

# A Field Guide to the Geology and Paleontology of Salmon Creek and Ludlowville Falls, Lansing, New York, USA



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**Running Header:** Central New York, Hamilton Group, Middle Devonian, Givetian, paleontology, stratigraphy

**Abstract:** While Ithaca, New York is famous for its spectacular geology, well-preserved Paleozoic Era fossils are generally rare due to poor exposure of the Hamilton Group at the south end of Cayuga Lake where Cornell University is situated. Just 16 kilometers north of campus, a series of discontinuous exposures at Salmon Creek in Lansing provide excellent examples of classic Middle Devonian stratigraphy and paleontology. These are accessible by foot at low stream stage, especially during the summer and fall. This field guide reflects a cooperative effort to document these features for education and outreach as well as student research projects at Cornell University and the Paleontological Research Institution.

**Disclaimer:** Anyone visiting Salmon Creek and Ludlowville Falls agrees to the following: (1) it is not permissible to litter, deface, or in any way detract from the original appearance of Salmon Creek and Ludlowville Falls; (2) it is not permissible to trespass onto private property; (3) it is not permissible to have alcoholic beverages or illegal drugs at Salmon Creek and Ludlowville Falls; (4) the authors and Paleontological Research Institution are not responsible for any injuries that may result from accidental, negligent, or intentional acts by participants, or by failure of any participants to observe these rules. Remember that you are responsible for minimizing environmental impact to Salmon Creek and Ludlowville Falls. Please be respectful of wildlife and private property and leave no trace. As this is a site of active paleontological research, refrain from over-collecting and/or undercutting outcrop (creek walls).

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# **Geology and Paleontology of Salmon Creek and Ludlowville Falls**

## **Tectonic Setting and Paleoenvironment of New York State During the Givetian Stage**

During the Givetian Stage (late Middle Devonian Period), the Acadian Orogeny occurred as a result of collision between the eastern margin of North America with the Avalon terranes. The uplift of the Acadian Mountains created an area of thickened crust to the East, driving flexural subsidence and the creation of a foreland basin called the Appalachian (Acadian) foreland basin (Fig. 1). New York State was situated in this basin during the Givetian, and an epeiric sea was formed as seawater filled it. Sediments shed from the Acadian Mountains formed the Catskill Delta, a thick section of marine to terrestrial sediments spanning the Middle and Late Devonian of New York. The sedimentary rocks exposed at Salmon Creek (Lansing, NY) represent the offshore equivalents of this deltaic sequence within the upper part of the Hamilton Group. These rocks are well known to contain a rich fossil fauna that record life in this ancient sea (Hall, 1947-1894; Wilson, 2014). They also contain a record of sea-level change, evident in cyclic packages of rock bound by surfaces of erosion or nondeposition (i.e., disconformities that reflect surfaces of wave base erosion/subaerial exposure or sediment starvation; Brett et al., 2012; 2023). These features are readily observable in a series of discontinuous outcrops exposed along the gorge walls and bed of Salmon Creek (Fig. 2).

## **Stratigraphic and Paleontological Features at Salmon Creek and Ludlowville Falls**

In general, the succession at Salmon Creek includes, in ascending order, the upper part of the Ludlowville Formation, Moscow Formation, and Tully Formation. These strata span the upper part of the Hamilton Group within the middle-upper Givetian (Rickard, 1975; Brett et al, 2023). The Ludlowville and Moscow formations consist of variably fossiliferous marine mudstone and occasional thin limestones. The overlying Tully Formation is characterized by carbonate mudstone to wackestones with thin dark shale partings along bedding planes. Collectively, these strata record repeated third (~1 million year-) and fourth-order (~100 to 400 thousand year-) cycles of deposition on a mixed carbonate-siliciclastic ramp, spanning sequences Giv-2, Giv-3, Giv-4, and Giv-5 of Brett et al. (2023; Fig. 3).

An overview of several key stratigraphic and paleontological features at Salmon Creek and Ludlowville Falls is provided below. For additional information about taxonomy, stratigraphic distribution and rarity, and identification of the fossil taxa, please refer to appendices I and II. For a complete field trip itinerary, please refer to Appendix III.

## Locality 1. Lower Salmon Creek

Spafford, Tichenor, “lower Moscow”, Deuel Road, and lower Windom members

Loc. 1 Parking Access: 42°32'23.3"N 76°32'42.1"W | Loc. 1a-1 Coords: 42°32'24.7"N 76°32'36.6"W | Loc. 1a-2 Coords: 42°32'26.9"N 76°32'35.8"W | Loc. 1a-T Coords: 42°32'29.4"N 76°32'35.5"W | Loc. 1b-T Coords: 42°32'33.7"N 76°32'27.5"W | Loc. 1b-1 Coords: 42°32'38.0"N 76°32'24.5"W

### *Locality 1a. Myers Road*

Spafford, Tichenor, and “lower Moscow” members

Loc. 1 Parking Access: 42°32'23.3"N 76°32'42.1"W | Loc. 1a-1 Coords: 42°32'24.7"N 76°32'36.6"W | Loc. 1a-2 Coords: 42°32'26.9"N 76°32'35.8"W | Loc. 1a-T Coords: 42°32'29.4"N 76°32'35.5"W

### **Locality 1a-1. *Modiomorpha-Ancyrocrinus* Bed (“lower Spafford” Member)**

Locality 1a Parking Access: 42°32'23.3"N 76°32'42.1"W | Locality 1a-1 Coords: 42°32'24.7"N 76°32'36.6"W

The Spafford Member of the Ludlowville Formation is the lowest unit of the Hamilton Group exposed at Salmon Creek (Fig. 4). This particular section of the Spafford is composed of a light gray to reddish brown, silty mudstone containing a faunal assemblage similar to the Ivy Point Member at Cascade Road Cut in Moravia, NY, about 32 kilometers to the northeast (Brett et al., 2023). As at Cascade, the lower Spafford Member at Myers Road contains an abundance of bivalves and spiriferid brachiopods, occasional phacopid trilobites, and rare cladid crinoids. Hence, we refer to this lower section of the Spafford as a new informal bed, the *Modiomorpha-Ancyrocrinus* Bed, recognized for its abundance of both the palaeoheterodont bivalve *Modiomorpha* and cladid crinoid *Ancyrocrinus*. This Bed contains not only the highest occurrence of *Ancyrocrinus* but also some of the youngest known specimens, as the genus disappeared from the fossil record shortly after the deposition of the overlying Tichenor Member and is absent from the rest of the Moscow Formation. We also use the *Modiomorpha-Ancyrocrinus* Bed to distinguish its lithological and paleontological content from the rest of the Spafford Member exposed at Myers Road (see ‘*Locality 1a-2. Main Outcrop*’ for further discussion).

Less silty and light gray in color, the lower strata of the *Modiomorpha-Ancyrocrinus* Bed are dominated by bivalves, particularly the palaeoheterodont *Modiomorpha* (*M. concentrica* and *M. mytiloides*) and heterodont *Cypricardella bellistriata*. *Orthonota undulata* is a very rare species of palaeoheterodont. Notably, the *Modiomorpha* display evidence of sublethal injuries from durophagous predators, such as ammonoids, phyllocarids, and potentially placoderms (Plate 1b). This is the first reported record of predation scars in the genus *Modiomorpha* and supports the “Middle Paleozoic Revolution” (Signor & Brett, 1984; Brett & Walker, 2002; Brett, 2003), a hypothesis that predation intensified during the Middle Devonian (see ‘*Paleoecology of Salmon Creek and Ludlowville Falls I*’ for further discussion). Spiriferid brachiopods, such as *Mucrospirifer mucronatus*, and chonetids (*Arcuaminetes*, *Longispina*) are also very common in these layers. However, only one lingulid, *Lingula delia*, has been recovered so far. Moreover, one very small, partial periderm test of an unidentified conulariid species (*Conularia* sp.) was found in the lower strata among the *Modiomorpha*.

Disarticulated tagmata, typically pygidia, of the phacopid trilobites *Eldredgeops rana* and *Greenops* are rare but occur in the upper layers of the outcrop where the mudstones are silty and rusty brown in color. During the time this stratum was deposited, the silty mud was firm enough for the holdfast (or cirral grapple) of *Ancyrocrinus bulbosus* to anchor securely, offering

in-situ support against the current. One well preserved specimen of these cirral grappels has been recovered from the upper *Modiomorpha-Ancyrocrinus* Bed (Plate 1a). In addition, cephalopods, though very rare, have been reported, the phragmocones of which were likely transported here after the death of the animal. The two cephalopod specimens include a small and relatively complete goniatite ammonoid *Tornoceras uniangulare* and an exceptionally preserved nautiloconic nautiloid *Nephriticeras magister* (Plate 1c).

### **Locality 1a-2. Main Outcrop (Spafford, Tichenor, and “lower Moscow” members)**

Locality 1 Parking Access: 42°32'23.3"N 76°32'42.1"W | Locality 1a-2 Coords: 42°32'26.9"N 76°32'35.8"W

The Spafford Member proper overlies the *Modiomorpha-Ancyrocrinus* Bed, forming an unseen disconformity between localities 1a-1 and 1a-2 (the contact is hidden beneath soil). The Spafford proper, together with the Tichenor Member and “lower Moscow” (an undifferentiated Deep Run-Kashong interval; Fig. 3) comprise the Main Outcrop at Myers Road (figs. 4 and 5a).

The Spafford Member proper is composed of gray, fossiliferous siltstones. This unit contains many brachiopods, mostly athyridids, spiriferids, and productids, typically found in discontinuous lags, or stringers, of shell material (Fig. 5b). Common species include *Ambocoelia umbonata*, *Athyris spiriferoides*, *Arcuaminctes* (*Devonochonetes*) *scitulus*, *Devonochonetes coronatus*, *Tropidoleptus carinatus* (Fig. 5d), and *Mucrospirifer mucronatus*. Four subclasses of bivalves are also present, including anomalodesmatans, heterodonts, palaeoheterodonts, and pteriomorphians. Typical taxa include *Modiomorpha* (*M. concentrica* and *M. mytiloides*) and *Cypricardella bellistriata*, which occur in similar abundance to the *Modiomorpha-Ancyrocrinus* Bed at Locality 1a-1. Large ovate calcareous concretions are abundant and occur along a ledge at just above the stream bank (~0-m height), but do not often contain well-preserved fossil material. However, split concretions will occasionally reveal calcitic assemblages of spiriferids, productids, and in one instance, a partially complete and pyritized phragmocone of the orthoconic nautiloid, *Spyroceras nuntium* (Plate 2f).

Along the concretionary ledge, the fodinichnia *Zoophycos* is uncommon, just above which brachiopods and bivalves can be sampled in great abundance. At about 1 m above the stream bank, uncompacted and complete specimens of the large spiriferid brachiopod *Spinocyrtia* (*S. cf. granulosa*, Fig. 5c; and potentially *S. granulifera*) occur, but are rare. Within this layer, the palaeoheterodont bivalve *Modiomorpha* (*M. concentrica*, *M. mytiloides* (Plate 2b), and *M. cf. subalata*) and the heterodont *Cypricardella* (Plate 2d) are common and sometimes found in “butterfly” position (valves spread open at the hinge). Rarer bivalve species here include the anomalodesmatan *Grammysioidea alveata*, palaeoheterodonts *Goniophora hamiltonensis* (Plate 2a) and *Orthonota undulata* (Plate 2c), and pteriomorphians *Pseudoaviculopecten princeps* (Plate 2e) and *Ptychopteria* (*Cornellites*) *fasiculata*. Several species of *Pseudoaviculopecten* probably occur within the Spafford Member, but these have largely been overlooked or misidentified in the field. Note that *P. fasiculata* is the first reported species possessing sublethal predation damage on Devonian bivalves (Nagel-Myers et al., 2009; see ‘*Paleoecology of Salmon Creek and Ludlowville Falls I*’ for further discussion). Gastropods are very rare, represented by the platyceratoid *Naticonema lineata* and pleurotomarioids *Glyptomaria capillaria* and *Mourlonia cf. lucina*. Disarticulated tagmata of the phacopid trilobite *Eldredgeops rana* and small stem fragments of vascular plants also rarely occur within the 1 m height stratum. In addition, one calyx of the pentremiid blastoid *Devonoblastus leda* was allegedly discovered in this section; this identification remains to be confirmed.

The Jaycox Member of the Ludlowville Formation, which overlies the Spafford Member, is not present at Salmon Creek. This unit, only present in sections further to the west, is about 2-5 meters thick and generally represents a shallowing water depth, a decrease in oxygen content, and an increase in relative abundance of marine faunas, including corals (Brett et al., 2012; 2023). Together, the Jaycox and Spafford members represent the upper part of sequence Giv-2, a major sea level cycle recognized throughout the Middle Devonian of North America (Fig. 3; Brett et al., 2012; 2023).

### **Locality 1a-T. Main Outcrop Seasonal Talus (Tichenor and “lower Moscow” members)**

Loc. 1 Parking Access: 42°32'23.3"N 76°32'42.1"W | Loc. 1a-T Coords: 42°32'29.4"N 76°32'35.5"W

The contact between the Spafford and Tichenor (basal Moscow Formation) members is a disconformity, above which there is a strong change in lithology to fossil-rich, silty limestone (Fig. 5a). The Tichenor, at about 0.5-m thick and the only carbonate unit present at Lower Salmon Creek (figs. 5e, 5f), indicates an abrupt change in environmental setting after the deposition of the Spafford. Limestones are typically deposited in settings with low siliciclastic input, so it is probable that the Tichenor formed in a warm, shallow sea. The presence of the tabulate coral *Favosites hamiltoniae* in the Tichenor at Lower Salmon Creek as well as at an equivalent exposure at Portland Point (about two kilometers to the southeast) demonstrates that the unit was likely deposited in a warm, shallow carbonate ramp setting during the mid-Givetian time (Fig. 6). The clear water conditions of the Tichenor are attributed to the beginnings of transgression following a major shallowing and erosional event (Brett et al. 2012; 2023). During sea level rise, rivers draining the Acadian Mountains were likely backed up, forming estuaries that served as coastal sediment traps. The sequestration of clastic sediments near shore resulted in offshore sediment starvation, allowing the skeletons of crinoids, corals, and other shelled invertebrates to gradually build up on the seafloor, forming shelly limestone (Fig. 5f).

The Tichenor Member can only be accessed at Myers Road via seasonal talus piles that accumulate along the western bank of Salmon Creek on the concretionary ledges of the Spafford Member. These accumulations often occur at the northern end of the Main Outcrop (42°32'29.4"N 76°32'35.5"W) following rock fall due to freeze-thaw cycles within the joints. The talus piles have been reliably accessed and extensively sampled over the past three freeze-thaw cycles (2023-2025), with falls occurring around mid- to late April each year. Strong storms in the late summer and early autumn will also occasionally bring down material. The most recent fall occurred in June 2025 and revealed that the uppermost Spafford is reworked by burrows in the overlying Tichenor Member.

The Tichenor Member records an abundance of marine life. Within the Tichenor (as well as the lower Moscow and upper Cuylerville Submember of the Windom Member), individual beds appear to follow a successional pattern: (1) large sweeping arcs of the fodinichnia *Zoophycos*; (2) well preserved molds of orthoconic nautiloids; and (3) high species diversity, particularly among spiriferid brachiopods, palaeoheterodont bivalves, and productid brachiopods. This pattern likely reflects a well-oxygenated bottom that enabled life to flourish both within and above the sediment interface. Small mounds were built up by colonies of the tabulate coral *Favosites* (*F. hamiltoniae* and *F. argus*). These supported epifaunal life, such as bivalves (rare, large *Pseudoaviculopecten* spp. and very rare uncompact *Grammysioidea* cf. *arcuata*; Plate 3e), brachiopods, gastropods (*Naticonema lineata*; Plate 3f), dendroid graptolites (*Dictyonema*

*hamiltoniae*; Plate 3c), and phacopid trilobites (uncommonly pygidia of *Greenops*). Interestingly, a relatively complete and large cephalon of the phacopid *Dipleura dekayi* was recovered with a pleurotomarioid gastropod *Glyptomaria capillaria* attached to the right compound eye lens, possibly representing a very rare example of gastropod feeding (i.e., scavenging) on a trilobite (Plate 3b; see ‘*Paleoecology of Salmon Creek and Ludlowville Falls III*’ for further discussion). The paleoenvironment of the Tichenor also supported pelagic life, including nektonic cephalopods (*Cyrtoceras* sp.; Plate 3d) and even phyllocarid “crustaceans.” Notably, one large and exceptionally complete specimen of the phyllocarid *Paraechinocaris (Echinocaris) punctata* (Plate 3a) was found. It is very unlikely that all these taxa, from infaunal burrowers to nektonic predators, lived together. Therefore, the Tichenor itself is likely highly time-averaged. This is further confirmed by the presence of very rare vascular plant material (Plate 3g) that must have drifted into this system as sea level rise flooded coastal areas to the east.

The Tichenor Member forms the base of the Moscow Formation. In general, the Moscow Formation is composed of gray, fossiliferous shale with silty concretionary horizons. Seasonal collapse of the Tichenor overhangs at the northern end of the Main Outcrop (42°32'29.4"N 76°32'35.5"W) will also bring down the overlying lower Moscow. It has been equally sampled over the past three freeze-thaw cycles (2023-2025). Together the Tichenor Member and lower Moscow compose a local stratigraphic unit called the Portland Point Subformation (Brett et al., 2023).

The lithology of the lower Moscow varies from bluish-gray calcareous mudstones to light gray silty shales, depending on the particular stratum that falls to the Spafford Member concretionary ledge below. In other sections in the Finger Lakes region, the lower part of the Moscow has been subdivided into the Deep Run, Menteth, and Kashong members (Fig. 3; Brett et al., 2023). However, distinct lithologic or paleontological features supporting a similar division are lacking at Salmon Creek. Like the underlying Tichenor Member, the lower Moscow follows the same successional *Zoophycos*-orthocone-diversity pattern when examining the individual beds, with well-preserved *Zoophycos* in the bluish-gray calcareous mudstones and siltstones (Plate 4e). Moreover, the lower Moscow also supported a sparse coral and bryozoan fauna. Instead of *Favosites* as in the Tichenor, however, the lower Moscow is dominated by large, disarticulated colonies of the branching tabulate coral *Thamnoptychia limbata* (Plate 4d) and thick, sheet-like mats of the trepostomate bryozoan *Leptotrypella furcata* (Plate 4b), suggesting more turbid conditions. Both taxa are often found hosting epibionts, including smaller tabulate coral (e.g., *Pleurodictyum americanum*) and bryozoan colonies, crinoids, and even gastropods.

Molluscan diversity is well represented in the lower Moscow. Among gastropods, uncompacted platyceratoids, such as *Naticonema lineata* and *Platyceras* spp. (Plate 4f), and rarely *Orthonychia* (Plate 4c), occur in the bluish-gray calcareous mudstones, whereas the internal molds of loxonematoids (*Palaeozygopleura delphicola* and *P. hamiltoniae*) can be found in the light gray silty shales. Very rarely, bellerophodontoids are represented by *Ptomatis patulus* and *Retispira leda*. Cephalopod diversity is also strong within the lower Moscow: the orthoconic nautiloids *Dolorthoceras exile*, *Michelinoceras telamon*, and *Spyroceras nuntium* are all uncommon finds. Even one complete phragmocone of the goniatite ammonoid *Tornoceras uniangulare* has been found. Bivalves, on the other hand, are not as diverse, potentially due to the increased silt in the system or perhaps collecting biases. Anomalodesmatans are represented

by *Glossites nuculoides*, rare uncompact specimens of *Grammysioidea* cf. *arcuata*, and very rare butterfly specimens of *Grammysioidea alveata*; palaeoheterodonts by *Modiomorpha* (*M. concentrica* and *M. mytiloides*), *Goniophora hamiltonensis*, and *Orthonota undulata*; and pteriomorphians by *Pseudoaviculopecten* spp.

Trilobites are represented mostly by *Greenops* (*G. grabau* and *G. barberi*) and *Eldredgeops rana*, and very rarely by pygidia of *Bellacartwrightia* and *Pseudodechenella rowi*. Within the bluish-gray calcareous mudstones, *Greenops* is more common than *Eldredgeops*, whereas the opposite trend occurs in the gray silty shales. One complete *Greenops barberi* has been found (Plate 4a), and large *Eldredgeops*, reminiscent of those of the Deep Run Member in Moscow Formation outcrops to the west (Mayer et al., 1991), are typical.

Spiriferid brachiopods are abundant throughout the lower Moscow, with *Mucrospirifer mucronatus* being very common and *Spinocyrtia* cf. *granulosa* much rarer. One internal mold of the strophomenid *Mesoleptostrophia junia* has been found. Also, one pyramidal test of the hyolithid *Hallotheca aclis* was recovered. Partial crinoid stalks are rare and sometimes taphonomically compressed (subrectangular) when found.

### *Locality 1b. Ridge Road*

Spafford, Tichenor, “lower Moscow”, Deuel Road., and lower Windom members

Loc. 1 Parking Access: 42°32'23.3"N 76°32'42.1"W | Loc. 1b-T Coords: 42°32'33.7"N 76°32'27.5"W | Loc. 1b-1 Coords: 42°32'38.0"N 76°32'24.5"W

The Givetian strata exposed at Salmon Creek gently dip to the northeast due to the Fir Tree anticline (Fig. 1a). This can best be observed by following the height of the Tichenor Member relative to water level. Moving upstream to Ridge Road, the older Ludlowville Formation disappears below Salmon Creek, replaced by the younger Moscow Formation. Along this stretch of Salmon Creek, the Moscow Formation includes the lower Moscow, Deuel Road, and lower Windom members (Cuylerville Smbr. *Ambocoelia* Beds of Brett et al., 2023).

### **Locality 1b-T. Rock Fall (Spafford, Tichenor, “lower Moscow”, Deuel Road., and lower Windom members)**

Loc. 1 Parking Access: 42°32'23.3"N 76°32'42.1"W | Loc. 1b-T Coords: 42°32'33.7"N 76°32'27.5"W

About halfway between the Main Outcrop and Ridge Road (42°32'33.7"N 76°32'27.5"W), the remains of a large rockfall are present on the southeastern bank of Salmon Creek. Collapse along a plane of weakness, likely a joint, brought down an approximate 10-m section of the Spafford, Tichenor, lower Moscow, Deuel Road, and lower Windom members. Large blocks of fallen Tichenor blocks are still present both on the Spafford concretionary ledge along the southeastern bank as well as in the creek bed itself. Within these particular Tichenor blocks, large prone individuals of the phacopid trilobite *Eldredgeops rana* occur rarely on the exposed surfaces. A collection of bluish-gray calcareous mudstones and light gray silty shales containing a similar faunal assemblage to the lower Moscow talus at the Main Outcrop can be accessed as float. The fauna of the lower Moscow at the Rock Fall requires further attention. Unusual taxa within these fissile-shale piles include more large *E. rana* (disarticulated tagmata, especially cephal), an unidentified partial gastropod whorl (very likely the same taxon as one found in the Spafford at the Main Outcrop), and a colony of *Pleurodictyum americanum*. Again, accessing these float

piles is dependent on seasonal freeze-thaw cycles, low stream stage, and slow stream flow. A small fall of the lower Moscow occurred here as recently as September 2025.

Basal in-situ exposures of the lower Moscow can be reasonably accessed just before reaching the Ridge Road bridge (42°32'37.0"N 76°32'24.6"W). Containing only spiriferid brachiopods, this section of the lower Moscow appears to lack a diverse fossil assemblage in contrast to the talus piles at the Main Outcrop and Rock Fall, though it remains to be thoroughly sampled for fossils. In one instance a partial uncompacted colony of the branching tabulate coral *Thamnoptychia limbata* was recovered, implying that taxonomic diversity must be higher than has been observed thus far.

The Deuel Road Member is a thick band of calcareous siltstone interposed between the lower Moscow and Windom members of the Moscow Formation (Fig. 5e). It represents a temporary shallowing of the Appalachian Basin before transgression continued in the overlying Windom. The Deuel Road is situated just out of reach for sampling, despite the northeastward dip towards Ridge Road. At Ridge Road, the Portland Point Subformation dips completely under the creek bed, allowing access to the lower Windom Member of the Moscow Formation. The Windom is a net transgressive to highstand sequence in which water depth increased, as a result of eustatic sea level rise followed by stillstand or falling conditions (Brett et al., 2012). Therefore, this unit is representative of an offshore marine environment.

#### **Locality 1b. Lower *Ambocoelia* Beds (Cuylerville Submember *Ambocoelia* Beds)**

Loc. 1 Parking Access: 42°32'23.3"N 76°32'42.1"W | Loc. 1b-1 Coords: 42°32'38.0"N 76°32'24.5"W

The Windom Member contains an abundance of fossils, with over 60 marine species described (Sang et al., 2013). At Ridge Road, fossils can be found readily in the *Ambocoelia* Beds (Cuylerville Smbr. of Brett et al., 2023), outcrops of fissile dark gray shale hosting extraordinary numbers of the small spiriferid *Ambocoelia umbonata*, for which the beds get their name (Plate 5f). In addition to *A. umbonata*, typical brachiopods include *Athyris spiriferoides*, *Mucrospirifer mucronatus*, and *Rhipidomella* (*R. vanuxemi* and *R. leucosia*). *Mediospirifer audaculus* and *Pseudoatrypa devonica* are much rarer, and only one specimen each of *Lingula delia* (Plate 5e) and *Mesoleptostrophia junia* have been found thus far. Three subclasses of bivalves (Anomalodesmata, Palaeoheterodonta, and Paleotaxodonta) are represented in the *Ambocoelia* beds, with *Nuculoidea corbuliformis* the most common. Compressed, partial phragmocones of the orthoconic nautiloid *Spyroceras nuntium* are typical, whereas uncompacted specimens of *Michelinoceras telamon* are rare. Incomplete phragmocones of a medium-sized goniatite ammonoid are uncommon and remain to be identified (Plate 5d; additional specimens have been reported from the upper Cuylerville Submember at Middle Salmon Creek). Two gastropod taxa, the bellerophodontoid *Retispira leda* and loxonematoid *Palaeozygopleura hamiltoniae* (Plate 5c), are known from the Cuylerville *Ambocoelia* Beds. Interestingly, three *P. hamiltoniae* specimens were found associated with the cubichnia *Rusophycus*, indicating feeding behavior (likely scavenging) by a trilobite on the shells of these gastropods (see '*Paleoecology of Salmon Creek and Ludlowville Falls II*' for further discussion). Corals (e.g., *Aulocystis dichotoma*; Plate 5g) and crinoids are rare. Notably, this horizon boasts a bounty of phacopid trilobites, including relatively common *Eldredgeops rana*, occasional *Greenops* (*G. grabau* and *G. barberi*), very rare *Bellacartwrightia*, and one meraspid (juvenile) *Dipleura dekayi* cephalon (Plate 5b). Disarticulated tagmata compose the majority of phacopid fossils; however, complete specimens

have also been found (Plate 5a). Among Incertae Sedis taxa, two pyramidal tests of *Hallotheca acilis* (Plate 5h) have been recovered.

## Locality 2. Middle Salmon Creek (Ludlowville Road)

Upper Cuylerville, Big Tree, and Bear Swamp submembers

Loc. 2 Parking Access: 42°33'02.2"N 76°32'17.7"W | Loc. 2-T Coords: 42°33'01.3"N 76°32'20.6"W | Loc. 2-1 Coords: 42°32'57.5"N 76°32'21.3"W

Moving upstream, the Givetian strata exposed at Salmon Creek continue their gentle downward dip to the northeast (Fig. 1a). At Middle Salmon Creek, the Portland Point Subformation and Deuel Road Member have completely disappeared. In their place is the lower Windom Member, containing the upper Cuylerville, Big Tree, and Bear Swamp submembers (Fig. 7). Situated between the creek bed and 2-m height, the upper Cuylerville and Big Tree submembers are the most accessible strata at Middle Salmon Creek. The Bear Swamp Member, on the other hand, is accessible just upstream of the Ludlowville Road bridge along the southern bank (42°33'02.9"N 76°32'15.4"W), but this unit has not been thoroughly sampled (only one partial goniatite ammonoid phragmocone and *Greenops* pygidia have been reported thus far). Exposure of the upper Windom Member continues at Upper Salmon Creek. The uppermost Moscow can be sampled in seasonal talus accumulations at Middle Salmon Creek (42°33'01.3"N 76°32'20.6"W).

### Locality 2. Main Bench (Upper Cuylerville and Big Tree submembers)

Loc. 2 Parking Access: 42°33'02.2"N 76°32'17.7"W | Loc. 2-1 Coords: 42°32'57.5"N 76°32'21.3"W

The concretionary horizon of the lower Windom Member at Middle Salmon Creek is generally inaccessible, as it is typically underwater. Another concretionary horizon can be more reliably accessed upstream at Green Road. However, during periods of extensive drought, such as summer 2025, the bed can be exposed. More sampling of this horizon is needed.

Just above this concretionary horizon is a 1.5-m thick series of light gray silty shale packages of the upper Cuylerville Submember, reworked by the foraminifera *Zoophycos*. The upper Cuylerville at Middle Salmon Creek has been extensively sampled for fossils. During low stream stage, the basal beds of the upper Cuylerville are exposed. Pavements of the athyridid brachiopod *Athyris spiriferoides*, similar to those seen in the Spafford Member at the Main Outcrop, are typical. Among spiriferids, *Mediospirifer audaculus* is commonly found in these lower horizons. *Spinocyrtia* cf. *granulosa*, though less common, is usually found with both valves preserved, which can occasionally be taphonomically deformed (shearing between valves). Note that *Ambocoelia umbonata* is largely absent from the upper Cuylerville, as the *Ambocoelia* Beds have dipped below the creek bed at Middle Salmon Creek. The orthid *Rhipidomella penelope* and atrypid *Pseudoatrypa devonica* are uncommon. Productids are commonly represented by *Arcuaminites* (*Devonochonetes*) *scitulus* and *Devonochonetes coronatus*. Among strophomenids, uncompact pedicle valves of *Megastrophia concava* (Plate 6-1c) are rare. Interestingly, *M. concava* occurs throughout the upper Cuylerville, unlike the other strophomenids. Phacopid trilobites, including *Eldredgeops rana* and *Greenops* (*G. grabau*i and *G. barberi*), are rare and restricted to the basal beds of the upper Cuylerville. Disarticulated tagmata are typical, especially among *Greenops*, but complete individuals of both species have also been found (plates 6-1a and 6-1b, respectively). Sometimes, long stalks (or runners) of crinoids can be found sandwiched between individual beds of *Zoophycos*-churned mudstone.

Faunal diversity appears to increase in the uppermost Cuylerville Submember. Again, taxonomic diversity is greatest within beds overlying *Zoophycos* churned and orthocone-dominated horizons, as seen in the Tichenor and lower Moscow members at Lower Salmon Creek. Mollusks are well represented here. Among bivalves, the palaeoheterodont *Modiomorpha* (*M. concentrica* and *M. mytiloides*) are the most common. The anomalodesmatan *Grammysioidea* cf. *arcuata*, often uncompact and with both valves enclosed (Plate 6-2g); paleotaxodont *Tellinopsis submarginata*, (Plate 6-2h); and smaller-sized valves of the pteriomorphian *Pseudoaviculopecten* spp. are rarer finds. Note that *G.* cf. *arcuata* occur throughout the upper Cuylerville, like *Megastrophia concava*. *Orthonota undulata* is a very rare species of palaeoheterodont, with even one specimen possessing regionalized deformations in the shell ribbing, potentially due to predation attempts. One very small specimen of the heterodont *Nyassa* cf. *arcuata* has been found. Gastropod diversity is restricted to two species: the platyceratoid *Naticonema lineata*, with well-preserved shell (Plate 6-2i), and the bellerophodontoid *Retispira leda*. Both ammonoid and nautiloid cephalopods are present in the uppermost Cuylerville, with *Spyrocreas nuntium* the most common among orthoconics. Interestingly, phragmocones of both *S. nuntium* and *Michelinoceras telamon* can sometimes be found fouled by tubes of the possible phoronid *Reptaria stolonifera* (plates 6-1d and 6-2f). A possible breviconic nautiloid was discovered, though this specimen, a large but partial phragmocone, remains to be identified. The goniatite ammonoid in the upper Cuylerville Submember, known from three partial phragmocones, is most likely the same medium-sized species as specimens recovered in the underlying *Ambocoelia* Beds at Ridge Road (Plate 5d). Proetid trilobites appear to be restricted to the uppermost Cuylerville Submember, separated from the phacopids. *Pseudodechenella rowi* is represented only by disarticulated tagmata, the vast majority being pygidia. Incertae Sedis taxa are very rare. They include one partial periderm test of the conulariid *Conularia undulata* (Plate 6-1e), one very small pyramidal test of *Hallotheca aclis*, and potentially a conical shell of the cornulitid tentaculite *Cornulites hamiltoniae*.

In addition to the fodinichnia *Zoophycos*, the upper Cuyerville Submember also contains the cubichnia *Rusophycus*. These resting traces are believed to have been constructed by arthropods, likely phacopid and proetid trilobites here. One *Rusophycus* specimen was recovered abutting a heavily phoronid-fouled orthoconic nautiloid *Michelinoceras telamon* (Plate 6-2f). This association of trace and body fossils is interpreted as trilobite scavenging (see '*Paleoecology of Salmon Creek and Ludlowville Falls II*' for further discussion).

Plant material within the upper Cuylerville Submember is very rare, with the only one decorticated stem of an unidentified lycophyte on record (Plate 6-2j).

Above the upper Cuylerville Submember lies the Big Tree Submember, which is subdivided into the Bay View Beds equivalent (lower) and Smoke Creek Bed (upper; Fig. 8a). The Bay View Beds interval is dominated by time-averaged assemblages of rugose and tabulate corals, as well as ossicles and partial stalks of crinoids (Fig. 8b). Rugose corals are very commonly represented by the stauriids *Stereolasma rectum* (Plate 7c) and *Streptelasma ungula* (Plate 7a), whereas tabulates are rarer and include small colonies of *Aulocystis jacksoni* (Plate 7b), *Pleurodictyum americanum* (Plate 7e), and one specimen of a bryozoan-fouled *Heliophyllum delicatum* (Plate 7d). In one instance, a partial calyx of the camerate crinoid *Megistocrinus depressus* (Plate 7f)

was recovered as float. This specimen represents the only crinoid calyx found at Salmon Creek. However, the camerate *Arthroacantha* has also been reported to come from this portion of the Windom Member (George McIntosh, pers. com.). Brachiopods are also uncommon, known so far by the atrypid *Pseudoatrypa devonica*. Pteriomorphian bivalves (*Pseudoaviculopecten* spp. and *Pterinopecten* cf. *conspectus*) and platyceratoid gastropods (e.g., smaller individuals of *Naticonema lineata*) occur but are rather rare. Cephalopods have not yet been documented in the Bay View Beds equivalent. A small pyramidal test of the hyolithid *Hyolithes striatus* has also been found (Plate 7g).

At about a 2-m height, limited sampling has occurred at the Smoke Creek Bed. The presence of in-filled burrows within the Smoke Creek Bed (Fig. 8c) emphasizes that the marine environment in which these animals lived had relatively low sedimentation rates and was well-oxygenated. These features likely reflect the lower boundary of cycle Giv-3d (Fig. 3; Brett et al., 2023), with the subsequent transgression permitting colonization by corals and diverse brachiopods, bryozoans, and crinoids (Fig. 8d).

### **Locality 2-T. Rock Chute (upper Moscow Formation)**

Loc. 2 Parking Access: 42°33'02.2"N 76°32'17.7"W | Loc. 2-T Coords: 42°33'01.3"N 76°32'20.6"W

Above the Big Tree Submember, sections of the uppermost Moscow Formation can be accessed via seasonal talus piles that accumulate along the northwestern bank of Middle Salmon Creek (42°33'01.3"N 76°32'20.6"W). For example, in October 2022, a silty section of the upper Windom and overlying Garrattsville Member (Brett et al., 2023) was brought down, including the Spezzano Gully Submember South Lansing Beds (figs. 2 and 11). The float contained an exceptionally preserved, large colony of the tabulate coral *Favosites hamiltoniae* (Plate 8e). The colony hosted an abundance of taxa, most notably an exceptionally rare, complete and prone specimen of the proetid trilobite *Pseudodechenella rowi* (Plate 8c), an uncompact shell of the spiriferid brachiopod *Spinocyrtia* cf. *granulosa*, and a few large phragmocone sections of the orthoconic nautiloid *Spyroceras nuntium* (Plate 8g). Unfortunately, this silty unit has since been swept away.

Another rockfall occurred in the same place in April 2023, where a large block of calcareous (concretionary) siltstone from the upper Taunton Submember (uppermost Windom Member, underlying the South Lansing Beds) was found as float. The following June, a period of torrential rainfall brought down additional pebbles of calcareous siltstone from this unit. Calcified crinoid ossicles compose the majority of fossil material in the upper Taunton Submember blocks. Cystoporate bryozoans are common. Calcified valves of spiriferid and tropidoleptid brachiopods are very common, including species such as *Mucrospirifer mucronatus* and *Tropidoleptus carinatus*, respectively. Interestingly, calcified pedicle valves of the large strophomenid *Mesoleptostrophia junia* (Plate 8d) and small *Strophodonta demissa* can be found in relative abundance. Mollusks are generally rare, with palaeoheterodont bivalves (*Goniophora hamiltonensis*), small platyceratoid (*Naticonema lineata*) and loxonematoid (*Palaeozygopleura hamiltoniae*; Plate 8d) gastropods, and orthoconic nautiloids representing this phylum thus far. In one instance, a split calcareous pebble yielded a relatively complete phragmocone of the orthoconic *Michelinoceras telamon* crosscut by veins of calcite (Plate 8f). Phacopid trilobites can also be found in relative abundance. Disarticulated pygidia of *Greenops* (*G. grabau* and *G. barberi*) are quite common; *Bellacartwrightia* (Plate 8a) is much rarer. Only one *Eldredgeops rana* and one very rare ventral specimen of *Odontocephalus* has been found. In addition, small to

very large thoracic segments of *Dipleura dekayi* are present (Plate 8b). Like the South Lansing Beds material, this accumulation of calcareous siltstones has been since washed downstream.

