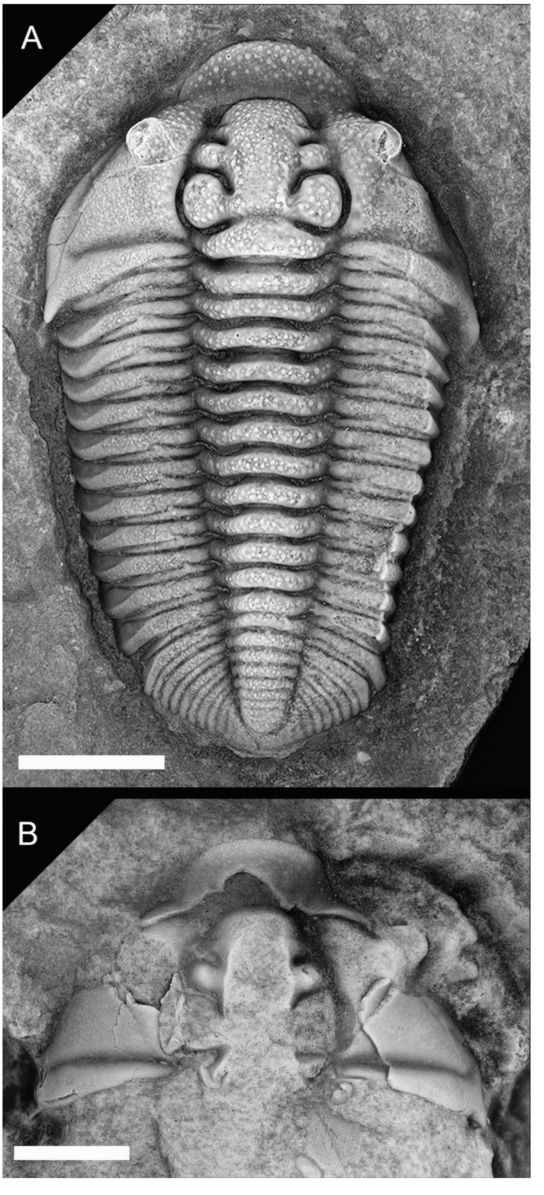

FIGURE 4. *Flexicalymene trentonensis*, n. sp., NY. **A.** Dorsal view of *F. trentonensis* from the Walcott-Rust Quarry, MCZ 111710 (paratype), scale bar = 5 mm. **B.** Cranidium of *F. trentonensis* from the Flat Creek Formation of Crum Creek (same locality as Brett and Baird, 2002, loc. 33b), eastern Mohawk Valley, NY, AMNH-FI-139592, scale bar = 3 mm.

Palpebral lobes hemispherical to slightly reniform, short (17% length of cephalon), anteriorly positioned with midpoint at S2, defined by shallow palpebral furrows, separated from glabella at distance similar to exsagittal position of fulcrum. Eye ridge not well developed. Preocular genal field strongly curved ventrally ("downsloping") toward anterior and lateral border furrows. Palpebral area of fixigena and

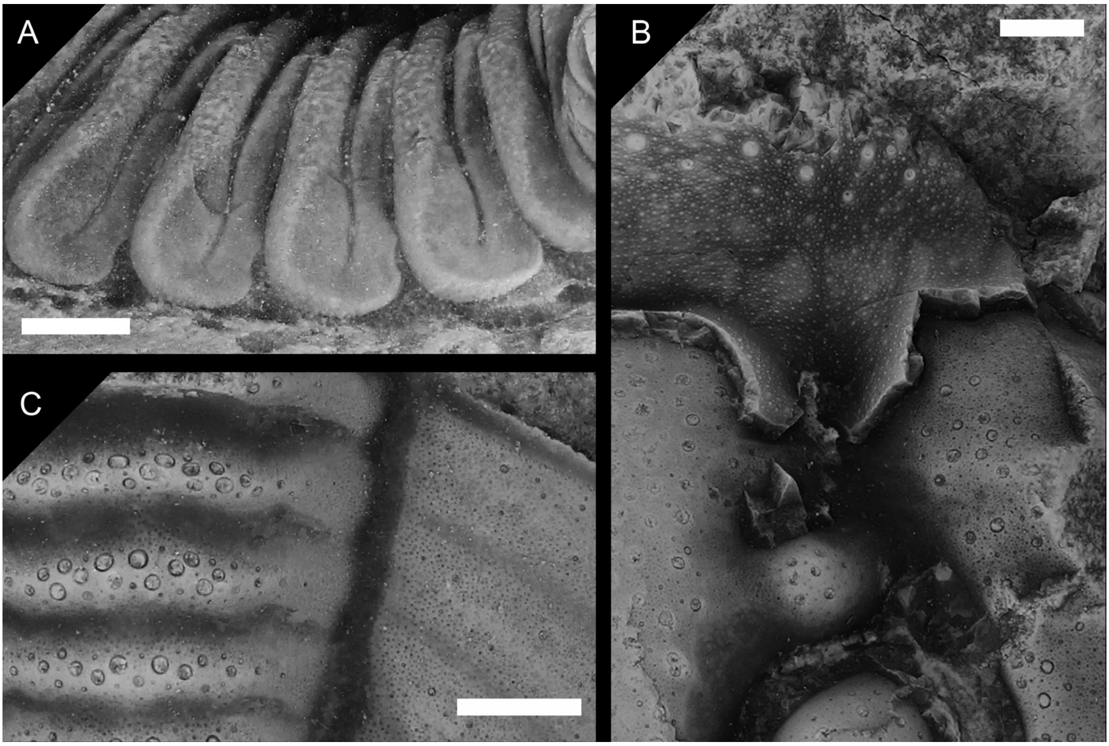

FIGURE 5. Anatomical detail of *Flexicalymene trentonensis,* n. sp. **A.** Lateral view of thoracic pleura, showing pleural furrow extending onto smooth facet. MCZ 111116, scale bar = 1 mm. **B.** Partially exfoliated and eroded cephalon, showing rings and pits in place of bimodal granulation. AMNH-FI 62196, scale bar = 1 mm. **C.** Exfoliated pygidial axis and part of pleura, showing rings and pits in place of bimodal granulation. AMNH-FI 62196, scale bar = 1 mm. Both specimens from Mohawk Valley, NY.

postocular field gently downsloping toward axial furrows. Glabella is higher than palpebral lobes. Eye surface is not preserved, but there is evidence of a vertical eye socle.

Anterior dorsal suture converges from anterior end of palpebral lobe at angle of 34° to sagittal line, meeting anterior border in line with maximum width of glabella. Posterior dorsal suture extends laterally, with first posterior angular inflection of 38° (54° from the transverse line) halfway to lateral margin and second posterior angular inflection of 23° (86° from the transverse line) at distal end of posterior border furrow; suture crosses at genal angle abaxially to genal spine. Apparent projection of posterior end of librigena is due to displacement relative to the cranidium (cf. fig. 4A). Genal spine triangular, short (11% length of cephalon).