No significant talus accumulations occurred during the 2024 and 2025 spring thaw seasons. In August 2024, new collapses were observed throughout Middle Salmon Creek, but the storm event must have been too severe to preserve any material on the stream bank.

## Locality 3. Upper Salmon Creek

Upper Windom, Garrattsville, Labrador Valley, Upperville, and Long Hill members

Loc. 3a Parking Access: 42°33'08.5"N 76°32'04.0"W | Loc. 3a Coords: 42°33'11.2"N 76°31'59.6"W | Loc. 3b Coords: 42°33'13.4"N 76°32'03.1"W | Loc. 3c Parking Access: 42°33'13.3"N 76°32'13.7"W | Loc. 3c-1 Coords: 42°33'17.2"N 76°32'10.8"W | Loc. 3c-2 Coords: 42°33'17.5"N 76°32'14.5"W

### *Locality 3a. Green Road*

Fisher Gully Submember

Loc. 3a Parking Access: 42°33'08.5"N 76°32'04.0"W | Loc. 3a Coords: 42°33'11.2"N 76°31'59.6"W

At Green Road, another concretionary horizon of the upper Windom Member (Fisher Gully Submember) can be accessed during low stream stage (figs. 9 and 10a). This unit has not been heavily sampled. It appears to lack a diverse fossil assemblage, similar to the ovate concretions within the Spafford Member at Myers Road. However, occasional fossils of the phacopid trilobite *Eldredgeops rana* have been found weathering out of the concretions (Plate 9a).

Between 1 and 2 m above the concretionary horizon, fissile and silty dark gray shales of the Fisher Gully Submember can be accessed. Again, this horizon requires further sampling, but so far finds have included small species of brachiopods and mollusks, all taphonomically compressed. Brachiopods are represented mostly by rhynchonellids (*Eumetabolotoechia multicostatum*; Fig. 10b) and tropidoleptids (*Tropidoleptus carinatus*). *E. multicostatum* is a characteristic indicator of relatively deep-water, dysoxic conditions within the Hamilton Group (Brett et al., 2023). Thus, these beds likely reflect an offshore environment within the highstand of cycle Giv-3e (Fig. 3). One craniid, *Petrocrania* cf. *hamiltoniae* has been recovered from this horizon. Mollusks are much rarer, with an unidentified bivalve and a partial spyroceratid phragmocone being the only two specimens reported thus far.

### *Locality 3b. Dug Road*

Taunton Submember lower Fall Brook Bed equivalent

Loc. 3b Coords: 42°33'13.4"N 76°32'03.1"W

The Fall Brook Bed equivalent of the Taunton Submember is a complex sedimentary package of dark gray, silty mudstone. It is composed of a series of thin shell beds dominated by spiriferid brachiopods. Large, calcareous concretionary burrows are present that cut across shell beds (Plate 9c), indicative of reworked sediments and a well-oxygenated environment. Both paleontological and mineralogical material have been found concentrated within these concretions, including spiriferid valves, *Eldredgeops rana* tagmata, and nodular pyrite growths (Plate 9d).

Spiriferids are represented most commonly by *Mediospirifer audaculus* and less often by *Spinocyrtia* cf. *granulosa*. Both species can be found either uncompacted (Plate 9b) or in butterfly. Fairly complete phragmocones of the orthoconic nautiloid *Spyroceras nuntium* occur in relative abundance; they are typically compressed, but, interestingly, one was found retaining original biological shape (Plate 9e). Small, compressed phragmocones of the orthoconic *Dolorthoceras exile* are quite rare. One incomplete phragmocone of the goniatite ammonoid *Tornoceras uniangulare* has been found. Bivalves thus far are limited to one specimen each of the anomalodesmatan *Grammysioidea alveata* and pteriomorphian *Mytilarca oviformis*. Tabulate corals are equally difficult to find, with only one specimen of the favositid *Pleurodictyum americanum* reported. Large, disarticulated tagmata of the phacopid trilobite *Eldredgeops rana* are uncommon, and those of *Greenops* (*G. grabau* and *G. barberi*) are rare. Pygidia of the proetid *Pseudodechenella rowi* are even rarer.

### *Locality 3c. Ludlowville Falls*

Taunton, Spezzano, Carpenter Falls, Taughannock Falls, and Moravia submembers

Loc. 3c Parking Access: 42°33'13.3"N 76°32'13.7"W | Loc. 3c-1 Coords: 42°33'17.2"N 76°32'10.8"W | Loc. 3c 2 Coords: 42°33'17.5"N 76°32'14.5"W

Depending on the amount of precipitation received, outcrops of the upper Moscow Formation, including the Fall Brook Bed equivalent (Windom Mbr: Taunton Smbr) and overlying South Lansing Beds (Garrattsville Mbr: Spezzano Gully Smbr), are seasonally accessible via a short but steep trail from Ludlowville Park, or by wading upstream from Dug Road. Like much of Salmon Creek, these units can be best seen during the summer months when stream stage is lowest.

#### **Locality 3c-1. Upper *Ambocoelia* Lags (Taunton Submember *Ambocoelia*-rich Fall Brook Bed equivalent)**

Loc. 3c Parking Access: 42°33'13.3"N 76°32'13.7"W | Loc. 3c-1 Coords: 42°33'17.2"N 76°32'10.8"W

An *Ambocoelia*-rich lens of the Fall Brook Bed equivalent (here termed ‘*Ambocoelia*-rich Fall Brook Bed equivalent’) can be accessed as a platform right along the northeastern bank of Upper Salmon Creek, just downstream of Ludlowville Falls. Like the Ridge Road outcrop, this section is composed of a fissile dark gray shale that contains a thin pavement of the small spiriferid *Ambocoelia umbonata* (Fig. 12d). In addition to *A. umbonata*, other brachiopods such as the athyridid *Athyris spiriferoides* and spiriferid *Mediospirifer audaculus* are very common (Fig. 12c). Orthids, such as *Rhipidomella penelope* are less common. Unlike Ridge Road, this bed contains an abundance of corals. Stauriid rugose corals, such as *Stereolasma rectum*, *Streptelasma ungula* (Fig. 12c), and *Stewartophyllum intermittens*, are much more typical than favositid tabulates, including *Pleurodictyum americanum*. Trilobites are represented by the phacopid *Eldredgeops rana* only. Disarticulated tagmata, especially pygidia, are relatively common; complete specimens are rare (Plate 9f). Mollusks appear to be very rare or absent entirely from this site.

Like the calcareous concretions in the Spafford Member (Myers Road) and lower Fall Brook Bed equivalent (Dug Road), the shales of the *Ambocoelia* lens at Ludlowville Falls host globular pyrite nodules, which can often be found encrusted to the fossils (e.g., Fig. 12b; Plate 9f). When exposed to the surface, these nodules rust in the presence of oxygen, changing color from yellow to reddish-brown.

### **Locality 3c-2. Ludlowville Falls Rock Shelter (Spezzano, Carpenter Falls, Taughannock Falls, and Moravia submembers)**

Loc. 3c Parking Access: 42°33'13.3"N 76°32'13.7"W | Loc. 3c-2 Coords: 42°33'17.5"N 76°32'14.5"W

Just upstream of the *Ambocoelia*-rich Fall Brook Bed equivalent, Salmon Creek plunges about 15 m over a fully exposed section of the Tully Formation, carving out the less resistant upper Moscow Formation below (Fig. 12a). Recall that the Moscow is primarily composed of shale, and since shale is much softer than limestone, freeze-thaw cycles weather the upper Moscow at a much faster rate than the Tully. This produces what is known as a caprock waterfall, where the Tully juts out as a thick (and precarious) overhang, and the upper Moscow is cut back into a rock shelter (recess cave).

The uppermost unit of the Moscow Formation exposed at Salmon Creek is the Garrattsville Member, which overlies the Windom Member. It most likely outcrops at the uppermost section of the Ludlowville Falls Rock Shelter, and is therefore generally inaccessible. However, the upper Taunton Submember and South Lansing Beds (Spezzano Gully Smbr.) have been identified at Middle Salmon Creek from seasonal talus accumulations in 2022 and 2023, respectively. Refer to ‘*Locality 2. Middle Salmon Creek (Ludlowville Road)*’ for further discussion.

The Tully Formation overlies the Garrattsville Member (figs. 11 and 12e), bringing an end to not only the Moscow Formation but also the entire Hamilton Group. Like the Spafford-Tichenor contact at Lower Salmon Creek, the Garrattsville-Tully contact at Ludlowville Falls is a disconformity. This surface forms the base of cycle Giv-5 (Fig. 3; Brett et al., 2023). Within the Tully Formation itself is a series of smaller disconformities, represented at contacts between the Carpenter Falls, Taughannock Falls, and Moravia members, which are further punctuated by thin shale partings (figs. 11 and 12a). Altogether, the Tully Formation represents about 500 thousand years of time (Sang et al., 2013).

Somewhat like the Tichenor Member at Lower Salmon Creek, it is probable that the Tully Formation formed in a warm, shallow sea; but in contrast to the Tichenor, the main carbonate sediment accumulating was lime mud. Tully fossils are actually rather scarce and scattered within the limestone. This could indicate a shallow but offshore setting in which green algae and/or bacteria produced large quantities of carbonate sediment. This evidence, together with the appearance of tropical warm water brachiopods derived from the more equatorial regions, indicates a relatively short period of warming perhaps lasting only 100 to 200 thousand years (Baird et al., 2012, 2023; Bartholomew et al., 2003; Zambito et al., 2012).

During low stream stage in the summer, the underside of the overhanging Tully Formation (Labrador Valley Mbr: Carpenter Falls Smbr) at Ludlowville Falls is accessible (42°33'17.5"N 76°32'14.5"W), either by walking along a concretionary ledge of the upper Moscow Formation or by swimming across the plunge pool (Fig. 12e). Large firm ground burrows, most likely produced by trilobites, can be seen by looking up at the base of the Carpenter Falls Submember (Fig. 12f). This reworking into the underlying Moscow indicates a well-oxygenated ocean bottom that supported a diversity of marine life during the time of deposition.

## Geologic History of Salmon Creek and Ludlowville Falls After the Givetian Stage

The last unit of strata exposed at Ludlowville Falls is the Tully Formation, which marks the end of the Hamilton Group and Givetian Stage. Above the Hamilton lies the Genesee Group and the start of the Frasnian (early Late Devonian). Just upstream of Ludlowville Falls along Salmon Creek Road there is an outcrop of the Genesee Formation, though inaccessible as it sits on private property. It contains fissile black shales, indicative of anoxic environmental conditions after the Taghanic Biocrisis, one of three “bioevents” that occurred over a 25-million-year period (late Middle to latest Devonian). Together the Taghanic (late-Givetian), Kellwasser (end-Frasnian in two large pulses), and Hangenberg (end-Famennian) and a series of lesser extinctions (e.g., the earliest Frasnian event) show the strong volatility of the Middle-Late Devonian interval. During this time, trees first appeared and began sequestering carbon from the atmosphere. Moreover, their deep roots released more nutrients from the soil, causing eutrophication of shallow seas and producing very widespread black shale deposits. The drawdown of carbon dioxide resulting from organic matter sequestration lowered global temperatures, transitioning Earth from a greenhouse to icehouse climate and causing episodes of sea level fall (Algeo et al, 1993; Algeo & Scheckler 1998). Sea level change and volcanism also contributed to increasing extinction and decreasing origination rates. This had severe consequences for marine invertebrates. Stromatoporoid sponges and corals suffered losses, with stromatoporoids becoming extinct at the end of the Famennian (latest Devonian). During the Taghanic Biocrisis specifically, odontopleurid, dalmanitid, and phacopid trilobites, as well as atrypid and pentamerid brachiopods disappear. The Tully-Genesee contact, during which this bioevent occurred, can be best seen at the Lower Falls at Taughannock Falls State Park (Trumansburg, NY). Predator-prey interactions escalated during the Devonian (Signor and Brett, 1984; Brett, 2003) (see *Paleoecology of Salmon Creek and Ludlowville Falls I* for further discussion), triggering rapid evolution among fishes, known as the nekton revolution (Klug, 2010), and ultimately the rise of vertebrate life on land.

Units younger than the Genesee Formation, such as the Ithaca Formation, can be seen on Cornell University campus (Ithaca, NY) at Fall Creek, Beebe Lake, and Cascadilla Gorge. Interestingly, new research led by E.M.C. in collaboration with the Paleontological Research Institution is demonstrating that phacopids did not actually disappear during the Taghanic Biocrisis, and instead persisted into the Frasnian, surviving in pocket refugia as young as the Ithaca (Brett et al., 2025). A full sequence from the Tully to Ithaca formations is again exposed at Taughannock Falls State Park.

The Ithaca Formation is one of the last Devonian units exposed in the central Finger Lakes area. By the end of the Frasnian, the Catskill Delta progradation completed and the Appalachian Basin was entirely filled with sediment. As a result, the Devonian marine record in New York State ended. From the Frasnian to the late Pleistocene Epoch, the rate of erosion generally outpaced the rate of deposition. Consequently, an enormous unconformity exists between the Devonian strata present at Salmon Creek (deposited around 385 Ma) and the overlying glacial till deposited during the late Pleistocene (11.7 Ka). An exception to this pattern occurs only in select localities, such as in Six Mile Creek (Ithaca, NY), where Jurassic- and Cretaceous-aged igneous dikes of

rock related to kimberlite, but lacking diamonds, can be found intruded into joints or fractures in the Frasnian-aged shales. Note that another kimberlite-like dike occurs at Upper Salmon Creek between Green and Dug Road, but the extrusion is located on private property and is therefore inaccessible.

During the Late Pleistocene, New York State experienced several successions of glacial advance and retreat. The latest glacial advance reached an acme around 21 Ka and final retreat began around 11 Ka. The Finger Lakes of central New York State originated as north-south river valleys. Glacial retreat ultimately deepened these pre-existing river valleys (Sang et al., 2013). Deposition of glacial till during episodes of retreat impounded meltwater, forming proglacial lakes. As glacial retreat continued, the proglacial lakes slowly drained and fell in elevation, carving steep sided valleys into the landscape. These steep inclines increased the distance from the base of the proglacial lakes to the height at which a stream, such as Salmon Creek, fed into it. Water follows the path of least resistance, so over time, Salmon Creek carved through sediment along its new path toward the present-day Cayuga Lake, exposing the Devonian strata beneath it. It cut into soft rock, such as the upper Moscow Formation shales, at a much faster rate than the harder rock, such as the Tully Formation. Ludlowville Falls formed this way as Salmon Creek cut deeply into the shale creating a natural rock shelter above which the Tully overhangs. Sediments shed from Ludlowville Falls (and throughout the creek) are deposited when they meet Cayuga Lake at Myers Point and stream velocity drops. Myers Point is a small delta that is currently prograding to the southwest as deposition continues.

## Paleoecology of Salmon Creek and Ludlowville Falls

### *I. New occurrences of sublethal injury in the shells of Devonian bivalves with the first record of predation scars in Modiomorpha (Modiomorphidae, Bivalvia)*

Predation scars provide direct evidence of ancient predatory interactions, allowing us to gauge predator-prey relationships and trends in deep time such as the major increase in durophagous predators during the Devonian, known as the “Middle Paleozoic Revolution” (Signor & Brett, 1984; Brett & Walker, 2002, Brett, 2003). While trace fossils (healed bite marks, peeling, and drilling) in mollusks increased in frequency from the Cambrian onward, showing a marked escalation in the later Paleozoic (Vermeij et al., 1981; Bond & Saunders, 1989; Brett & Walker, 2002, Brett, 2003), certain forms of sublethal damage continue to be rare in literature. The overall rarity of sublethal breakage in Devonian bivalves specifically made the documentation of healed injuries on the pterineid bivalve genus *Ptychopteria* a significant finding, recognized as the first report of sublethal predation damage on Devonian (Hamilton Group; New York, USA) bivalves (Nagel-Myers et al., 2009). In this guide, we continue to update the known literature and report new evidence of Devonian predation scars in the bivalve genus *Modiomorpha* (Plate 1b) from the *Modiomorpha-Ancyrocrinus* Bed (Ludlowville Fm: lower Spafford Mbr; Locality 1a-1) of Salmon Creek. This marks the first evidence of predation scars in *Modiomorpha* bivalves, and continues to be only other reported predation scar evidence in Devonian bivalves besides those reported in Nagel-Myers et al. (2009).

Predation scars on bivalve shells are recognized primarily as evidence of sublethal, breakage-induced injuries that the animal survived and successfully repaired (Nagel-Myers et al., 2009). These repair scars are distinguished from non-biological breakage, such as taphonomic effects, by several characteristic features of the damage and subsequent repair (Brett & Walker, 2002; Brett, 2003; Alexander & Dietl, 2003; Nagel-Myers et al., 2009). A key identifying characteristic is the scar geometry, which typically appears as scalloped and V-shaped or, less frequently, as embayments where a large piece of the shell margin has been removed (Alexander & Dietl, 2003; Nagel-Myers et al., 2009). These scalloped and embayed shapes resemble traces made by modern shell-breaking predators, such as decapod arthropods, suggesting a similar mechanism of attack by durophagous Devonian predators (Alexander & Dietl, 2003; Nagel-Myers et al., 2009). Further identification evidence includes the pattern of shell regrowth, which may involve changes in growth line banding and the loss or offsetting of radial surface ornamentation in the area immediately surrounding the repair scar (Nagel-Myers et al., 2009). Finally, a biological origin is supported by the stereotyped positioning of the wounds occurring on the posterior/medial region, which indicates active site selection by predators, possibly targeting the exhalant and inhalant current regions (Nagel-Myers et al., 2009).

Shell damage in bivalves lacking protective traits is often lethal because the exposure of the mantle following sublethal breakage creates an open invitation for bacteria or parasites, while simultaneously signaling the injured individual's vulnerability to other predators. This inherent risk results in typically low repair frequencies for most bivalve taxa compared to groups like gastropods, unless they possess specialized defenses such as the retractable mantle and tight valve closure observed in some Devonian bivalves like *Ptychopteria* (Nagel-Myers et al., 2009). Potential culprits of this type of predation evidence include Devonian shell-crushing predators that diversified during this time, such as ammonoid cephalopods and phyllocarid arthropods (both with documented occurrences at Salmon Creek), and jawed placoderm fishes (yet undocumented) (Brett & Walker, 2002; Brett, 2003; Nagel-Myers et al., 2009). These new data from our sites affirm the Paleozoic bivalve record as an essential, though historically underutilized, resource for testing hypotheses concerning the evolutionary influence of specialized predator-prey interactions (Nagel-Myers et al., 2009).

The discovery of frequent repair scars in *Ptychopteria* was high compared to most modern bivalves and supports the hypothesis that predation pressure intensified in the middle Paleozoic (Nagel-Myers et al., 2009). While understudied, the predation scar evidence found at Salmon Creek is noteworthy in that there are multiple specimens all from the same site and geologic unit. *Modiomorpha* species are very common from this particular site (Appendix II), but remain undersampled relative to their occurrence due to various collection biases. As such, the available rates of predation scar evidence cannot be conclusively studied like in Nagel-Myers et al. (2009; however, we contend that they may experience similarly high rates of predation evidence due to multiple predated specimens being found in the same site as opposed to the previous study's sampling from across the states Devonian (Hamilton Group) exposures. A more detailed collection of *Modiomorpha* bivalves at the site should help to answer some of these crucial questions, while occurrences in new genera of bivalves show that overall sampling for predation scars in bivalves should be further studied.

## II. *An overview of invertebrate feeding traces with specific focus on new associations of Rusophycus and mollusk shells*

The traces *Zoophycos* and *Rusophycus* are key ichnofossils used in interpreting ancient marine environments, including those found throughout the various deposits exposed on Salmon Creek and Ludlowville Falls. *Zoophycos* is morphologically characterized by helical or tongue-shaped spreiten burrows (Seilacher, 1967; Wetzel & Werner, 1981; Sedorko et al., 2018) produced by endobenthic worm-like organisms (Wetzel & Werner, 1981; Ekdale & Lewis, 1991), representing a specialized deposit-feeding behavior (Seilacher, 1967; Bouchemla et al., 2021). *Rusophycus*, conversely, is typically a bilobed impression resulting from the resting (cubichnia) or digging activities of arthropods, primarily trilobites (Osgood, 1970; Seilacher, 1970; Pickerill, 1995), often displaying characteristic transverse scratches (Bjerstedt, 1987; Tarhan et al., 2011). In the Devonian marine environment, *Zoophycos* experienced its first significant expansion in shelfal deposits (Miller, 1991; Zhang et al., 2015; Sedorko et al., 2018; Bouchemla et al., 2021), a phenomenon sometimes linked to increased food supply correlated with the rise of land plants (Kotake, 2014; Sedorko et al., 2018). Ecologically, while dense occurrences in storm deposits might be interpreted opportunistically (Sedorko et al., 2018), *Zoophycos* generally reflects behavior of k-selected, equilibrium species capable of long-term activity (Ekdale, 1985; Sedorko et al., 2018). *Rusophycus* highlights critical ecological interactions, as composite traces known as “hunting burrows” demonstrate that trilobites actively entered the sediment in search of infaunal prey (Jensen, 1990; Tarhan et al., 2011). Furthermore, the tracemakers responsible for these deep structures significantly impact their environment through bioturbation (Cribb et al., 2019), a crucial ecosystem engineering behavior. This process, particularly through deep burrows, involves bioirrigation. Bioirrigation allows the circulation or continuous ventilation of water (Wetzel, 1991; Wetzel & Werner, 1981) that flushes reduced chemicals, such as iron and sulfur, from the sediment and thereby increases oxygen penetration depth and overall oxygenation in the substrate (Wetzel, 1991).

Both *Zoophycos* and *Rusophycus* are instrumental in interpreting depositional environments, particularly within the ichnofacies scheme. *Rusophycus* is a key indicator of the Cruziana Ichnofacies (Seilacher, 1967; Bjerstedt, 1987; Bouchemla et al., 2021), typically ascribed to shallow-marine settings such as offshore-to-lower shoreface environments or restricted-bay facies (Bjerstedt, 1987; Sedorko et al., 2018). Historically, *Zoophycos* has been associated with the eponymous *Zoophycos* Ichnofacies, traditionally indicating deeper water (sublittoral to bathyal depths) below wave base (Seilacher, 1964; Osgood & Szmuc, 1972; Marintsch & Finks, 1982). However, given its frequent appearance in Paleozoic shelfal settings, its strict bathymetric reliability is debated (Sedorko et al., 2018). In the Devonian Paraná Basin, for example, *Zoophycos* is interpreted as a component of the distal expression of the Cruziana Ichnofacies (Miller, 1991; Sedorko et al., 2018; Bouchemla et al., 2021). Ichnological analyses integrating trace type and bioturbation degree serve as proxies for reconstructing bottom-water oxygen levels and sedimentation rates (Wetzel, 1991); the association of *Zoophycos* with low-diversity assemblages including *Chondrites* suggests tolerance to dysoxic conditions in deeper offshore beds (Sedorko et al., 2018; Casanova-Arenillas et al., 2021). Caution remains necessary, as

*Rusophycus* has been documented in deep-water flysch sequences (Seilacher, 1967; Pickerill, 1995), indicating that reliance on a single trace fossil for definitive depth assignment can be misleading (Pickerill, 1995).

The findings of *Rusophycus* from Salmon Creek that include one specimen abutting a phragmocone of the orthoconic nautiloid *Michelinoceras telamon* from the upper Cuylerville Submember (Locality 2; Plate 6-2f), and three encompassing the loxonematoid gastropod *Palaeozygopleura* from the Cuylerville Submember *Ambocoelia* Beds (Locality 1b; Plate 5c) provide direct ichnological evidence of feeding behaviors by the tracemaker (Jensen, 1990; Tarhan et al., 2011). Such composite traces, known as “hunting burrows,” indicate intentional stationary digging into the substrate in search of infaunal animals (Bergström, 1973; Jensen, 1990; Tarhan et al., 2011). The association of *Rusophycus* with a cephalopod shell is most likely related to scavenging, where the trilobite exploits the organic remains of an already dead organism (Fortey & Owens, 1999; Neto de Carvalho, 2006). Additionally, the three gastropods found directly encompassed within the burrow trace may also point to scavenging, if not active predation by the trilobite trace maker (Tarhan et al., 2011). The act of digging (*Rusophycus*) to reach infaunal or shallowly buried food (gastropods) demonstrates a controlled, directed behavior by the trilobite (Jensen, 1990). This ability of trilobites to tackle shelled prey is consistent with the finding of calcareous invertebrate fragments, such as ostracods and echinoderms, in the gut of the Ordovician trilobite *Bohemolichas incola*, indicating that these arthropods possessed an alkaline gut capable of consuming shelled organisms indiscriminately (Kraft et al., 2023). These findings reinforce the interpretation that the trilobite taxa found at Salmon Creek are capable of feeding behaviors directed toward shelled invertebrates, including consumption of hard shell material. This further supports the conclusion that *Rusophycus* traces found encompassing the gastropod taxon, *Palaeozygopleura*, are not the result of chance association, but instead represent plausible feeding behavior by the tracemaker. Overall, *Rusophycus* traces found at Salmon Creek provide new insights into the feeding behaviors of trilobites, expanding the known possible food options for these trilobites and solidifying their presumed generalist feeding behaviors.

### III. *Parasitism and the role of platyceratoid gastropods in the broader ecology*

The study of platyceratoid gastropods within the Middle Devonian Hamilton Group strata of Salmon Creek provides an invaluable regional lens through which to examine the dynamics of Paleozoic parasitism and the broader ecological structure of these ancient marine communities. Platyceratoids occur across multiple sites and stratigraphic units within Salmon Creek. *N. lineata* is the most abundant species; it has been reported from the Spafford Member, Portland Point Subformation, upper Cuylerville Submember, Bay View Beds equivalent, and upper Taunton Submember (localities 1a-2, 1a-T, 2, and 2-T, respectively). The highest density and greatest diversity of platyceratoid genera (including *N. lineata*, *Platyceras* spp., and rare *Orthonychia* sp.) are found in the lower Moscow (Locality 1a-T), accessed via seasonal talus piles. These sites exhibit high crinoid fossil density and good diversity, including the presence of the cladid *Ancyrocrinus bulbosus* in the *Modiomorpha-Ancyrocrinus* Bed (Locality 1a-1) and camerate *Megistocrinus depressus* in the Bay View Beds equivalent (Locality 2). However, the

depositional settings typically resulted in disarticulated remains, resulting in low collection and a bias in the recorded number of crinoid species. This also means that direct preservation of the host-parasite interactions is usually lacking in the Salmon Creek fossil record.

Platyceratoidea represent an extinct superfamily of gastropods with a record spanning from the Middle Ordovician to the Late Permian, tentatively extending into the Triassic (Thomka & Brett, 2021). Traditionally viewed as commensal organisms that engaged in coprophagy, feeding harmlessly on the host crinoid's waste as inferred by their positioning over the anal vent (Bowsher, 1955), this interpretation has been largely supplanted by evidence suggesting a detrimental parasitic relationship, potentially kleptoparasitism (Rollins & Brezinski, 1988; Baumiller, 2003). Key evidence supporting parasitism includes the smaller size or stunted growth of infested crinoid individuals (Rollins & Brezinski, 1988) and the discovery of non-predatory drill holes penetrating the crinoid test directly beneath the attached gastropod (Baumiller, 1990). This boring behavior, which allows the gastropod to access nutrients (such as partially digested food) within the crinoid's digestive tract (Baumiller, 1990; Thomka & Brett, 2021), indicates a specialized parasitic strategy. Phylogenetic analysis, including the study of soft tissue preserved in a Silurian platyoceratid, suggests the group had an attached, symbiotic mode of life, possibly related to extant patellogastropods (Sutton et al., 2006). This specialization varied among genera, with early forms such as *Cyclonema* and *Naticonema* possessing relatively unspecialized shells with smooth apertural margins compared to the complex, irregular shells of later *Platyceras* and *Orthonychia* species (Bowsher, 1955; Rollins & Brezinski, 1988).

The shell morphology of *Naticonema lineata*, the most commonly documented platyoceratoid at Salmon Creek, is relevant to its ecological role. Species like *Naticonema*, possessing less specialized shell morphology, were likely less restricted to a single host and may have employed a more vagile lifestyle, including opportunistic scavenging or kleptoparasitism (Brett, 2003). The pervasive occurrence of *N. lineata* across varied lithologies, from the silty mudstones of the Spafford Member to the calcareous mudstones of the lower Moscow, supports the notion that these species were more mobile and adaptable, allowing them to exploit different environments and prey availability, which correlates with their higher frequency of discovery. Their ecological function in Salmon Creek, therefore, is expected to be that of opportunistic scavengers or kleptoparasites. Furthermore, the presence of other sessile platyoceratoids may have contributed to a broader evolutionary dynamic known as the "targeting hypothesis" (Brett, 2003; Syverson et al., 2018). This hypothesis posits that the platyoceratoids themselves, rather than the crinoids, became the target of durophagous predators, such as the ammonoid cephalopods or phyllocarid arthropods documented at Salmon Creek. Predation pressure intensified during this time (Signor & Brett, 1984), and organisms would select for increased defensive mechanisms. This included the increased spinosity in the crinoids which was likely used to deter predators from attacking the attached gastropods and inflicting collateral damage upon the host (Syverson et al., 2018). Thus, even without articulated evidence of direct host-parasite drilling in the Salmon Creek crinoids, the platyoceratoids played a critical, complex ecological role by acting as vital members of the trophic ecology, and contributing to the selective pressures that shaped crinoid macroevolution in this Middle Devonian environment.

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### Field Guide

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### Exhibit

*‘Science in Your Backyard: The Fossils of Salmon Creek’* was a temporary exhibition on display at the Museum of the Earth in Ithaca, NY from August 2024 to January 2025. Written and curated by W.C.H., the exhibit complemented *‘NY Rocks! Ancient Life of the Empire State’* (December 2023–January 2025) by highlighting a local and publicly accessible site of geological and paleontological significance. I (W.C.H.) would first like to thank Warren Allmon for making this exhibition possible. I am also deeply grateful to Leon Apgar for his invaluable assistance in constructing the exhibit case, which accommodated more than 30 fossil specimens. My thanks extend to Whitney Ribeiro, Robert Ross, Jonathan Hendricks, and C.E.B. for their thoughtful feedback and support in developing the exhibit’s text, language, font, and design. I am especially indebted to A.I.E., E.M.C., and Heath Cook for generously loaning specimens, and to Maureen Bickley for her mentorship in the Fossil Lab, where she taught me the fossil preparation techniques essential for readying these specimens for display (now featured in the plates of this field guide).

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### **Author Contributions**

W.C.H. provided overall project leadership and wrote most of the first draft manuscript. C.J.H. and C.E.B. provided stratigraphic interpretations for the main text and contributed expertise on the Hamilton Group rocks and fossils. A.I.E. wrote the paleoecology sections of the main text. C.J.H. created all the figures for the main text, and W.C.H. produced all the plates for the main text and plates and figures for the appendices. W.C.H., C.J.H., A.I.E., and E.M.C. all spent countless hours in the field documenting the stratigraphic and paleontological features discussed in the main text. They all collected and contributed specimens to W.C.H.’s private fossil collection, which are now housed in the research collection of the Paleontological Research Institution in Ithaca, NY under PRI Acc. 1973, unless otherwise noted. All authors commented on the final draft and made modifications to it.

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# Figures and Figure Captions

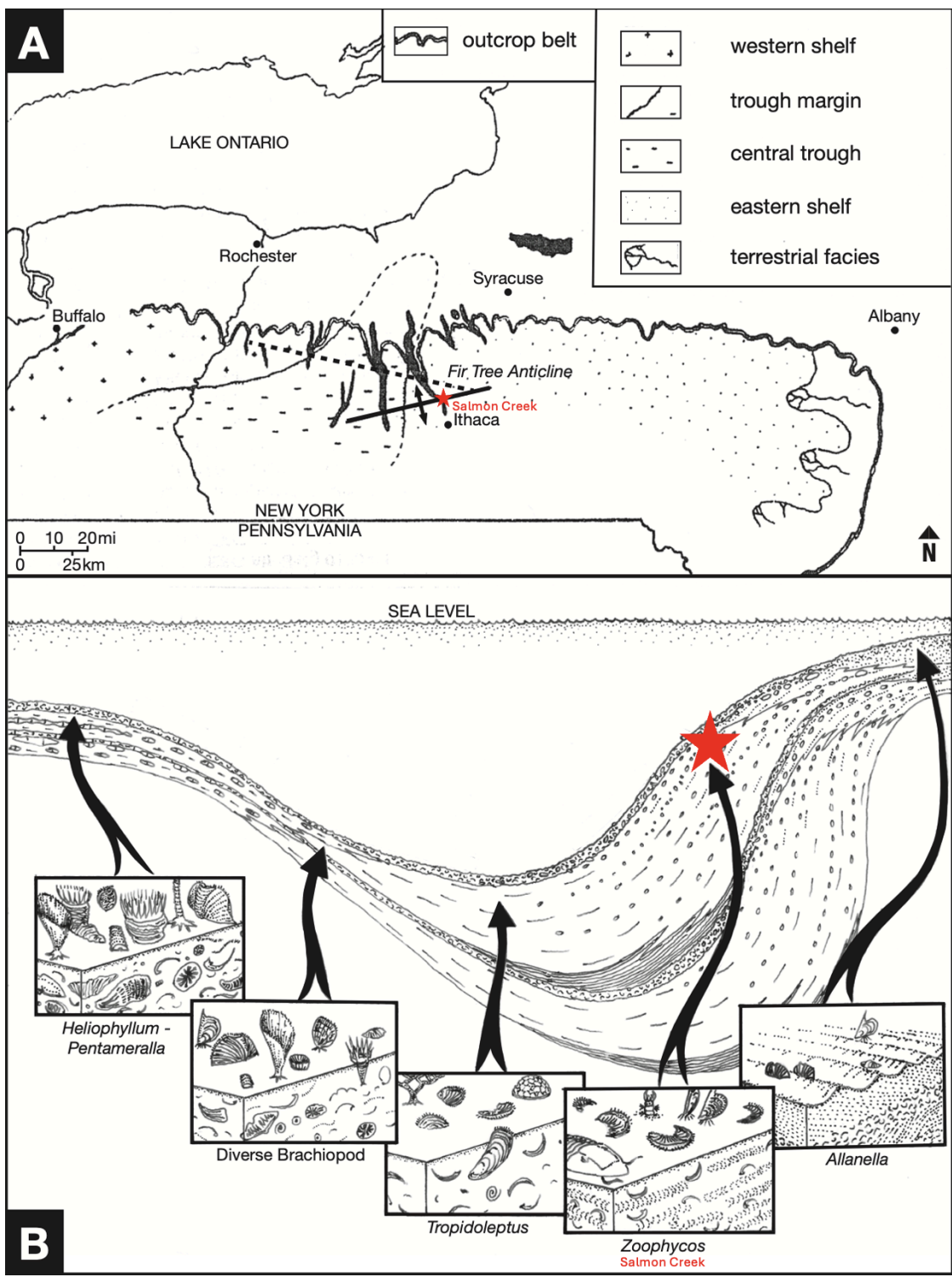
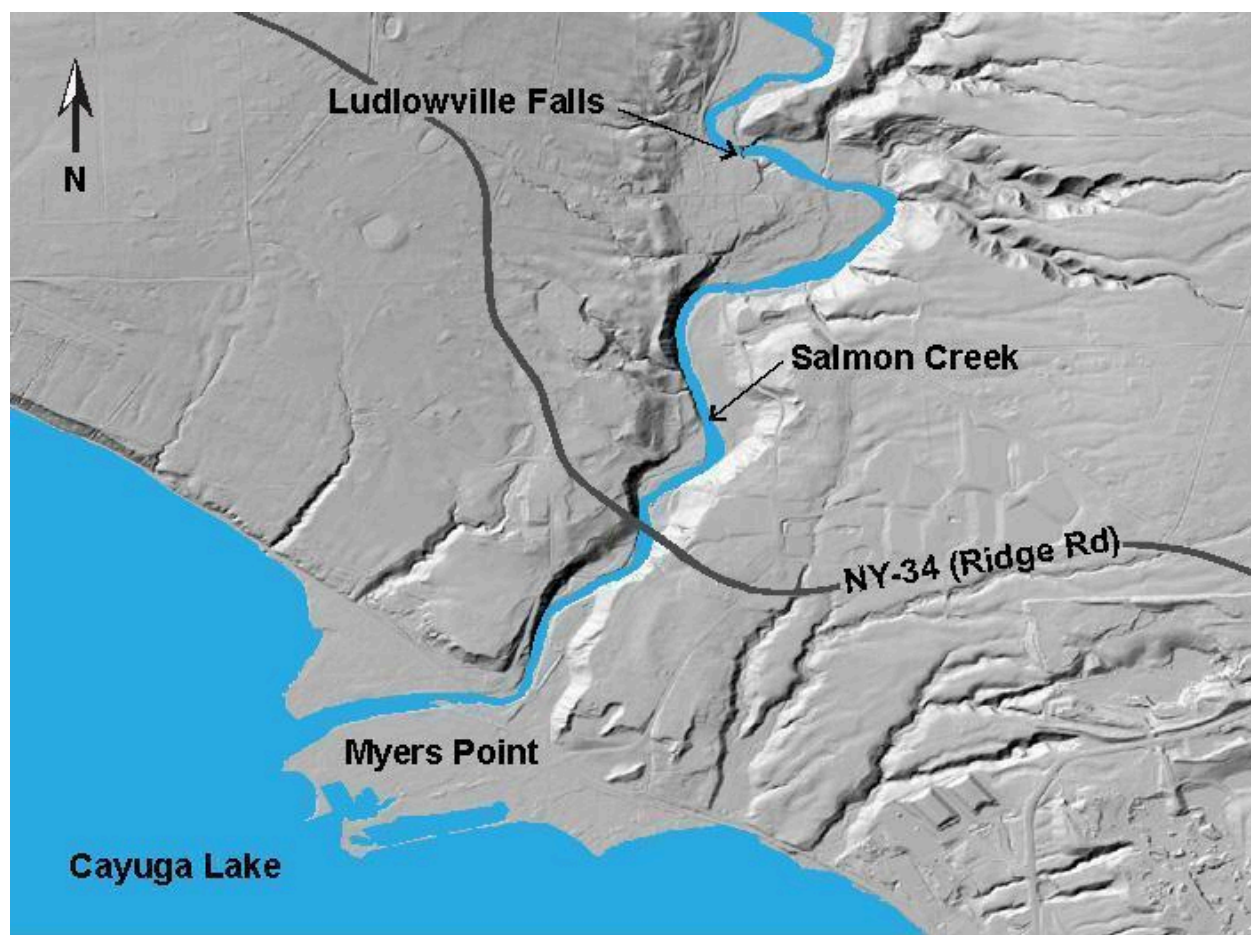