Border sector of rostral plate narrow (sag.), as wide as glabella at L2, strongly curved along anterior margin, with straight connective sutures (fig. 6A). Two hypostomes from the Walcott-Rust Quarry are tentatively assigned to *F. trentonensis* (fig. 6B, C). These specimens are subrectangular in outline. Anterior border wide (sag.) and extends from middle body, curving very gently ventrally. Anterior wings extend laterodorsally, with deep pit on ventral side near the anterolateral edge. Lateral margins slightly waisted, so that hypostome is wider at anterior and posterior wings. Lateral border furrow most strongly expressed along anterior lobe of the middle body, which is oval in overall shape; separated from posterior lobe by shallow furrow. Posterior furrow deepest at lateral edges and at sagittal axis. Posterior border flat, forked, the notch reaching anteriorly almost to the posterior border furrow.

Thorax with 13 tergites,[11] narrowing posteriorly, so that posteriormost tergite is 65% the width of the anteriormost segment. Axis narrowing progressively from anterior to posterior of trunk, ranging from 40% to 36% of thoracic width. Axial rings with articulating furrow; furrow is deeper abaxially than medially. Posterior margin of axial ring mimics shape of posterior margin of occipital ring. Anterior margin of pleura with prominent fulcral process, abaxial to which pleura is strongly curved ventrally ("downturned"). Pleural furrow extends weakly posteriorly from axial furrow; strongly expressed until shallowing onto facet (fig. 3A). Anterior and posterior bands rounded, of similar height, but posterior band is wider (exsag.) adaxially than anterior band. Facet broad, smooth; pleural tips broadly rounded (fig. 5A).

Pygidium subrhomic with length:width ratio of 0.60. Axis tapers posteriorly with six or seven distinct rings and rounded terminal piece, occupying 90% of the pygidial length. On some specimens, including the holotype, a shallow furrow indicative of an additional seventh or eighth ring is visible. Shape of pygidial axial rings mimics those of thorax, although inter-ring furrows are more transverse than articulating furrows of thorax. Axial furrow strongly expressed; shallowing at sagittal axis on posterior margin of terminal piece. Pleural region horizontal adaxial to fulcrum, curving strongly ventrally abaxially toward border. Pleural and interpleural furrows expressed from axial furrow to margin; extend posterolaterally at 62° to sagittal axis until reaching border where they start curving more posteriorly. Pleural and interpleural furrows similar in width and depth on border region, but interpleural furrows are progressively shallower and narrower toward the axial furrow. First five sets of furrows visible; additional posterior furrows visible only as traces. Fulcral process on anterior margin (fig. 3).

Granulation on the exoskeleton bimodal in size with random (i.e., not paired) distribution of larger (300–350 μm) granules surrounded by more densely packed small (110–130 μm) granules. The larger-sized granules are concentrated on the cephalic border, the glabella, the interocular fixigenal area, the axial rings of the entire trunk, and the proximal pleural region of the thoracic tergites (figs. 2, 5B, C), but are largely absent from the preglabellar field, the distal parts of the fixigena, distal parts of the thoracic tergites, and the pleura of the pygidium. The pattern of granulation is evident on internal molds and weathered surfaces as rings representing the large granules and pitting representing the small granules (fig. 5B, C). The style of granulation is similar to that of the *Flexicalymene senaria* material that Evitt and Whittington (1953: pl. 9) described from Chazy, NY.

The largest articulated specimen that we have found in museum collections (AMNH-FI-62196) is 51.3 mm in total body length with cephalon:thorax:pygidium at 14.5:28.1:8.7. This size is comparable to the largest specimens we are aware of in private collections. We are not aware of any disarticulated material that would imply a larger total body size.

[11] Traditionally, the articulated sclerites in the thorax of the trilobite exoskeleton have been called "thoracic segments." Throughout this manuscript, we refer to the thoracic segments as "tergites" to reflect their anatomical similarity to other arthropods and to distinguish them from body segments, which may not be positionally synchronous (see, for example, Ortega-Hernández and Brena, 2012).

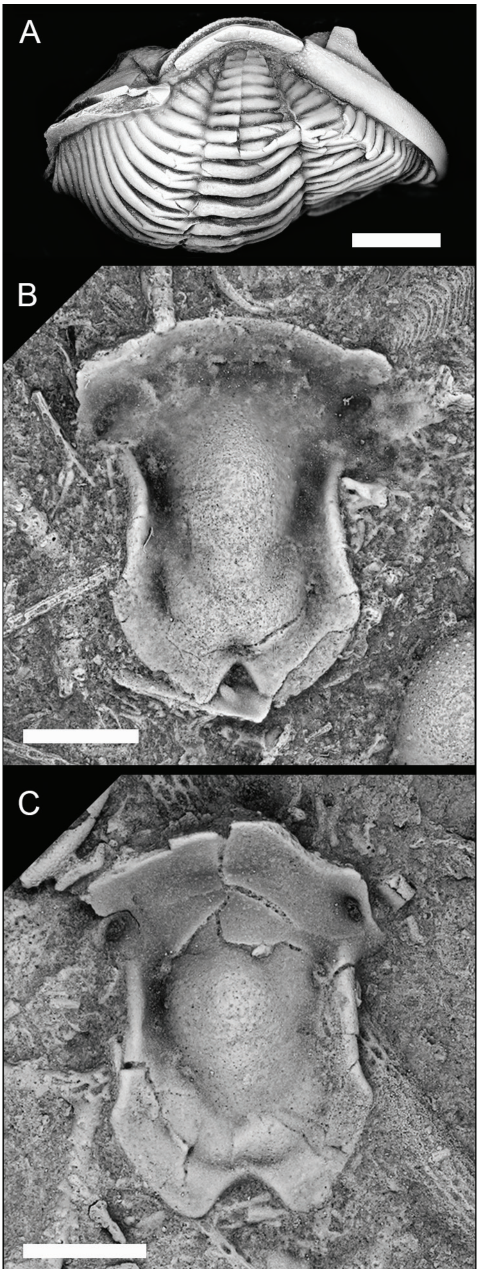

FIGURE 6. Ventral morphology of *Flexicalymene trentonensis*, n. sp. **A.** View of rostral plate, AMNH-FI-140955 (paratype), scale bar = 5 mm. **B.** ?Hypostome, MCZ 201041, scale bar = 2 cm. **C.** ?Hypostome, MCZ 201403, scale bar = 2 mm. MCZ specimens are from the Walcott-Rust Quarry; AMNH-FI-140955 is from the type locality in Quebec (see text).

Discussion: *Flexicalymene trentonensis* may be differentiated from *Flexicalymene senaria* by the extended anterior shape and weak dorsal curvature of the anterior border of the cephalon and the presence of short genal spines (fig. 7). Both species have bimodally sized granulation, but on *F. trentonensis*, the granulation is more highly concentrated on the axial lobe and the larger class of granules is larger than those of *F. senaria*. On average, *F. trentonensis* has more pygidial axial rings (fig. 7D, H), but the variation in expression across specimens (table 1) makes this difference useful primarily in combination with other traits. If the assignment of the two isolated hypostomes from the Walcott-Rust Quarry is correct, then the two species also differ in the expression of the forked posterior margin of the hypostome. In *F. trentonensis*, the margin is more smoothly curved into the median notch, whereas in *F. senaria* from Virginia, the margin extends into two pointed spines (Whittington, 1941: pl. 72, figs. 34, 40, 43; Evitt and Whittington, 1953: pl. 9, figs. 8–10; Chatterton et al., 1990: figs. 5.13, 5.18).

The holotypes of each species differ in the size of L2 relative to L1, and this is the case on average despite variation within both species (fig. 8A, table 2). Interestingly, there is an association between cephalic length and relative size of L2 in *F. senaria* that is not observed in *F. trentonensis* (fig. 8B, table 2). The relative length of the genal spines also changes during ontogeny (fig. 8C, table 2). Although genal spines are present in small specimens of *F. senaria*, they are reduced during ontogeny and the genal angle is smooth in cranidia larger than 3 mm (Whittington, 1941). Thus the presence of the genal spines in *F. trentonensis* holaspides can be a useful diagnostic character in combination with the other differences, particularly because it is retained on the cranidium. We are not aware of any meraspid specimens of *F. trentonensis*. The smallest articulated specimen that we have observed (MCZ 186292) is

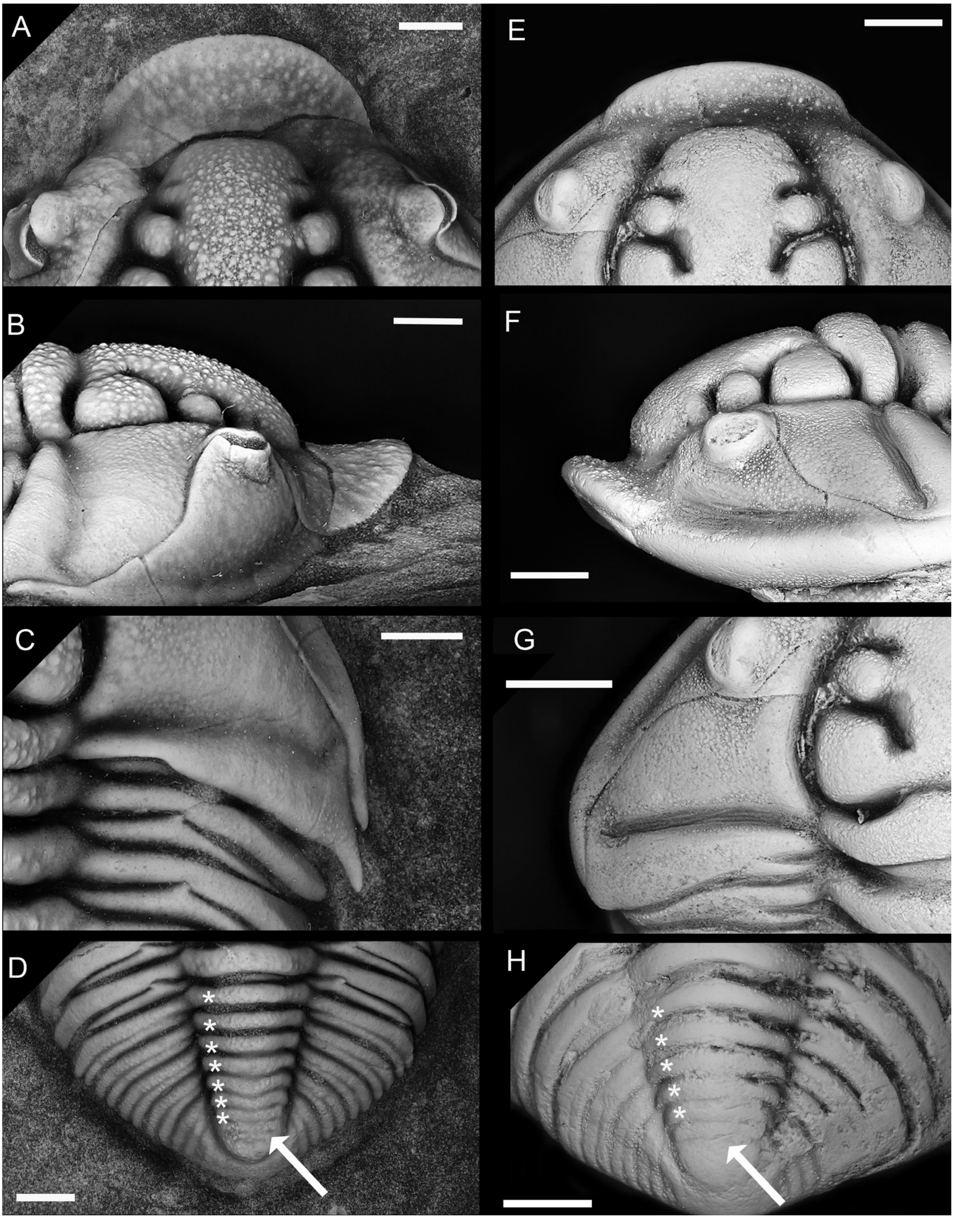

FIGURE 7. Comparison of features distinguishing *Flexicalymene trentonensis*, n. sp. (A–D) and *Flexicalymene senaria* (Conrad, 1841) (E–H). **A, E.** Anterior border in dorsal view. **B, F.** Anterior border in lateral view. **C, G.** Genal angle. **D, H.** Pygidium. Asterisks indicate distinct axial rings; arrow points to shallow furrow indicative of an additional but less well-defined axial ring. Specimens pictured are the respective holotypes (*F. senaria*: AMNH-FI-29474; *F. trentonensis*: AMNH-FI-140954; see also figs. 2 and 3). Scale bar = 2 mm.

TABLE 1. Number of pygidial rings expressed on specimens of *Flexicalymene senaria* and *Flexicalymene trentonensis*. See text for repository abbreviations and the online supplement (https://doi.org/10.5531/sd.sp.71) for more information about specimens.