Figure 1



500 m

Figure 2

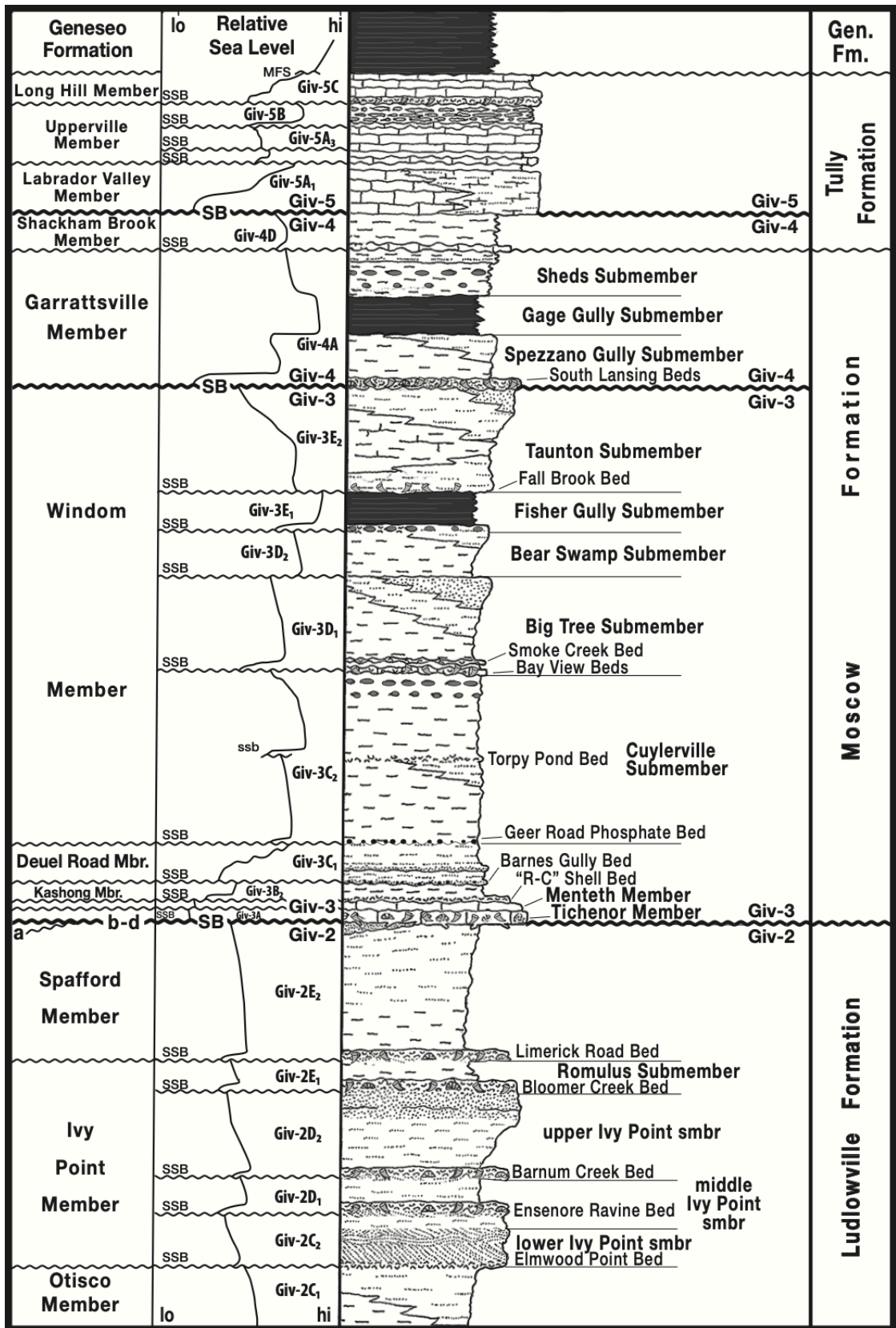


Figure 3

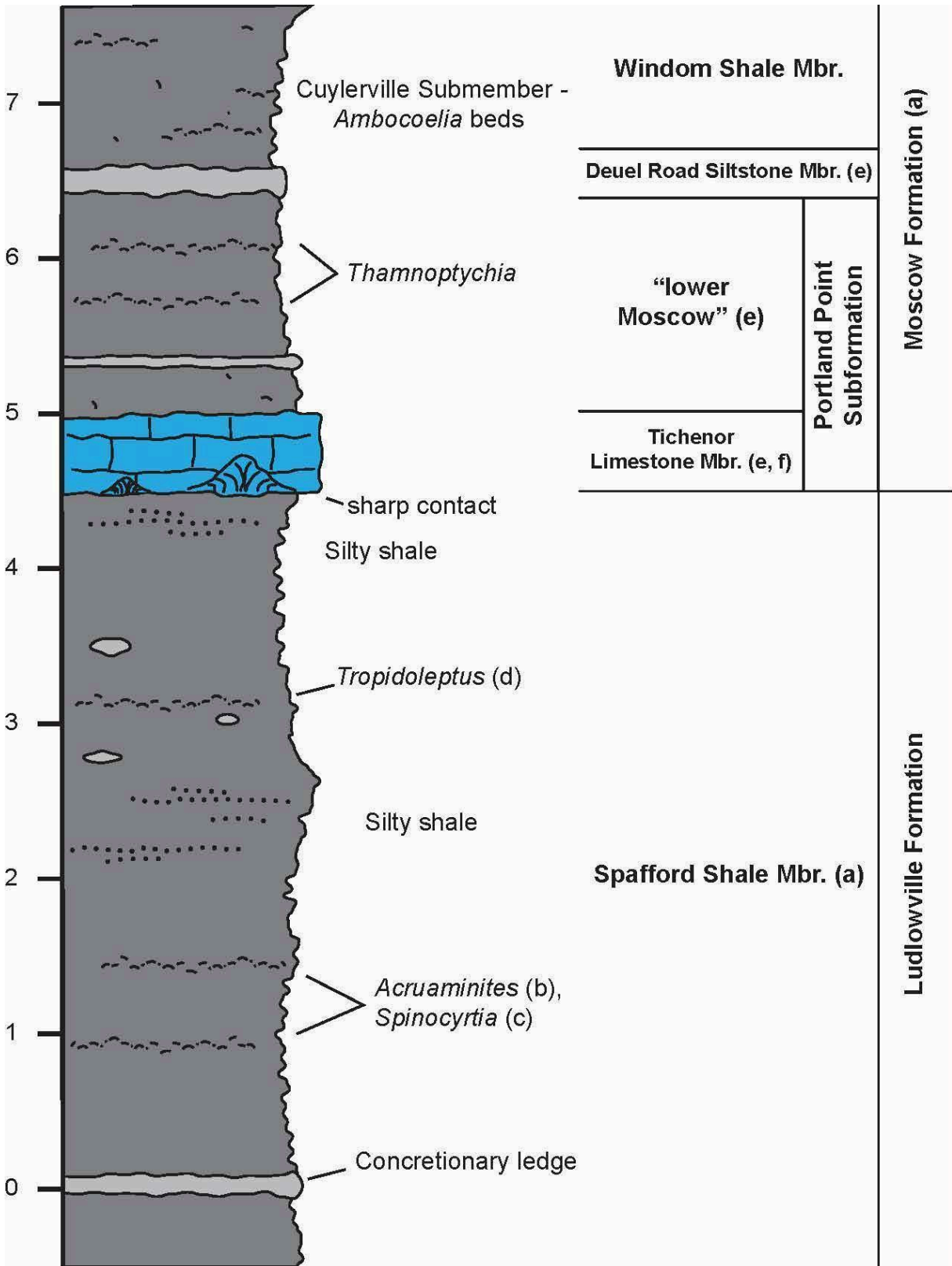


Figure 4

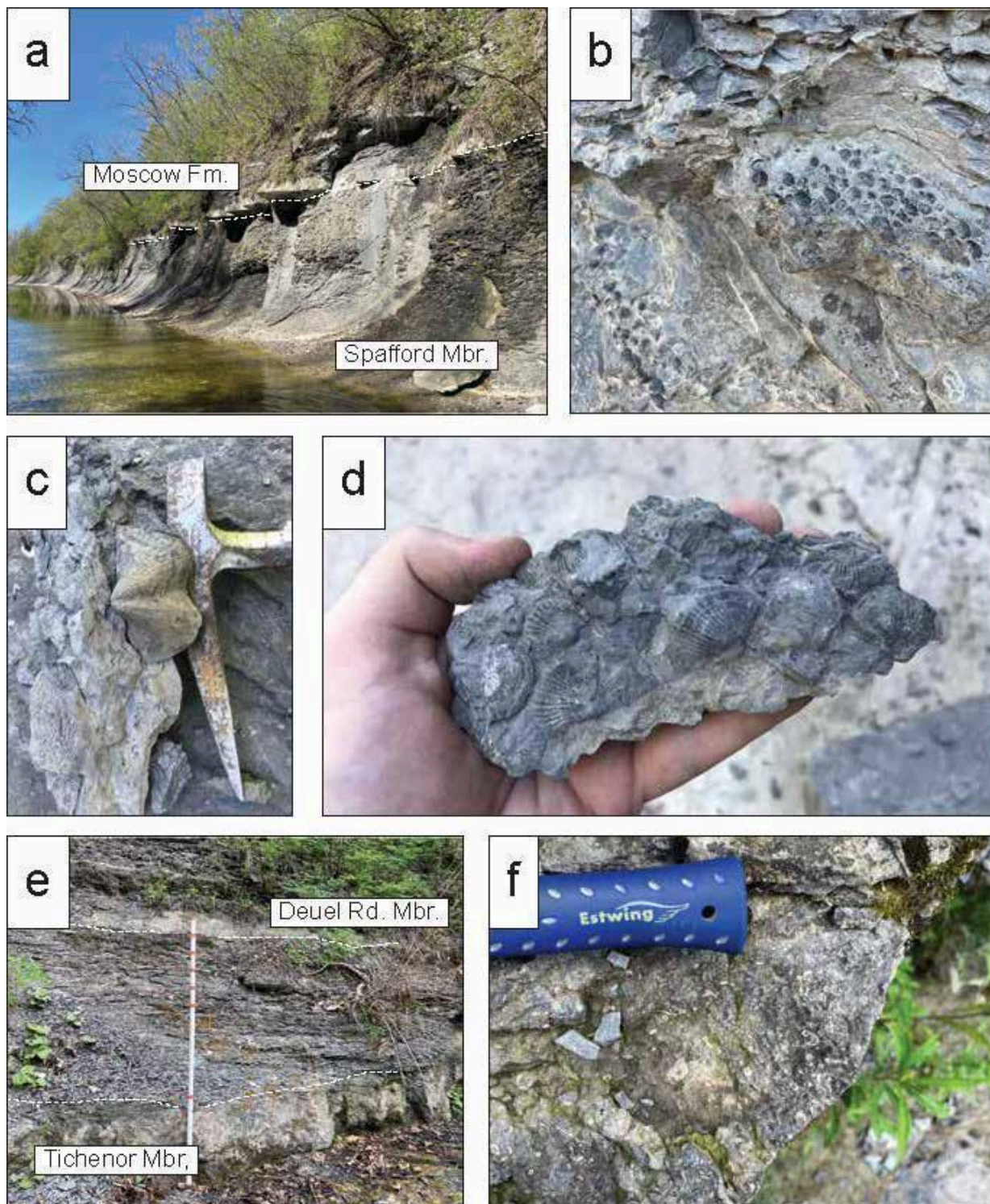


Figure 5



**Figure 6**

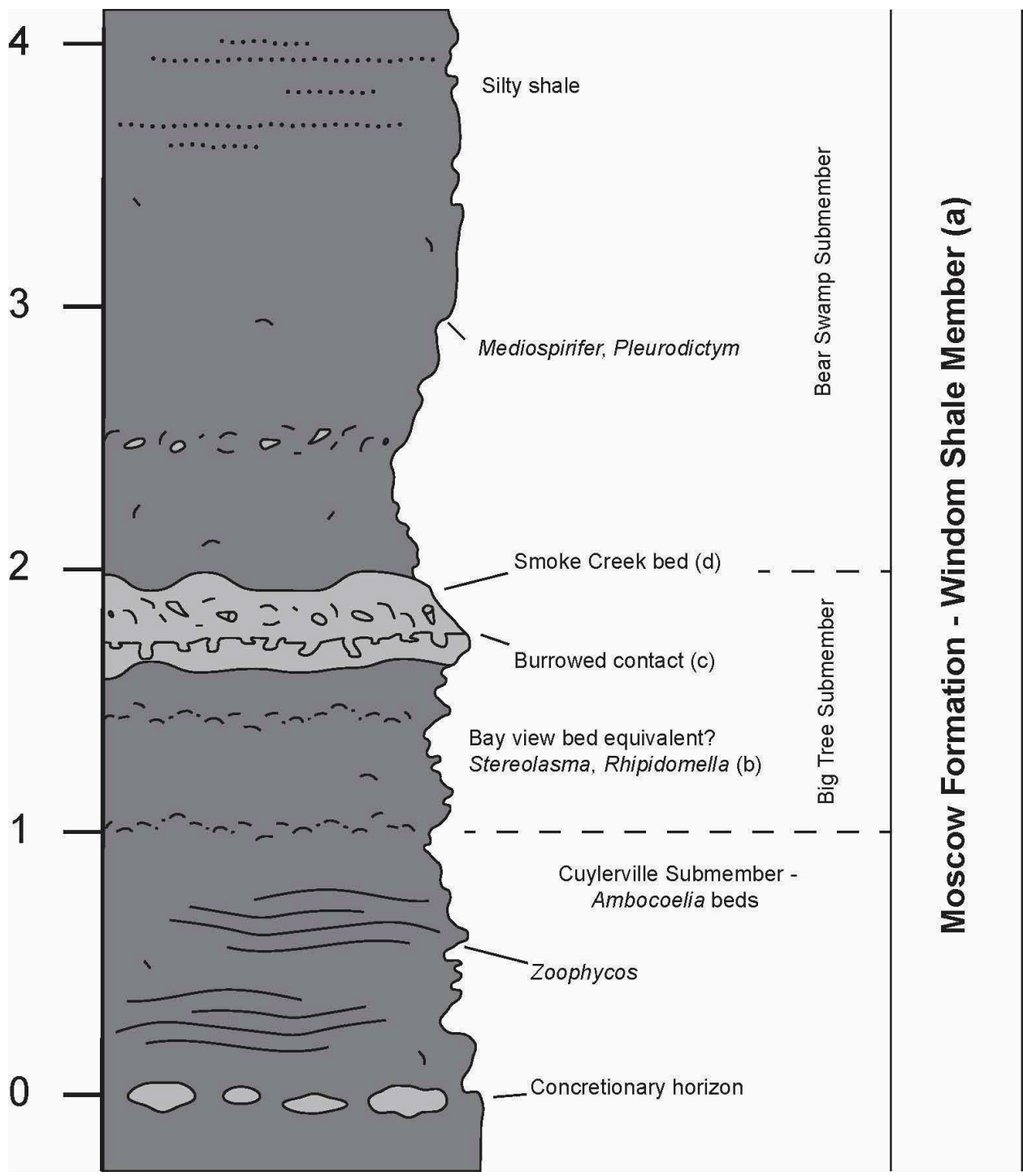


Figure 7

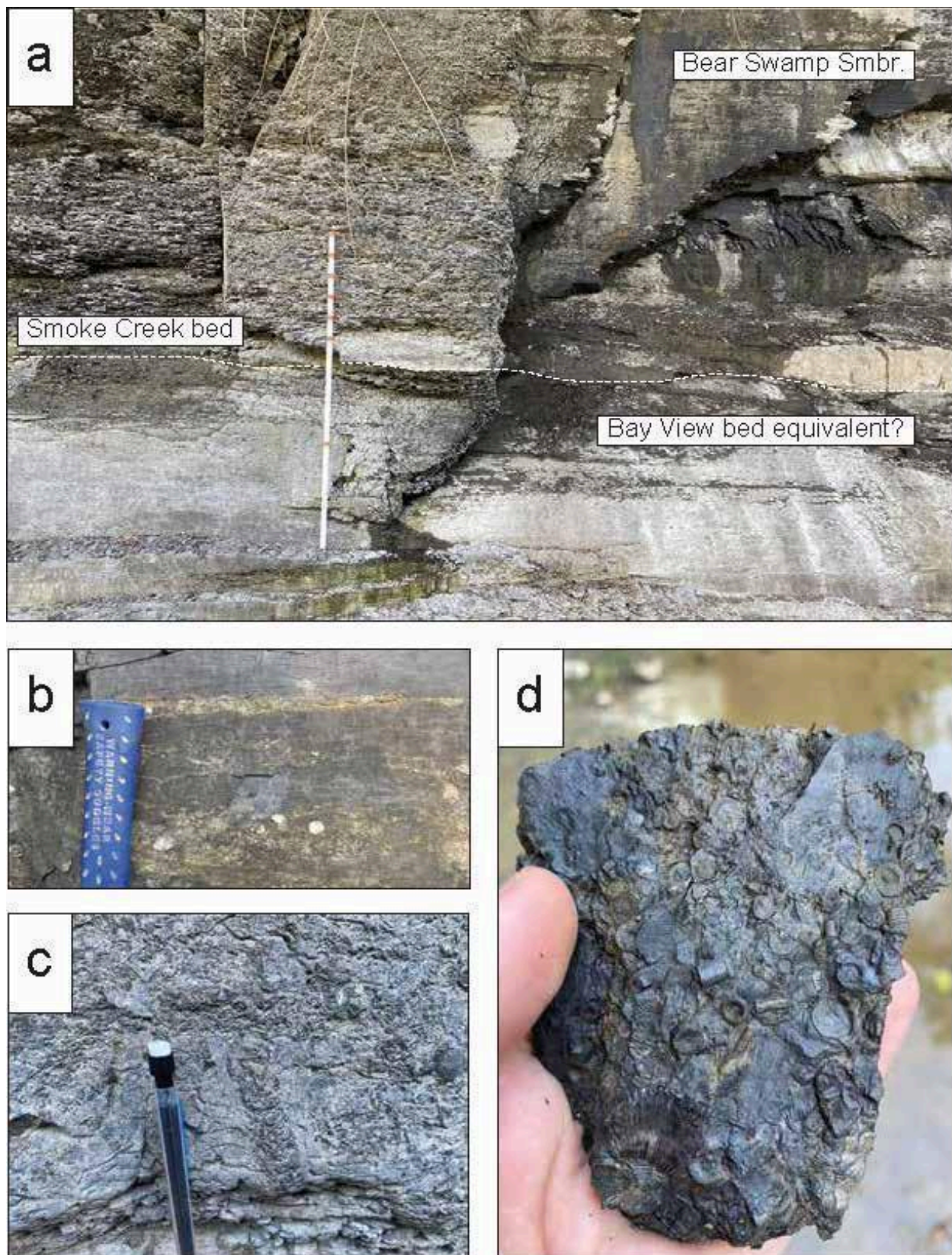
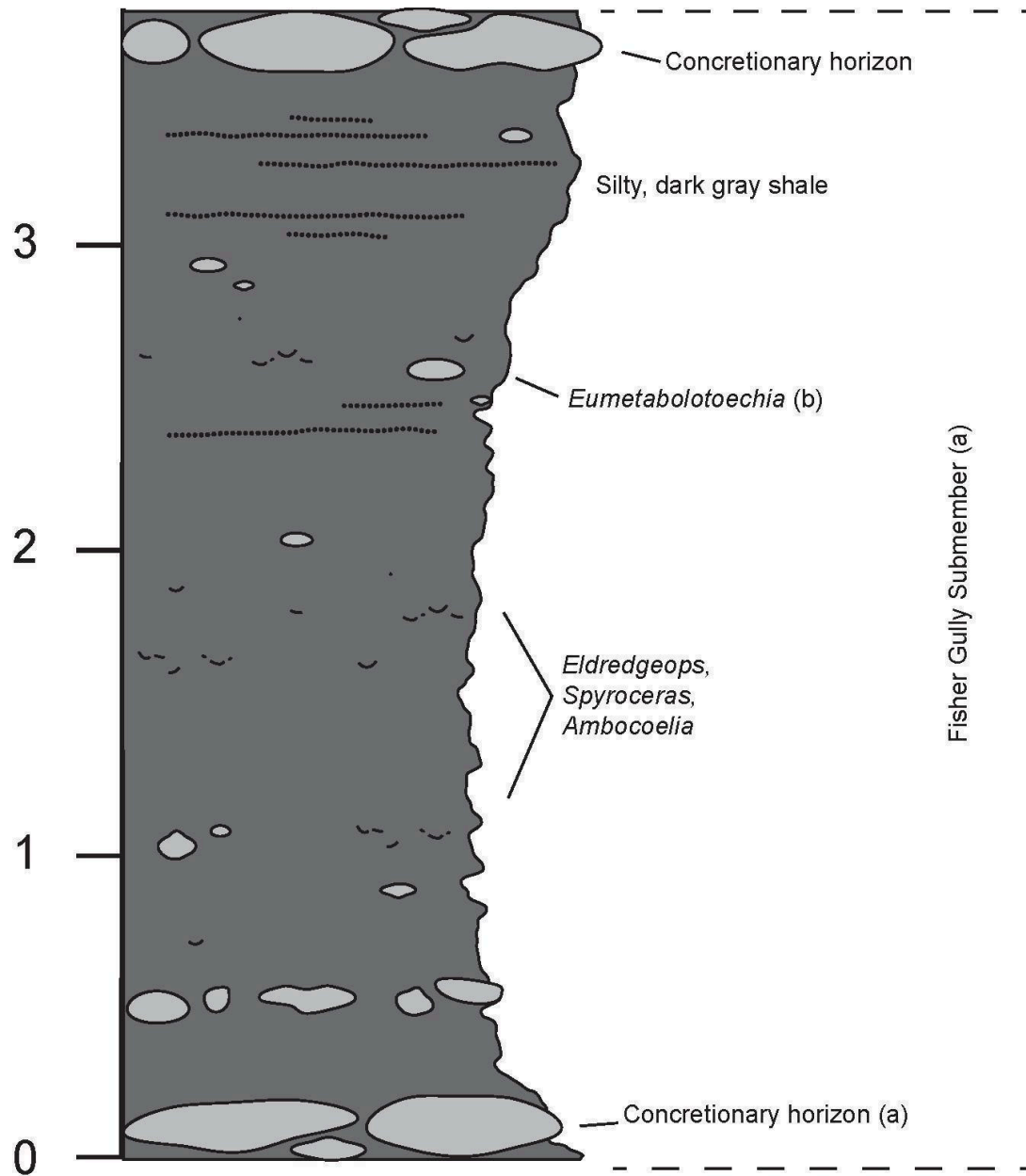


Figure 8



Fisher Gully Submember (a)

**Moscow Formation - Windom Shale Member**

**Figure 9**

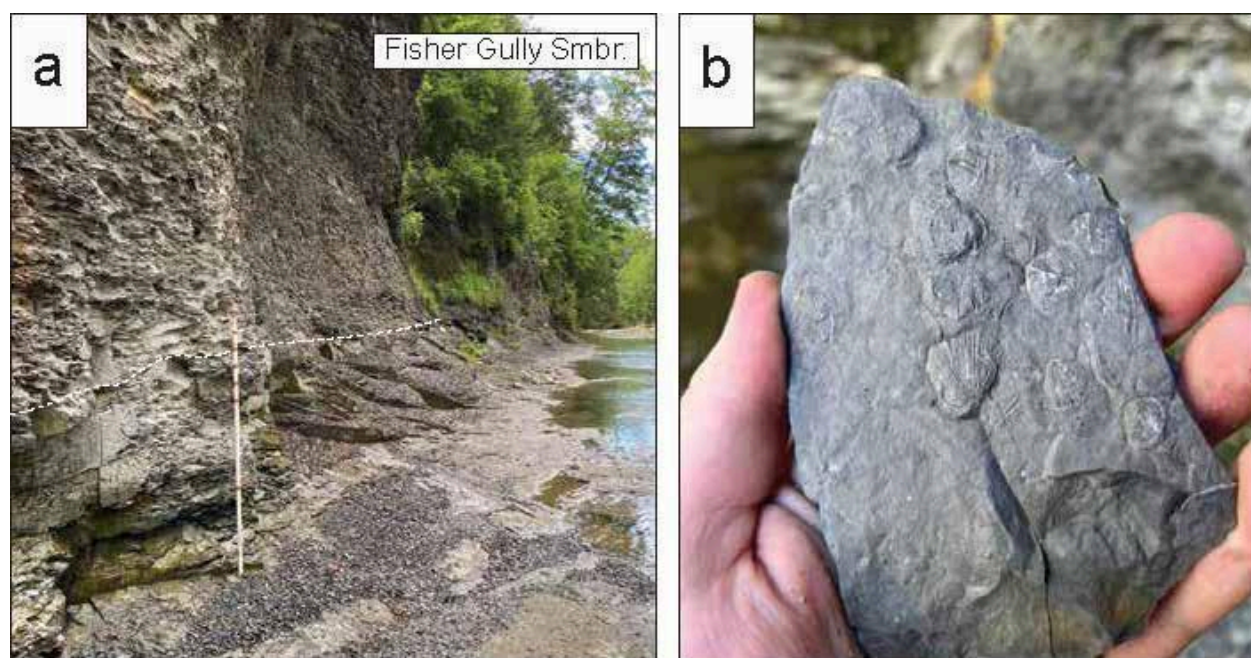


Figure 10

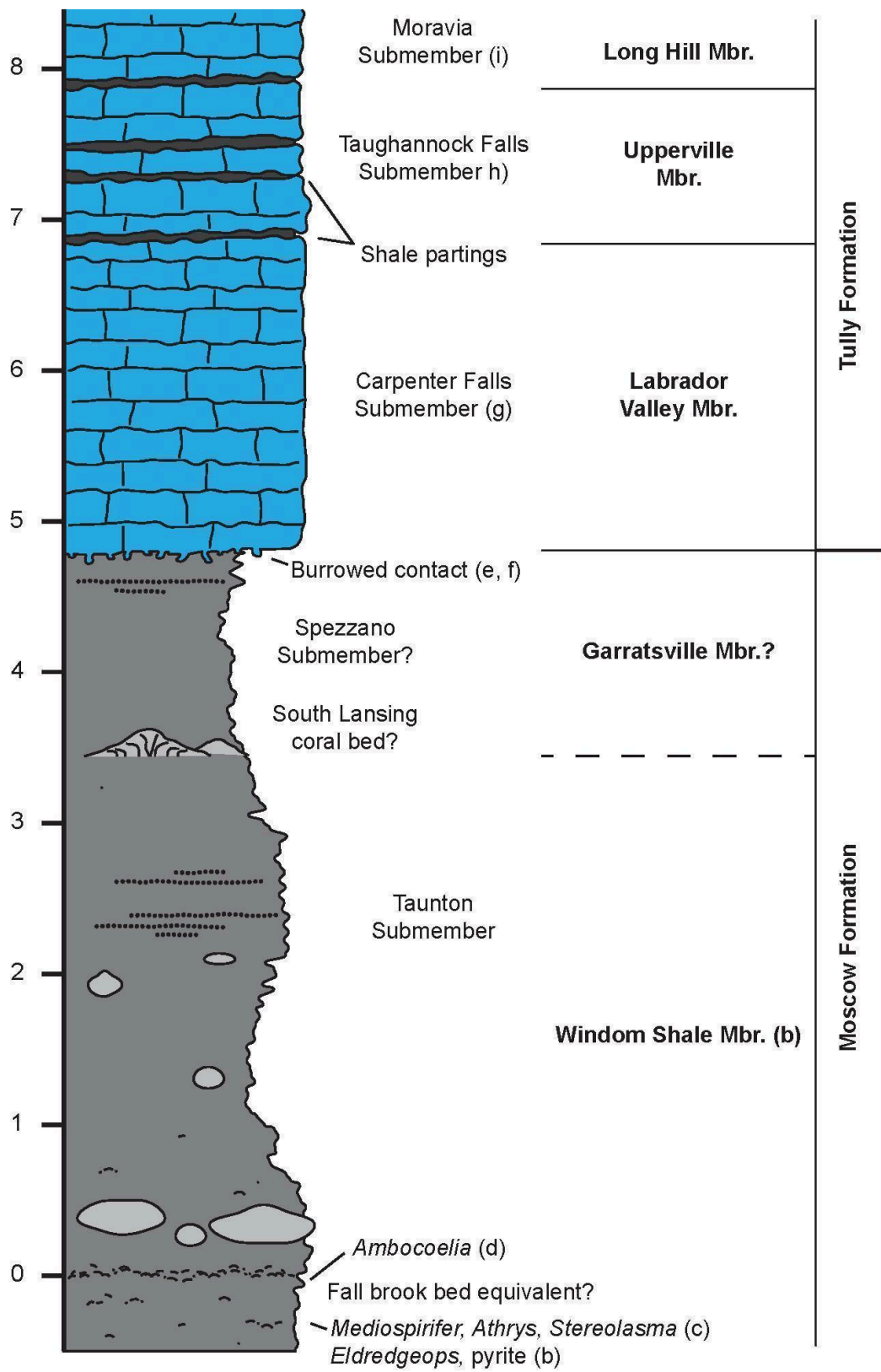


Figure 11

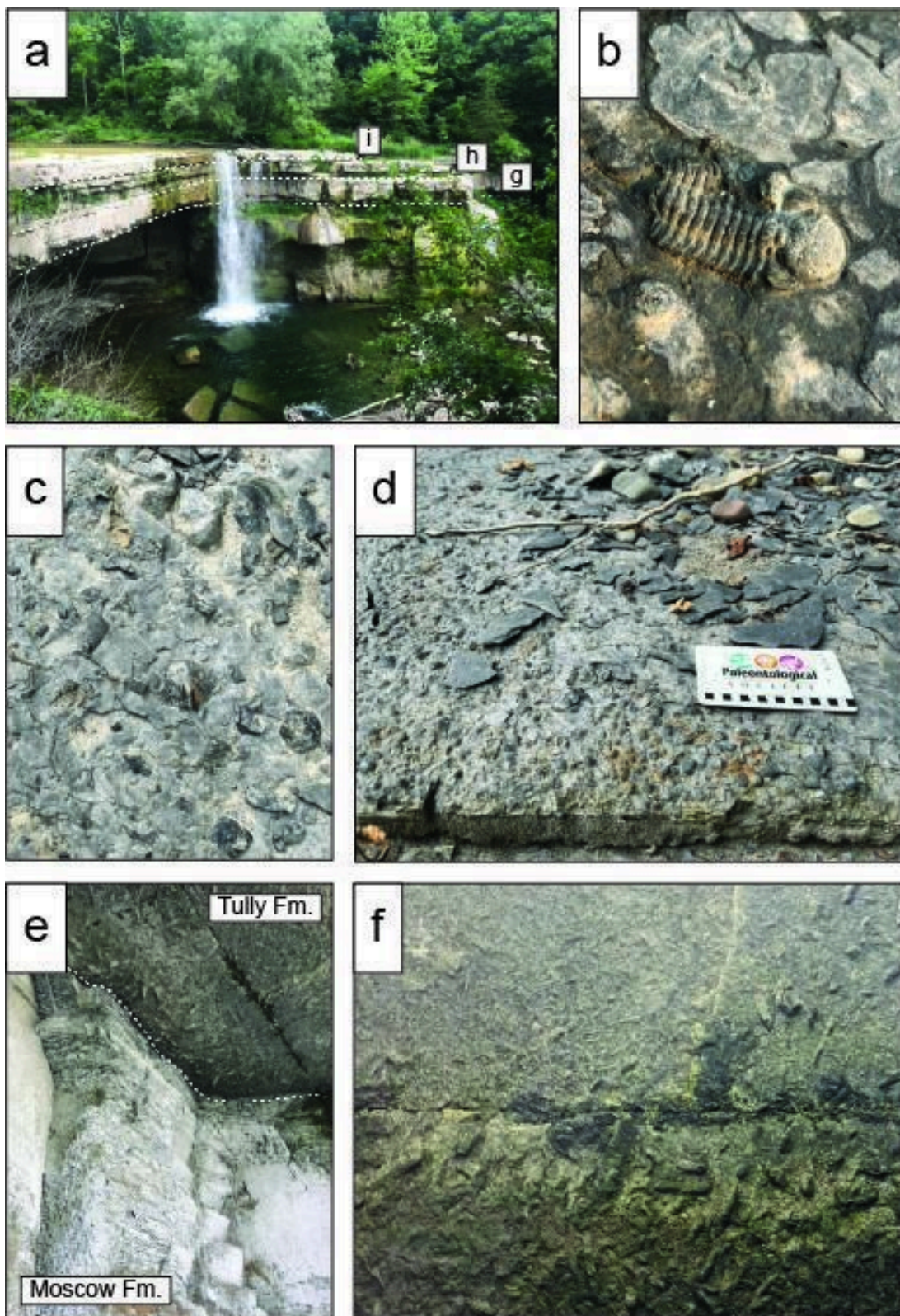


Figure 12

**Figure 1.** Paleogeography of western and central New York State during the Middle Devonian (modified from Brett et al., 2023, text-fig. 3). **(A)** Outcrop belt of the Hamilton Group across western and central New York State, including the position of Salmon Creek (red star). Note that Salmon Creek is heavily influenced by the Fir Tree anticline (dashed line), the crest of which is exposed along the railroad cut just to the south at Portland Point (Lansing, NY). The Fir Tree anticline is a north-south upward-arching fold that formed during the Alleghanian Orogeny, a succession of mountain-building events that culminated in the creation of the supercontinent Pangea by the Late Permian (Prucha, 1968; Hatcher, 2010). This folding uplifted the Middle Devonian strata of the Hamilton Group, and over time, erosion along the crest of the anticline removed the overlying younger rocks. As a result, the older Hamilton Group rocks are now exposed at the surface near Salmon Creek, where the stream has further cut into the uplifted fold. Consequently, older rocks are visible to the north, while progressively younger units appear toward the south. The solid line shows the orientation of the cross-section in B. **(B)** Cross-section of the Appalachian foreland basin facies profile during periods of relative lowstand (well oxygenated seafloor). Salmon Creek (red star) was positioned along the edge of the eastern shelf in the *Zoophycos* facies. Note that the vertical scale of the basin is exaggerated here.

**Figure 2.** Middle Devonian sequence stratigraphy (left) and lithostratigraphy (right) of western and central New York State (modified from Brett et al., 2023, text-fig. 60). Strata exposed at Salmon Creek includes units of the Ludlowville, Moscow, and Tully formations. At Locality 1, the upper Ludlowville (Spafford Member) and lower Moscow (Tichenor, “lower Moscow”, Deuel Road, and lower Windom members) formations are present. At Localities 2 and 3, the upper Moscow (upper Windom and Garrattsville members) and Tully formations are present. Note that the lower Moscow, Deuel Road, and Garrattsville members are not illustrated. Inferred trends in relative sea level are illustrated by the middle curve.

**Figure 3.** Hillshade model of the lower Salmon Creek Valley, Lansing NY. Note the sharp cornering of the stream meanders, indicating that Salmon Creek is strongly joint controlled in its expression. Scale bar = 500 m.

**Figure 4.** Measured section of the upper Ludlowville and lower Moscow formations at Locality 1. Labeled features refer to field photographs in Figure 5. Note that “lower Moscow” is used here to refer to an undifferentiated Deep Run-Kashong interval (Fig. 2; Brett et al., 2023).

**Figure 5.** Field photographs of the upper Ludlowville and lower Moscow formations at Locality 1. **(A)** Outcrop photo of Locality 1a-2, illustrating the disconformable contact (dashed line) between the Ludlowville and Moscow formations. **(B)** Abundant productid brachiopods *Arcuaminctes* (*Devonochonetes*) *scitulus* found along discontinuous surfaces within the Spafford Member. **(C)** Large, rare specimen of the spiriferid brachiopod *Spinocyrtia* cf. *granulosa*, found scattered throughout the Spafford Member. **(D)** Abundant tropidoleptid brachiopod *Tropidoleptus carinatus*, found along discontinuous surfaces within the Spafford Member. **(E)** Outcrop photograph, illustrating the extent of the lower Moscow (dashed lines between the Tichenor and Deuel Road members of the Moscow Formation). **(F)** Crinoid material exposed along the weathered surface of the Tichenor Member at Locality 1b.

**Figure 6.** Large colony of the tabulate coral *Favosites hamiltonae* within the Tichenor Member at the nearby section at Portland Point, approximately 2 km from Locality 1. A small, weathered colony was also noted within the Tichenor Member at Locality 1b.

**Figure 7.** Measured section of the Bay View-Smoke Creek interval (Big Tree Submember) of the Windom Member at Locality 2. Labeled features refer to field photographs in Figure 8.

**Figure 8.** Field photographs of the Bay View-Smoke Creek interval (Big Tree Submember) of the Windom Member at Locality 2. (A) Outcrop photograph of Locality 2, illustrating the contact of the Bay View and Smoke Creek equivalent beds of the Big Tree Submember, as well as the overlying Bear Swamp Submember. (B) Coral and shell rich lenses within the Bay View equivalent. (C) Burrowed horizon within the Smoke Creek Bed equivalent. (D) Hand sample of crinoid hash collected from Smoke Creek Bed.

**Figure 9.** Measured section of the Fisher Gully Submember of the Windom Member at Locality 3a. Labelled features refer to field photographs in Figure 10.

**Figure 10.** (A) Field photograph of the Fisher Gully Submember of the Windom Member at Locality 3a. The lower concretionary horizon is indicated by the dashed line. (B) Flattened specimens of the rhynchonellid brachiopod *Eumetabolatoechia multicostatum* in silty, dark gray shale.

**Figure 11.** Measured section of upper Moscow-Tully interval at Locality 3. Labeled features refer to field photographs in Figure 12. Note the tentative placement of the Garrattsville Member (Spezzano Gully Smbr. South Lansing Beds) based on the probable stratigraphic origin of the tabulate coral *Favosites hamiltonae* found in rock fall (Plate 8e).