Specimen Number	**Identification**	**Pygidial Rings (no.)**
MCZ 201040	*F. senaria*	5
MCZ 111065	*F. senaria*	7
MCZ 186339	*F. senaria*	8
NYSM 19432	*F. senaria*	6–7
NYSM 19433	*F. senaria*	5–6
NYSM 19434	*F. senaria*	6–7
NYSM 19453	*F. senaria*	5–6
AMNH-FI-140957	*F. senaria*	5–6
AMNH-FI-140958	*F. senaria*	5
AMNH-FI-140959	*F. senaria*	5–6
AMNH-FI-136680	*F. senaria*	5-6
AMNH-FI-25305	*F. senaria*	4–5
AMNH-FI-843/4	*F. senaria*	6–7
AMNH-FI-843/1	*F. senaria*	5
AMNH-FI-139620	*F. senaria*	5
MCZ 186363	*F. senaria?*	6
MCZ 186401	*F. senaria?*	5–6
MCZ 186404	*F. senaria?*	6
AMNH-FI-62195	*F. senaria?*	6
AMNH-FI-136706	*F. senaria?*	6–7
AMNH-FI-62200	*F. senaria?*	6–7
AMNH-FI-843/3	*F. senaria?*	5–6
MCZ 201044	*F. trentonensis*	6
MCZ 201047	*F. trentonensis*	6
MCZ 186411	*F. trentonensis*	7
MCZ 186365	*F. trentonensis*	6–7
MCZ 186420	*F. trentonensis*	8
MCZ 186368	*F. trentonensis*	7–8
MCZ 186421	*F. trentonensis*	7
MCZ 186423	*F. trentonensis*	7
MCZ 186400	*F. trentonensis*	7–8
MCZ 186403	*F. trentonensis*	6–7
MCZ 186430	*F. trentonensis*	5–6
MCZ 111116	*F. trentonensis*	6–7
MCZ 111710	*F. trentonensis*	6–7

TABLE 1 *continued*

Specimen Number	**Identification**	**Pygidial Rings (no.)**
NYSM 12717	*F. trentonensis*	6
NYSM 19413	*F. trentonensis*	6
NYSM 19440	*F. trentonensis*	7–8
PRI 109205	*F. trentonensis*	6
PRI 09203.3	*F. trentonensis*	7
AMNH-FI-140954	*F. trentonensis*	7
AMNH-FI-140955	*F. trentonensis*	7
AMNH-FI-62196	*F. trentonensis*	7
MCZ 186415	*F. trentonensis?*	6
MCZ 186390	*F. trentonensis?*	7
MCZ 186413	*F. trentonensis?*	7
AMNH-FI-136709	*F. trentonensis?*	7

13.8 mm in total body length with a 4.0 mm long (sag.) cranidium and has the full complement of thoracic tergites.

Other species that have extended preglabellar areas include *Flexicalymene verecunda* Dean, 1979, *Flexicalymene cambrensis* (Salter, 1865), and *Flexicalymene planilabra* Stumm and Kauffmann, 1958. *Flexicalymene trentonensis* is distinguished from *F. cambrensis* by the shape and pattern of tuberculation on the anterior border, which is wider (tr.) and shorter (sag.) in the latter and has a consistent distribution of granulation instead of a concentration along the margin and axial lobe (Whittard, 1961: pl. XXII). *Flexicalymene trentonensis* is similar to *F. verecunda* in having a genal spine but the anterior border is wider in *F. verecunda* and there is no evidence of coarse granulation. Dean (1979) considered the decrease in the width of the anterior lobe (which he referred to as a "step" in the glabellar outline) to be diagnostic of *F. verecunda*, but we observe it in some specimens of *F. senaria* (fig. 2B) and perhaps very gently in some specimens of *F. trentonensis* (fig. 4A). The type specimen for *F. planilabra* is a partial cranidium (UMMP 34244, fig. 9), and is the only specimen known for the species. The relative size of the glabellar lobes is just within the range of *F. trentonensis* (table 2), but there is no evidence of any granulation. Both *F. senaria* and *F. trentonensis* differ from *Flexicalymene croneisi* (Roy, 1941) by lacking a transverse ridge in the preglabellar area (Whittington, 1954: pl. 62, fig. 14).

Flexicalymene Species at the Walcott-Rust Quarry

Specimens previously assigned to *"Flexicalymene senaria"* belong to a relatively small number of trilobite species for which appendages have been preserved. The earliest descriptions of the appendages were based on material collected from a quarry at Gray's Brook, near Trenton Falls, NY, by Charles Walcott in the late 19th century (e.g., Walcott, 1881). This quarry is currently referred to as the "Walcott-Rust Quarry" (Brett et al., 1999) or the "Walcott Quarry"

TABLE 2. Variation in diagnostic cephalic characters in *Flexicalymene senaria* and *Flexicalymene trentonensis*. The area of L1 and L2 were estimated from length and width measurements. NA = indicates posterior margin too broken to assess presence and/or length of genal spine. See text for repository abbreviations and the online supplement (https://doi.org/10.5531/sd.sp.71) for more information about specimens.

Specimen Number	Identification	Cephalic Length (mm)	Area L2/ Area L1	Genal Spine Length (mm)	Type Status
AMNH-FI-136843	*F. senaria*	3.04	0.35	0.40	
AMNH-FI-140968	*F. senaria*	3.41	0.40	0.16	
AMNH-FI-140966	*F. senaria*	4.86	0.46	0	
AMNH-FI-140967	*F. senaria*	5.37	0.49	NA	
MCZ 201040	*F. senaria*	6.15	0.34	0	
MCZ 186418	*F. senaria*	6.46	0.39	0	
AMNH-FI-139626	*F. senaria*	6.80	0.47	0.13	
AMNH-FI-136842	*F. senaria*	7.01	0.35	0.32	
AMNH-FI-139620	*F. senaria*	7.22	0.39	0	
AMNH-FI-140597	*F. senaria*	8.64	0.40	0.14	
AMNH-FI-29474	*F. senaria*	8.76	0.48	0	holotype
AMNH-FI-140965	*F. senaria*	9.25	0.42	0	
AMNH-FI-139624	*F. senaria*	9.84	0.55	0	
AMNH-FI-140598	*F. senaria*	10.48	0.48	0	
AMNH-FI-843/1	*F. senaria*	11.59	0.45	0	
NYSM-19434	*F. senaria*	11.99	0.44	0	
MCZ 201051	*F. trentonensis*	4.27	0.30	0.51	
PRI-109194.1	*F. trentonensis*	4.65	0.34	NA	
MCZ 201047	*F. trentonensis*	4.90	0.37	0.56	
MCZ 186377	*F. trentonensis*	5.19	0.33	0.65	
MCZ 186376	*F. trentonensis*	5.56	0.35	0.29	
NYSM-12717	*F. trentonensis*	6.39	0.34	NA	
PRI-109205	*F. trentonensis*	6.69	0.29	0.70	
MCZ 201045	*F. trentonensis*	6.97	0.40	0.92	
MCZ 201046	*F. trentonensis*	7.30	0.36	0.78	
MCZ 111710	*F. trentonensis*	7.49	0.33	1.11	paratype
MCZ 111116	*F. trentonensis*	8.47	0.25	0.63	
NYSM_19436	*F. trentonensis*	9.89	0.35	0.89	
NYSM-19445	*F. trentonensis*	10.36	0.36	NA	
MCZ 201053	*F. trentonensis*	10.42	0.35	1.07	
MCZ 201048	*F. trentonensis*	10.52	0.26	1.47	
AMNH-FI-140954	*F. trentonensis*	11.49	0.33	1.29	holotype
MCZ 201054	*F. trentonensis*	11.62	0.40	1.05	

TABLE 2 *continued*

Specimen Number	Identification	Cephalic Length (mm)	Area L2/ Area L1	Genal Spine Length (mm)	Type Status
NYSM-19413	*F. trentonensis*	12.11	0.42	0.71	
MCZ 201050	*F. trentonensis*	12.24	0.32	NA	
MCZ 201052	*F. trentonensis*	12.41	0.37	1.07	
NYSM-19424	*F. trentonensis*	12.87	0.26	NA	
NYSM-19410	*F. trentonensis*	12.94	0.26	1.13	
PRI-108722	*F. trentonensis*	13.78	0.31	NA	
AMNH-FI-140955	*F. trentonensis*	13.97	0.36	NA	paratype
MCZ 201049	*F. trentonensis*	14.19	0.38	1.35	
AMNH-FI-62196	*F. trentonensis*	14.50	0.34	NA	
MCZ 186379	*F. trentonensis*	14.65	NA	1.52	
NYSM-19428	*F. trentonensis*	16.53	0.33	NA	
NYSM-19452	*F. trentonensis*	17.30	0.31	NA	
UMMP 34244	*F. planilabra*	NA	0.25	NA	holotype

(Brett and Baird, 2002); see also Yochelson (2007) for history of the quarry. The rocks exposed at the quarry are in the lower Spillway Member of the Rust Formation (Brett et al., 1999, Brett and Baird, 2002).

Brett et al. (1999: 301) noted that specimens of *Flexicalymene* from the Walcott-Rust Quarry are "pustulose and all have short genal spines." Indeed, a commonly figured specimen from the Walcott-Rust Quarry (MCZ 111710, fig. 4A; see also Brett et al., 1999: fig. 9.2; Whiteley et al., 2002: pl. 69; and Losso et al., 2023a: fig 1a) is without question *F. trentonensis* and designated as a paratype herein. Interestingly, Walcott (1881: pl. 4, fig. 7) illustrated a specimen with an intermediate morphology and his diagrammatic line drawings that reference the thin-section cuts (pl. 5, figs. 5, 6) show a calymenid with a short anterior border and no genal spines.

The Walcott Collection at the Harvard Museum of Comparative Zoology (MCZ) includes calymenid specimens from "locality 51," which was determined to be the quarry at Gray's Brook by Thomas E. Whiteley and his colleagues in the late 1990s (Jessica Cundiff, personal commun., 2023). There were over 100 calymenid specimens in this lot available for study in June 2023. Of those that are sufficiently well preserved to make species determinations (35%), over 85% are confirmed or likely *Flexicalymene trentonensis* (see "Walcott Collection" in the online supplement). One specimen appears to be a transitional form between *F. senaria* and *F. trentonensis* (MCZ 186418; fig. 8A).

Whiteley also donated specimens he had collected from the Walcott-Rust Quarry to the MCZ. Three specimens donated in the 1990s are all *F. trentonensis* from Layer 3, the lowest layer in which calymenid specimens may be found, and also where they are most abundant (Brett et al., 1999: table 1). Most of the specimens in later donations (mid to late 2000s) are *Ceraurus* or unprepped, but there is one lot of 15 prepared *Flexicalymene* specimens, in which

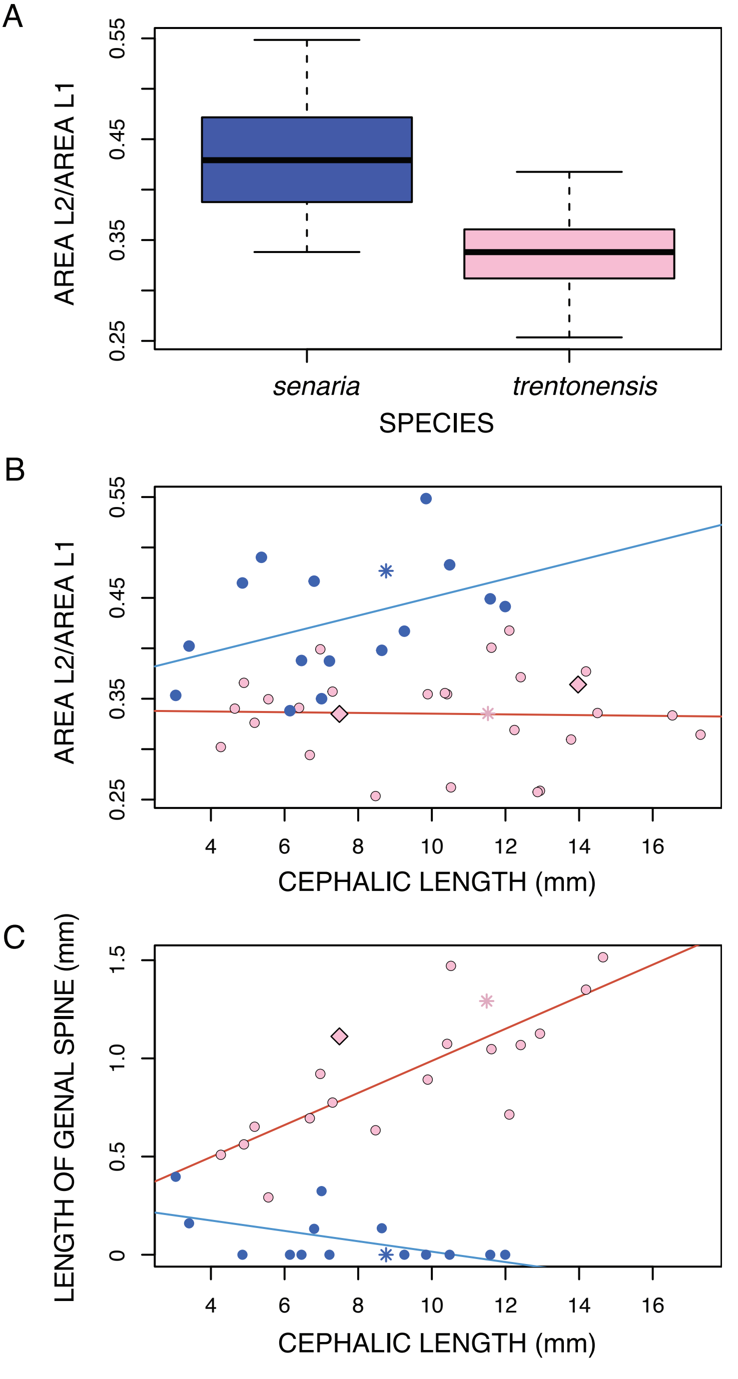

FIGURE 8. Variation in diagnostic characters in *F. senaria* and *F. trentonensis*. **A.** Boxplots showing variation in the size of L2 relative to L1 in each species. **B.** Association between cephalic length and relative size of L2. **C.** Association between cephalic length and genal spine length. Dark blue = *F. senaria*; pale red = *F. trentonensis*; asterisks = holotypes; diamonds = paratypes.