**Figure 12.** Field photographs of the upper Moscow-Tully interval at Locality 3. (A) Outcrop photo of Ludlowville Falls, illustrating the Carpenter Falls (g) Taughannock Falls (h) and Moravia (i) submembers. (B) Pyrite-encrusted specimen of the phacopid trilobite *Eldredgeops rana* within the *Ambocoelia*-rich Fall Brook Bed equivalent (Windom Mbr: Taunton Smbr) at Locality 3c-1. (C) Common fossils *Mediospirifer audaculus* (Brachiopoda: Spiriferida), *Athyris spiriferoides* (Brachiopoda: Athyridida), and *Streptelasma ungula* (Cnidaria: Rugosa) along a bedding surface within the *Ambocoelia*-rich Fall Brook Bed equivalent (Windom Mbr: Taunton Smbr) at Locality 3c-1. (D) Thin *Ambocoelia* shell bed within the Fall Brook Bed equivalent (Windom Mbr: Taunton Smbr) at Locality 3c-1. (E) Moscow-Tully contact (dashed line) exposed at the overhang of Ludlowville Falls at Locality 3c-2. (F) Worms-eye view of burrows, most likely made by large trilobites, along the lower surface of the Tully Formation at Locality 3c-2.

## Plates and Plate Captions

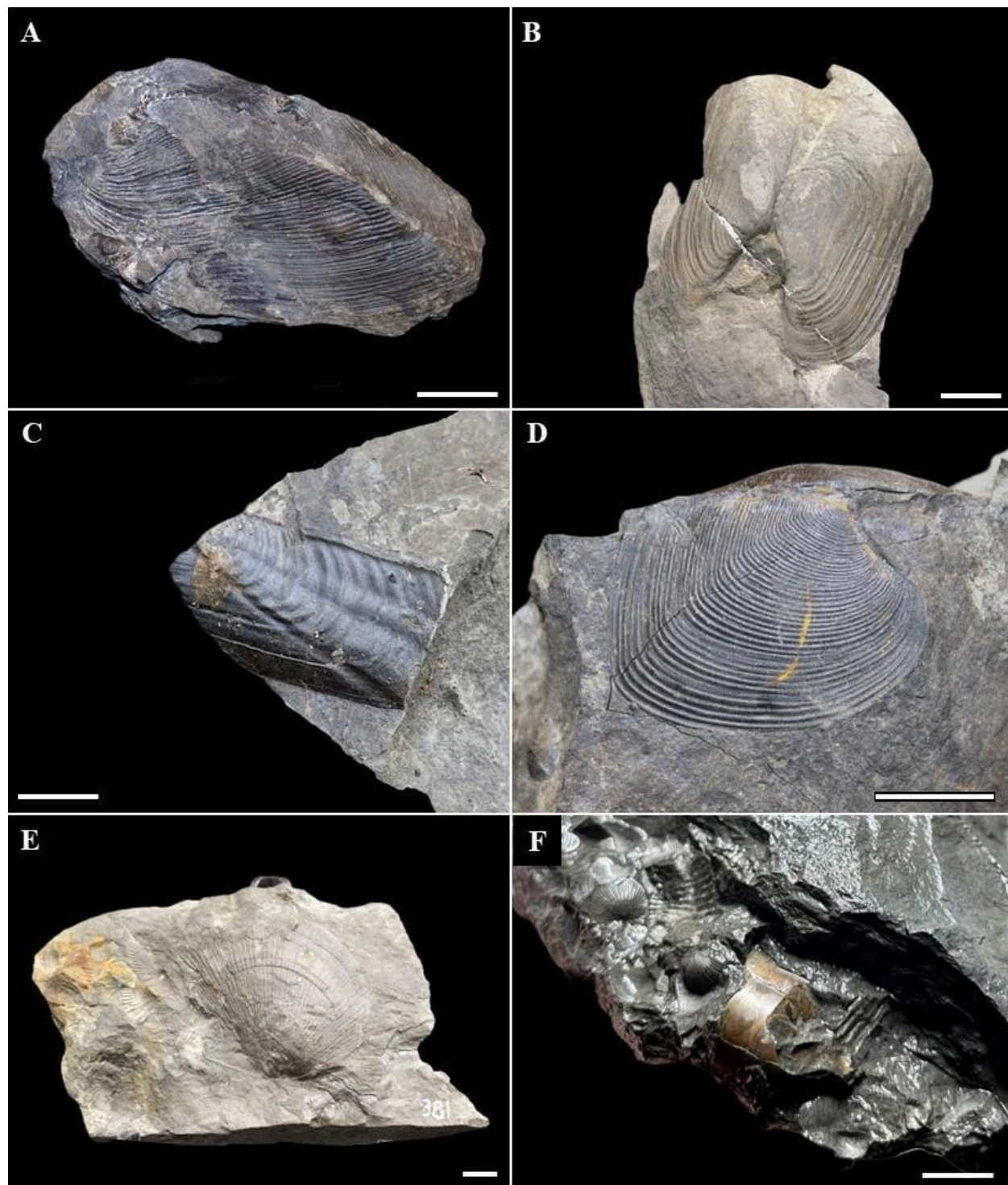
Unless a collector name is designated (“col.”), all fossils figured in plates 1-9 are part of the private collection of William C. Hooker (“WCH XXX”), deposited at the Paleontological Research Institution under PRI Acc. 1973 for conservation and future study. The one exception is PRI 111630 (formerly WCH 820; Plate 3a), which is on permanent display at the Museum of the Earth in Ithaca, NY (New Acquisitions case; PRI 111630). All figured specimens in the WCH private collection are tabulated below (Table 1).

PRI no.	WCH no.	Plate	Determination	Stratum	Locality	Collector(s)	Date Collected
PRI Acc. 1973	WCH 9351	1a	<i>Ancyrocrinus bulbosus</i> Hall, 1862	<i>Modiomorpha-Ancyrocrinus</i> Bed	1a-1	William C. Hooker	02.03.2025
	WCH 941b	1b	<i>Modiomorpha concentrica</i> (Conrad, 1838)	<i>Modiomorpha-Ancyrocrinus</i> Bed	1a-1	Emily M. Cavanaugh	03.01.2025
	WCH 3351	2a	<i>Goniophora hamiltonensis</i> (Hall, 1870)	Spafford Member	1a-2	William C. Hooker	10.09.2022
	WCH 472	2b	<i>Modiomorpha mytiloides</i> (Conrad, 1841)	Spafford Member	1a-2	William C. Hooker	04.13.2023
	WCH 667	2d	<i>Cypricardella bellistriata</i> (Conrad, 1842)	Spafford Member	1a-2	William C. Hooker	08.19.2023
	WCH 381	2e	<i>Pseudoaviculopecten princeps</i> (Conrad, 1838)	Spafford Member	1a-2	William C. Hooker	10.16.2022
WCH 508	2f	<i>Spyroceras nuntium</i> (Hall, 1861)	Spafford Member	1a-2	Corey J. Hensen	04.22.2023	
PRI 111630	WCH 820	3a	<i>Paraechinocaris (Echinocaris) punctata</i> Hall, 1863	Tichenor Member	1a-T	Adam I. Eliezer & William C. Hooker	05.01.2024
PRI Acc. 1973	WCH 828	3b	<i>Dipleura dekayi</i> (Green, 1832)	Tichenor Member	1a-T	Adam I. Eliezer	05.08.2024
	WCH 833	3c	<i>Dicyonema hamiltoniae</i> (Hall, 1896)	Tichenor Member	1a-T	William C. Hooker	05.16.2024
	WCH 823	3d	<i>Cyrtoceras</i> Conrad, 1838	Tichenor Member	1a-T	Adam I. Eliezer	05.01.2024
	WCH 832	3g	Tracheophytes Sinnott, 1935 ex Cavalier-Smith, 199	Tichenor Member	1a-T	Adam I. Eliezer	05.16.2024
	WCH 817	4b	<i>Leptotrypella furcata</i> (Hall, 1877)	"Lower Moscow" (Deep Run-Kashong interval)	1a-T	William C. Hooker	05.01.2024
	WCH 816	4c	<i>Orthonychia</i> Hall, 1843	"Lower Moscow" (Deep Run-Kashong interval)	1a-T	Adam I. Eliezer	04.27.2024
	WCH 811	4d	<i>Thamnoptychia limbata</i> (Eaton, 1832)	"Lower Moscow" (Deep Run-Kashong interval)	1a-T	William C. Hooker	04.27.2024
	WCH 819	4f	<i>Platyceras cf. bucculentum</i> Hall, 1861	"Lower Moscow" (Deep Run-Kashong interval)	1a-T	William C. Hooker	05.01.2024
	WCH 601	5a	<i>Eldredgeops rana</i> Green, 1832	Cuylerville Submember <i>Ambocoelia</i> Beds	1b	William C. Hooker	07.30.2023
	WCH 602	5a	<i>Eldredgeops rana</i> Green, 1832	Cuylerville Submember <i>Ambocoelia</i> Beds	1b	William C. Hooker	08.07.2023
	WCH 1020	5b	<i>Dipleura dekayi</i> (Green, 1832)	Cuylerville Submember <i>Ambocoelia</i> Beds	1b	Adam I. Eliezer	08.08.2025
	WCH 1023	5c	<i>Rusophycus</i> J. Hall, 1852	Cuylerville Submember <i>Ambocoelia</i> Beds	1b	Adam I. Eliezer	08.08.2025
	WCH 475	5d	<i>Goniatitida</i> Hyatt, 1884	Cuylerville Submember <i>Ambocoelia</i> Beds	1b	Corey J. Hensen	04.13.2023
	WCH 481	5e	<i>Lingula delia</i> Hall, 1867	Cuylerville Submember <i>Ambocoelia</i> Beds	1b	William C. Hooker	05.19.2024
	WCH 422	5g	<i>Aulocystis dichotoma</i> (Grabau, 1899)	Cuylerville Submember <i>Ambocoelia</i> Beds	1b	Corey J. Hensen	12.07.2022
	WCH 558	5h	<i>Hallothea acilis</i> (Hall, 1876)	Cuylerville Submember <i>Ambocoelia</i> Beds	1b	William C. Hooker	06.23.2023
	WCH 804	6-1c	<i>Megastrophia concava</i> (Hall, 1857)	Upper Cuylerville Submember	2	William C. Hooker	04.23.2024
	WCH 857	6-1d	<i>Reptaria stolonifera</i> Rolle, 1851	Upper Cuylerville Submember	2	Adam I. Eliezer	06.23.2024
	WCH 854	6-1e	<i>Conularia undulata</i> (Conrad, 1841)	Upper Cuylerville Submember	2	William C. Hooker	06.23.2024
	WCH 860	6-2f	<i>Rusophycus</i> J. Hall, 1852	Upper Cuylerville Submember	2	Adam I. Eliezer	06.23.2024
	WCH 856	6-2g	<i>Grammysioidea cf. arcuata</i> (Conrad, 1841)	Upper Cuylerville Submember	2	William C. Hooker	06.23.2024
	WCH 846	6-2h	<i>Tellinopsis submarginata</i> (Conrad, 1842)	Upper Cuylerville Submember	2	Adam I. Eliezer	05.21.2024
	WCH 855	6-2i	<i>Naticonema lineata</i> Conrad, 1842	Upper Cuylerville Submember	2	William C. Hooker	06.23.2024
	WCH 476	7a	<i>Streptelasma unguia</i> Hall, 1876	Bay View Beds equivalent	2	William C. Hooker	04.13.2023
	WCH 772	7b	<i>Aulocystis jacksoni</i> (Grabau, 1899)	Bay View Beds equivalent	2	William C. Hooker	02.27.2024
	WCH 916	7c	<i>Stereolasma rectum</i> Hall, 1876	Bay View Beds equivalent	2	William C. Hooker	08.18.2024
	WCH 923	7d	<i>Heliophyllum delicatum</i> Oliver & Sorauf, 1994	Bay View Beds equivalent	2	William C. Hooker	08.31.2024
	WCH 924	7d	<i>Heliophyllum delicatum</i> Oliver & Sorauf, 1994	Bay View Beds equivalent	2	William C. Hooker	08.31.2024
	WCH 398	7e	<i>Pleurodictyum americanum</i> Roemer, 1876	Bay View Beds equivalent	2	Corey J. Hensen	10.31.2022
	WCH 918	7g	<i>Hyoilthes striatus</i> Hall, 1876	Bay View Beds equivalent	2	William C. Hooker	08.18.2024
	WCH 551	8a	<i>Bellacartwrightia</i> Lieberman & Kloc, 1997	Upper Taunton Submember	2-T	William C. Hooker	06.22.2023
	WCH 552	8b	<i>Dipleura dekayi</i> (Green, 1832)	Upper Taunton Submember	2-T	William C. Hooker	06.22.2023
	WCH 733	8d	<i>Mesoleptostrophia junia</i> (Hall, 1867)	Upper Taunton Submember	2-T	William C. Hooker	09.23.2023
	WCH 403	8e	<i>Favosites hamiltoniae</i> Hall, 1876	Spezzano Gully Submember South Lansing Beds	2-T	William C. Hooker	11.05.2022
	WCH 751	8f	<i>Michelinoceras telamon</i> (Hall, 1879)	Upper Taunton Submember	2-T	William C. Hooker	09.30.2023
	WCH 401	8g	<i>Spyroceras nuntium</i> (Hall, 1861)	Spezzano Gully Submember South Lansing Beds	2-T	Corey J. Hensen	10.31.2022
	WCH 573	9a	<i>Eldredgeops rana</i> Green, 1832	Fisher Gully Submember	3a	William C. Hooker	06.30.2023
	WCH 566	9b	<i>Spinocyrtia granulosa</i> (Conrad, 1839)	Lower Fall Brook Bed equivalent	3b	William C. Hooker	06.29.2023
	WCH 861	9d	Calcareous concretion with pyrite nodular growth	Lower Fall Brook Bed equivalent	3b	William C. Hooker	06.27.2024
	WCH 568	9e	<i>Spyroceras nuntium</i> (Hall, 1861)	Lower Fall Brook Bed equivalent	3b	Corey J. Hensen	06.29.2023

Table 1. All figured specimens from the WCH private fossil collection featured in plates 1-9.



**Plate 1.** Fossils from the *Modiomorpha-Ancyrocrinus* Bed at Locality 1a-1.



**Plate 2.** Fossils from the Spafford Member at Locality 1a-2.

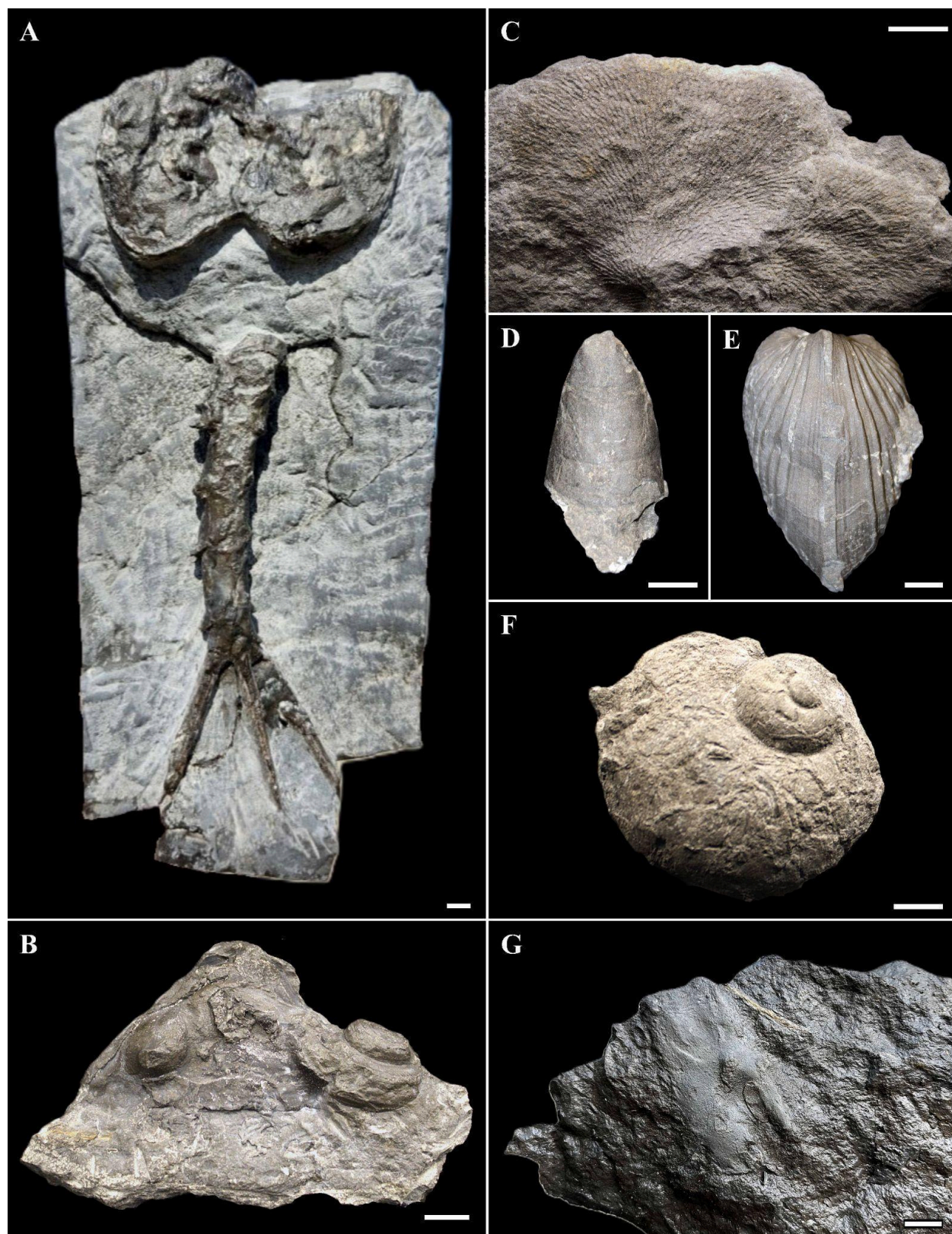
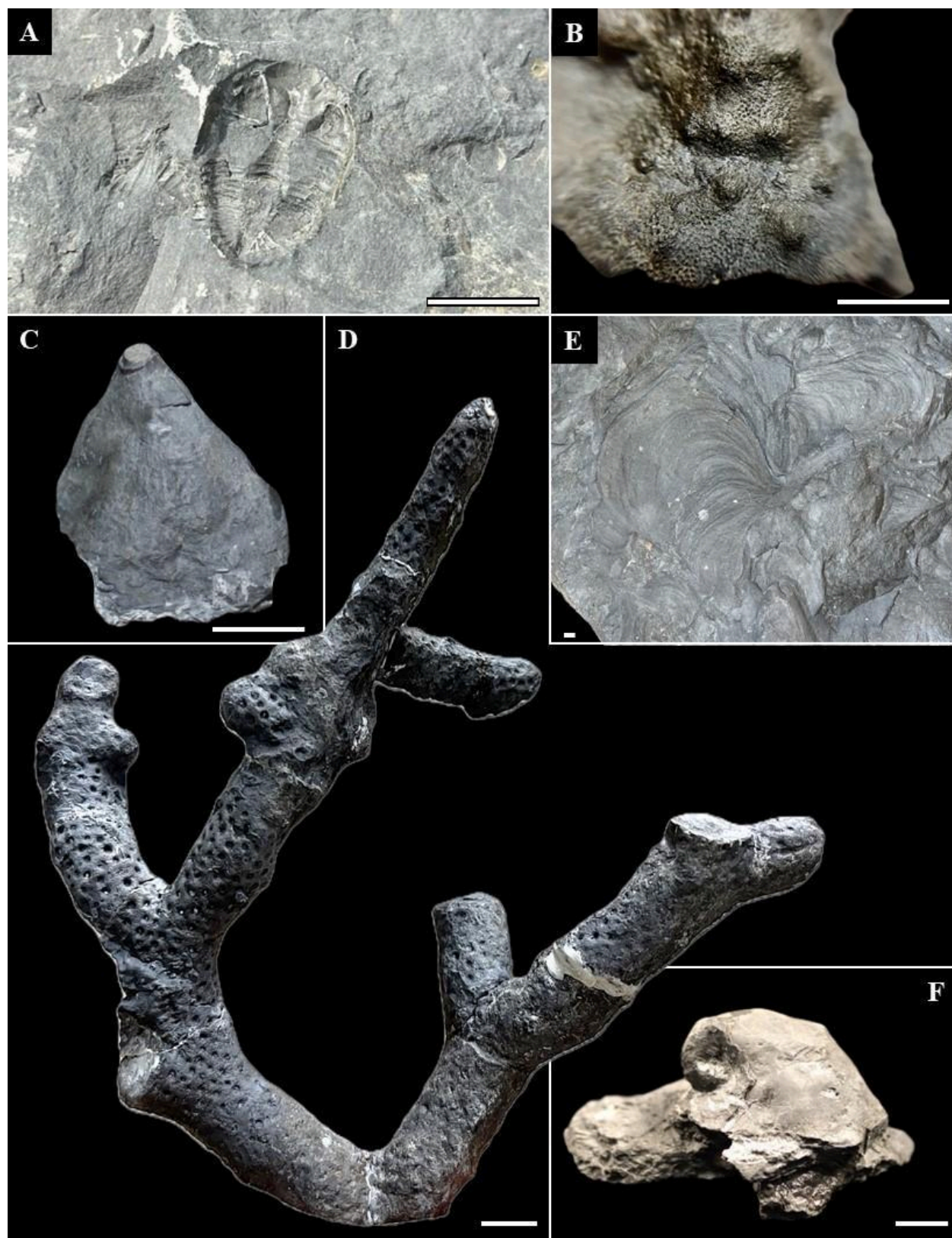
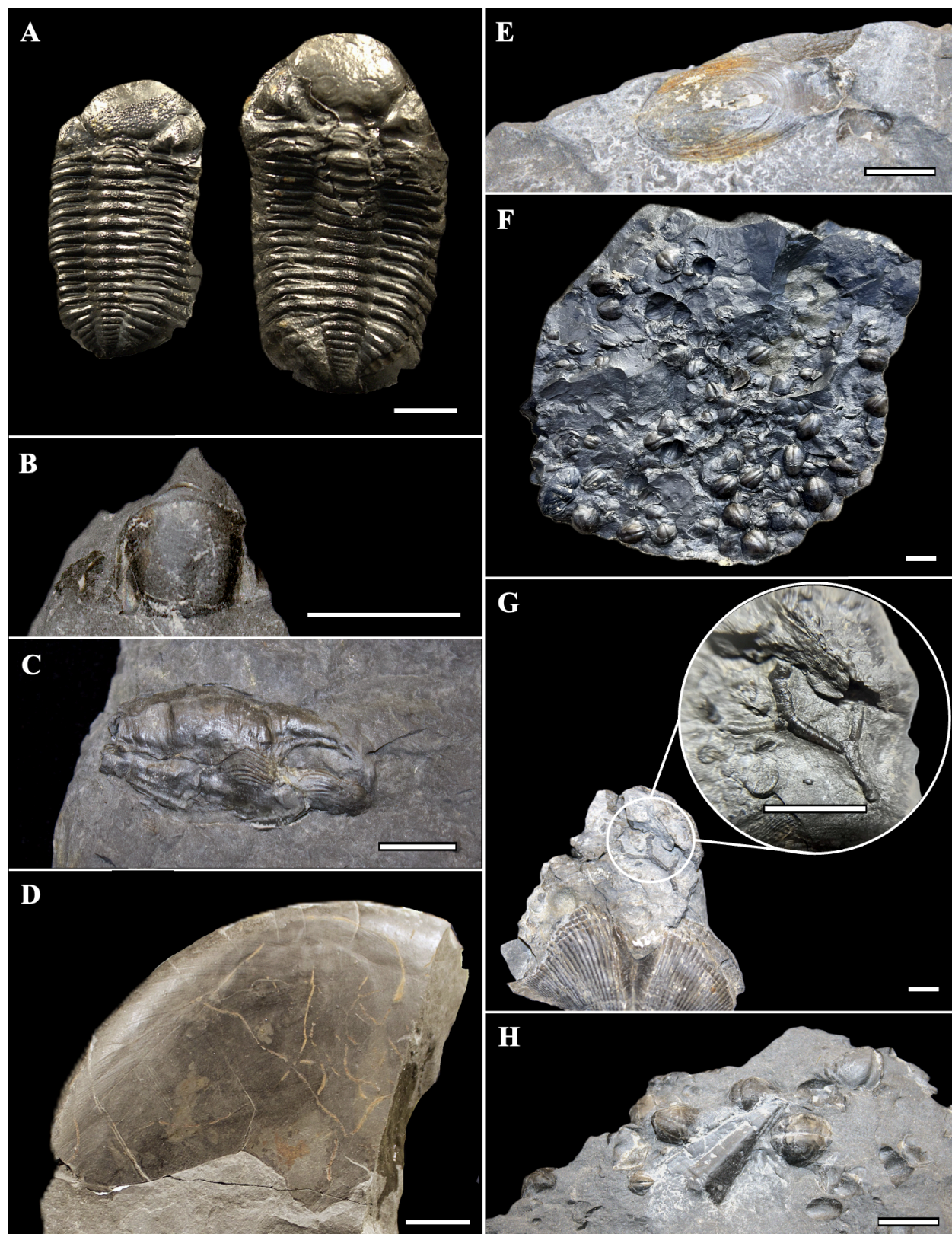


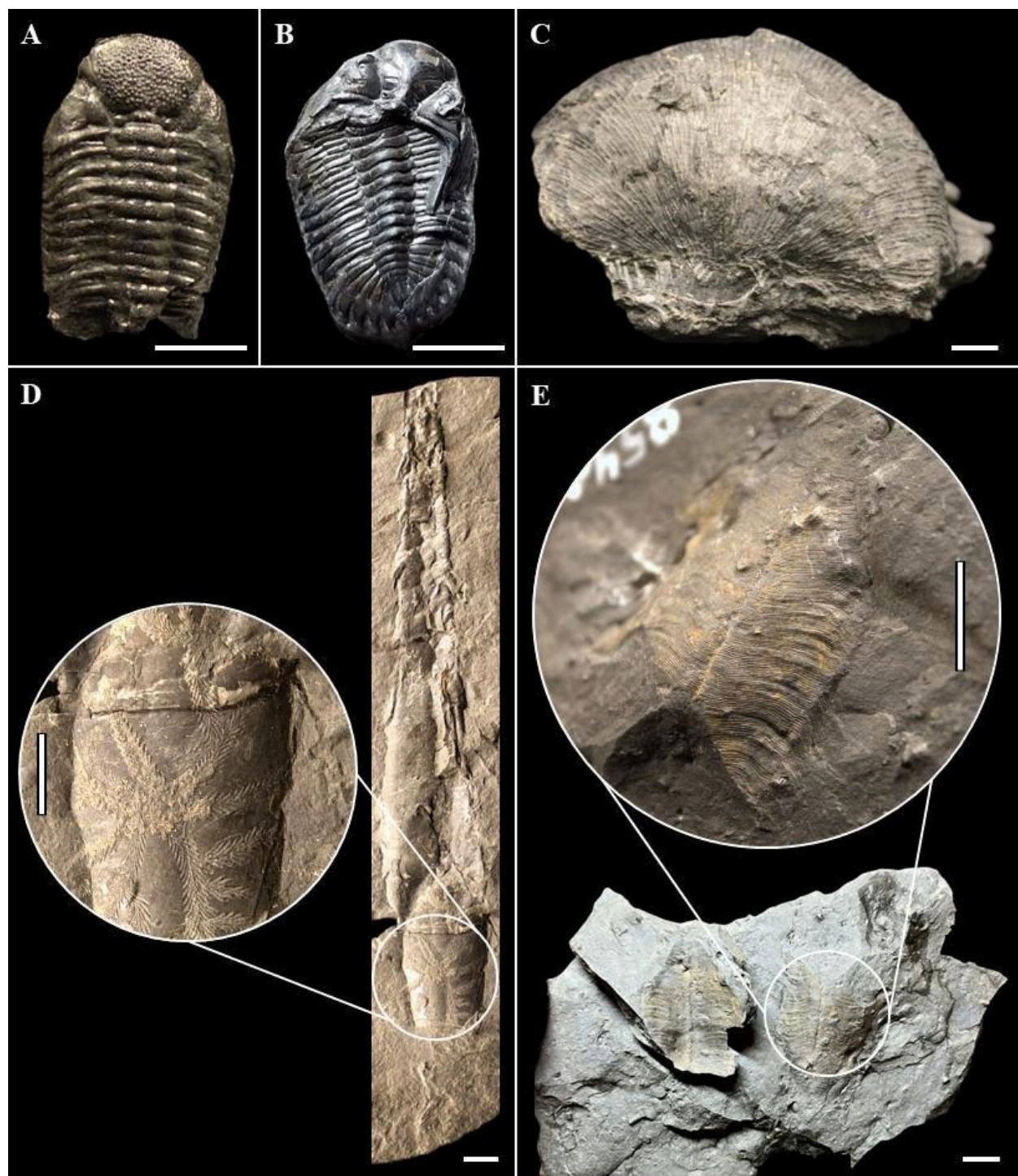
Plate 3. Fossils from the Tichenor Member at Locality 1a-T.



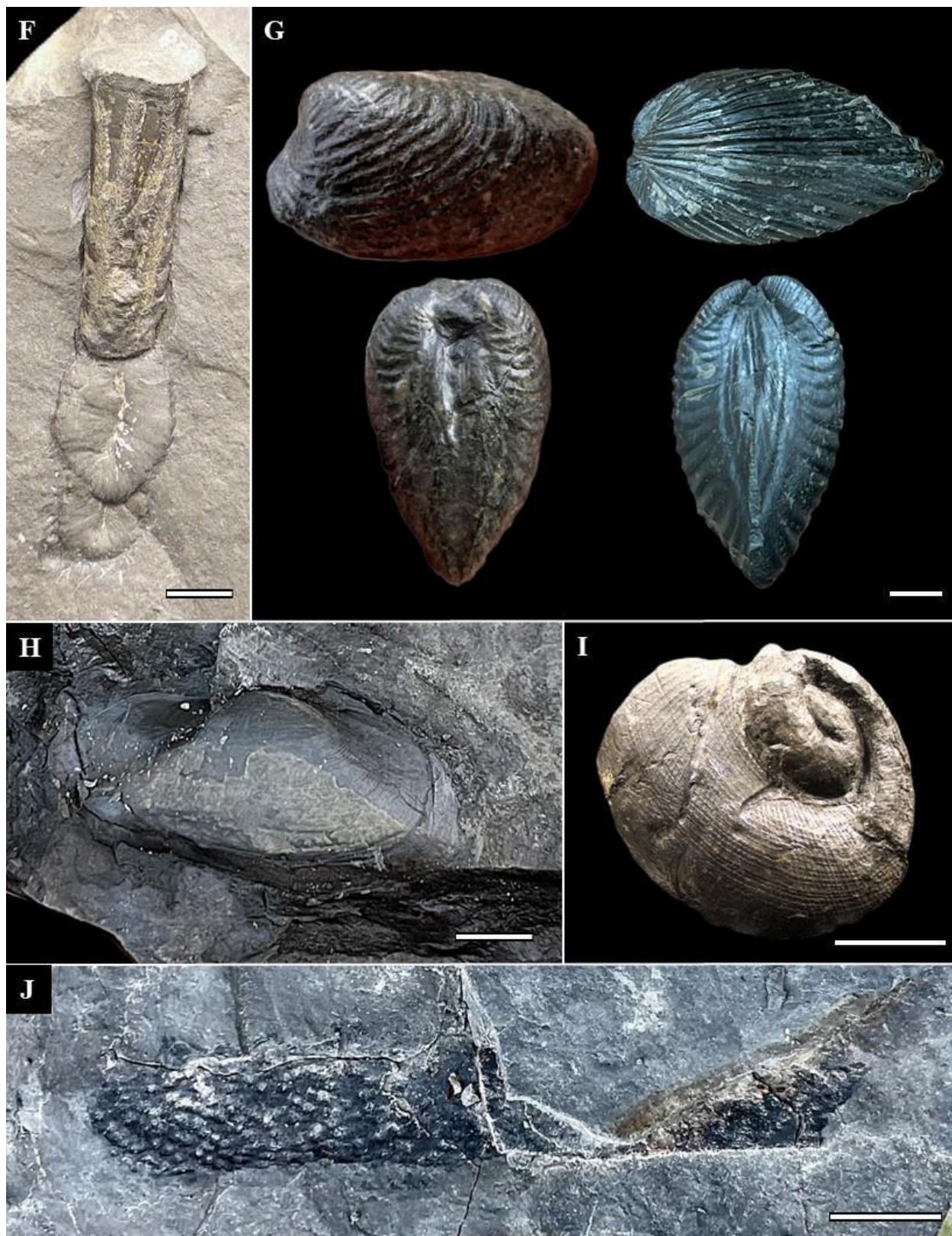
**Plate 4.** Fossils from the “lower Moscow” at Locality 1a-T.



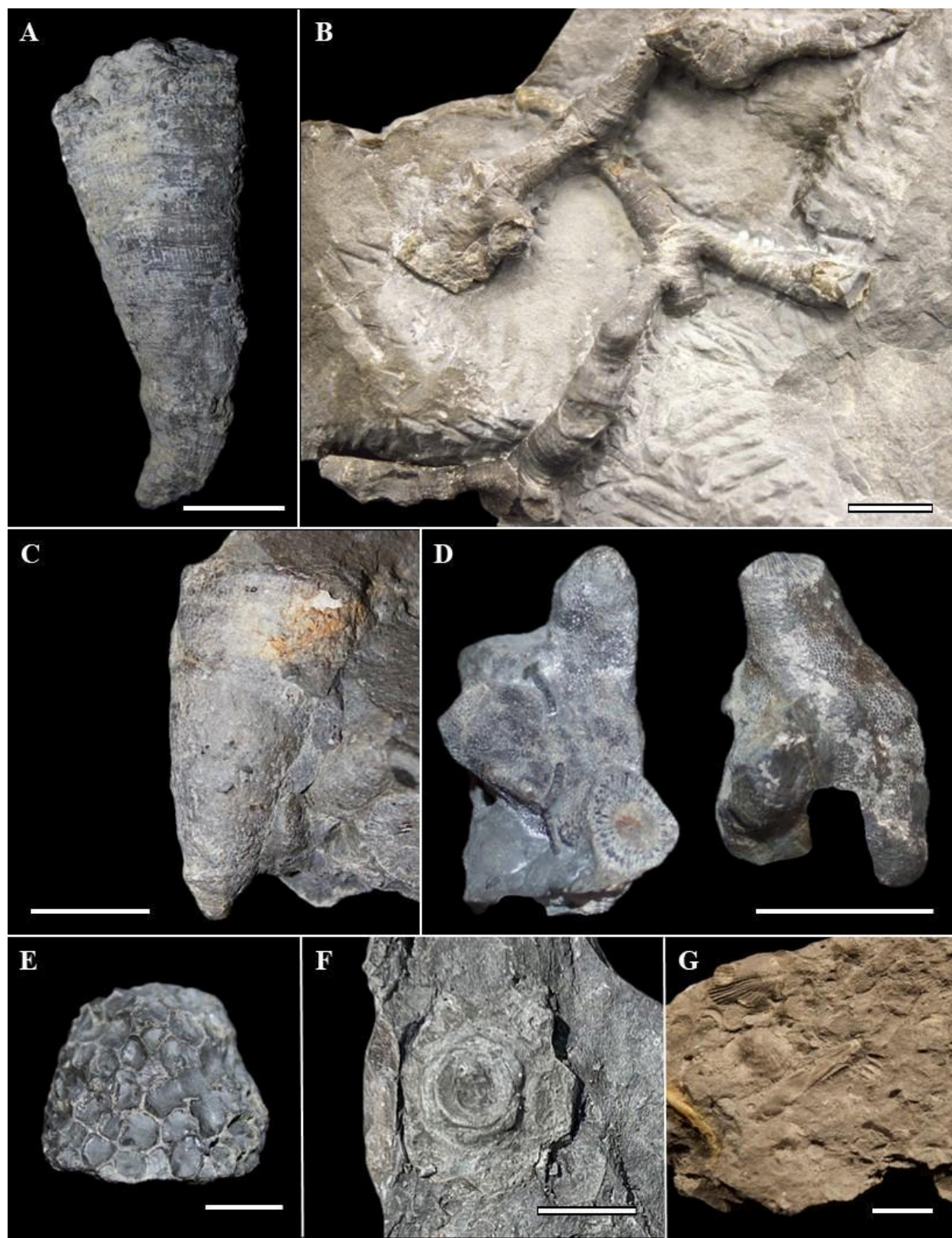
**Plate 5.** Fossils from the Cuylerville Submember *Ambocoelia* Beds at Locality 1b.