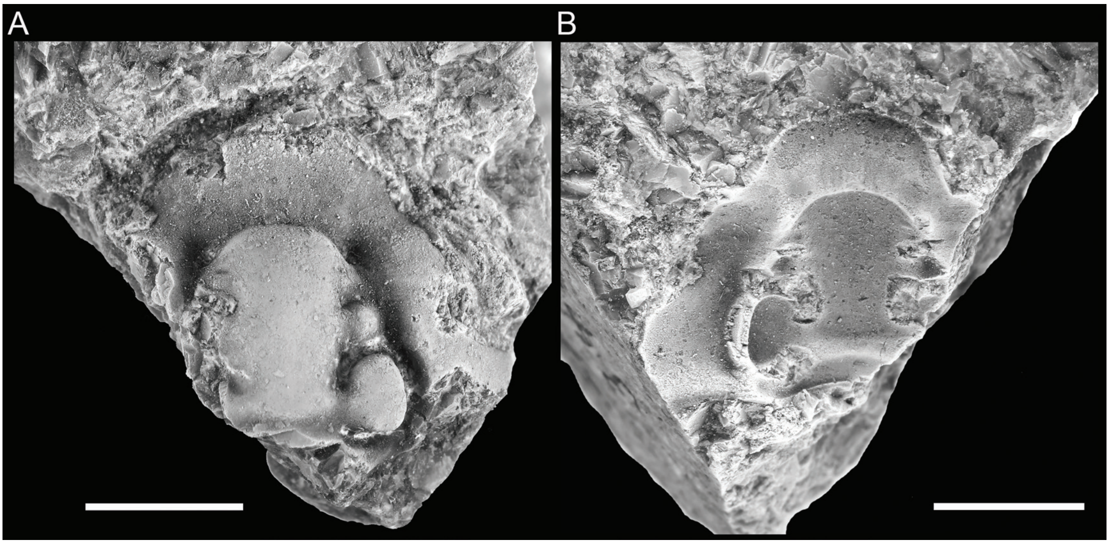

FIGURE 9. Part (A) and counterpart (B) of holotype of *Flexicalymene planilabra* (UMMP IP 34244). Images provided by the University of Michigan Museum of Paleontology. Scale bar = 2 mm.

there are three complete exoskeletons, two partial exoskeletons, five cranidia, and one pygidium of *F. trentonensis*; two hypostomes tentatively assigned to *F. trentonensis* (fig. 5B, C); and only one complete *F. senaria* (MCZ 201040, fig. 2D).

Based on this survey of MCZ collections made by Walcott and Whiteley, *F. senaria* either co-occurs with *F. trentonensis* at the Walcott-Rust Quarry, or occurred above *F. trentonensis* at this locality. Regardless, because *F. senaria* is common in older formations in the region, the stratigraphic range for *F. senaria* must encompass at least part of that of *F. trentonensis*.

Because appendages are preserved through calcite replacement, study of these specimens has largely been pursued using thin sections (Brett et al., 1999; Losso et al., 2023a, b; Walcott, 1879). Except in unusual cases where diagnostic characters are captured in the plane of the thin section (e.g., fig. 4c of Losso et al., 2023b, which has the weakly curved preglabellar field of *F. trentonensis*), it may be impossible to determine which species was preserved (e.g., the transverse cut shown in Losso et al., 2023b: fig. 5c). However, while collections of thin sections from the Walcott-Rust Quarry almost certainly comprise a mix of the two species, the survey described above indicates that the majority of the specimens are expected to be *Flexicalymene trentonensis*. For this reason, all equivocal specimens in thin section from the Walcott-Rust Quarry are questionably listed in the synonymy for *F. trentonensis*.

Transitional Forms and Cisne et al.'s Transitional Time Series

Some specimens appear to be morphologically transitional between *Flexicalymene senaria* and *Flexicalymene trentonensis* in the shape of the anterior border, expression of genal spines, and the distribution of granulation. For example, a small specimen (20 mm) in the MCZ collected by Walcott, and likely from the Walcott-Rust Quarry (see Discussion above), has a broad

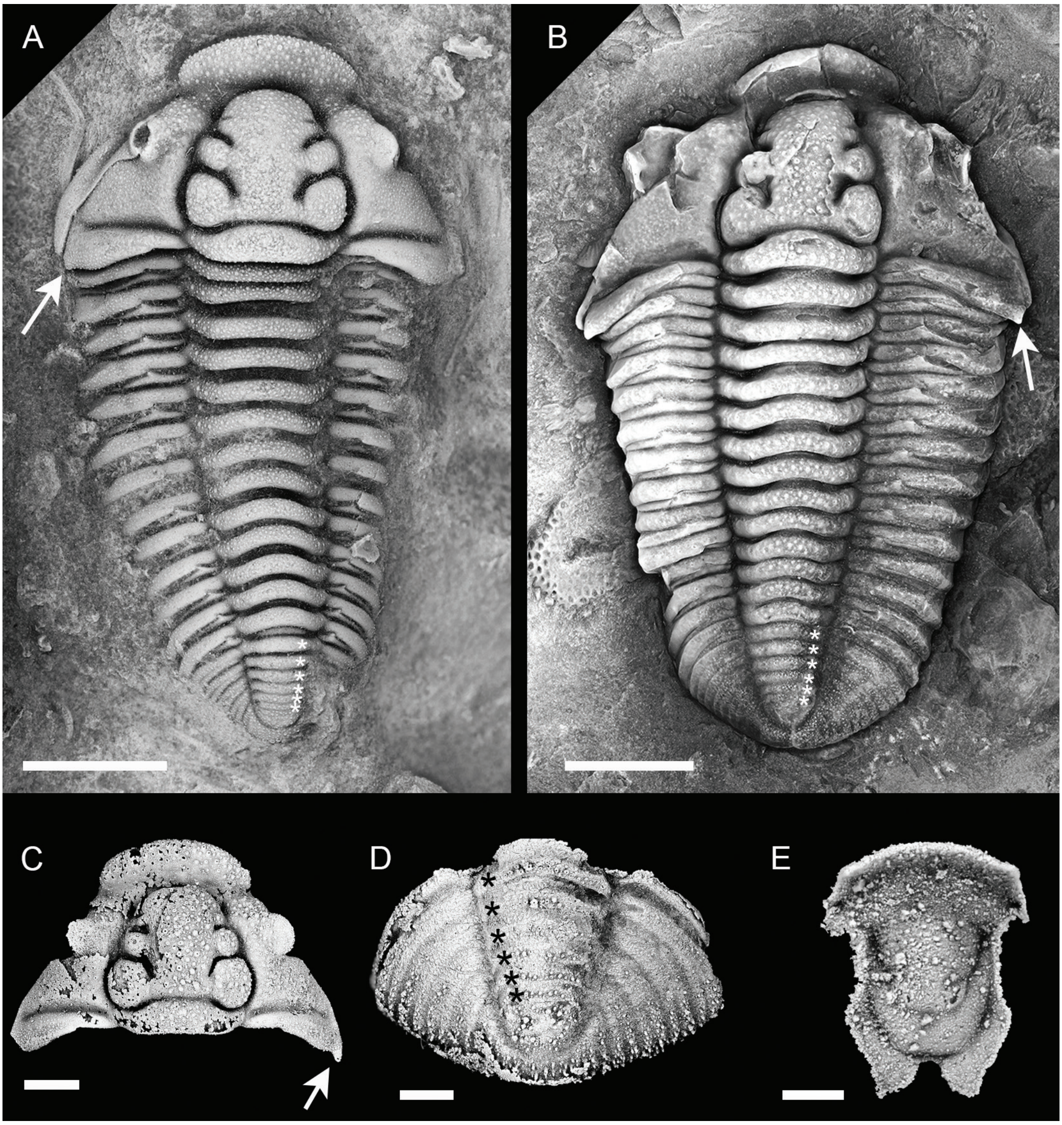

FIGURE 10. Transitional forms between *Flexicalymene senaria* and *F. trentonensis*. These specimens have a somewhat broader anterior border than the neotype of *F. senaria* (but not as broad as *F. trentonensis*), a small swelling at the genal angle (but not a full spine, see arrows), and six axial rings on the pygidium (asterisks). The hypostome from Chazy, NY, however, aligns the occurrence there with *F. senaria*. **A.** Specimen collected by Walcott, and most likely from the Walcott-Rust Quarry, NY (see text), MCZ 186418, scale bar = 4 mm. **B.** Specimen from the Lindsay Formation, Ontario, AMNH-FI-140957, scale bar = 5 mm. **C–E.** Specimens collected from the late Sandbian Glens Fall Formation near Chazy, NY. AMNH locality 4066. **C.** Cranidium, AMNH-FI-136842, scale bar = 2 mm. **D.** Pygidium, AMNH-FI-136841, scale bar = 2 mm. **E.** Hypostome, AMNH-FI-136868, scale bar = 500 µm. See also Whiteley et al., 2002: pl. 68.

anterior border and swelling at the genal angle, but lacks the distinctively large mode of granules (fig. 10A). Another much larger (43 mm) specimen collected by Gerald Kloc has a moderately expanded anterior border, an emergent genal spine on the right side of the cephalon, and six to seven pygidial axial rings (Whiteley et al., 2002: pl. 68). The latter specimen is from the Denley Formation and is reportedly characteristic of the *F. senaria* found in the lower and middle Trenton Group at Trenton Falls. A similar combination of characteristics is also seen in a specimen from the Lindsay Formation of Ontario, which overlies the Verulum Formation and is likely equivalent to the upper Denley and/or Rust formations (fig. 10B). Large *Flexicalymene* specimens from the older Glens Fall Formation (Sandbian: Macdonald et al., 2017; Sell et al., 2015) of the Champlain Valley have a moderately broad anterior border, short genal spines, and six to seven axial rings (fig. 10C, D). They also have a hypostome with a sharply forked posterior margin (fig. 10E, compare with Whittington, 1940: pl. 72, figs. 34, 40, 43, 46), which align them more strongly with *F. senaria* than *F. trentonensis*.

This pattern of increasing average number of axial rings from early *F. senaria* to *F. trentonensis* is consistent with the dataset presented by Cisne et al. (1982a), who showed a shift in average number of axial rings at 20 m in a composite section, where "zero" represented a bentonite bed near the base of the Denley Formation and additional bentonite beds are counted in turn up-section. Although some doubts have been raised about the graptolite correlation used by Cisne and colleagues (Goldman et al., 1994), Cisne et al.'s "M8" bentonite is the lower Sherman Falls K-bentonite, which is 5.7 m above the base of the Denley Formation (Brett and Baird, 2002: 243). In addition, the part of Cisne et al.'s "standard section" above "M8" is represented by the exposure at Trenton Falls (Cisne et al., 1982b: 233). Based on this, it seems possible that the transition that Cisne et al. (1982a) reported at 20 m occurred within the Russia Member of the Denley Formation and represents a shift from collections dominated by *F. senaria* to those dominated by *F. trentonensis*. Given the frequency of *Gravicalymene* specimens in museum collections labeled "*senaria*," however, the possibility that the collections used by Cisne and colleagues also included *Gravicalymene* specimens cannot be rejected.

SUMMARY

The complicated taxonomic history of *Flexicalymene senaria* effectively obscured the true diversity of calymenid taxa in Late Ordovician fossil assemblages of the Trenton Group in eastern North America. A detailed review of the literature revealed that parallel conceptions of this species were sustained for decades, and examination of historic museum collections revealed additional diversity that had been suspected but unconfirmed for 180 years. Additional fieldwork was required to better determine the spatial and temporal range of *Flexicalymene senaria* as well as the new species, *Flexicalymene trentonensis*, described herein. Previously described clinal variation in *Flexicalymene senaria* may be better interpreted as a transition in abundance from *F. senaria* to *F. trentonensis* in the assemblages from outcrops exposed near Trenton, NY, including the historic Walcott-Rust Quarry.

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APPENDIX

Review of Literature Describing "*senaria*" from Conrad (1841) to Ross (1967)

For the type assignment, type 1 indicates morphology consistent with *Flexicalymene senaria* as diagnosed herein and type 2 indicates morphology consistent with *Flexicalymene trentonensis* n. sp.

Year	Author	Formation	Location/Geography	Specimens	Evidence	Remarks
1841	Conrad	Trenton		type 2	description of frontal area (p. 49)	
1842	Vanuxem	Trenton	"of frequent occurrence, especially towards the Mohawk, being more rare north of Trenton Falls"	both	states outright that there is more than one species in collections	notes that *C. blumenbachii* = *C. senaria* of Conrad was sent to Brongniart in Paris
1842	Emmons	Trenton	Glen's Falls, Essex, Plattsburgh, Cumberland Head, NY	type 1	illustration on page 390, fig 100.2 seems to have 15 thoracic segments, making count of pygidial segments unreliable	reproduced in Emmons, 1844, 1855; additional comments are made about similar specimens being found in Cincinnati and Madison, IN, but Emmons confines *senaria* to the Trenton limestone
1847	Hall	Trenton and others (see next cell)	"This species is abundant in the Trenton limestone, at many localities...It occurs also at Herkimer, Jacksonburgh, Turin, Lowville and Watertown; and at Plattsbirgh, Glen's falls, and other places in the Hudson and Champlain valley. It is likewise common in the same rock at Bay Quinta and other places in Canada. It is found in the Hudson-river group at Turin, Lowville and elsewhere, and it appears to be almost equally abundant in the Avestern extension of this group; occurring at Cincinnati, Lebanon, Oxford and other places in Ohio; at Maysville and Frankfort, Kentucky; at Madison, Indiana; and at Mineral Point, Wisconsin."	both	"regularly rounded in front, or slightly projecting in in front of the glabella"	very broad species concept, including *meeki*, *C. selenecephala* and *C. callicephala*.