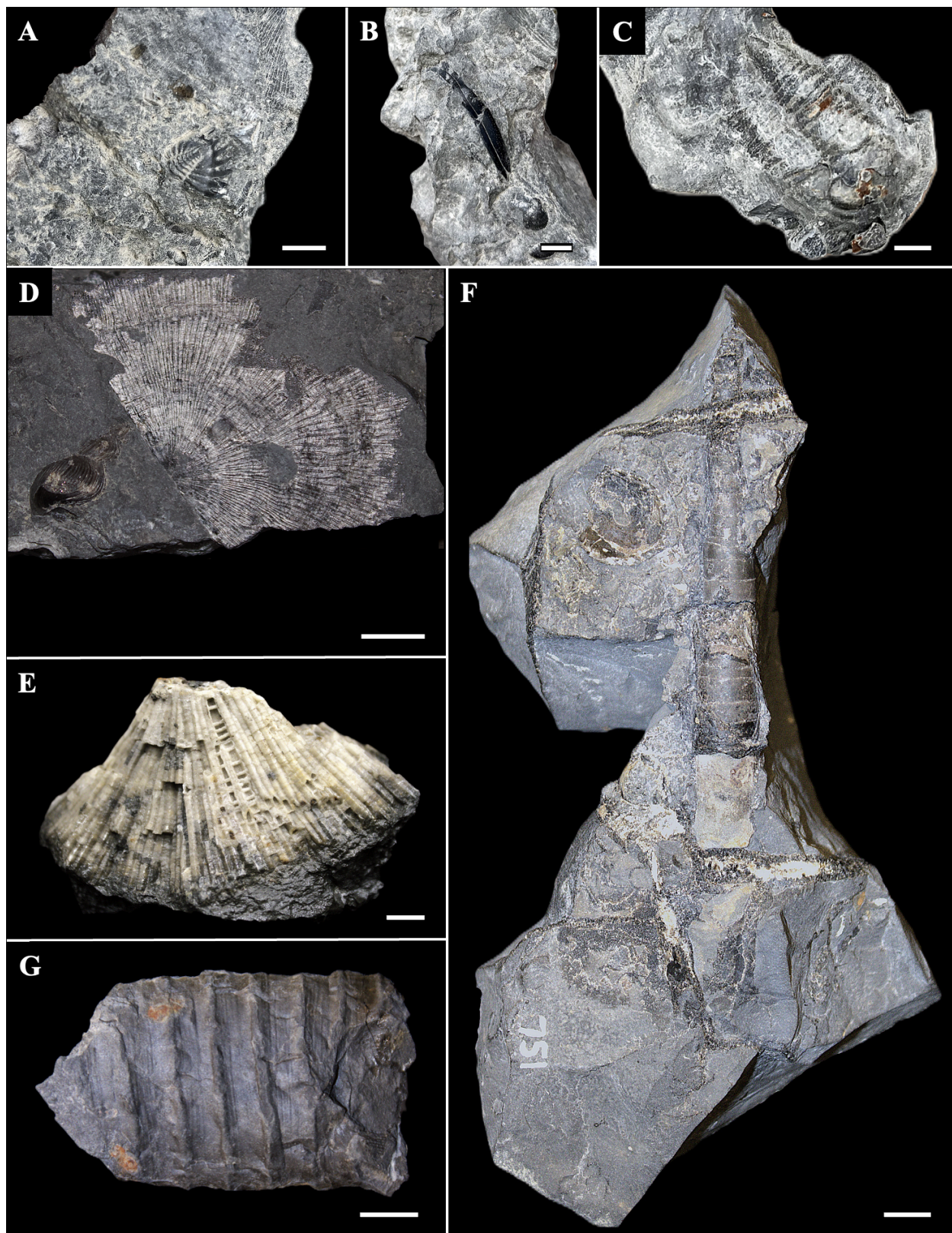


**Plate 6-1.** Fossils from the upper Cuylerville Submember at Locality 2. Continues on Plate 6-2.

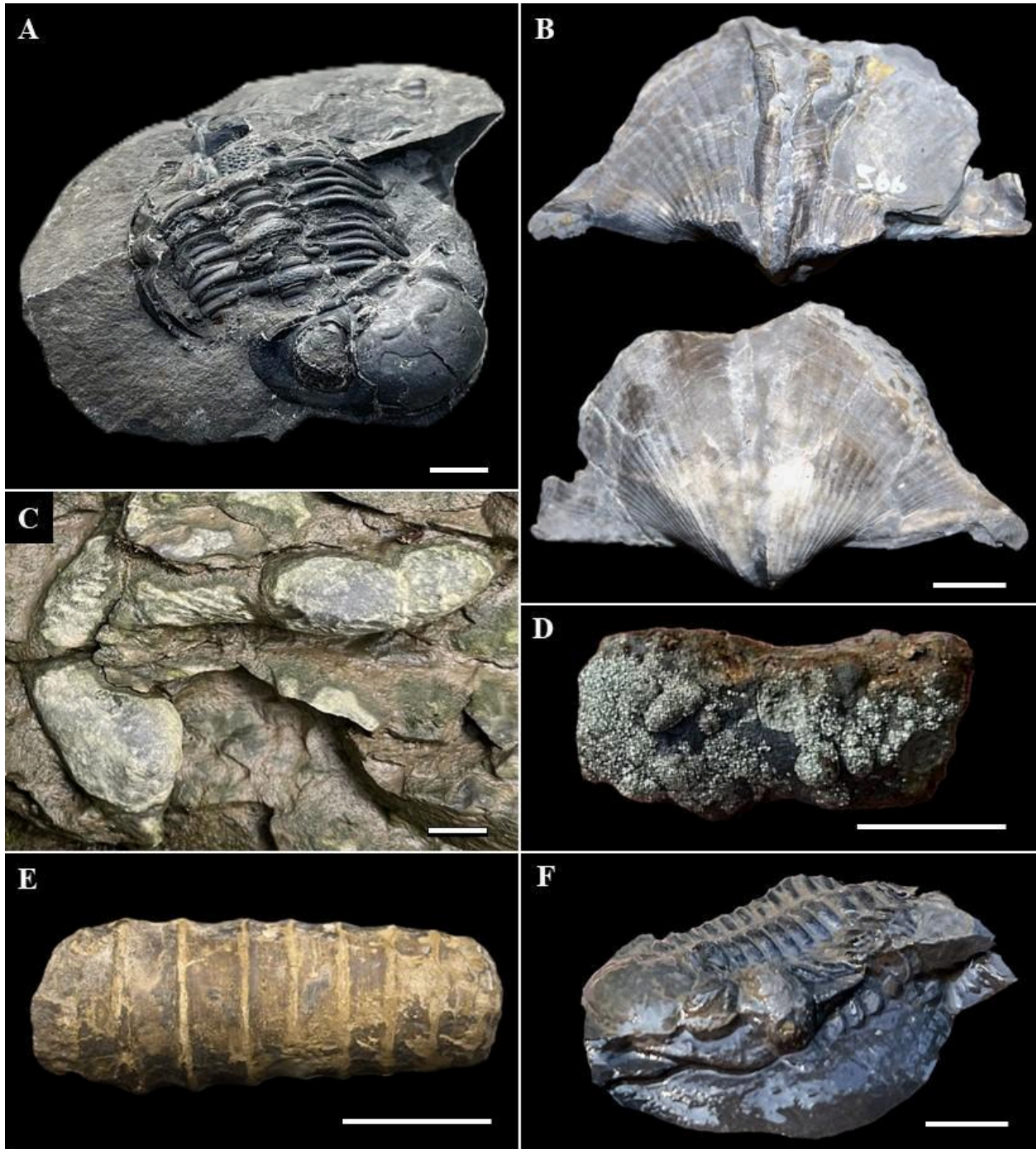


**Plate 6-2.** Fossils from the upper Cuylerville Submember at Locality 2. Continued from Plate 6-1.





**Plate 8.** Fossils from the upper Moscow Formation, including the South Lansing Beds (Garrattsville Mbr: Spezzano Gully Smbr) at Locality 2-T.



**Plate 9.** Fossils from the (A) Fisher Gully Smbr. lower concretionary horizon (0-m height) at Locality 3a, (B-E) lower Fall Brook Bed equivalent at Locality 3b, and (F) *Ambocoelia*-rich Fall Brook Bed equivalent at Locality 3c-1.

**Plate 1.** Fossils from the *Modiomorpha-Ancyrocrinus* Bed at Salmon Creek Locality 1a-1: (A) a cirral grapple of the cladid crinoid *Ancyrocrinus bulbosus* (WCH 9351); (B) a right valve of the palaeoheterodont bivalve *Modiomorpha concentrica* (WCH 941b) with a healed predation scar on the older growth lines; and a relatively complete phragmocone of the nautiloconic nautiloid *Nephriticeras magister* (col. E.M. Cavanaugh). Scale bar = 1 cm.

**Plate 2.** Fossils from the Spafford Member at Salmon Creek Locality 1a-2: (A-E) Bivalves include: (A) an uncompact palaeoheterodont *Goniophora hamiltonensis* (WCH 3351); (B) valves of the palaeoheterodont *Modiomorpha mytiloides* (WCH 472) in butterfly; (C) a right valve of the palaeoheterodont *Orthonota undulata* (col. Y. Cao); (D) valves of the heterodont *Cypricardella bellistriata* (WCH 667) in butterfly, with the left valve in focus; and (E) a right valve of the pteriomorphian *Pseudaviculopeecten princeps* (WCH 381); and (F) a pyritized partial phragmocone of the orthoconic nautiloid *Spyroceras nuntium* (WCH 508) within a split calcareous concretion. Scale bar = 1 cm.

**Plate 3.** Fossils from the Tichenor Member at Salmon Creek Locality 1a-T, accessed via a seasonal talus pile (42°32'30.1"N 76°32'34.8"W): (A) a large and relatively complete specimen of *Paraechinocaris (Echinocaris) punctata* (WCH 820/PRI 111630); (B) a cephalon of the phacopid trilobite *Dipleura dekayi* (WCH 828) with the pleurotomarioid *Glyptomaria capillaria* attached to the right compound eye lens; (C) a rhabdosome of the dendroid graptolite *Dictyonema hamiltoniae* (WCH 833); (D) an apex of the phragmocone of the cyrtoconic nautiloid *Cyrtoceras* (WCH 823); (E) an uncompact anomalodesmatan bivalve *Grammysioidea cf. arcuata* (col. A.I. Eliezer); (F) a complete shell of the platyceratoid gastropod *Naticonema lineata* (col. A.I. Eliezer); and (G) crushed vascular plant material (WCH 832). Scale bar = 1 cm.

**Plate 4.** Fossils from the “lower Moscow” at Salmon Creek Locality 1a-T, accessed via a seasonal talus pile (42°32'29.4"N 76°32'35.5"W): (A) a mold of the phacopid trilobite *Greenops barberi* (col. A.I. Eliezer); (b) a closeup of zooids belonging to a sheet colony of the stenolaemate bryozoan *Leptotrypella furcata* (WCH 817); (C) a relatively complete shell of the platyceratoid gastropod *Orthonychia* (WCH 816); (D) a branching colony of the tabulate coral *Thamnoptychia limbata* (WCH 811) encrusted by at least six species of epibionts, including two tabulate corals (*Aulocystis dichotoma*, *Pleurodictyum americanum*), two bryozoans (*Leptotrypella furcata*, one unidentified), and an unidentified gastropod and crinoid; (E) the fodinichnia *Zoophycos*; and (F) a complete shell of the platyceratoid gastropod *Platyceras cf. bucculentum* (WCH 819). Scale bar = 1 cm.

**Plate 5.** Fossils from the Cuylerville Submember *Ambocoelia* Beds at Salmon Creek Locality 1b: (A) two prone and relatively complete specimens of the phacopid trilobite *Eldredgeops rana* (left to right: WCH 601, 602); (B) a partial cephalon of a meraspid (juvenile) phacopid trilobite *Dipleura dekayi* (WCH 1020); (C) the cubichnia *Rusophycus* with an associated partial shell of the loxonematoid gastropod *Palaeozygopleura hamiltoniae* (WCH 1023); (D) a partial phragmocone of an unidentified goniatite ammonoid (WCH 475); (E) a pedicle valve of the lingulid brachiopod *Lingula delia* (WCH 841); (F) a hand sample of the Cuylerville Submember *Ambocoelia* beds, featuring the exuberant spiriferid brachiopod *Ambocoelia umbonata* (col. R. Brinkerhoff); (G) a branching colony of the tabulate coral *Aulocystis dichotoma* (WCH 422)

encrusted on the spiriferid brachiopod *Mediospirifer audaculus*; (**H**) and a pyramidal test of the hyolithid *Hallotheca aclis* (WCH 558). Scale bar = 1 cm.

**Plate 6-1.** Fossils from the upper Cuylerville Submember at Salmon Creek Locality 2: prone and complete specimens of the phacopid trilobites (**A**) *Eldredgeops rana* (col. A.I. Eliezer) and (**B**) *Greenops grabau* (col. A.I. Eliezer); (**C**) an uncompacted pedicle valve of the strophomenid brachiopod *Megastrophia concava* (WCH 804); (**D**) tubes of the possible phoronid *Reptaria stolonifera* (WCH 857) encrusted on a complete phragmocone of the orthoconic nautiloid *Spyroceras nuntium*; and (**E**) part and counterpart of a partial periderm test of the conulariid *Conularia undulata* (WCH 854). Scale bar = 1 cm. Continues on Plate 6-2.

**Plate 6-2.** Fossils from the upper Cuylerville Submember at Salmon Creek Locality 2 (continued from Plate 6-1): (**F**) the cubichnia *Rusophycus* (WCH 860) abutting a complete phragmocone of the orthoconic nautiloid *Michelinoceras telamon* encrusted by tubes of the possible phoronid *Reptaria stolonifera*; (**G**) uncompacted anomalodesmatan bivalves *Grammysioidea* cf. *arcuata* (left to right: col. E.M. Cavanaugh, WCH 856); (**H**) a right valve of the paleotaxodont *Tellinopsis submarginata* (WCH 846); (**I**) a large shell of the platyceratoid gastropod *Naticonema lineata* (WCH 855); and (**J**) a decorticated stem of an unidentified lycophyte. Scale bar = 1 cm.

**Plate 7.** Fossils from the Bay View Beds equivalent at Salmon Creek Locality 2: (**A**) a complete corallum of the rugose coral *Streptelasma ungula* (WCH 476); (**B**) a branching colony of the tabulate coral *Aulocystis jacksoni* (WCH 772); (**C**) a complete corallum of the rugose coral *Stereolasma rectum* (WCH 916); (**D**) a branching colony of the rugose coral *Heliophyllum delicatum*, fouled by an unidentified bryozoan colony (WCH 923 and 924); (**E**) a massive colony of the tabulate coral *Pleurodictyum americanum* (WCH 398); (**F**) a partial calyx (columnal insertion and infrabasals) of the camerate crinoid *Megistocrius depressus* (col. E.M. Cavanaugh); and (**G**) a pyramidal test of the hyolithid *Hyolithes striatus* (WCH 918). Scale bar = 1 cm.

**Plate 8.** Fossils from the upper Moscow Formation, including the South Lansing Beds (Garrattsville Mbr: Spezzano Gully Smbr) at Salmon Creek Locality 2-T, accessed via a seasonal talus pile (42°33'01.3"N 76°32'20.6"W): a pygidium and thoracic segment of the phacopid trilobites (**A**) *Bellacartwrightia* (WCH 551) and (**B**) *Dipleura dekayi* (WCH 552), respectively; (**C**) a complete specimen of the proetid trilobite *Basidechenella rowi* (col. S.E. Echavarría); (**D**) a pedicle valve of the strophomenid brachiopod *Mesoleptostrophia junia* and body chamber of the loxonematoid gastropod *Palaeozygopleura hamiltoniae*, both replaced by calcite (WCH 733); (**E**) an exceptionally preserved colony of the tabulate coral *Favosites hamiltoniae* (WCH 403); (**F**) a relatively complete phragmocone of the orthoconic nautiloid *Michelinoceras telamon* (WCH 751) crosscut by veins of calcite within a split calcareous limestone; and (**G**) a partial phragmocone of the orthoconic nautiloid *Spyroceras nuntium* (WCH 401). Scale bar = 1 cm.

**Plate 9.** Fossils from the lower concretionary horizon (0-m height) of the Fisher Gully Submember at Salmon Creek Locality 3a: (**A**) two specimens of the phacopid trilobite *Eldredgeops rana* (WCH 573), including one relatively prone and complete individual and one shed cephalon. Fossils from the lower Fall Brook Bed equivalent: (**B**) branchial (top) and pedicle (bottom) views of an uncompacted spiriferid brachiopod *Spinocyrtia* cf. *granulosa* (WCH 566); (**C**) an irregular concretion that likely follows burrows; (**D**) a concretion (burrow?) with nodular

pyrite growth on the surface (WCH 861); and (E) an uncompacted mold of a partial phragmocone of the orthoconic nautiloid *Spyroceras nuntium* (WCH 568). Fossils from the *Ambocoelia*-rich Fall Brook Bed equivalent at Salmon Creek Locality 3c-1: (F) a complete specimen of the phacopid trilobite *Eldredgeops rana* with nodular pyrite growth on the left pleural lobe (col. C.J. Hensen). Scale bar = 1 cm.

## Appendices

### Appendix I. The Fossils of Salmon Creek and Ludlowville Falls

This appendix summarizes the occurrences and rarities of the known fossil animals and plants sampled from Salmon Creek and Ludlowville Falls. Animal taxa are organized according to phylum and are ordered alphabetically as opposed to phylogenetically, beginning with Arthropoda and ending with Porifera. Note ichnological taxa (“Ichnotaxa,” or trace fossils) and Incertae Sedis taxa (Problematica, or problematic fossils) are treated here as phyla even though Ichnotaxa have their own taxonomy separate from body fossils, and Incertae Sedis is not a monophyletic clade (by definition, it is a polyphyletic clade of taxa with uncertain affinities to the known animal phyla). Brief, phylogenetic contexts for some broad animal subclades (Parahoxozoa, Bilateria, Protostomia, Deuterostomia, Ecdysozoa, and Lophotrochozoa) are provided prior to description of the first phylum to fall within that subclade (e.g., Arthropoda is the first phylum described that is a member of Parahoxozoa, Bilateria, Protostomia, and Ecdyzoa, so these subclades are described first before discussion of Phylum Arthropoda). Descriptions of each phylum are split into subclades where appropriate; these are also presented alphabetically (e.g., Arthropoda is divided into sections on first “Crustacea” and second †Trilobita), when appropriate. Stratigraphic occurrences and rarities are summarized for each fossil taxon by phylum subclade; these are presented in tabulated form in Appendix II. Identification plates, modified from Wilson (2014), are provided for all fossil taxa known from Salmon Creek identified to the species level. The dagger symbol (†) is used to represent wholly extinct clades, for which there are no living representatives (e.g., †Trilobita). Any fossil taxa identified to the genus or species levels (italicized here and throughout this field guide; e.g., *Eldredgeops rana*) are all assumed to be extinct and will not display the dagger symbol in front of their genus name to spare additional text. Parentheses (“ ”) are used to denote paraphyletic (non-monophyletic) clades (e.g., “Crustacea”). Plant taxa (Tracheophytes) are summarized after the animals. Note that plant systematists use the “division” as an equivalent taxonomic rank to the “phylum” for animals.

Seven animal phyla and one plant division have been documented at Salmon Creek and Ludlowville Falls. The animals include Arthropoda, Brachiopoda, Bryozoa, Cnidaria, Echinodermata, Hemichordata, and Mollusca (as well as Incertae Sedis taxa and Ichnotaxa); the plants include Tracheophytes. Although Chordata and Porifera have not been documented, these taxa are included for complete discussion on all the fossil-forming animal phyla that can potentially occur at Salmon Creek.

For more information about the fossils of Salmon Creek and Ludlowville Falls, please visit the [Devonian Atlas of Ancient Life](#), a free educational resource created by the Paleontological Research Institution and supported by the National Science Foundation under Grant No. 2127427. Links to the Atlas for each available animal clade are provided as they appear throughout this appendix.



**Phylogenetic context on Clade Bilateria:** Bilateria is an extant clade of parahoxozoan that first appeared in the Ediacaran. Bilaterians include the clades Protostomia (discussed below) and Deuterostomia (see ‘*Phylum Chordata*’ for further discussion). They are all triploblastic (composed of three cell layers: endo-, meso-, and ectoderm) and possess left-right, or mirror-image, symmetry (Martindale et al., 2004). This is known as bilateral symmetry, where the animal body is organized along only one plane of symmetry and lacks any additional axes of symmetry (Holló, 2015). This is in contrast to poriferans (sponges), which are asymmetrical, and cnidarians (jellies, corals, and allies), which are radially symmetrical (have one axis of symmetry and an unlimited number of planes of symmetry) (Holló, 2015). Some bilaterians, such as echinoderms (sea stars, sea urchins, and allies) have evolved a special type of bilateral symmetry known as pentaradial (also pentamous or pentamerous) symmetry (Benton & Harper, 2020).

**Phylogenetic context on Clade Protostomia:** Protostomia (“mouth first”) is an extant clade of bilaterian where the blastopore becomes the mouth during development (Benton & Harper, 2020; Martín-Durán et al., 2016). Protostomes first appeared in the Ediacaran. They include two superphyla: (1) Ecdysozoa (discussed below) and (2) Lophotrochozoa (see ‘*Phylum Brachiopoda*’ for further discussion).

**Phylogenetic context on Clade Ecdysozoa:** Ecdysozoa is an extant superphylum of protostome that first appeared in the Ediacaran. Ecdysozoans all shed their exoskeletons via a process called ecdysis (Telford et al., 2008). Ecdysozoa includes the phyla Arthropoda, Nematoda, Onychophora (velvet worms), Tardigrada (water bears), and allies.

### Phylum Arthropoda (“jointed limbs”)

Arthropoda is an extant phylum of ecdysozoan protostome and the most speciose clade of the animal phyla (Giribet & Edgecombe, 2013). Arthropod body fossils first appeared in the fossil record during the Cambrian Explosion (Stage 3), though arthropod-like traces such as *Rusophycus* are known from Stage 2, potentially extending the record by another eight million years (Edgecombe, 2010). All arthropods share jointed appendages, a segmented body, and an exoskeleton made of chitin or sclerotin (Smarandache-Wellmann, 2016).

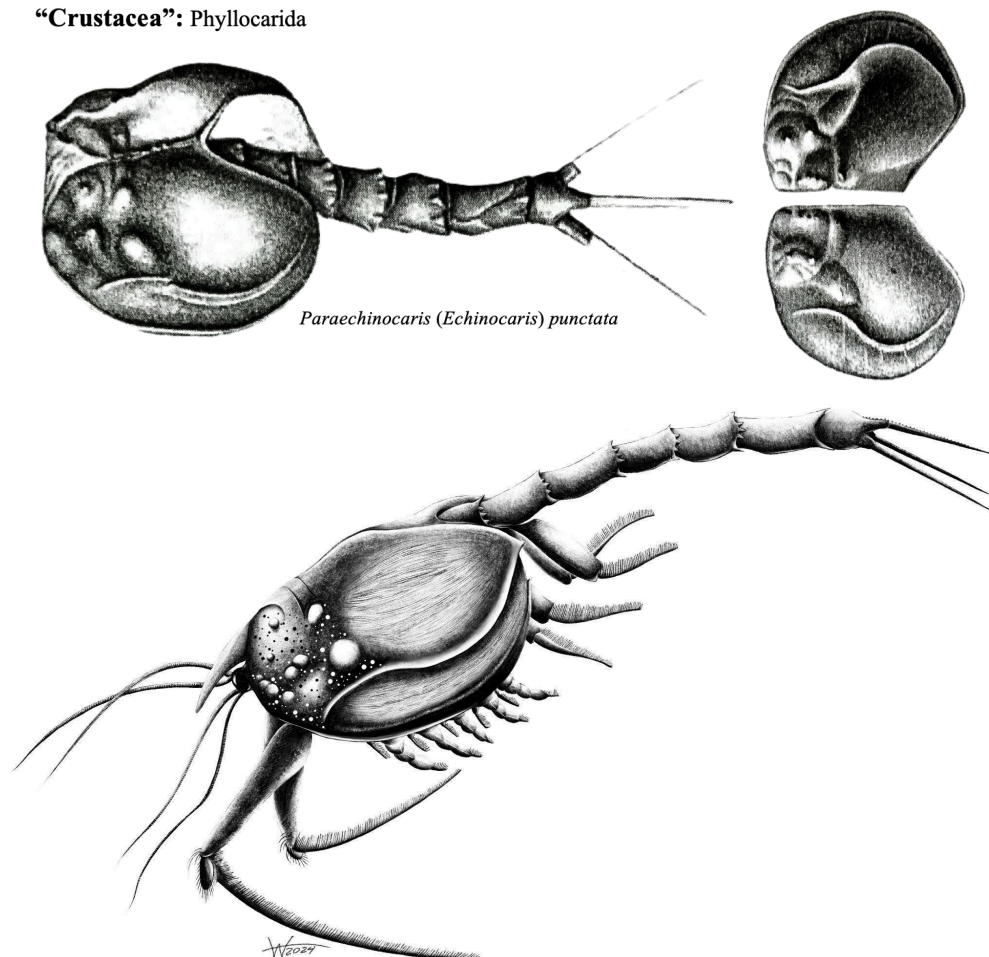
Arthropoda is traditionally divided into five subphyla: (1) †Trilobitomorpha (trilobites, agnostids, and naroids), (2) Chelicerata (eurypterids, horseshoe crabs, spiders, mites, and scorpions), (3) Myriapoda (centipedes and millipedes), (4) “Crustacea” (crabs, lobsters, “shrimps”, barnacles, and allies), and (5) Hexapoda (insects and allies) (Benton & Harper, 2020). Fossils of phyllocarids (a subclass of crustaceans) and trilobites can be found at Salmon Creek.

### Subphylum “Crustacea”: crabs, lobsters, “shrimps”, barnacles, and allies

“Crustacea” is an extant subphylum of marine arthropod that includes decapods (crabs, lobsters, “shrimps”), cirripedes (barnacles), and allies (amphipods, branchiopods, copepods, isopods, ostracods, etc.). “Crustaceans” first appeared in the Cambrian. Recent work has revealed “Crustacea” to be a paraphyletic clade that excludes Hexapoda. Rather than sink Hexapoda within “Crustacea,” Pancrustacea has been proposed as the monophyletic name for this broader group of arthropods (Schram & Koenemann, 2021; Bracken-Grissom & Wolfe, 2020). As a result, both subphyla names are retained, with “Crustacea” referring to all non-hexapod crustaceans as it has done so historically.

## Subclass Phyllocarida (“leaf shrimp”)

“Crustacea”: Phyllocarida



**Appendix I Plate 1-1.** Phylum Arthropoda: Subphylum “Crustacea”: Subclass Phyllocarida: *Paraechinocaris (Echinocaris) punctata*. Modified from Wilson (2014). Life reconstruction of *Paraechinocaris punctata* by W.C.H.

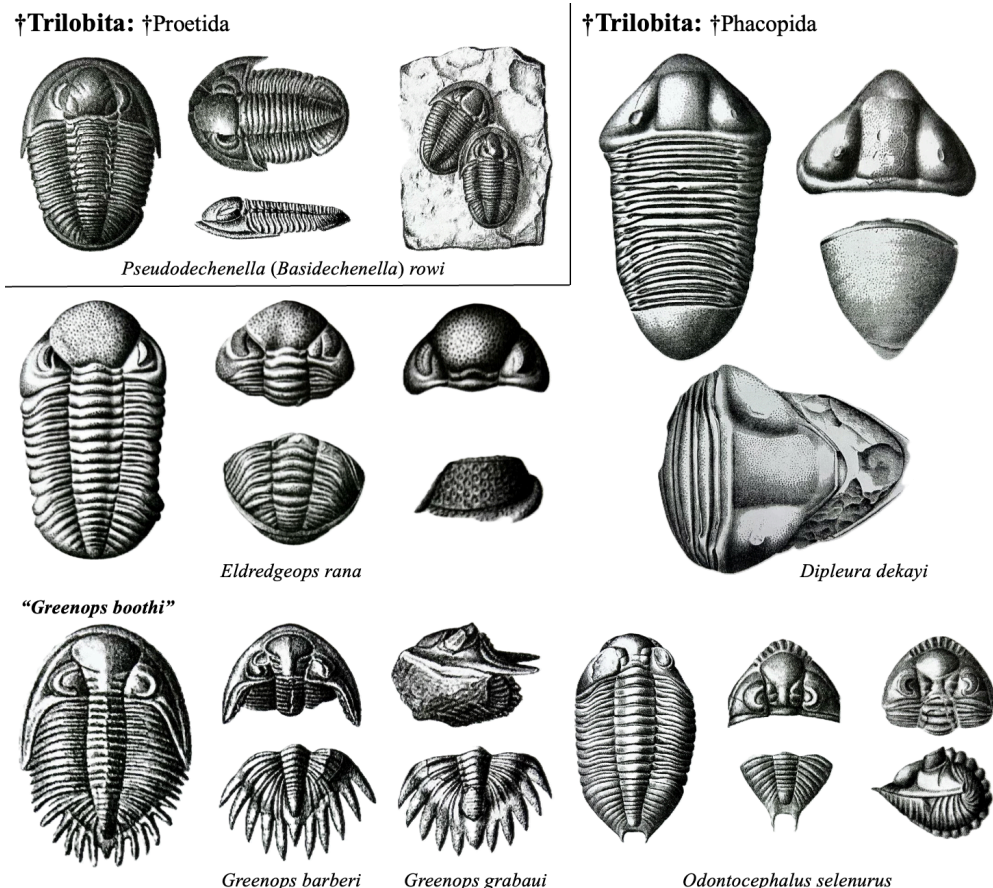
Phyllocarida is an extant subclass of shrimp-like “crustacean” that all share a large, bivalved carapace and a fan-shaped telson (Bergmann & Rust, 2014). Although this clade first appeared in the Silurian, the large durophagous forms first appeared in the Devonian, crushing shelled prey such as brachiopods and bivalves with their mandibles (Kaplan, 2023). Unlike trilobites, phyllocarids are still around today. They have a global distribution and inhabit a range of water depth and climate (Rode & Lieberman, 2002).

Phyllocarids are rather rare throughout the Hamilton Group. Partial carapace valves of *Rhinocaris columbina*, often confused for crushed ammonoid phragmocones, are relatively common finds in the Geer Road Beds (Moscow Fm: Windom Mbr) exposed near Hamilton, NY; however, this species has not been found at Salmon Creek. In fact, only one phyllocarid fossil has been recovered thus far: an exceptionally rare and relatively complete specimen of *Paraechinocaris (Echinocaris) punctata* with both carapace valves as well as the abdomen and telson spines preserved (Plate 3a). It came from the Tichenor Member at Locality 1a-T, and now

is on permanent display at the Museum of the Earth in Ithaca, NY (New Acquisitions case; PRI 111630).

## Subphylum †Trilobitomorpha: trilobites, agnostids, and naroids

### Class †Trilobita (“three-lobed rocks”): trilobites



**Appendix I Plate 1-2.** Phylum Arthropoda: Subphylum †Trilobitomorpha: Class †Trilobita. Order †Phacopida: *Dipleura dekayi*, *Eldredgeops (Phacops) rana*, *Greenops barberi*, *Greenops grabau*, and *Odontocephalus selenurus*. Order †Proetida: *Pseudodechenella (Basidechenella) rowi*. Modified from Wilson (2014).

†Trilobita is an extinct class of marine arthropod. Trilobites first radiated in the Early Cambrian, shortly after the appearance of the arthropods; they did not disappear until the end of the Permian, about 270 million years later (Schoenemann et al., 2024). Trilobites are composed of three basic parts: the (1) cephalon (head), (2) thorax (body segments), and (3) pygidium (tail) (Bergström, 1973). The body can also be divided into two lateral pleural lobes (PL) and one medial axial lobe (AL); this is where the name “tri-lob-ite” (“three-lobed rocks”) is derived (Wilson, 2014).

The most common type of trilobite fossil at Salmon Creek are incomplete molts (shed exoskeletons). These can be sampled throughout Salmon Creek, though they are more common in the Moscow (localities 1a-T, 1b-T, 1b, 2, 3a, 3b, 3c-1) than the Ludlowville Formation (localities 1a-1, 1a-2). Complete trilobite specimens (either prone or enrolled) are much rarer.

These are known from the lower Moscow (Locality 1a-T; Plate 4a), Cuylerville Submember *Ambocoelia* Beds (Locality 1b; Plate 5a), upper Cuylerville Submember (Locality 2; Plate 6-1a, 6-1b), Fisher Gully Submember lower concretionary horizon (0-m height) (Locality 3a; Plate 9a), *Ambocoelia*-rich Fall Brook Bed equivalent (Locality 3c-2; Plate 9f), and Spezzano Gully Submember South Lansing Beds (Locality 2-T; Plate 8c).

### Order †Phacopida (“lens-face”)

†Phacopida is an extinct order of trilobite that first appeared in the Furongian (latest Cambrian). Phacopids experienced rapid radiation in the Silurian, reaching peak diversity in the Devonian (Adrain, 2013). Phacopids are the most common trilobite order found in the Hamilton Group. At Salmon Creek, *Eldredgeops* and *Greenops* are well represented in both the Ludlowville and Moscow formations. *Bellacartwrightia*, *Dipleura*, and *Odontocephalus*, however, are very rare and restricted to only a few stratigraphic units. Phacopids disappeared at the end of the Famennian as a result of the Hangenberg Biocrisis.

### *Eldredgeops rana*

*Eldredgeops (Phacops) rana* is the most common trilobite species from the Hamilton Group of western and central New York State. This is particularly true for the Windom Member, a unit that not only contains several *E. rana*-bearing beds (Brett et al., 2013) but is also heavily exposed throughout Salmon Creek (localities 1b-T, 1b, 2, 3a, 3b, 3c). The species epithet “*rana*,” in fact, means “frog,” referring to the frog-like appearance of this trilobite when viewed from the front (Priesendorf, 2021). *E. rana* occurs in relative abundance in the Cuylerville Submember *Ambocoelia* Beds, and several complete specimens (prone and enrolled) have been documented from this unit (Locality 1b; Plate 5a). Other strata that reliably contain *E. rana* fossils include the Tichenor Member (Locality 1b-T), lower Moscow (localities 1a-T, 1b-T), upper Cuylerville Submember (Locality 2; Plate 6-1a), Fisher Gully Submember lower concretionary horizon (0-m height) (Locality 3a; Plate 9a), and *Ambocoelia*-rich Fall Brook Bed equivalent (Locality 3c-2; Plate 9f). Note that the *E. rana* from the lower Moscow (localities 1a-T, 1b-T), known only from disarticulated tagmata thus far, are reminiscent of those of the Deep Run Member in Moscow Formation outcrops to the west (Mayer et al., 1991). *E. rana* are rare in the Ludlowville Formation (Locality 1a), and are absent (undocumented thus far) from the Spezzano Gully Submember South Lansing Beds (Locality 2-T).

### *Greenops* spp.

*Greenops* is an uncommon phacopid genus at Salmon Creek, represented by *G. grabau* and *G. barberi*, with the former more common than the latter. These species differ according to the size and shape of the terminal lappet (the single pygidial spine on the AL). This structure is short and subrectangular in *G. grabau*, and long and triangular in *G. barberi* (Wilson, 2014; Bignon & Crônier, 2014). Well preserved pygidia exemplifying these character differences can be found in the upper *Modiomorpha-Ancyrocrinus* Bed at Locality 1a-1. *Greenops* is more abundant than *Eldredgeops rana* in certain layers of the lower Moscow (Locality 1a-T; Plate 4a). Rarely, complete specimens have been found in the Cuylerville Submember *Ambocoelia* beds (Locality 1b) and upper Cuylerville Submember (Locality 2; Plate 6-1b).

### *Bellacartwrightia* sp.

*Bellacartwrightia* is morphologically quite similar to *Greenops*, and thus is probably undersampled at Salmon Creek (both taxa are united within the family †Acastidae). Unlike *Greenops*, *Bellacartwrightia* has medially curved PL pygidial spines that are much longer than the terminal lappet, a terminal lappet as wide as the AL, and genal spines as long as the cephalon (Bignon & Crônier, 2014). Only pygidia of this taxon have been found thus far from the lower Moscow (Locality 1a-T), Cuylerville Submember *Ambocoelia* Beds (Locality 1b), and Spezzano Gully Submember South Lansing Beds (Locality 2-T; Plate 8a).

### ***Odontocephalus* sp.**

*Odontocephalus* is a very rare phacopid genus diagnosed by elongated perforations (process-like projections) that radiate from an expanded border on the anterior margin of the cephalon (Holloway, 2011). When the cephalon is absent, the pygidium, bearing medially curved PL spines, resembles that of *Bellacartwrightia*. Thus far, only one complete ventral specimen of *Odontocephalus* has been found in the upper Taunton Submember (Locality 2-T).

### *Dipleura dekayi*

*Dipleura dekayi* is one of the largest trilobite species of the Hamilton Group, reaching lengths of up to 22 cm (Saul, 1967). At Salmon Creek, *D. dekayi* is very rare, known only from disarticulated tagmata. It is much more common in units to the east, such as the Cole Hill Beds (Skaneateles Fm: Delphi Station Mbr) and Geer Road Beds (Moscow Fm: Windom Mbr) exposed near Hamilton, NY. Thus far, two cephalons have been recovered: one from the Tichenor Member (Locality 1a-T) and another from the Cuylerville Submember *Ambocoelia* Beds. Interestingly, the Tichenor specimen includes a pleurotomarioid gastropod *Glyptomaria capillaria* attached to the right compound eye lens, representing a very rare example of gastropod feeding (i.e., scavenging) on a trilobite (Plate 3b; see ‘*Paleoecology of Salmon Creek and Ludlowville Falls III*’ for further discussion). The *Ambocoelia* Beds specimen is a meraspid (juvenile) (Plate 5b). Large, individual thoracic segments of *D. dekayi* have been recovered from the Spezzano Gully Submember South Lansing Beds (Locality 2-T; Plate 8b).