APPENDIX *continued*

Year	Author	Formation	Location/Geography	Specimens	Evidence	Remarks
1855	Emmons	Trenton limestone; Blue Limestone	NY, OH, VA, TN	type 1	pl. 15, fig. 16; fig. 72.9d–g	pl. 15, fig. 16 reproduced from Emmons, 1842
1856	Billings	Trenton limestone	Chaudiere Falls, near Ottawa	type 1	fig. 10; describes seven segments (includes terminal piece?) in pygidium	notes that some workers consider the same as *C. blumenbachii* (but Billings doesn't appear to)
1860	Emmons	Trenton		type 1	fig. 87 (p. 98)	reproduced from Emmons, 1842. Groups with gastropods!
1861	Hitchcock	Trenton	Larrabee's Point, Chimney Point, Frost's Landing, McNeil's Point, South Hero, Grand Isle, Isla la Motte, VT	Both?	"regularly rounded in front, or slightly projecting in in front of the glabella"	copied from Hall? Illustration is terrible
1865	Salter	Trenton	NY, OH, United Kingdom	type 1?	"the front produced and elevated," also fig. 21 (but note examples are from OH and Britain, not NY), pl. 9 with North American specimen from Blue Limestone (Ohio) with type 1 border. Other specimens neither type 1 or type 2	excludes Green's 1932 cast no. 2 from *C. senaria*. Specimen from Caernarvonshire might be *Gravicalymene* (bell-shaped glabella; wide, flat preglabellar area; large number of axial rings)
1870	Billings		OH	unclear	enrolled cross section	paper is about possible eggs in tightly enrolled material from Ohio
1878	Etheridge		Greenland	unclear		questionably associated with *senaria*; cephalon poorly preserved, no illustration
1881	Walcott	Trenton limestone	Trenton Falls, NY	type 2	pl. 4, fig. 7 shows cephalon with extended medial section and short genal spines; pl. 5 shows cross sections with broad, shallowly curved preglabellar area; pl. 6, fig. 1 shows graphical illustration of ventral side	graphical illustration of appendages (ventral and/or cross section) reproduced in Walcott 1884, 1894; Beecher, 1902

APPENDIX *continued*

Year	Author	Formation	Location/Geography	Specimens	Evidence	Remarks
1889	Lesley	Trenton limestone, Hudson River beds, Lorraine shale	NY, OH, PA	type 1	illustrations p. 110 reproduced from other sources, show both types (and possibly a *Gravicalymene*)	type 1 reproduced from Emmons, 1842
1897	Clarke	Trenton	Trenton Falls, NY	type 2	fig. 3 (p. 700) shows expanded medial section and genal spines—listed as Conrad's Trenton Falls form	publication reprinted from 1894; distinguishes between Trenton and Ohio form, but the "usual Trenton species must retain the name proposed for it by Conrad"; Green's *C. blumenbachii* (cast no. 1) is from Trenton Falls; Green's *C. callicephala* is distinct from both; Minnesota forms are granular (granulosa?)
1894	Keyes		Missouri	Cincinnatian species?	"anterior outline being more or less regularly rounded"	
1894	Bernard			type 2		cross-sectional drawings reproduced from Walcott 1881, pl. 5, fig. 3
1901	Ruedemann	Trenton	Rysedorph Hill, Rensselaer County, NY	type 2	"long shovel-shaped anterior expansion"	"belonging rather to [*C. senaria*] than to *C. callicephala* Green was found in the black limestone. This is the common Trenton form, while *C. callicephala* occurs in the Trenton as well as the Lorraine beds."
1903	Weller	Trenton	Jacksonburg, NJ	type 1?	"Head sub-semi circular of sublunate in outline, the anterior and lateral margins being more or less regularly rounded"	allies with Ohio specimens; notes that Clarke refers to as *C. callicephala*, but that pygidium is distinct from Ohio forms. Figures only pygidium
1910	Grabau and Shimer	Trenton	NY, NJ, OH, MN, etc.	type 2	"anterior extension of cephalon narrowed and shovel-shaped, not abruptly concave. Pleural segments of pygidium grooved"	notes that "*senaria*" differs from *C. callicephala* in broad and abruptly concave anterior extension of cephalon, absence of genal spines, and absence of grooving on the pleural segments of the pygidium. Puts *C. callicephala* in Trenton-Lorraine of NY, VA, OH, IN, MN, etc. Illustrations copied from Clarke, 1987

APPENDIX *continued*

Year	Author	Formation	Location/Geography	Specimens	Evidence	Remarks
1910	Foerste	Trenton	Trenton Falls, NY	type 2	pl. 2, fig. 14, showing extended border; description on p. 82 with extended border. Pygidium has seven segments plus terminal piece	description is of AMNH specimen labeled *callicephala* and numbered 843-7 (missing); includes comparison to specimen figured by Clarke, 1897
1912	Ruedemann	Canajoharie Shale	Canajoharie and Sprakers, Montgomery Co., NY		pl. 9, figs. 6, 10	*Gravicalymene magnotuberculata* (see Ruedemann 1926; Whiteley et al., 2002: 133)
1915	Bassler	Trenton	"New York, New Jersey, Ohio, Minnesota, etc."	both?		seems to embrace broad conception based on bibliography; lists USNM 4916, 5004 as plastotypes; includes Green's *C. blumenbachii* (cast 1) and *C. selenocephala* (cast 3) in *C. senaria*
1918	Walcott	Trenton	New York	type 2	pl. 28, fig. 7–8; pl. 33; pl. 26, fig. 1–7, 9–13; pl. 27, fig. 4–14	illustrations in pls. 28 and 33 reproduced from Walcott, 1881; others are in cross section
1919	Foerste	Trenton	New York	type 2	based on comparison with another species	compares *C. whittakeri* as less elongate (lip) and with rounded genal angles compared with *C. senaria*
1926	Ruedemann					reports *C. senaria granulosa* [= *Flexicalymene granulosa*] in Whetstone Gulf, *C. meeki* in Pulaski; proposes *C. senaria var. magnotubeculata* [= *Gravicalymene magnotuberculata*] for Canajoharie specimens; *C. conradi* = *C. meeki*
1941	Whittington		Spring Hill, Augusta County, VA	type 1	pl. 72, description includes mention of tubercle as "remnant of genal spine," narrow margin, and strongly recurved preglabellar field	Whittington placed *senaria* in *Flexicalymene*; IDs VA species based on age "the Trenton species of calymenid," points reader to Bassler, 1915: 169, for reference to writings on *senaria*
1953	Evitt and Whittington	Trentonian age	Staunton and Harrisberg, VA; Chazy, NY	unclear	pl. 10, fig. 1	silicified material

APPENDIX *continued*

Year	Author	Formation	Location/Geography	Specimens	Evidence	Remarks
1958	Stumm and Kauffmann		MI, northern PA	type 1	pl. 123, figs. 1–11	"Specimens of *Flexicalymene senaria* (Conrad) illustrated by James Hall (1847), were examined, and, as the repository of Conrad's types is unknown, the original of Hall's pl. 64, figs. 3b-c is refigured as it is a characteristic and well preserved specimen." They use Ross' neotype as representative. Also refer readers to Whittington's 1941 description. Note that the catalog number and locality stated in plate caption is incorrect.
1967	Ross			both	pl. 4	neotype = type 1; type 2 figured from NYSM (figs. 11–13)

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