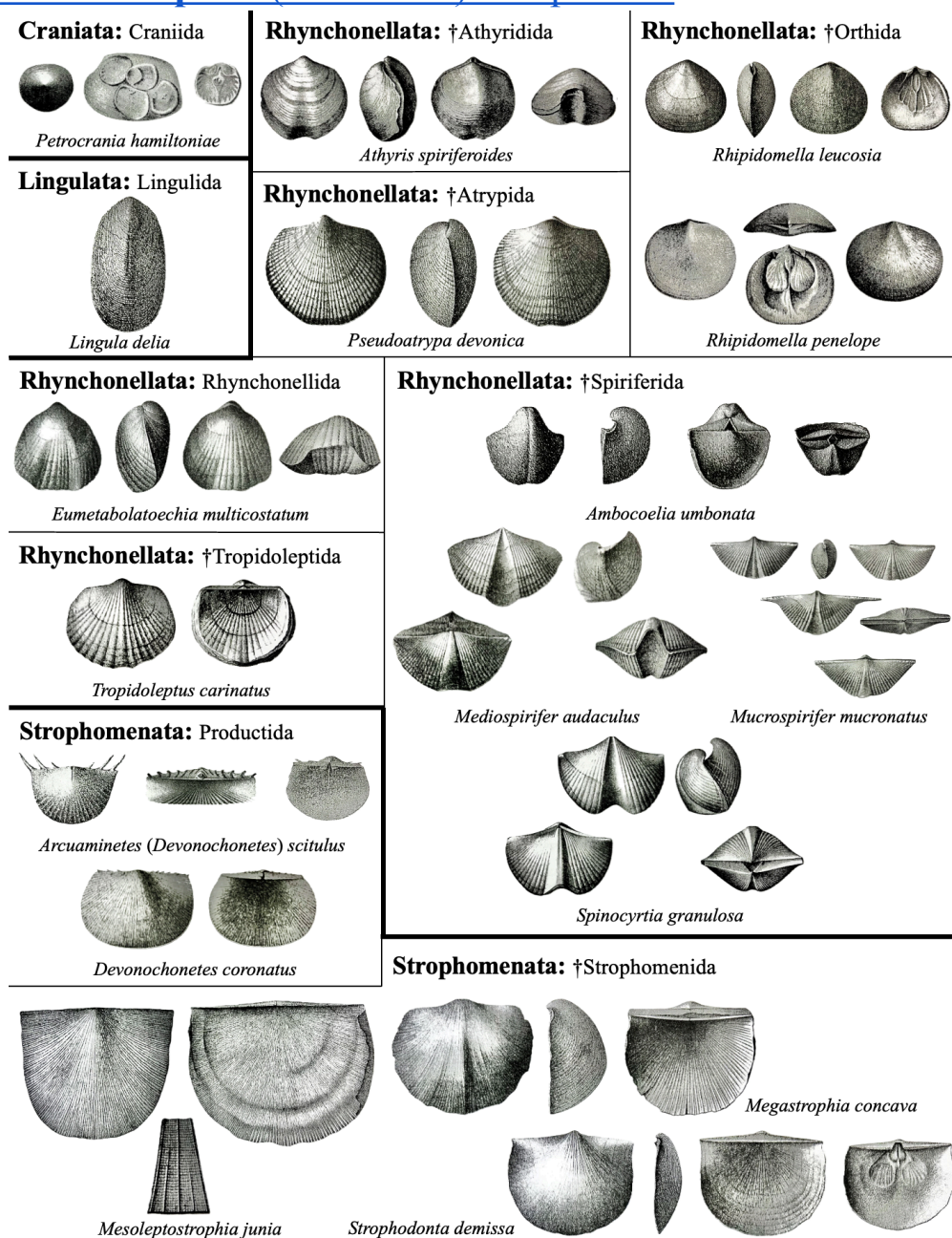
### Order †Proetida

†Proetida is an extinct order of trilobite that first appeared in the Early Ordovician. Proetids are very rare; among amateur and professional collectors, proetids are said to occur once for every one hundred phacopids found. They are also often mistaken for phacopids, especially *Greenops*. One differentiating character is a distant glabella from the rostral plate (anterior border) (Lamsdell & Selden, 2015). So far, the species *Pseudodechenella* (*Basidechenella*) *rowi* has been found at Salmon Creek, though genera such as *Monodechenella* are probably also present and yet to be identified. Fossils of *P. rowi* are generally represented by disarticulated tagmata, especially pygidia (often confused for *Eldredgeops rana* pygidia at a cursory glance), and most reliably occur in the upper Cuylerville Submember and Bay View Beds equivalent (Locality 2). In one instance, a complete specimen was recovered from the Spezzano Gully Submember South Lansing Beds (Locality 2-T; Plate 8c). Unlike phacopids, proetids persisted after the Late Devonian mass extinction. They did not disappear until the end of the Permian.

**Phylogenetic context on Superphylum Lophotrochozoa:** Lophotrochozoa *sensu lato* (= Spiralia *sensu stricto*) is an extant but unresolved (polytomous) superphylum of protostome

including Annelida (segmented worms, including marine polychaetes and soil-dwelling oligochaetes), Brachiopoda, Bryozoa, Mollusca, Phoronida, and other smaller phyla (Kocot, 2016). Lophotrochozoans first appeared during the Early Cambrian. They all undergo spiral cleavage during ontogeny (Martín-Durán & Marlétaz, 2020). Most either have a lophophore (a coiled feeding and respiratory organ; Kuzmina & Malakhov, 2007) or a trochophore stage (a ciliated, planktonic ontogenetic stage; Nielsen, 2018); some even possess both characters.

## Phylum Brachiopoda (“arm feet”): lamp shells



**Appendix I Plate 2.** Phylum Brachiopoda: Subphylum Craniiformea: Class Craniata: *Petrocrania hamiltoniae*. Subphylum Linguliformea: Class Lingulata: Order Lingulida: *Lingula delia*. Subphylum Rhynchonelliformea: Class Rhynchonellata: Order †Arthyridida: *Athyris*

*spiriferoides*; Order †Atrypida: *Pseudoatrypa devonica*; Order †Orthida: *Rhipidomella leucosia* and *R. penelope*; Order Rhynchonellida: *Eumetabolatoechia multicostatum*; Order †Spiriferida: *Ambocoelia umbonata*, *Mediospirifer audaculus*, *Mucrospirifer mucronatus*, *Spinocyrtia cf. granulosa*; Order †Tropidoleptida: *Tropidoleptus carinatus*. Class Strophomenata: Order Productida: *Arcuaminites (Devonochonetes) scitulus* and *Devonochonetes coronatus*; Order †Strophomenida: *Megastrophia concava*, *Mesoleptostrophia junia*, and *Strophodonta demissa*. Modified from Wilson (2014).

Brachiopoda is an extant phylum of lophotrochozoan that first appeared in the Early Cambrian. Brachiopods are characterized by a bivalved shell and a lophophore. The presence of a lophophore makes brachiopods more closely related to bryozoans and phoronids, united as Lophophorata, than to annelids and mollusks, members of Trochozoa (Santagata, 2015). The shared appearances, and functions, between brachiopods and bivalve mollusks is therefore an example of convergent evolution. Brachiopods first appeared in the Cambrian and achieved peak diversity during the Paleozoic before being displaced by bivalves after the Mesozoic Marine Revolution (Benton & Harper, 2020). Extant brachiopods are represented by less than 500 species and are generally restricted to cryptic, deep-water environments (Carlson, 2016; Giles, 2012). The deep sea as a refuge for outcompeted taxa is known as Sar's Paradigm (Ameziane & Roux, 1997).

Brachiopods are the most speciose and abundant phylum present at Salmon Creek, with each of the three subphyla (Craniiformea, Linguliforma, Rhynchonelliformea) represented. They can be sampled at every locality, especially the orders †Spiriferida, †Athyridida, Productida, and Terebratulida. Craniida, Lingulida, and †Strophomenida, on the other hand, are generally rare. Other orders are likely undersampled, including †Atrypida, †Orthida, and Rhynchonellida.

Both brachiopods and bivalve fossils can be found at Salmon Creek. These taxa can be differentiated by symmetry: brachiopods are symmetrical across valves whereas bivalves are symmetrical between valves. In other words, a single brachiopod shell is symmetrical, and a single bivalve shell is asymmetrical.

## **Subphylum Craniiformea**

Craniiformea is an extant subphylum of inarticulate brachiopod that first appeared in the Middle Cambrian. Both craniiforms and linguliforms lack diductor muscles (in contrast to rhynchonelliforms, which possess both adductor and diductor muscles). Both subphyla were once referred to as “Inarticulata”, or the inarticulate brachiopods, but this clade name is now outdated (Wilson, 2014). In the following sections, we use the terms “inarticulate” and “articulate” to differentiate craniiforms and linguliforms from rhynchonelliforms, respectively.

## **Class Craniata**

### **Order Craniida**

Craniida is an extant order of craniiform brachiopod that first appeared in the Ordovician. It is represented by one species at Salmon Creek, *Petrocrania cf. hamiltoniae*, which is often found attached to the shells of larger brachiopods and bivalves (e.g., *Cypricardella bellistriata*) (Wilson, 2014). Only one specimen has been identified thus far and comes from the Fisher Gully Submember (Locality 3a).

## Subphylum Linguliformea

Linguliformea is an extant subphylum of inarticulate brachiopod that first appeared in the Early Cambrian. Linguliforms all possess equally sized valves as well as a long pedicle for burrowing in sediments (Santagata, 2015). Like craniiforms, linguliforms lack diductor muscles. Unlike other brachiopods, which often possess calcitic or aragonitic shells, linguliforms are more typically preserved by apatite (calcium phosphate), the same mineral that composes the vertebrate skeleton.

### Class Lingulata

#### Order Lingulida

Lingulida is an extant order of linguliform brachiopod where larvae have modified the lophophore for swimming and dispersion (Kuzmina & Malakhov, 2007). Lingulids are very rare at Salmon Creek and are represented by the species *Lingula delia*. The genus name “*Lingula*” is derived from Latin, meaning “little tongue”, in reference to its small, equally sized valves. It has long been considered a “living fossil” because *Lingula*-shaped brachiopods are known from the Cambrian to the Recent; all of these forms likely led similar epifaunal lifestyles as adult *Lingula*, with a long pedicle rooted in the sediment (Craig, 1952). Only three specimens of *L. delia* thus far are known: one from the lower *Modiomorpha-Ancyrocrinus* Bed (Locality 1a-1), one from the Tichenor Member (Locality 1a-T), and another from the Cuylerville Submember *Ambocoelia* Beds (Locality 1b; Plate 5e). Interestingly, the shell of the Tichenor specimen is apatitic.

## Subphylum Rhynchonelliformea

Rhynchonelliformea is an extant subphylum of articulate brachiopod (“Articulata”) that first appeared in the Early Cambrian. Rhynchonelliforms all possess an upward-facing pedicle valve, a rigid pedicle for attaching to hard substrate, and a brachidium, a calcified structure that supports the lophophore (Santagata, 2015). The brachidium is especially evident when preserved in spiriferids (Yuan et al., 2020).

### Class Rhynchonellata

#### Order †Athyridida

†Athyridida is an extinct order of rhynchonelliform brachiopod that first appeared in the Early Silurian. This taxon is best represented by the common species *Athyris spiriferoides*, formerly considered to be a spiriferid. *A. spiriferoides* are typically found with both pedicle and branchial valves intact but taphonomically deformed (dorsoventrally compressed). Stringers of *A. spiriferoides* commonly occur throughout the Spafford Member at Locality 1a-2. Individual, dorsoventrally compressed specimens are relatively abundant in both the Cuylerville Submember *Ambocoelia* Beds (Locality 1b) and *Ambocoelia*-rich Fall Brook Bed equivalent (Locality 3c-1; Fig. 12c). Athyridids disappeared in the Early Jurassic.

#### Order †Atrypida

†Atrypida is an extinct order of rhynchonelliform brachiopod that first appeared in the Middle Ordovician. Atrypids are represented by the species *Pseudoatrypa devonica*. *P. devonica* is a rather uncommon find at Salmon Creek, best documented at Locality 2 (upper Cuylerville Submember and Big Tree Submember Bay View Beds equivalent). However, it is probably

overlooked and occurs more frequently throughout Salmon Creek. More sampling for this species is required. Atrypids disappeared in the Frasnian as a result of the Kellwasser Biocrisis.

### Order †Orthida

†Orthida is an extinct order of rhynchonelliform brachiopod that first appeared in the Botomian (Cambrian Stage 4). Orthids are represented by two species of *Rhipidomella*: *R. leucosia* and *R. penelope*. Both species occur in the Cuylerville Submember *Ambocoelia* Beds (Locality 1b), with *R. leucosia* more common than *R. penelope*. *R. penelope* also occurs in the *Ambocoelia*-rich Fall Brook Bed equivalent (Locality 3c-1), but it is a rare find. Orthids disappeared in the Permian.

### Order Rhynchonellida

Rhynchonellida is an extant order of rhynchonelliform brachiopod that first appeared in the Late Ordovician. Rhynchonellids are represented by the species *Eumetabolatoechia multicostratum*, a characteristic indicator of relatively deep-water, dysoxic conditions within the Hamilton Group (Brett et al., 2023). Taphonomically deformed (dorsoventrally compressed) valves are very common in the Fisher Gully Submember (Locality 3a; Fig. 10b). *E. multicostratum* also occurs in the *Ambocoelia*-rich Fall Brook Bed equivalent (Locality 3c-1).

### Order †Spiriferida

†Spiriferida is an extinct order of rhynchonelliform brachiopod that first appeared in the Late Ordovician. Spiriferids are the most abundant brachiopod found at Salmon Creek. Generally, *Mucrospirifer mucronatus* is the most common spiriferid, especially in the Ludlowville Formation at Locality 1a. Within the Moscow Formation, *Ambocoelia umbonata* is exuberant, defining both the Cuylerville Submember *Ambocoelia* Beds (Locality 1b; Plate 5f) and *Ambocoelia*-rich Fall Brook Bed equivalent (Locality 3c-1; Fig. 12d). Uncommon spiriferids include the larger species *Mediospirifer audaculus* (Fig. 12c) and *Spinocyrtia* cf. *granulosa* (both of which are members of family †Spinocrytidae). Uncompacted specimens of *S.* cf. *granulosa* are rare finds in the Spafford Member (Locality 1a-2; Fig. 5c) and lower Fall Brook Bed equivalent (Locality 3b; Plate 9b). Sheared specimens have been occasionally found in the upper Cuylerville Submember (Locality 2). Spiriferids disappeared in the Triassic.

### Order †Tropidoleptida

†Tropidoleptida is an extinct order of rhynchonelliform brachiopod. Tropidoleptids are represented by one species, *Tropidoleptus carinatus*, which was historically considered an orthid. The family †Tropidoleptidae has now been elevated to ordinal status within Rhynchonellata (Harper et al., 2010). *T. carinatus* is quite common in the Ludlowville Formation (Locality 1a). It is also well represented by calcitic valves in the upper Taunton Submember (Locality 2-T). This species is probably undersampled throughout Salmon Creek and requires further searching.

## Class Strophomenata

### Order Productida

Productida is an extant order of rhynchonelliform brachiopod that first appeared in the Silurian. Productids are represented by the species *Arcuaminetes* (*Devonochonetes*) *scitulus* and *Devonochonetes coronatus*. Both species are common finds, and they even co-occur in the upper Cuylerville Submember (Locality 2). Stringers of *D. coronatus* are typical in the Spafford

Member (Locality 1a-2; Fig. 5b). This species is also found in great abundance within split calcareous concretions in this unit (Plate 2f). Productids disappeared in the Early Triassic.

### **Order †Strophomenida**

†Strophomenida is an extinct order of rhynchonelliform brachiopod that first appeared in the Ordovician. Strophomenids are known for their large, inflated pedicle valves and thin branchial valves. Three species of strophomenid are known from Salmon Creek: *Megastrophia concava*, *Mesoleptostrophia junia*, and *Strophodonta demissa*. *S. demissa* is the most common species, occurring in the Ludlowville Formation (Locality 1a) and upper Taunton Submember (Locality 2-T) with calcitic valves preserved. *M. concava* and *M. junia*, on the other hand, are much rarer, generally restricted to the lower Windom Member (Plate 6-1c). However, calcitic valves of *M. junia* are rather uncommon in the upper Taunton Submember (Locality 2-T; Plate 8d). Strophomenids disappeared in the Permian.

### **Phylum Bryozoa (“moss animals”)**

Bryozoa (Ectoprocta) is an extant phylum of colonial lophophorate that resemble corals and hydroids. It was long thought to be the only major animal phylum absent during the Cambrian Explosion, appearing later in the Early Ordovician, but new evidence suggests a Stage 3 origin that agrees with molecular clock estimates (Zhang et al., 2021). About 6,000 species can be found today, often attached to other organisms such as macroalgae (seaweeds) in the subtidal zone (Liuzzi & Gappa, 2011).

An individual bryozoan is known as a zooid, and each zooid is enclosed in a calcareous exoskeleton and attached to the colony by a stolon. Each zooid has a specialized function to serve the larger colony, such as feeding, defending, reproducing, or removing excess sediments. Bryozoan colonies come in many different shapes, from encrusting and sheet-like to branched forms (Benton & Harper, 2020).

Bryozoans are generally rare finds at Salmon Creek. They are much more common in nearby outcrops to the south, such as the Ithaca Formation (Frasnian) at Cascadilla Gorge and Six Mile Creek in Ithaca, NY.

### **Class Stenolaemata: tubular bryozoans**

Stenolaemata is an extant class of bryozoan that first appeared in the Ordovician. Stenolaemates typically possess cylindrical, or tube-like, zooids (hence their common name, the tubular bryozoans) (Bock et al., 2018). Two orders of stenolaemate are present at Salmon Creek – all are generally rare and occur in select stratigraphic units.

### **Order †Cystoporata**

†Cystoporata is an extinct order of branching stenolaemate bryozoan that first appeared in the Ordovician. Cystoporates very rarely occur in the Spafford Member (Locality 1a-2), but are very common in the upper Taunton Submember (Locality 2-T). The upper Moscow specimens are even colored dark blue due to preservation of their calcitic exoskeletons. The Salmon Creek cystoporates have yet to be identified to the species level. In the Ithaca Formation (Frasnian) at Cascadilla Gorge and Six Mile Creek to the south (Ithaca, NY), the cystoporates *Sulcoretepora* cf. *incisurata* and *Taenipora* cf. *exigna* are very common in shell lags. They often co-occur with

crinoid ossicles and spiriferid valves, and are colored bright red as a result of iron oxide replacement. Cystoporates disappeared in the Triassic.

### **Order †Trepostomata**

†Trepostomata is an extinct order of encrusting stenolaemate bryozoan that first appeared in the Early Ordovician. Trepostomates are represented at Salmon Creek by the species *Leptotrypella furcata*. Sheet-like mats of *L. furcata* can be found in relative abundance in particular sections of the lower Moscow (Locality 1a-T; Plate 4b). This species can sometimes be confused with stromatoporoid sponges, which possess similar mound-like structures called mamelons. Trepostomates disappeared in the Triassic.

**Phylogenetic context on Clade Deuterostomia:** Deuterostomia (“mouth second”) is an extant clade of bilaterian metazoan where the blastopore becomes the anus during development (Benton & Harper, 2020; Martín-Durán et al., 2016). Deuterostomes first appeared in the earliest Cambrian. They include two subclades: (1) Ambulacaria (see ‘*Phylum Echinodermata*’ for further discussion) and (2) Chordata.

### **Phylum Chordata: lancelets, tunicates and salps, and vertebrates**

Chordata is an extant phylum of deuterostome that first appeared during the Cambrian Explosion (Stage 3). Chordates include three subphyla: Cephalochordata (lancelets, such as *Branchiostoma*), Urochordata (tunicates and salps), and Vertebrata (vertebrates: “fishes”, amphibians, “reptiles”, birds, and mammals). All chordates possess a notochord (a midline structure that provides support and regulates embryonic development), a dorsal nerve cord, an endostyle (a secretory and locomotor organ), and a postanal tail (Satoh et al., 2014; Corallo et al., 2015; Olsson, 1963). Some of these characters are only present in the embryological stage of the chordate subphyla. Urochordates, for instance, resorb the notochord, nerve cord, and postanal tail during their metamorphosis from free-swimming larvae to sessile adults, retaining only the endostyle throughout ontogeny (Paululat & Purschke, 2025).

### **Subphylum Vertebrata: “fishes”, amphibians, “reptiles”, birds, mammals**

Vertebrata is an extant subphylum of chordate that first appeared during the Cambrian Explosion (Stage 3). All vertebrates possess a head, a tripartite brain, a muscular pharynx, and vertebrae (Bemis et al., 2023). Note that vertebrae are not notochord. The notochord is greatly reduced in most adult vertebrates, the remnants of which can be found in the intervertebral disks. Most vertebrate characters (head, tripartite brain, muscular pharynx) decay much earlier than chordate features (notochord), making many early diverging vertebrates, such as “agnathans” (jawless fishes), appear “less evolved” and more like ancestral forms. This phenomenon is known as stemward slippage, where taphonomic processes bias our understanding of the timing of vertebrate origins (Benton & Harper, 2020; Sansom et al., 2010).

During the Givetian, vertebrates are represented only by “fishes”, as tetrapods (four-limbed terrestrial vertebrates) do not originate until the subsequent Frasnian. Evidence of the invasion of land by tetrapods can be seen as locally as outcrops of the Catskill Formation (Famennian) in northcentral Pennsylvania. In the Appalachian Basin of western and central New York State, several classes of fishes can be found as fossils: †Conodonts, †“Placoderms”, Chondrichthyes (Acanthodii), and Sarcopterygii.

## **Infraphylum “Agnatha” (“without jaws”): jawless vertebrates**

### **Class †Conodonta (“cone teeth”)**

†Conodonta is an extinct class of “agnathan” (jawless vertebrates) that first appeared in the Middle Cambrian. Conodonts are typically represented by individual tooth-like structures called conodont elements. Owing to their widespread geographic distributions, short time ranges, and diagnostic types (e.g., platforms, bars and blades, cones), these elements are the most important index fossils for biostratigraphic correlation, and have been used to define hundreds of biozones throughout the Paleozoic and Mesozoic geological records (e.g., Cambrian and Ordovician, Tai-Xiang, 1981; Silurian-Devonian boundary, Carls et al., 2007; Carboniferous, Barrick et al., 2022; Permian, Henderson, 2018; Permian-Triassic boundary, Nicoll et al., 2002; Triassic, Sweet et al., 1970). More locally, conodont elements have been used to refine the stratigraphy of the Middle and Upper Devonian of the southern Appalachian Basin (Over, 2007) as well as the Devonian-Mississippian boundary (Corradini et al., 2017).

Despite their biostratigraphic utility, the conodont animal was not known until 1983, where various element types were found in-situ within the head of an elongate, soft-bodied animal from the Lower Carboniferous of Edinburgh, Scotland (Briggs et al., 1983). It was later determined that the conodont animal was a relative of, albeit much more derived than, extant cyclostomes (lampreys and hagfishes) (Donoghue et al., 2000). Conodonts disappeared during the Hattengian (earliest Jurassic) following the end-Triassic mass extinction event. After the extinction of conodonts, ammonites and calcareous nannoplankton (protists) are used for biostratigraphic correlation for the remainder of the Mesozoic and subsequent Cenozoic, among other taxa.

Due to their small size, conodonts have not been sampled for at Salmon Creek, though they are more than likely present throughout the exposed Ludlowville and Moscow formations.

### **Infraclass Gnathostoma (“jaw mouth”): jawed vertebrates**

No gnathostome (jawed vertebrate) fossils have been found at Salmon Creek thus far. The absence of large fish material from Salmon Creek is likely due to the central position of Salmon Creek in the Appalachian Basin during the Givetian – fish diversity was likely greatest along the nearshore margins, to the east and west of Salmon Creek (Fig. 1b). Those that ventured into the central basin probably did not spend much time there, or were restricted to the pelagic realm. However, the presence of fossilized plant material, including even one lycophyte specimen (Plate 6-2j), represents the potential for large fish material (e.g., the armored plates of “placoderms”, fin spines of acanthodians, or phosphatic teeth of sarcopterygians) to occasionally be transported to the central basin from elsewhere. These fossils, if found, would represent exceptionally rare specimens.

### **Class †“Placodermi” (“plated skin”)**

Although vertebrate macrofossils have not been documented at Salmon Creek thus far, there have been two local reports of large fish material, both plates (dermal armor) of “placoderms”. †“Placodermi” is an extinct class of gnathostome (jawed vertebrates) that first appeared in the Llandovery (earliest Silurian). Despite paraphyly, all “placoderms” share simple jaws composed of two or three pairs of gnathals (bony tooth plates) that were used to crush armored prey, such as shelled invertebrates and bony vertebrates (Goujet & Young, 2004). The first locally reported

“placoderm” is a posterior dorsolateral (PDL) plate of the arthrodire *Dinichthys*. It came from an older section of the Ludlowville Formation, the Ashantee (lower Centerfield Member), exposed at Reeder Creek (eastern drainage of Seneca Lake) in Romulus, NY, about 55 km northwest of Lansing. The other specimen is an undetermined plate of another arthrodire, *Holonema*. The plate was found in the upper Ithaca Formation (Frasnian) exposed at Fall Creek on Cornell University campus in Ithaca, NY. Both specimens, particularly the *Dinichthys* PDL plate, demonstrate the potential, albeit exceptionally rare, for vertebrate material to be found at Salmon Creek. “Placoderms” disappeared at the end of the Devonian as a result of the Hangenberg Biocrisis.

### Phylum Cnidaria (“nettle bearers”): jellies, corals, and allies

Cnidaria is an extant phylum of parahoxozoan that includes jellies, corals, and allies. Cnidarians first appeared in the Ediacaran. They are all radially symmetric, and possess cnidocytes (stinging cells) and a mouth surrounded by tentacles. Most alternate life cycles between a polyp (sessile) and medusa (mobile) stage, a life history pattern known as alteration of generations (Paululat & Purschke, 2025). In contrast to bilaterians, which are triploblastic (possess three cell layers: endo-, meso-, and ectoderm), cnidarians are generally considered to be diploblastic (two cell layers: endo- and ectoderm). However, this may be an oversimplification of reality, as cnidarians possess mesoderm-like genes that may represent a secondary loss of triploblasty during their evolutionary history (Martindale et al., 2004).

At Salmon Creek, fossil cnidarians are represented by two subclasses of anthozoans (corals) as well as †conulariids, an extinct order of Problematica (see ‘*Incertae Sedis*’ for further discussion).

### Class Anthozoa: corals and sea anemones

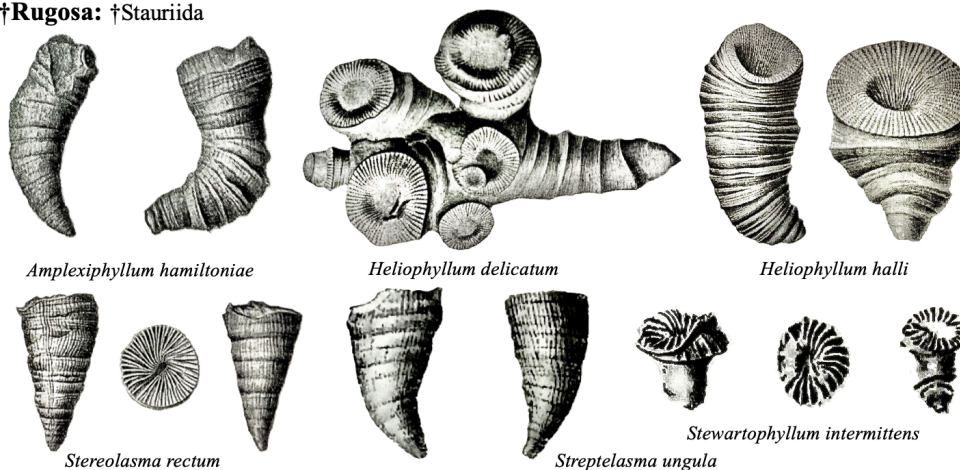
Anthozoa is an extant class of cnidarian that first appeared in the Ediacaran. Anthozoans include fossil and living corals (Scleractinia). Two subclasses of fossil corals can be found at Salmon Creek, (1) †Rugosa and (2) †Tabulata. Both rugose and tabulate corals first appeared in the Ordovician and went extinct during the end-Permian mass extinction event (Benton & Harper, 2020). Interestingly, after the disappearance of rugose and tabulate corals, there were no corals in the oceans for at least 14 million years until the appearance of modern scleractinian corals (Stanley, 2003).

#### **Subclass †Rugosa: horn corals**

†Rugosa is an extant subclass of anthozoan that first appeared in the Ordovician. Rugosans include both solitary and colonial corals. Rugose corals were nestlers that sat in the mud on the ocean bottom. Some rugose corals, like *Amplexiphyllum*, grew tall rapidly and would regrow vertically when fallen over (Wilson, 2014); these are called geniculate corals. Others, like *Stereolasma*, almost always grew vertically in a steep-sided conical shape that rarely toppled or showed kinks.

## Order †Stauriida

†Rugosa: †Stauriida

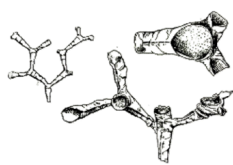


**Appendix 1 Plate 3-1.** Phylum Cnidaria: Class Anthozoa: Subclass †Rugosa: Order †Stauriida: *Amplexiphyllum hamiltoniae*, *Heliophyllum delicatum* and *H. halli*, *Stereolasma rectum*, *Streptelasma unguia*, and *Stewartophyllum intermittens*. Modified from Wilson (2014).

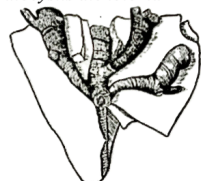
†Stauriida is an extinct order of rugosan represented by seven species at Salmon Creek. Both genticulate and non-genticulate types can be found in the Bay View Beds equivalent at Locality 2. Here, the non-genticulates *Stereolasma rectum* (Plate 7c) and *Streptelasma unguia* (Fig. 12c; Plate 7a) are more common than the genticulates *Amplexiphyllum hamiltoniae* and *Heliophyllum delicatum* (Plate 7d). Stauriids also typically occur in the *Ambocoelia*-rich Fall Brook Bed equivalent at Locality 3c-1. These include *S. unguia* and *Stewartophyllum intermittens*. On one rare occasion, a large specimen of the solitary rugose coral *Heliophyllum halli* was recovered from the Spezanno Gully Submember South Lansing Beds (Locality 2-T).

## Subclass †Tabulata

†Tabulata: †Auloporida

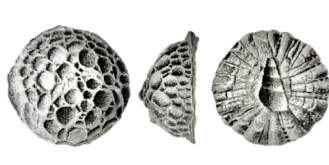


*Aulocystis dichotoma*



*Aulocystis jacksoni*

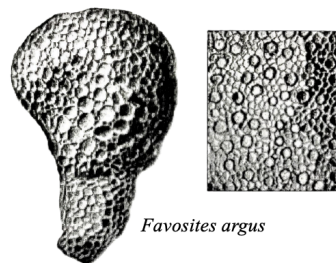
†Tabulata: †Favositida



*Pleurodictyum americanum*



*Thamnopychia limbata*



*Favosites argus*



*Favosites hamiltoniae*

**Appendix 1 Plate 3-2.** Phylum Cnidaria: Class Anthozoa: Subclass †Tabulata: Order †Auloporida: *Aulocystis dichotoma* and *A. jacksoni*. Order Favositida: *Favosites argus* and *F. hamiltoniae*, *Pleurodictyum americanum*, and *Thamnopychia limbata*. Modified from Wilson (2014).

†Tabulata is an extinct subclass of anthozoan that first appeared in the Ordovician. Tabulate corals are entirely colonial. The shape of a colony varies from sheet-like to branching forms. It has been proposed that tabulate corals, like their scleractinian relatives, may have had photosymbionts (Zapalski, 2014; Jung et al., 2024).

### **Order †Auloporida**

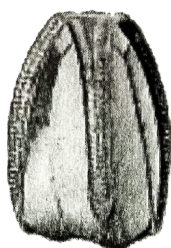
†Auloporida is an extinct order of branching tabulate coral that possess tube-like corallites often found encrusted on biological substrates, such as brachiopods, stromatoporoid sponges, and other corals. At Salmon Creek, auloporids are represented by two species of *Aulocystis*: *A. dichotoma* and *A. jacksoni*. Both are very rare finds, with *A. dichotoma* documented from the lower Moscow (Locality 1a-T; Plate 4c), Cuylerville Submember *Ambocoelia* Beds (Locality 1b; Plate 5g) and upper Taunton Submember (Locality 2-T); and *A. jacksoni* from the upper Cuylerville Submember (Locality 2; Plate 7b). The lower Moscow specimen of *A. dichotoma* was found encrusted on a larger tabulate coral *Thamnoptychia limbata* along with other epibionts (Plate 4d), and one from the *Ambocoelia* Beds is encrusted on the spiriferid brachiopod *Mediospirifer audaculus* (Plate 5g).

### **Order †Favositida**

†Favositida is an extinct order of tabulate coral that first appeared in the Ordovician. Tabulates are represented by three genera at Salmon Creek: *Favosites*, *Pleurodictyum*, and *Thamnoptychia*. The honeycomb coral (genus *Favosites*) forms massive colonies throughout the Tichenor Member (localities 1a, 1b; Fig. 6). It is especially abundant in the Spezzano Gully Submember South Lansing Beds (Locality 2-T; Plate 8e). *Pleurodictyum americanum* is a smaller, massive type that can be found in the lower Moscow (Locality 1b-T), Bay View Beds equivalent (Locality 2; Plate 7e), lower Fall Brook Bed equivalent (Locality 3b), and *Ambocoelia*-rich Fall Brook Bed equivalent (Locality 3c), though it is generally quite rare. In certain sections of the lower Moscow, large branching colonies of the favositid *Thamnoptychia limbata* are common (Locality 1a-T; Plate 4d). These colonies host a diversity of epibionts, including colonies of smaller tabulate corals (e.g., *P. americanum*) and bryozoans, crinoids, and even gastropods. *T. limbata* is also recorded from the Spafford Member (Locality 1a-2), but from very limited occurrences.

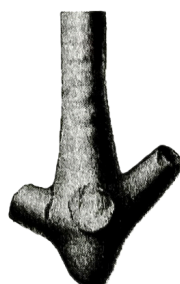
## **Phylum Echinodermata (“spiny skin”): sea stars, sea urchins, and allies**

### **Echinodermata:** †Blastoidea

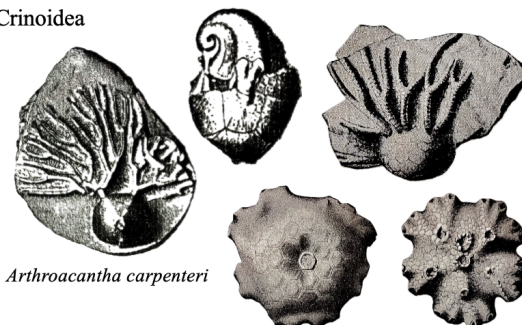


*Devonoblastus leda*

### **Echinodermata: Crinoidea**



*Ancyrocrinus bulbosus*



*Arthroacantha carpenteri*

*Megistocrinus depressus*

**Appendix 1 Plate 4.** Phylum Echinodermata: Class †Blastoidea: Order †Pentremitida: *Devonoblastus leda*. Class Crinoidea: Subclass †Camerata: *Ancyrocrinus bulbosus* and

*Arthroacantha carpenteri*; Subclass Pentacrinoidea: *Megistocrinus depressus*. Modified from Wilson (2014).

Echinodermata is an extant phylum of deuterostome that first appeared during the Cambrian Explosion (Stage 3). Echinoderms are united by the presence of pentaradial (also pentamous, pentamerous) symmetry (five-part symmetry, a unique type of bilateral symmetry), an internal water vascular system, and tube feet modified for locomotion, respiration, and digestion (Benton & Harper, 2020). They are a strictly marine radiation with no freshwater or terrestrial descendants.

Echinodermata is the sister group to Hemichordata. Sometimes these phyla are collectively referred to as Ambulacraria, as they both undergo two larval stages during ontogeny. They begin as (1) planktotrophs (ciliated filter feeding larvae) and then metamorphose into (2) reserve-trophs (non-ciliated and non-feeding larvae) before becoming adults (Malakhov et al., 2025).

Crown Echinodermata include five classes: Asteroidea (sea stars), Crinoidea (sea lilies), Echinoidea (sea urchins and sand dollars), Holothuroidea (sea cucumbers) Ophiuroidea (brittle stars). †Blastoidea (sea buds), †Edrioasteroidea, and †Homoiosteala (solutes) are three examples of echinoderm stem classes. Of these, blastoids and crinoids can be found at Salmon Creek. Crinoids are very common throughout the Hamilton Group, whereas blastoids are much rarer.

### **Class †Blastoidea: sea buds**

†Blastoidea is an extinct class of stem echinoderm (Subphylum †Blastozoa) that all possess pentaradial symmetry, short stalks, hydrospires (respiratory structures), and five spiracles surrounding the mouth (Benton & Harper, 2020), vaguely resembling small hickory nuts (hence their common name, the sea buds). They first appeared in the Middle Ordovician and disappeared at the end of the Permian. Generally, blastoids are rare finds throughout the Hamilton Group of western and central New York State. Thus far, only one potential blastoid specimen, the calyx of the pentremiid *Devonoblastus leda*, has been reported from the Spafford Member (Locality 1a-2). Blastoids occur in greater relative abundance in outcrops to the west, such as the Kipp Road Beds (Moscow Fm: Deep Run Mbr) along Canandaigua Lake (Mayer et al., 1991).

### **Class Crinoidea: sea lilies**

Crinoidea is an extant class of crown echinoderm (Subphylum Crinozoa) that resemble flowering plants (angiosperms). Crinoids first appeared in the Early Ordovician, and both stalked and stalkless forms were abundant throughout the Paleozoic. Today they are less common, with stalked forms inhabiting cryptic habitats such as deep-water environments, like brachiopods. This is another example of Sar's Paradigm (Amezziane & Roux, 1997).

Some crinoids have root-like holdfasts to attach themselves to the seafloor. This structure has been derived into the anchor-like cirral grapple of the cladid *Ancyrocrinus bulbosus* to secure itself against the current. Interestingly, the cirral grapple of *A. bulbosus* has four-part symmetry, as opposed to the typical pentaradial symmetry seen in other echinoderms. One of these cirral grapples have been recovered from the upper *Modiomorpha-Ancyrocrinus* Bed (Locality 1a-1; Plate 1a).

The stalk, or stem, is made up of many individual components called ossicles (or columnals). Crinoid ossicles are probably the second most abundant fossil in western and central New York State, after brachiopods. This is especially true for Frasnian outcrops to the south (e.g., Ithaca Formation at Cascadilla Gorge and Six Mile Creek), where time-averaged “death assemblages” of ossicles occur in dense shell lags, numbering in the hundreds to thousands. Similar assemblages of crinoid ossicles can be most reliably found in the Bay View Beds equivalent (Locality 2; Fig. 8b) and overlying Smoke Creek Bed. Like their sea star relatives, crinoids disarticulate after death, which is why they are so commonly found as individual ossicles. Unfortunately, identifying crinoid ossicles lower taxonomic ranks (e.g., species) is very difficult and often impossible.

Sometimes, crinoids are immediately buried after death, allowing for preservation of articulated stalks and even calyces. Crinoid runners (long articulated sections of stalks) occur sandwiched between individual beds of *Zoophycos*-churned mudstone in the upper Cuylerville Submember (Locality 2). In the lower Moscow (Locality 1a-T), small taphonomically deformed runners have been recovered that are compressed (subrectangular) in shape.

Typically, five arms arise from the crinoid calyx and may branch multiple times, providing a large area for suspension feeding tube feet (Wilson, 2014). In one instance, a partial calyx (columnal insertion and infrabasals) of the camerate crinoid *Megistocrinus depressus* was recovered as float from the Bay View Beds equivalent (Locality 2; Plate 7f). This specimen represents the only crinoid calyx found at Salmon Creek. However, the camerate *Arthroacantha* has also been reported to come from the Windom Member, though the bed it occurs in has yet to be identified by the authors. Crinoid calyces are generally more common in outcrops to the west. At the Kipp Road Beds (Moscow Fm: Deep Run Mbr) along Canandaigua Lake, for example, calyces of the genera *Gennaeocrinus*, *Griphocrinus* (*Rhodocrinus*), *Dolatocrinus*, and *Megistocrinus* are well documented (Mayer et al., 1991).

Complete crinoid fossils (holdfasts, stalk, and calyx all articulated) are very rare owing to the requirements necessary for preservation. They have not yet been documented from Salmon Creek.

### **Class †Soluta: “carpoids”**

†Soluta (†Homioστεlea) is an extinct class of stem echinoderm (Subphylum †Blastozoa), though they have also been interpreted as stem chordates (Smith, 2005). Solutes are one of four “carpoid” classes. They are diagnosed by an asymmetrical body with two appendages. The posterior tail-like appendage is longer and bilaterally symmetric; it sometimes served a similar rooting function as the holdfast in crinoids. The anterior antenna-like appendage is offset laterally and may have served a feeding role (Rahman, 2009). Solutes first appeared in the Drumian (Middle Cambrian) and were once thought to have disappeared in the Early Devonian until two specimens were discovered in the Smoke Creek Bed at Penn Dixie Quarry (near Buffalo, NY) in 2023, extending their stratigraphic range into the Givetian. No solutes have been found at Salmon Creek thus far; more searching of the Smoke Creek Bed, though much thinner at Salmon Creek than Penn Dixie, is certainly warranted.

## Phylum Hemichordata (“half string”): acorn worms and allies

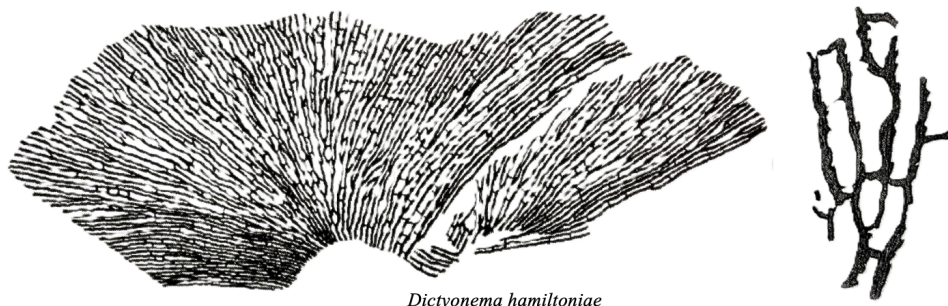
Hemichordata is an extant phylum of bilaterally symmetric and non-segmented ambulacrarian deuterostome that first appeared during the Cambrian Explosion (Stage 3). There are two classes of hemichordate: Enteropneusta (acorn worms) and Pterobranchia, both of which are extant. Enteropneusts are infaunal burrowers that are commonly found in the muddy intertidal zone (e.g., *Balanoglossus*). However, they also occur in deeper waters (Kaul-Strehlow & Röttinger, 2015). It has been proposed that enteropneusts represent the ancestral condition of Deuterostomia; i.e., a benthic vermiform bilaterian that undergoes direct development and possesses a mouth, an anus, and a pharynx with gill slits, among other characters (Cameron, 2005). Owing to their soft bodies and absence of hard parts, enteropneusts are exceptionally rare throughout the fossil record and therefore would not be found at Salmon Creek.

### Class Pterobranchia: *Rhabdopleura*, *Cephalodiscus*, and allies

Pterobranchs are very small colonial animals that function similarly to corals and bryozoans. Like enteropneusts, pterobranchs have a global distribution and occur at all depths (Kaul-Strehlow & Röttinger, 2015). Unlike enteropneusts, however, pterobranchs are very derived, having lost many of their basal deuterostome features, opting instead for tubes for colonial living (Cameron, 2005). Modern pterobranchs are sessile and restricted to the benthos (e.g., *Rhabdopleura*, *Cephalodiscus*), whereas many fossil forms (e.g., graptolites) were planktonic (Benton & Harper, 2020).

### Subclass Graptolithinia (“written rocks”): graptolites

**Pterobranchia:** Graptolithinia



*Dictyonema hamiltoniae*

**Appendix 1 Plate 5.** Phylum Hemichordata: Class Pterobranchia: Subclass Graptolithinia: *Dictyonema hamiltoniae*. Modified from Wilson (2014).

Graptolithinia is an extant subclass of pterobranchs whose appearance can be confused for bryozoans. Graptolites were once believed to be extinct until *Rhabdopleura* was demonstrated to be the sole living graptolite genus (Mitchell et al., 2012).

A graptolite colony is referred to as a rhabdosome (or tubarium). Rhabdosomes grow outwards from the sicula, either as one unit or from branching stipes. Lateral dissepiments sometimes connect the stipes. Thecae develop along the stipes, housing the individual zooids (note that this term is shared with Bryozoa) (Benton & Harper, 2020).

Like conodonts, graptolites are among the most useful index fossils for biostratigraphic correlation, especially in the early Paleozoic, owing to their widespread geographic distributions, short time ranges, and diagnostic forms (Storch et al., 2024).

At Salmon Creek, graptolites are very rare. Two rhabdosomes of the dendroid (branching, tree-like) *Dictyonema hamiltoniae* have been recovered from the Tichenor Member (Locality 1a-T; Plate 3c).

## **Ichnotaxa: trace fossils**

As opposed to body fossils, which preserve the hard, and sometimes soft, parts of organisms from the past, trace fossils record the behavior of an organism in the past (Seilacher, 1967). Trace fossils include all sorts of activities, such as locomotion, dwelling, resting, feeding, and predation. Three “ichnomorphological classes” (our term for the ethological classes from Seilacher, 1953; i.e., groups of trace fossils with a shared morphology, proxying a shared behavior) are documented at Salmon Creek: cubichnia (resting traces), fodinichnia (feeding traces), and repichnia (locomotion traces).

Since many different kinds of organisms could have made the trace fossils seen at Salmon Creek (e.g., polychaetes, enteropneusts, arthropods), and all trace fossils more generally, trace fossil taxonomic names refer to the morphology of the structure and not the maker of it. For example, *Zoophycos* is a fodinichnia found from the Early Ordovician to the present, implying that many organisms (and not just one species) could produce this structure throughout deep time.

### **Ichnomorphological Class Cubichnia: resting traces**

Cubichnia (Seilacher, 1953) are a class of trace fossil represented by *Rusophycus*, inferred to be the resting trace of a marine arthropod (Donovan, 2010), most likely a small trilobite at Salmon Creek. *Rusophycus* can be found in the Cuylerville Submember *Ambocoelia* Beds (Locality 1b) as well as the overlying upper Cuylerville Submember (Locality 2). Interestingly, three *Ambocoelia* Beds specimens are associated with the loxonematoid *Palaeozygopleura hamiltoniae*, indicating feeding behavior (likely scavenging) by a trilobite on the shells of these gastropods (Plate 5c). Further, the upper Cuylerville specimen abuts a heavily phoronid-fouled orthoconic nautiloid *Michelinoceras telamon* (Plate 6-2f). This association of trace and body fossils is interpreted as another instance of trilobite scavenging. See ‘*Paleoecology of Salmon Creek and Ludlowville Falls II*’ for further discussion about all three specimens.

### **Ichnomorphological Class Fodinichnia: feeding traces**

Fodinichnia (Seilacher, 1953) are a class of trace fossil represented by *Zoophycos*, inferred to be the systematic probing motions of a proboscis of an endobenthic “worm” feeding on organic detritus in the sediment to provide the greatest area for food while spending the least amount of energy when feeding. *Zoophycos* occur in great abundance in the lower Moscow (Locality 1a-T; Plate 4e). It is also quite common along the concretionary ledge of the Spafford Member (Locality 1a-2), Tichenor Member (Locality 1a-T), and upper Cuylerville Submember (Locality 2). Within the Tichenor, lower Moscow, and upper Cuylerville Submember of the Windom Member, individual beds appears to follow a successional pattern: (1) large sweeping arcs of *Zoophycos*; (2) well preserved molds of orthoconic nautiloids; and (3) high species diversity, particularly among spiriferids, palaeoheterodonts, and productids. This pattern likely reflects a

well-oxygenated bottom that enabled life to flourish both within and above the sediment interface at all three stratigraphic units. However, this may alternatively be simply a taphonomic artefact of storm beds in highstand systems as opposed to opportunistic strategy exploited by an animal (Sedorko et al., 2018).

### **Ichnomorphological Class Repichnia: locomotion traces**

Repichnia (Seilecher, 1953) are a class of trace fossil represented by simple burrows, a form of bioturbation where sediment is reworked by the movement of organisms. Small, in-filled burrows can be found in the Smoke Creek Bed (Locality 2; Fig. 8c). Similarly, medium-sized concretions, likely following the path of burrows, can be seen cutting across individual shell beds of spiriferids in the lower Fall Brook Bed equivalent (Locality 3b; plates 9c, 9d). Very large burrows, most likely made by trilobites, can be seen underneath Ludlowville Falls within the base of the Tully Limestone (Locality 3c-2; Fig. 12f).

### **Incertae Sedis (Problematica): problematic fossils**

Problematic fossils such as *Plumalina*, †Conulariida, †Hyolitha, and †Tentaculita are collectively referred to as “Problematica” or Incertae Sedis taxa, as they all are extinct clades with uncertain broader relationships to the 36 currently recognized animal phyla (Foote et al., 2007). In Appendix I Figure 1, the Problematica documented from Salmon Creek have been placed within their respective least inclusive taxon based on the most recent phylogenetic (morphological) evidence: †Conulariida as basal Medusozoa, †Hyolitha as basal Lophotrochozoa, and †Tentaculita as basal Lophophorata.

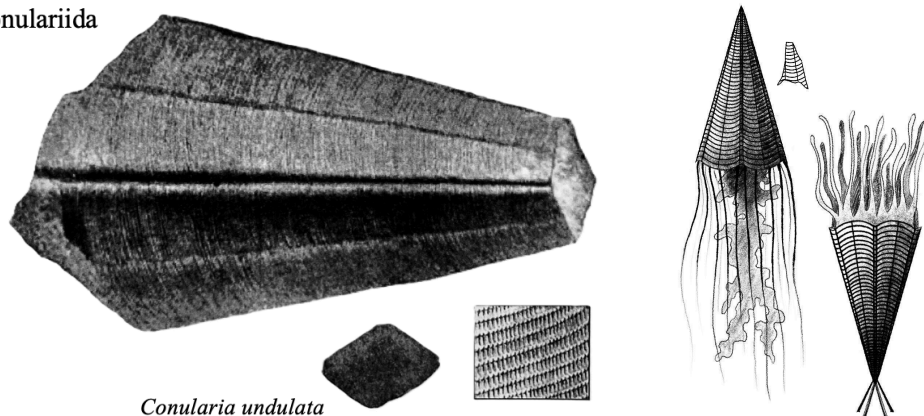
#### ***Plumalina* spp.**

Note that *Plumalina* is absent from Salmon Creek. Locally, two species of *Plumalina*, *P. brevis* and *P. plumaria*, occur just to the south in Ithaca Formation (Frasnian) outcrops. *Plumalina* is believed to be a genus of colonial leptothebate hydrozoan (Medusozoa), but it has also been described as a coral, crinoid, and graptolite (Maletz et al., 2025). Each individual consists of a feather-like frond called a hydrocalus that connects to the rest of the colony via a stolon. Each frond includes many hydrocladia that branch off from the central stalk (Muscente & Allmon, 2013). Often, hydrocali are found aligned in the same direction. Thus, the orientation of *Plumalina* can be used to infer the direction of marine currents during the Frasnian of central New York State.

*P. brevis* co-occurs with *P. plumaria* at Fall Creek, Cascadilla Gorge, and Six Mile Creek (Ithaca, NY). *P. brevis* can be differentiated from *P. plumaria* by the length of the hydrocladia, and both species are never found in the same horizon.

## Order †Conulariida

Incertae Sedis: †Conulariida



*Conularia undulata*

**Appendix 1 Plate 6-1.** Incertae Sedis: Order †Conulariida: *Conularia undulata*. Modified from Wilson (2014). Life reconstruction of *Conularia undulata* depicting both hypothesized lifestyles (nektonic and jelly-like; and sessile and coral-like) by WCH.

†Conulariida is an extinct order of Problematika that first appeared during the Ediacaran. They are known primarily from external pyramidal shells called tests, or periderm (Mergl et al., 2016). The tests possess a unique four-fold (tetramous) symmetry, and each test face contains many rows of calcium phosphate rods, referred to as either lamellae or transverse ribs (Wilson, 2014). As durophagy intensified during the “Middle Paleozoic Revolution” (Signor & Brett, 1984; Brett & Walker, 2002; Brett, 2003), some conulariids responded by reinforcing their tests with phosphatic tubercles (Mergl et al., 2016). They persisted until the end of the Triassic (Van Iten et al., 2014), when they were most likely overwhelmed by the new durophagous predators of the Mesozoic.

Exceptional preservation of soft tissue reveals that tentacles emerged from the apertural end of the conulariid test (Marques & Collins, 2004; Van Iten et al., 2006). Thus, conulariids likely share affinities with Medusozoa, the cnidarian class that includes jellies and allies (Appendix 1 Fig. 1). If true, conulariid tentacles likely contained cnidocytes to aid with immobilizing prey. It is unclear whether conulariids were nektonic or sessile. Soft preservation of a holdfast-like structure on the apical end indicates that conulariids lived attached to substrates, convergently resembling anthozoans, particularly sea anemones (Brood, 1995; Appendix 1 Plate 7-1).

Two conulariids have been recovered from Salmon Creek. The first is a very small periderm test (that is too small to identify to the species level, but most likely *Conularia* sp.) from the lower *Modiomorpha-Ancyrocrinus* Bed (Locality 1a-1), and the second is a partial periderm test of *Conularia undulata* from the upper Cuylerville Submember (Locality 2; Plate 6-1e).

Like *Eldredgeops* and *Plumalina*, conulariids are also components of the Recurrent Hamilton Fauna, persisting into the Frasnian after the Taghanic Biocrisis. Locally, a well preserved periderm test face of *Conularia continens* was found just south of Salmon Creek in the Ithaca Formation exposed at Six Mile Creek in Ithaca, NY.

## Class †Hyalitha

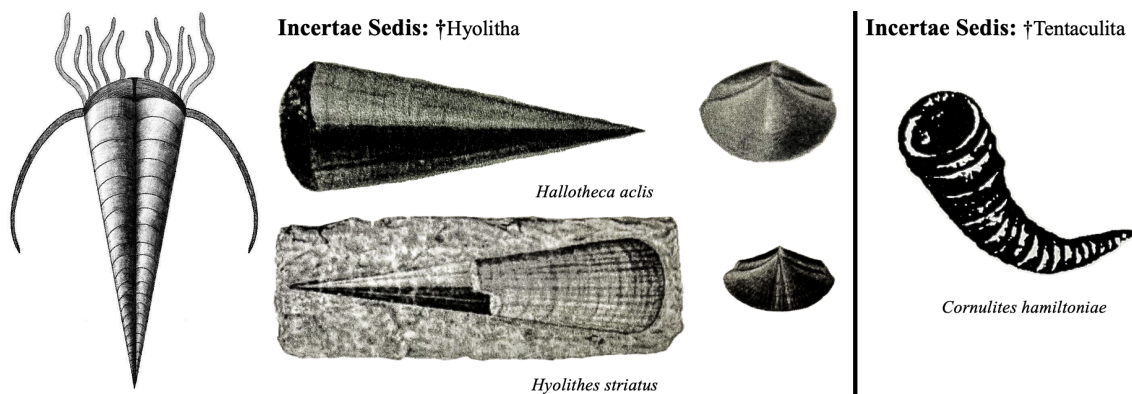
†Hyalitha is an extinct class of Problematica that first appeared in the Cambrian and disappeared during the end-Permian. Hyoliths are known from calcareous pyramidal tests with thin lamellae. They are generally much smaller than conulariids, and uniquely possess an operculum (a trapdoor-like structure also seen in many gastropods and used to seal off the exposed soft parts from predators) and sometimes paired helens (supportive structures that emerge from slits in the test commissure, presumed to give hyoliths a slight vertical advantage over other epifaunal filter feeders, such as lingulid brachiopods) (Martí Mus & Bergström, 2005). Hyoliths were long thought to be related to mollusks due to the presence of an operculum. However, recent discovery of lophophores in exceptionally preserved specimens revealed that hyoliths may actually be lophophorates (Moysiuk et al., 2017). Since they possess qualities of both groups, hyoliths have been tentatively placed as basal Lophotrochozoa (Liu et al., 2020; Appendix 1 Fig. 1).

Hyaliths are very rare at Salmon Creek. Four specimens of *Hallotheca acilis* have been recovered thus far: one from the lower Moscow (Locality 1a-T); two from the Cuylerville Submember *Ambocoelia* Beds (Locality 1b; Plate 5h); and from the uppermost Cuylerville Submember (Locality 2). Only one specimen of *Hyolithes striatus* has been found from the Bay View Beds equivalent (Locality 2; Plate 7g).

## Class †Tentaculita

†Tentaculita is an extinct class of Problematica that first appeared in the Ordovician and disappeared in the Middle Jurassic. Tentaculites are small calcareous tubes once believed to have been constructed by marine worms. Others have noted a similarity between the ribbing of tentaculites and the annulations of orthoconic nautiloids, such as *Spyroceras nuntium*. Moreover, perforations in the “septae” have furthered the argument for tentaculites as small-bodied nautiloids (Bouček, 1964; Vinn et al., 2024). However, recent work has overturned the nautiloid hypothesis (Vinn et al., 2025; Vinn et al., 2023), and instead supports tentaculites as lophophorates (Vinn & Zatoń, 2012; Appendix 1 Fig. 1).

Only one potential tentaculite has been reported from Salmon Creek thus far. This specimen is believed to be the cornulitid *Cornulites hamiltoniae* and comes from the uppermost Cuylerville Submember (Locality 2).



**Appendix 1 Plate 6-2.** Incertae Sedis: Class †Hyolitha: Order †Hyolithida: *Hallotheca aclis* and *Hyolithes striatus*. Class †Tentaculita: Order †Cornulitida: *Cornulites hamiltoniae*. Modified from Wilson (2014). Life reconstruction of *Hallotheca aclis* with soft tissues (operculum, tentacles, and helens) by WCH.

## Phylum Mollusca

Mollusca is a phylum of extant lophotrochozoan that first appeared in the Early Cambrian. It includes three major classes (Bivalvia, Gastropoda, Cephalopoda), five minor classes (Aplacophora, Monoplacophora, Polyplacophora, Scaphopoda), and one wholly extinct class (†Rostroconchia). Many mollusks are segmented and all are soft-bodied. They all share a radula (except bivalves), a foot, visceral mass, and a mantle. The radula is a feeding organ composed of chitin used to scrape and drill. Gastropods use the radula to drill into the shells of bivalves, brachiopods, other gastropods, and even crinoids, and feed on the soft tissues within. The foot is a sole-like structure on which the animal crawls. It has been derived into many structures in the major classes, such as the arms and funnel in cephalopods and operculum in gastropods. The visceral mass encloses the digestive, excretory, and circulatory organs. Overlying the visceral mass is the mantle, which secretes the shell. The mantle has been modified into the siphon in bivalves, used for respiration, feeding, and excrement (Benton & Harper, 2020; Paululat & Purschke, 2025).

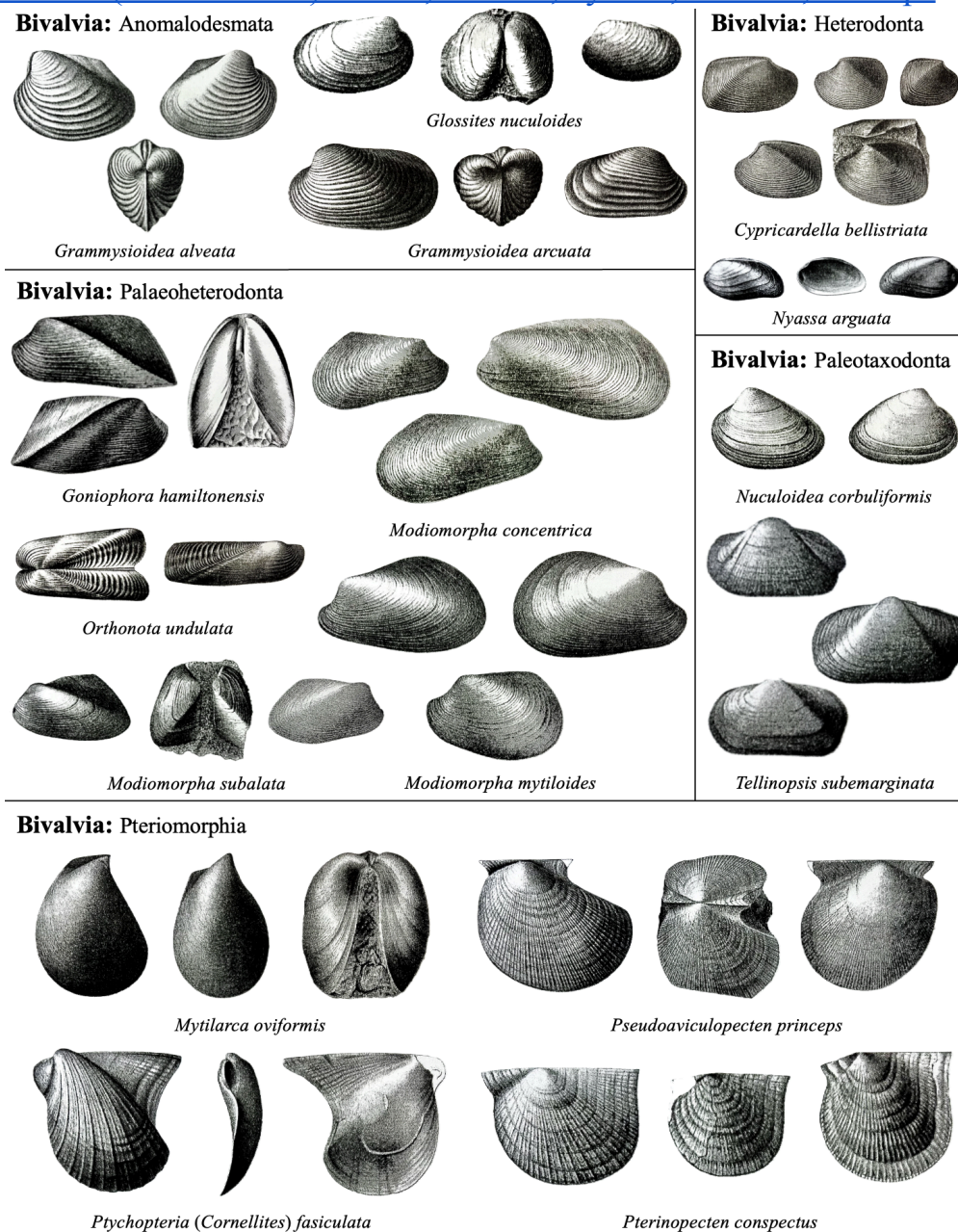
The mollusk shell is secreted as aragonite, a polymorph (mineral variety) of calcium carbonate ( $\text{CaCO}_3$ ), with an organic matrix and an outer organic layer (Falini et al., 1996). This is in contrast to brachiopods, which are made of calcite, another polymorph of calcium carbonate (Roda et al., 2019). Aragonite is more soluble and less thermodynamically stable than calcite (Wray & Daniels, 1957; Falini et al., 1996). The aragonite compensation depth (ACD), or the depth at which the rate of aragonite dissolution exceeds the rate of deposition, is 1-2 km, whereas the calcite compensation depth (CCD) is 4-5 km (Benton & Harper, 2020). In other words, in the same water body at constant temperature, aragonite dissolves at a faster rate and shallower depth than calcite. As a result, brachiopods and other calcite-secreted shells are often better preserved than mollusks and other aragonitic-based invertebrates. This phenomenon is well demonstrated at Salmon Creek, where calcitic body fossils of brachiopods, bryozoans, and trilobites readily occur, especially within calcareous concretions, yet mollusks, especially bivalves and gastropods, are preserved as natural casts and molds. This is best seen in the Spafford Member at Locality 1a-2 (Plate 2f) and upper Taunton Submember at Locality 2-T (Plate 8).

Recent systematic work places Bivalvia and Gastropoda as sister taxa (Pleistomollusca), more closely related to each other than either is to Cephalopoda. As the taxonomy of each major class continues to be resolved, older subclade names remain in use in the literature and among paleontologists. For this reason, we, as does Wilson (2014), follow the taxonomy presented in Newell (1965) that uses tooth hinge morphology to diagnose bivalve subclades. When bivalve species are introduced in the next section below, their most up-to-date parent taxon is denoted in parentheses (e.g., Modiomorphidae). These taxonomic names are typically families unless it is a basal member of Bivalvia or large bivalvian subrank. These order names follow Bouchet et al. (2010), compiled using both genetic and morphological data. This taxonomy is the current classification system adopted by WoRMS (World Register of Marine Species). The same is done for the subclades of gastropods and cephalopods in the subsequent sections after the bivalves.

Gastropods are organized according to Ponder & Lindberg (1997). Cephalopods follow parts K and L of the *Treatise on Invertebrate Paleontology* (Teichert et al., 1996 and Wright et al., 1996, respectively).

The three major mollusk classes are present at Salmon Creek, with bivalves the most common and gastropods the rarest. All are generally restricted to the Spafford Member, Portland Point Subformation, and lower Windom Member, exposed at Localities 1 and 2, with the greatest diversity within the Portland Point Subformation. With the exception of the upper Moscow talus, no gastropods have been reported from the upper Windom and overlying Garattsville members, and bivalves and cephalopods are quite rare in these units.

## Class Bivalvia (“two valves”): clams, cockles, oysters, mussels, scallops



**Appendix 1 Plate 7-1.** Phylum Mollusca: Class Bivalvia: Clade Anomalodesmata: *Glossites nuculoides*, and *Grammysioidea alveata* and *G. arcuata*. Clade Heterodonta: *Cypricardella bellistriata* and *Nyassa arguata*. Clade Palaeoheterodonta: *Goniophora hamiltonensis*, *Modiomorpha concentrica*, *M. mytiloides*, and *M. subalata*, and *Orthonota undulata*. Clade Paleotaxodonta: *Nuculoidea corbuliformis* and *Tellinopsis submarginata*. Clade Pteriomorpha: *Mytilarca oviformis*, *Pseudoaviculopecten princeps*, *Ptychopteria (Cornellites) fasciculata*, and *Pterinopecten conspectus*. Modified from Wilson (2014).

Bivalvia (Pelecypoda, Lamellibranchia) is an extant class of marine and freshwater mollusk that first appeared in the Early Cambrian. Bivalves include clams, cockles, oysters, mussels, scallops,

and allies. Most are suspension feeders, primarily living on or in the sediment in shallow marginal marine settings (Smolowitz, 2021). However, others, such as oysters and mussels, live attached to hard substrates via byssal threads or cement secreted by the foot, whereas others, such as scallops, are free living (Gosling, 2015). The group first appeared in the Cambrian and rapidly diversified after the end-Permian mass extinction, displacing brachiopods as the dominant component of marine benthic communities (Fraiser & Bottjer, 2016). All bivalves have two-hinged shells (hence the name “bi-valve”) secreted in the dorsum by two mantle lobes that surround the body organs, such as the stomach, foot, and gills (Abbott, 1968; Gosling, 2015).

Newell’s bivalve subclades present at Salmon Creek include Anomalodesmata, Heterodonta, Palaeoheterodonta, Paleotaxodonta, and Pteriomorphia. All (except for the paleotaxodonts) can be found in great abundance in the Ludlowville Formation (Locality 1a; plates 1b and 2a-e). These taxa are mostly represented by individual valves, though butterfly (spread valves) specimens (*Cypricardella bellistriata*, Plate 2d; *Modiomorpha mytiloides*, Plate 2b; and *M. cf. subalata*) and uncompacted forms (*Goniophora hamiltonensis*, Plate 2a) have been occasionally found. In strata above the Ludlowville Formation, bivalve diversity and abundance generally decreases.

**Clade Anomalodesmata:** [grammysiids](#) and [modiomorphids](#)

Anomalodesmata is an extant clade of bivalve that includes marine clams. Anomalodesmatans first appeared in the Tremadocian (earliest Ordovician). They are represented by three species at Salmon Creek: *Glossites nuculoides*, *Grammysioidea alveata*, and *G. cf. arcuata*. *G. nuculoides* (†Modiomorphidae; see ‘*Modiomorphid palaeoheterodonts*’ for further discussion) is a small anomalodesmatan that is probably overlooked and thus undersampled at Salmon Creek. It is a rare find in both the lower Moscow (Locality 1a-T) and Cuylerville Submember *Ambocoelia* Beds (Locality 1b). *Grammysioidea* (†Grammysiidae) is a medium- to large-sized anomalodesmatan often found uncompacted, though sometimes taphonomically deformed, with valves compressed flat. *G. alveata* occurs very rarely in the Spafford Member (Locality 1a), Cuylerville Submember *Ambocoelia* Beds (Locality 1b), and lower Fall Brook Bed equivalent (Locality 3b), whereas *G. cf. arcuata* can be found in the Tichenor Member (Locality 1a-T; Plate 3e) and upper Cuylerville Submember (Locality 2; Plate 6-2g). Both species rarely occur in the lower Moscow (Locality 1a-T).

**Clade Heterodonta:** crassatellids and nyassids

Heterodonta is an extant clade of bivalve that includes clams, cockles, shipworms, and allies. All heterodonts share equally sized valves (Wilson, 2014). This taxon is represented by two species at Salmon Creek: *Cypricardella bellistriata* and *Nyassa arguata*. *C. bellistriata* (†Crassatellidae) are very common throughout the Ludlowville Formation (Locality 1a). Specimens of *C. bellistriata* can be found as either individual valves or in butterfly (Plate 2d). *N. arguata* (Nyassidae) is a very small, and likely overlooked, species of heterodont. It is a very rare find in the upper Cuylerville Submember (Locality 2).

**Clade Palaeoheterodonta:** [modiomorphids](#) and orthonotids

Palaeoheterodonta is an extant clade of freshwater and marine bivalve that includes unionids (freshwater mussels), trioniids, and allies. Palaeoheterodonts first appeared in the Devonian.

They are represented by five species at Salmon Creek: *Goniophora hamiltonensis*, *Modiomorpha concentrica*, *M. mytiloides*, *M. cf. subalata*, and *Orthonota undulata*.

### **Modiomorphid palaeoheterodonts**

*G. hamiltonensis* is a medium- to large-sized palaeoheterodont diagnosed by a trapezoidal valve and a sharp ridge running from the umbo to posterior margin (Wilson, 2014). It is generally rare, and can be sampled from the Spafford Member (Locality 1a-2), lower Moscow (Locality 1a-T), and upper Taunton Submember (Locality 2-T). Large, relatively uncompacted specimens of *G. hamiltonensis* have been recovered from the Spafford Member (Plate 2a).

### **Modiomorpha spp.**

*Modiomorpha* is a medium-sized bivalve and the most abundant palaeoheterodont found at Salmon Creek. It is a typical find in the Ludlowville Formation (Locality 1a). *M. concentrica* is by far the most common species. It has a complete stratigraphic record from the “lower Spafford” to upper Cuylerville Submember, becoming rarer as the strata gets younger. *M. mytiloides* (Plate 2b) is slightly less common than *M. concentrica*, also disappearing after the upper Cuylerville Submember. The species epithet “*mytiloides*” is in reference to the mussel-like appearance this taxon shares with mytilids (mussels). *M. cf. subalata*, on the other hand, is exclusively found in butterfly in the Spafford Member (Locality 1a-2).

Notably, the Locality 1a-1 *Modiomorpha* display evidence of sublethal injuries from durophagous predators, such as ammonoids, phyllocarids, and potentially placoderms (Plate 1b). This is the first reported record of predation scars in the genus *Modiomorpha* and supports the “Middle Paleozoic Revolution” (Signor & Brett, 1984; Brett & Walker, 2002; Brett, 2003), a hypothesis that predation intensified during the Middle Devonian (see ‘*Paleoecology of Salmon Creek and Ludlowville Falls I*’ for further discussion).

### **Orthonotid palaeoheterodonts**

*O. undulata* (†Orthonotidae) is distinct from other palaeoheterodont species by its extremely elongate and ornamented shell (Wilson, 2014). This morphology is convergent with modern pharids (razor clams). For this reason, it is probable that *O. undulata* lived similarly to pharids, burrowing into soft sand to feed on smaller organisms within the sediment. Like *G. hamiltonensis*, *O. undulata* is generally rare, and occurs in the Ludlowville Formation (Locality 1a; Plate 2c), lower Moscow (Locality 1a-T), and upper Cuylerville Submember (Locality 2).

### **Unionid palaeoheterodonts**

Unionida is an extant order of bivalve that first appeared in the Devonian. Unionids include freshwater mussels. Although unionid fossils cannot be found at Salmon Creek, both extinct and extant forms can be found at the New York-Pennsylvania border, with the modern taxa living on the stream bottom and the fossil taxa encased within rock along the stream bank. In the Catskill Formation (Famennian) of northcentral Pennsylvania, large death assemblages of *Archanodon catskillensis* can be found in or near channel bar lags, often preserved oriented in the direction of the paleocurrent (like *Plumalina*) and sometimes even in undisturbed life position (Broussard et al., 2018). *A. catskillensis* is morphologically analogous to the extant freshwater pearl mussel (*Margaritifera*). Thus, it is interpreted to have lived a similar lifestyle; *A. catskillensis* may have even parasitized the gills of fishes (e.g., “placoderms”, acanthodians, sarcopterygians) with

mature larvae (1-4 million per female) to ensure upstream dispersal of its offspring during the Famennian (Rinehart & Lucas, 2013). In addition to body fossils, escape burrows of *A. catskillensis* are also common occurrences in the Catskill Formation, interpreted to represent responses to small scale sedimentation events (Knoll et al., 2017).

**Clade Paleotaxodonta:** ctenodontids and nuculids

Paleotaxodonta is an extant clade of bivalve that is probably overlooked, and thus undersampled, at Salmon Creek. This taxon is represented by two species: *Nuculoides corbuliformis* and *Tellinopsis submarginata*. Both are rare finds and are restricted to one stratum each: *N. corbuliformis* (†Nuculidae) to the Cuylerville Submember *Ambocoelia* Beds (Locality 1b), and *T. submarginata* (†Ctenodontidae) to the upper Cuylerville Submember (Locality 2; Plate 6-2h).

**Clade Pteriomorphia:** myalinids, ostreids, and pectinids

Pteriomorphia is an extant clade of bivalve that includes limids (file shells), mytilids (mussels), ostreids (true oysters), pectinids (scallops), and allies. Some pteriomorphians, such as ostreids and mytilids, live attached to hard substrates via byssal threads or cement secreted by the foot. Others, like pectinids, are free living (Gosling, 2015). Rudimentary to complex photoreceptors occur in 11 families and have arisen independently at least five times (Audino et al., 2020). Pteriomorphia is represented by at least four species at Salmon Creek: *Mytilarca oviformis*, *Pseudoaviculopecten princeps*, *Ptychopteria* (*Cornellites*) *fasiculata*, and *Pterinopecten* cf. *conspetus*.

**Pterinopectinid pteriomorphians**

*Pseudoaviculopecten* is the most typical pteriomorphian at Salmon Creek, and especially large valves of this genus can be found in the Spafford Member (Locality 1a-2; Plate 2e) and Portland Point Subformation (Locality 1a-T). There are likely several species of *Pseudoaviculopecten* present at Salmon Creek. So far, only *P. princeps* has been identified to the species level with confidence. *P. cf. conspectus* is represented by only one specimen from the Bay View Beds equivalent (Locality 2), but this unit requires further sampling, as it appears to harbor a diversity of yet to be identified pterinopectinid species (e.g., *Pseudoaviculopecten* spp.).

**Non-pterinopectinid pteriomorphians:** [ambonychiids](#) and pterinids

Non-pterinopectinid pteriomorphians are much rarer at Salmon Creek. Thus far, only one *M. oviformis* (†Ambonychiidae) has been documented from the lower Fall Brook Bed equivalent (Locality 3b). *P. fasiculata* (†Pterineidae) is a rare medium-sized shell in the Spafford Member (Locality 1a-2), co-occurring with *Pseudovaculopecten*. Notably, *P. fasiculata* is the first reported species possessing sublethal predation damage on Devonian bivalves (Nagel-Myers et al., 2009; see ‘*Paleoecology of Salmon Creek and Ludlowville Falls I*’ for further discussion).

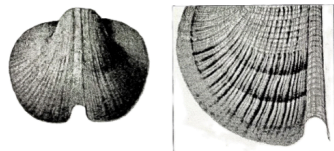
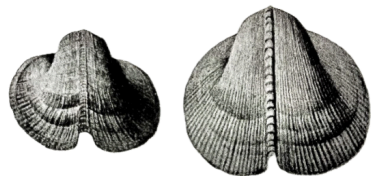
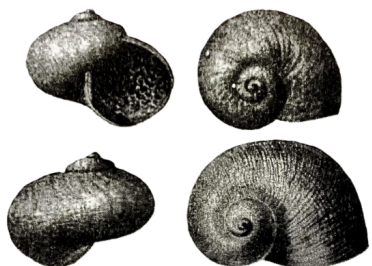
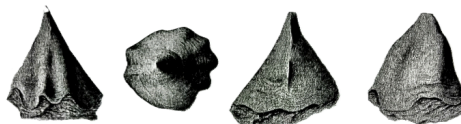
**[Class Gastropoda \(“stomach foot”\): snails and slugs](#)**

Gastropoda is an extant class of marine, freshwater, and terrestrial mollusk that first appeared in the Cambrian. Gastropods include snails and slugs. Nearly all gastropods have a head and a single, typically helically coiled, valve (gastropods are sometimes referred to as “univalves” to further distinguish them from bivalves). An operculum is typically present on the foot (Poutiers, 2016). Gastropods experience torsion during ontogeny, producing an asymmetrical body in which the visceropallium (the posterior half that includes the mantle cavity, containing the anus,

gills, and other visceral organs), generally rearward in primitive mollusks, are rotated up and over the cephalopallium (the anterior half that includes the head and foot) or to one side (Page, 2003). The shell has been extensively modified (in terms of elongation and coiling) by various subclades of gastropods. Some gastropods, like the marine nudibranchs, even lost their shells, opting instead to obtain chemical defenses from their environment, such as the unfired cnidocytes of cnidarians; a process referred to as kleptocnidy (Greenwood, 1988).

The radula is present in all gastropods, and is specialized in various groups allowing them to have a variety of feeding types (herbivory, carnivory, detritivory, scavenging, and parasitism). Carnivorous gastropods use the radula to drill into shelled prey, including bivalves, brachiopods, other gastropods, and even crinoids, leaving behind drillholes called borings. Modern gastropod borers primarily include the muricids (murex snails) and naticids (moon snails), among others (Rayment, 1967). In the Devonian, platyceratoid gastropods such as *Naticonema lineata* were parasites of crinoids when small (early adulthood) and active predators of bivalves, brachiopods, and other gastropods when large (late adulthood); this has been interpreted as a form of niche partitioning and is evident at Salmon Creek (see '*Naticonema lineata*' for further discussion).

Four subclades of gastropods are known from Salmon Creek: †Bellerophodontoidea, †Loxonematoidea, Platyceratoidea, and Pleurotomarioidea. Generally, gastropod fossils are rare and are restricted to the lower Moscow Formation (with the platyceratoid *Naticonema lineata* as the only exception). The stratigraphic unit with the most abundant and diverse gastropod assemblage is the lower Moscow (Locality 1a-T), where all four subclades are represented.

**Gastropoda: †Bellerophodontoidea***Ptomatis patulus**Retispira leda***Gastropoda: †Loxonematoidea***Palaeozygopleura delphicola**Palaeozygopleura hamiltoniae***Gastropoda: Pleurotomarioidea***Glyptomaria capillaria***Gastropoda: †Platyceratoidea***Naticonema lineata**Orthonychia conicum**Platyceras bucculentum*

**Appendix 1 Plate 7-2.** Phylum Mollusca: Class Gastropoda: Clade †Bellerophodontoidea: *Ptomatis patulus* and *Retispira leda*. Clade †Loxonematoidea: *Palaeozygopleura delphicola* and *P. hamiltoniae*. Clade †Platyceratoidea: *Naticonema lineata*, *Orthonychia conicum*, and *Platyceras bucculentum*. Clade Pleurotomarioidea: *Glyptomaria capillaria*. Modified from Wilson (2014).

**Clade †Bellerophodontoidea:** bellerophodontids and plectonotids

†Bellerophodontoidea is an extinct clade of globose, marine gastropod that first appeared in the Late Cambrian. Bellerophodontoids are diagnosed by an involute shell whose apertural end flares out into a flattened ridge (Wilson, 2014). This taxon is represented by two species at Salmon Creek: *Ptomatis patulus* and *Retispira leda*. Both are very rare finds. Only one specimen of *P. patulus* (†Plectonotidae) is known from the lower Moscow, where it co-occurs with *R. leda* (†Bellerophontidae). *R. leda* can also be found in the Cuylerville Submember (both the *Ambocoelia* Beds at Locality 1b and upper horizon at Locality 2). Bellerophodontoids disappeared in the Triassic.

**Superfamily †Loxonematoidea: palaeozygopleurids**

†Loxonematoidea is an extinct superfamily of marine gastropod with high-spired shells (analogous to *Turritella*). It is united with Pleurotomarioidea under Order Pleurotomariida. Loxonematoids are represented at Salmon Creek by two species of *Palaeozygopleura*: *P. delphicola* and *P. hamiltoniae*. Both are members of †Palaeozygopleuridae and are generally

rare. However, in the light gray silty shales of the lower Moscow (Locality 1a-T), internal molds of *Palaeozygopleura* can be found in relative abundance. Within the Cuylerville Submember *Ambocoelia* Beds (Locality 1b), at least three specimens of *P. hamiltoniae* have been found in association with the cubichnia *Rusophycus*, indicating feeding behavior (likely scavenging) by a trilobite on the shells of these gastropods (Plate 5c; see ‘*Paleoecology of Salmon Creek and Ludlowville Falls II*’ for further discussion). Interestingly, split pebbles of calcareous siltstone from the upper Taunton Submember (Locality 2-T) has yielded calcitic shells of *P. hamiltoniae* (Plate 8d).

**Superfamily †Platyceratoidea:** cyrtoneritomorphans and [euomphalins](#)

†Platyceratoidea is an extinct superfamily of predatory marine gastropod that first appeared in the Middle Ordovician and disappeared in the Permian. Platyceratoids are often found parasitizing crinoids. They are represented by at least three species at Salmon Creek: *Naticonema lineata*, *Orthonychia* sp., and *Platyceras* cf. *bucculentum*.

**Ornthonychiid platyceratoids**

*Orthonychia* is known from two specimens from the bluish-gray calcareous mudstones of the lower Moscow (Locality 1a-T; Plate 4c). It is probably overlooked, and therefore undersampled, due to poor preservation of the shell and tendency to break when the host rock is split.

**[Platyceratid platyceratoids](#)**

*Platyceras*, with several species, is definitely undersampled at Salmon Creek. It is relatively uncommon in the bluish-gray calcareous mudstones of the lower Moscow (Locality 1a-T), like *Orthonychia*. Thus far, only one specimen has been identified to species, *P. cf. bucculentum* (Plate 4f).

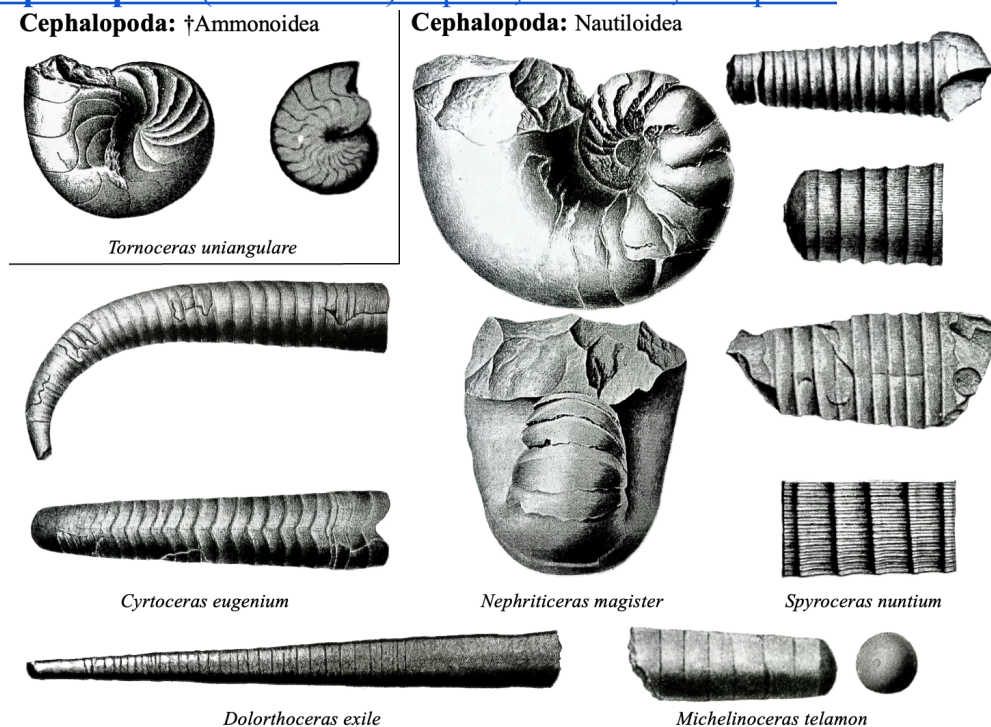
***Naticonema lineata***

*N. lineata* is a medium- to large-sized shell and the most common platyceratoid species, with known occurrences in the Spafford Member, Portland Point Subformation, upper Cuylerville Submember, Bay View Beds equivalent, and upper Taunton Submember (localities 1a-2, 1a-T, 2, and 2-T, respectively). The largest *N. lineata* specimens come from the lower Moscow (Locality 1a-T; Plate 3f), where they were most likely benthic and served active predatory roles. The smallest specimens come from the Bay View Beds equivalent (Locality 2), where they co-occur with an abundant crinoid assemblage, including disarticulated ossicles and even calyces (one identified as the camerate *Megistocrinus depressus*; Plate 7f). It is probable that these *N. lineata* parasitized crinoids within this unit, either stealing nutrients directly from the stomach (kleptoparasitism) or feeding off wastes excreted from the anal tube (commensal coprophagy). Direct evidence of *N. lineata* parasitizing crinoids, such as the camerate *Griphocrinus* (*Rhodocrinus*) *nodulosus*, can be seen in relative abundance in outcrops to the west, such as the Kipp Road Beds (Moscow Fm: Deep Run Mbr) along Canandaigua Lake (Mayer et al., 1991). The separation of parasitic and active predatory roles has been interpreted as a form of niche partitioning for *N. lineata*. See ‘*Paleoecology of Salmon Creek and Ludlowville Falls III*’ for further discussion about the role of platyceratoids in the broader ecology.

### Clade Pleurotomarioidea: gosseletinids

Pleurotomarioidea is an extant superfamily of marine gastropod that first appeared in the Cambrian. This taxon is represented by two species of †Gosseletinidae at Salmon Creek: *Glyptomaria capillaria* and *Mourlonia* cf. *lucina*. *G. capillaria* is rare, occurring only in the Portland Point Subformation (Locality 1a-T). Interestingly, within the Tichenor Member, a relatively complete and large cephalon of the phacopid *Dipleura dekayi* was recovered with *G. capillaria* attached to the right compound eye lens. This association represents a very rare example of gastropod feeding (i.e., scavenging) on a trilobite (Plate 3b; see ‘*Paleoecology of Salmon Creek and Ludlowville Falls III*’ for further discussion). *M. cf. lucina* is thus far only known from one uncompact specimen from the Spafford Member (Locality 1a-2).

### Class Cephalopoda (“head foot”): squids, cuttlefish, octopuses



**Appendix 1 Plate 7-3.** Phylum Mollusca: Class Cephalopoda: Subclass Ammonoidea: *Tornoceras uniangulare*. Subclass Nautiloidea: *Cyrtoceras eugenium*, *Dolorthoceras exile*, *Michelinoceras telamon*, *Nephriticeras magister*, and *Spyroceras nuntium*. Modified from Wilson (2014).

Cephalopoda is an extant class of active marine predatory mollusk that first appeared in the Cambrian. All cephalopods share a funnel, arms (tentacles) surrounding the mouth, and a chitinous beak. The funnel functions both for locomotion (jet propulsion) and excretion of waste products. The arms often bear suckers or hooks, used to immobilize and manipulate prey towards the mouth. The beak is a jaw-like apparatus, within which is the radula (Guerra et al., 2014).

### Subclass †Ammonoidea

†Ammonoidea is an extinct subclass of shelled cephalopod. They first appeared in the Devonian and disappeared in the Paleocene, just after the end-Cretaceous mass extinction event (Landman

et al., 2015). There are three groups of ammonoids, but only goniatites, those lacking subdivided saddles and lobes along their sutures, can be found in the Hamilton Group. Goniatites are a basal order of ammonoids that first appeared in the Eifelian (early Middle Devonian). They are best characterized by the presence of “goniatitic” sutures, or undivided saddles and lobes on the shell, arranged in the shape of a zigzag (Lacchia, 2012).

Increases in ammonoid suture complexity over time, from goniatitic to “ceratitic” to “ammonitic”, was once believed to be related to strengthening of the ammonoid shell against implosion and predators (the Buckland hypothesis), but it is now thought to be related to buoyancy control and swimming capabilities (Saunders, 1995). Both their shell shape and basal phylogenetic position indicate that goniatites were poor swimmers relative to ceratites and ammonites. Despite this, goniatites likely had well developed vision for capturing live prey.

Goniatites disappeared during the end-Permian mass extinction event, replaced by the ceratites in the subsequent Triassic, which were in turn replaced by the ammonites in the wake of the end-Triassic mass extinction event (Miller, 1938). This step-wise succession of ammonoid turnover is very useful for biostratigraphy: without knowing anything about the local geology of a sedimentary outcrop, you can determine its relative age by examining the suture pattern of the fossil ammonoids contained within.

At Salmon Creek, goniatites are represented by *Tornoceras uniangulare* and an unidentified species, known from medium-sized partial phragmocones that are distinct from *T. uniangulare*. The unidentified species comes from the Cuylerville Submember *Ambocoelia* Beds (Locality 1b; Plate 5d) and upper Cuylerville Submember (Locality 2).

### ***Tornoceras uniangulare***

*Tornoceras uniangulare* is a small goniatite with a distinct sigmoidal (S-shaped) goniatitic suture pattern. The shell is discoidal (flat) and involute, with the last whorl overlapping prior whorls. The umbilicus (shell center) is depressed inwards (Wilson, 2014). *T. uniangulare* is a very rare find throughout Salmon Creek. It is known from five stratigraphic units: upper *Modiomorpha-Ancyrocrinus* Bed, lower Moscow, Cuylerville Submember *Ambocoelia* Beds, upper Cuylerville Submember, and lower Fall Brook Bed equivalent (localities 1a-1, 1a-T, 1b, 2, and 3b, respectively).

### **Subclass Nautiloidea: *Nautilus*, argonauts, and allies**

Nautiloidea is an extant subclass of shelled cephalopod that first appeared in the Late Cambrian. Straight shelled nautiloids, called orthoconics, are the most common cephalopod fossil from central New York State, but there are many other coiling forms of nautiloid; at Salmon Creek, breviconics, cyrtconics, and nautiloconics are also represented. Though the orthoconics are extinct, nautiloids as a group are not. The Chambered Nautilus (*Nautilus pompilius*), for example, is a living relative of the Givetian-aged nautiloids at Salmon Creek.

Unlike coleoids (squids, cuttlefish, octopuses, vampire squid), nautiloids have external shells called phragmocones (coleoids have reduced and internalized this structure – referred to as the cuttlebone). The individual chambers of the phragmocone are divided by thin, concave-forward curved walls of aragonite, termed septa. Each septa is perforated by a hole, typically in the center

through which a tube or cord of tissue, the siphuncle, present in all cephalopods, passes. The siphuncle enabled cephalopods to regulate the amount of fluid and gas in their chambers to control their buoyancy in the water column, like a submarine. The siphuncle is considered a key innovation for Cephalopoda, freeing them from the benthos (Kröger, 2003). Five species of nautiloid can be found at Salmon Creek. They are presented below according to their coiling form; note that these are evolutionary grades not phylogenetic clades.

### **Breviconic nautiloids**

Breviconic (short and stout, cone-shaped) nautiloids are represented by one potential specimen from the upper Cuylerville Submember (Locality 2). This specimen, a large but partial phragmocone with expanded ribbing, remains to be identified.

### **Orthoconic nautiloids:** orthoceratids and spyroceratids

Orthoconics are the most common form of nautiloid at Salmon Creek, represented by three species: *Dolorthoceras exile*, *Michlinoceras telamon*, and *Spyroceras nuntium*. All are constituents of the *Zoophycos*-orthocone-diversity pattern of individual beds in the Tichenor Member, lower Moscow, and upper Cuylerville Submember, with *S. nuntium* generally the most typical.

### ***Dolorthoceras* spp.**

*D. exile* (†Spyroceratidae) is diagnosed by a regularly expanding, slender and straight shell (Wilson, 2014). It occurs throughout the Hamilton Group. For a fossil cephalopod, *D. exile* is relatively common. It is an uncommon occurrence in the lower Moscow, Tichenor Member, and upper Cuylerville Submember (localities 1a-T and 2, respectively), and is very rare in the upper Taunton Submember and lower Fall Brook Bed equivalent and (localities 2-T and 3b, respectively).

*D. exile* is very small when compared to its sister taxon, *D. cayuga* (sometimes referred to as a variant or subspecies of *Orthoceras bebryx* in older literature; Williams, 1884). This species is not present at Salmon Creek but can be found just to the south in the Ithaca Formation exposed at Six Mile Creek in Ithaca, NY. Owing to both its size and tendency to occur in the bedload, incomplete specimens (partial chambers of the phragmocone) are typical. Moreover, the phragmocone is often found taphonomically deformed (dorsoventrally compressed).

### ***Michlinoceras telamon***

*M. telamon* (†Orthoceratidae) is characterized by a phragmocone that expands regularly from the apex. The surface of the phragmocone itself is smooth, in contrast to the annulations present in *Spyroceras* (see ‘*Spyroceras nuntium*’ for further discussion). Cross sections of the phragmocone of *M. telamon* are circular. Occasionally, the siphuncle can be seen in these cross sections, positioned at about one-third of the length of diameter (Wilson, 2014). *M. telamon* is generally rare at Salmon Creek. It is an uncommon occurrence in the Portland Point Subformation (Locality 1a-T), and is rare in the Cuylerville Submember *Ambocoelia* Beds and upper Cuylerville Submember (localities 1b and 2, respectively). Within the upper Cuylerville Submember, one specimen of *M. telamon* was found fouled by tubes of the possible phoronid *Reptaria stolonifera* and abutted by the cubichnia *Rusphycus* (Plate 6-2f), representing trilobite scavenging (see ‘*Paleoecology of Salmon Creek and Ludlowville Falls II*’ for further discussion).

Even more unusual, a relatively complete phragmocone of *M. telamon* crosscut by veins of calcite (Plate 8f) was discovered in a split calcareous pebble from the upper Taunton Submember (Locality 2-T).

### ***Spyroceras nuntium***

*S. nuntium* (†Spyroceratidae) is diagnosed by screw-like annulations and coarse longitudinal striae on the phragmocone (Wilson, 2014). This species is the most common nautiloid found at Salmon Creek, often encountered as partial, taphonomically deformed (dorsoventrally compressed) phragmocones. Generally, it occurs throughout the Moscow Formation, and is most reliably found in the Portland Point Subformation and upper Cuylerville Submember (localities 1a-T and 2, respectively). It is very rare in the Ludlowville Formation, with one very partial, pyritized phragmocone recovered from a split calcareous concretion in the Spafford Member (Locality 1a-2; Plate 2f). Larger individuals of *S. nuntium* come from the upper Taunton Submember (Locality 2-T; Plate 8g) Several complete phragmocones are known from the upper Cuylerville Submember, where one has even been found fouled by tubes of the possible phoronid *Reptaria stolonifera* (Plate 6-1d). Uncompacted specimens have also been recovered in the lower Fall Brook Bed equivalent (Locality 3b; Plate 9e).

### **Cyrtocoenic nautiloids:** basal cephalopods

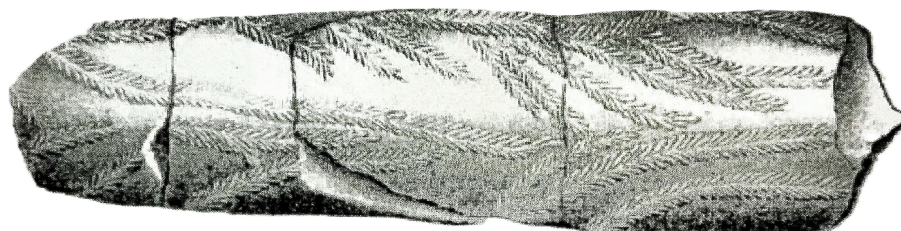
Cyrtocoenic (curved) nautiloids are represented by one very rare specimen of *Cyrtoceras* (basal Cephalopoda) from the Tichenor Member (Locality 1a-T; Plate 3d). This specimen includes just the apex (tip) of the phragmocone. The complete phragmocone would appear orthoconic at the apertural end (the opening into the living chamber in which the animal resided), curving downwards until the apical end (opposite the aperture) is perpendicular to the aperture. As a basal cephalopod, *Cyrtoceras* may represent an early evolutionary step towards the coiled form.

### **Nautiloconic nautiloids:** “barrandeocerids”

Nautiloconic (coiled) nautiloids are represented by one exceptionally rare specimen of *Nephriticeras magister* (†Nephriticeratidae) from the upper *Modiomorpha-Ancyrocrinus* Bed (Locality 1a-1; Plate 1c). Most of the phragmocone is preserved, with the simple nautiloid suture pattern present. *N. magister*, similar in size and coiling form, probably looked and behaved similarly to the modern *N. pompilius*.

## **Phylum Phoronida:** horseshoe worms

### **Phoronida:**



*Reptaria stolonifera*

**Appendix 1 Plate 8.** Phylum Phoronida: *Reptaria stolonifera*. Modified from Wilson (2014).

Phoronida is a phylum of extant lophophorate that first appeared in the Silurian. Phoronids are small worm-like animals that possess a lophophore and build chitinous tubes to protect their soft

bodies. They are most closely related to brachiopods, and thus both phyla are united as members of Brachiozoa. Phoronids are represented at Salmon Creek by one species, *Reptaria stolonifera*, which has historically been considered a branching cyclostomate (Bryozoa: Stenolaemata). This taxon exclusively occurs on the phragmocones of orthoconic nautiloids. At Salmon Creek, phragmocones of both *Spyroceras nuntium* and *Michelinoceras telamon* have been found fouled by tubes of *R. stolonifera* in the upper Cuylerville Submember (Locality 2; Plate 6-1d, 6-2f).

### **Phylum Porifera (“pore-bearers”): sponges**

Porifera is a phylum of extant non-parahoxozoan (Parazoa) that first appeared in the Ediacaran. Poriferans include sponges as well as †Archaeocyatha and †Stromatoporoidea. All poriferans are asymmetrical and lack true differentiated tissues and organs. They are composed of calcareous or siliceous spicules that reinforce the skeleton (Benton & Harper, 2020). Porifera has long been thought to be the most basal animal phylum. However, recent work has proposed Ctenophora (ctenophores, or “comb-bearers”) as the first diverging animal clade (Whelan et al., 2017).

Generally, poriferans are very rare fossils across New York State. They have not yet been documented at Salmon Creek. However, the hexactinellid (glass sponge) *Hydnoceras* (*H. tuberosum* and *H. bathense*), a relative of the modern Venus’ Flower Basket (*Euplectella*), has been found just to the south in the Ithaca Formation exposed in Ithaca, NY. Specimens of the Ithaca *Hydnoceras* (e.g., PRI 76741) can be seen on permanent display at the Museum of the Earth.

### **Division Tracheophytes: vascular plants**

Occasionally, plant material was transported from the terrestrial realm to the sea, where they would ultimately be deposited in the Appalachian Basin and preserved as fossils. Salmon Creek during the Givetian was positioned near the center of this basin, and far from land (Fig. 1b). As a result, fossil plant material is very rare. However, small unidentified stems are known from the Spafford Member (1 m height; Locality 1a-2), and larger crushed material has come from the Tichenor Member (Locality 1a-T; Plate 3g). Most unusual, a decorticated stem of an unidentified lycophyte, a primitive tracheophyte and component of the first coastal swamps, was found in the upper Cuylerville Submember (Locality 2; Plate 6-2j).

## Appendix II. Summary Chart of the Fossils at Salmon Creek and Ludlowville Falls

This appendix tabulates the occurrences and rarities of the known fossil animals and plants sampled from Salmon Creek and Ludlowville Falls. Animal taxa are organized according to phylum and are ordered alphabetically as opposed to phylogenetically, beginning with Arthropoda and ending with Porifera. Note ichnological taxa (“Ichnotaxa,” or trace fossils) and Incertae Sedis taxa (Problematica, or problematic fossils) are treated here as phyla even though Ichnotaxa have their own taxonomy separate from body fossils, and Incertae Sedis is not a monophyletic clade (by definition, it is a polyphyletic clade of taxa with uncertain affinities to the known animal phyla). The dagger symbol (†) is used to represent wholly extinct clades, for which there are no living representatives (e.g., †Trilobita). Any fossil taxa identified to the genus or species levels (italicized here and throughout this field guide; e.g., *Eldredgeops rana*) are all assumed to be extinct and will not display the dagger symbol in front of their genus name to spare additional text. Parentheses (“ ”) are used to denote paraphyletic (non-monophyletic) clades (e.g., “Crustacea”). Plant taxa (Tracheophytes) are tabulated after the animals. Note that plant systematists use the “division” as an equivalent taxonomic rank to the “phylum” for animals.

We use the following symbols to describe relative rarity for a fossil taxon within a particular stratigraphic unit at Salmon Creek and Ludlowville Falls: VC (very common), C (common), U (uncommon), R (rare), and VR (very rare), with VC fossils discoverable with minimal effort during an outing and VR fossils known from very few specimens, typically three or less collected over the past three years of dedicated sampling effort. ER is reserved for exceptionally rare specimens that are very unlikely to ever be found again owing to their state of preservation. ER specimens include *Paraechinocaris* (*Echinocaris*) *punctata* (WCH 820/PRI 111630) from the Tichenor Member (Locality 1a-T; Plate 3a), *Pseudodechenella* (*Basidechenella*) *rowi* (col. S.E. Echavarría) from the Spezzano Gully Submember South Lansing Beds (Locality 2-T; Plate 8c), and *Nephriticeras magister* (col. E.M. Cavanaugh) from the upper *Modiomorpha-Ancyrocrinus* Bed (Locality 1a-1; Plate 1c). Blank cells represent stratigraphic units for which a fossil taxon has not been reported from, but importantly it does not represent absence from those units. Black cells represent stratigraphic units for which little to no sampling has occurred, representing future directions for research at Salmon Creek. These undersampled units include the Deuel Road Member, Smoke Creek Bed, Bear Swamp Submember, Taughannock Falls Submember, and Moravia Submember. The former three units are the most likely candidates for future sampling effort, especially in the Bear Swamp Member is accessible just upstream of Locality 2. The latter two units, submembers of the Tully Formation exposed at Locality 3c-2, are generally inaccessible.

Salmon Creek Locality Number	1a	1a/b	1b	2	3a	3b	3c	2 (talus)	3c				
<b>Stratigraphic Unit</b>	Hamilton Group								Tully Formation				
	Ludlowv Fm.	Moscow Formation											
	Modiomorpha-Ancyrocrinus Bed ("lower Spafford")	Spafford Member	Tichenor Member	"Lower Moscow" (Deep Run-Kashong interval)	Deuel Road Member	Windom Member				Gar Mbr	Lab Vall	Upp Mbr	Lon Hill
						Cuylerville Submember <i>Ambocoelia</i> Beds	Upper Cuylerville Submember	Big Tree Smbr.	Smoke Creek Bed				
	Lower Fall Brook Bed equivalent	<i>Ambocoelia</i> -rich Fall Brook Bed equivalent	Upper Taunton Submember	Spezzano Gully Submember	South Lansing Beds								
	Carpenter Falls Submember												
	Taughanock Falls Submember												
	Moravia Submember												

**Arthropoda:****Phyllocarida ("Crustacea"):***Paraechinocaris (Echinocaris) punctata*

ER

**†Trilobita:****†Phacopida:***Bellacartwrightia* sp.

VR

VR

VR

*Dipleura dekayi*

VR

VR

VR

*Eldredgeops (Phacops) rana*

R

R

R

U

C

R

R

U

U

R

VR

*Greenops* spp. (*G. barberi*, *G. grabau*)

R

U

C

R

R

R

VR

U

*Odontocephalus* sp.

VR

**†Proetida:***Pseudodechenella (Basidechenella) rowi*

VR

R

VR

VR

VR

ER

Salmon Creek Locality Number	1a	1a/b	1b	2	3a	3b	3c	2 (talus)	3c			
<b>Stratigraphic Unit</b>	Hamilton Group								Tully Formation			
	Ludlowv Fm.	Moscow Formation										
	Modiomorpha-Ancyrocrinus Bed ("lower Spafford")	Spafford Member	Tichenor Member	"Lower Moscow" (Deep Run-Kashong interval)	Deuel Road Member	Windom Member			Gar Mbr	Lab Vall	Upp Mbr	Lon Hill
						Cuylerville Submember <i>Ambocoelia</i> Beds	Upper Cuylerville Submember	Big Tree Smbr.				
	Bay View Beds equivalent	Smoke Creek Bed	Bear Swamp Submember	Fisher Gully Submember	Lower Fall Brook Bed equivalent				<i>Ambocoelia</i> -rich Fall Brook Bed equivalent	Upper Taunton Submember	Spezzano Gully Submember	South Lansing Beds

**Brachiopoda:****Craniida (Craniata):***Petrocrania* cf. *hamiltoniae*

VR

**Lingulida (Lingulata):***Lingula delia*

VR

VR

VR

**Rhynchonellata:**†**Athyridida:***Athyris spiriferoides*

C

VC

C

C

C

R

†**Atrypida:***Pseudoatrypa devonica*

R

U

U

†**Orthida:***Rhipidomella leucosia*

R

*Rhipidomella penelope*

U

U

R

**Rhynchonellida:***Eumetabolatoechia multicostatum*

VC

U

†**Spiriferida:***Ambocoelia umbonata*

VC

VC

*Mediospirifer audaculus*

C

C

R

U

U

C

VC

*Mucrospirifer mucronatus*

VC

VC

VC

VC

VC

*Spinocyrtia* spp. (*S. granulifera*, *S. cf. granulosa*)

U

R

R

U

U

VR

†**Tropidoleptida:***Tropidoleptus carinatus*

C

C

U

C

**Strophomenata:****Productida:***Arcuaminetes (Devonochonetes) scitulus*

C

*Devonochonetes coronatus*

C

C

†**Strophomenida:***Megastrophia concava*

R

R

*Mesoleptostrophia junia*

VR

VR

U

*Strophodonta demissa*

C

C

U

Salmon Creek Locality Number	1a	1a/b	1b	2	3a	3b	3c	2 (talus)	3c				
<b>Stratigraphic Unit</b>	Hamilton Group								Tully Formation				
	Ludlowv Fm.	Moscow Formation											
	Modiomorpha-Ancyocrinus Bed ("lower Spafford")	Spafford Member	Tichenor Member	"Lower Moscow" (Deep Run-Kashong interval)	Deuel Road Member	Windom Member				Gar Mbr	Lab Vall	Upp Mbr	Lon Hill
						Cuylerville Submember <i>Ambocoelia</i> Beds	Upper Cuylerville Submember	Big Tree Smbr.	Smoke Creek Bed				
	Bay View Beds equivalent	<i>Ambocoelia</i> -rich Fall Brook Bed equivalent	Upper Taunton Submember	Spezzano Gully Submember	South Lansing Beds					Carpenter Falls Submember	Taughanock Falls Submember	Moravia Submember	

**Bryozoa:****Stenolaemata:****†Cystoporata:**

Unidentified cystoporate spp.

VR

C

**†Trepstomata:***Leptotrypella furcata*

R

**Cnidaria:****†Stauriida (†Rugosa):***Amplexiphyllum hamiltoniae*

R

*Heliophyllum delicatum*

VR

*Heliophyllum halli*

VR

*Stereolasma rectum*

R

VC

*Stewartophyllum intermittens*

C

*Streptelasma ungula*

C

C

**†Tabulata:****†Auloporida:***Aulocystis dichotoma*

VR

VR

VR

*Aulocystis jacksoni*

VR

**†Favositida:***Favosites argus*

VR

*Favosites hamiltoniae*

R

VC

*Pleurodictyum americanum*

VR

U

VR

R

*Thamnoptychia limbata*

VR

C





Salmon Creek Locality Number	1a	1a/b	1b	2	3a	3b	3c	2 (talus)	3c			
<b>Stratigraphic Unit</b>	Hamilton Group								Tully Formation			
	Ludlowv Fm.	Moscow Formation										
	Modiomorpha-Ancyrocrinus Bed ("lower Spafford")	Spafford Member	Tichenor Member	"Lower Moscow" (Deep Run-Kashong interval)	Deuel Road Member	Windom Member			Gar Mbr	Lab Vall	Upp Mbr	Lon Hill
						Cuylerville Submember <i>Ambocoelia</i> Beds	Upper Cuylerville Submember	Big Tree Smbr.				
	Bay View Beds equivalent	Smoke Creek Bed	Bear Swamp Submember	Fisher Gully Submember	Lower Fall Brook Bed equivalent				<i>Ambocoelia</i> -rich Fall Brook Bed equivalent	Upper Taunton Submember	Spezzano Gully Submember	South Lansing Beds

**Mollusca:****Gastropoda:****†Bellerophodontoidea:**

<i>Ptomatis patulus</i>				VR															
<i>Retispira leda</i>				VR		VR	VR												

**†Loxonematoidea:**

<i>Palaeozygopleura</i> spp. ( <i>P. delphicola</i> , <i>P. hamiltoniae</i> )				U		VR								VR					
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**†Platyceratoidea:**

<i>Naticonema lineata</i>		VR	R	U			R	R							R				
<i>Orthonychia</i> sp.				R															
<i>Platyceras</i> spp. (e.g., <i>P. cf. bucculentum</i> )				U															

**Pleurotomaroidea:**

<i>Glyptomaria capillaria</i>		VR	VR	R															
<i>Mourlonia</i> cf. <i>lucina</i>		VR																	

**Mollusca:****Cephalopoda:****†Ammonoidea:**

<i>Tornoceras uniangulare</i>	VR			VR		VR	VR				VR								
Unidentified gonaititic sp.						VR	VR												

**Nautiloidea**

Unidentified breviconic sp.							VR												
<i>Cyrtoceras</i> sp.			VR																
<i>Dolorthoceras exile</i>			U	U			U				VR		VR						
<i>Michelinoceras telamon</i>			U	U			VR	R					VR						
<i>Nephriticeras magister</i>	ER																		
<i>Spyroceras nuntium</i>		VR	U	U			R	C			R	R			R				

Salmon Creek Locality Number	1a	1a/b	1b	2	3a	3b	3c	2 (talus)	3c			
<b>Stratigraphic Unit</b>	Hamilton Group								Tully Formation			
	Ludlowv Fm.	Moscow Formation										
	Modiomorpha-Ancyrocrinus Bed ("lower Spafford")	Portland Point	Windom Member						Gar Mbr	Lab Vall	Upp Mbr	Lon Hill
			Spafford Member	"Lower Moscow" (Deep Run-Kashong interval)	Deuel Road Member	Cuylerville Submember <i>Ambocoelia</i> Beds	Upper Cuylerville Submember	Big Tree Smbr.	Taunton Smbr.			
	Tichenor Member	Bay View Beds equivalent	Smoke Creek Bed							Bear Swamp Submember	Fisher Gully Submember	Lower Fall Brook Bed equivalent
	Spezzano Gully Submember	South Lansing Beds	Carpenter Falls Submember	Taughanock Falls Submember	Moravia Submember							
	<b>Phoronida:</b>											
	<i>Reptaria stolonifera</i>					VR						
	<b>Tracheoptyes:</b>											
	Unidentified Tracheophytes spp.		VR	VR		VR						

## Appendix III. Field Trip Itinerary

This appendix provides a complete field trip itinerary to observe all the described stratigraphic and paleontological features present at Salmon Creek and Ludlowville Falls. The itinerary starts at Lower Salmon Creek (Locality 1), where Salmon Creek empties into Cayuga Lake at Myers Point. Here, the oldest stratigraphic unit, the *Modiomorpha-Ancyrocrinus* Bed (the lower Spafford Member) of the Ludlowville Formation, is exposed. The itinerary ends at Upper Salmon Creek (Locality 3) at Ludlowville Falls. The Tully Formation, the youngest unit, outcrops here. Driving directions from Snee Hall (Department of Earth and Atmospheric Sciences at Cornell University) to Locality 1, and from Locality 3 back to Snee Hall, are provided. For each locality, walking instructions to stratigraphic and paleontological sites of interest are given. Maps (figs. 1-4) are intended to supplement the directions.



**Appendix 3 Figure 1.** Physical map of Salmon Creek (Lansing, NY), with all documented fossil occurrences colored by locality.

The first edition of this itinerary (and field guide) was written by W.C.H. in spring 2023 for the first annual Pangea Club at Cornell (PCC) field trip to Salmon Creek and Ludlowville Falls in collaboration with the Snee Graduate Organization (SGO). Since then, PCC and SGO have run trips to Salmon Creek each spring. In addition to these trips, PCC runs regular field trips both on and off Cornell University's campus during the fall and spring semesters. Destinations in the past have included Cascadilla Gorge, Six Mile Creek, Tuaghannock Falls State Park, and Penn Dixie Quarry. PCC was led by W.C.H. from fall 2021 to spring 2024, and then by E.M.C. from fall 2024 to spring 2025. It is currently co-led by Eric Zhang and Giovanni D'Orazio. Joint Salmon Creek field trips with SGO leadership include C.J.H., Olivia Paschall, and Matthew Pruden in spring 2023; Francesca Riley in spring 2024; and Sarah Nolan in spring 2025.

Before traveling to Salmon Creek and Ludlowville Falls, please wear appropriate clothing and footwear. Wading through Salmon Creek is required to access many of the localities (i.e., all but Locality 1a). Do not wade across Salmon Creek if conditions are hazardous (e.g., high stream flow and stage). Visit Salmon Creek during the summer and fall, when stream flow and stage are both low, and avoid during the winter and spring, when freeze-thaw cycles are in effect. If collecting fossils, consider bringing plastic bags and/or paper towels, as well as sharpies for labeling locality and stratigraphic information. Note that hammers and chisels are unnecessary, as there is ample opportunity to surface collect at most localities. While walking to each locality and when collecting, always be aware of your surroundings at all times. Take note of and avoid walking underneath precarious overhangs (e.g., Tichenor Member at Locality 1a-2, Tully Member at Locality 3c-2). Be aware of private property and do not trespass.

Anyone visiting Salmon Creek and Ludlowville Falls agrees to the following: (1) it is not permissible to litter, deface, or in any way detract from the original appearance of Salmon Creek and Ludlowville Falls; (2) it is not permissible to trespass onto private property; (3) it is not permissible to have alcoholic beverages or illegal drugs at Salmon Creek and Ludlowville Falls; (4) the authors and Paleontological Research Institution are not responsible for any injuries that may result from accidental, negligent, or intentional acts by participants, or by failure of any participants to observe these rules. Remember that you are responsible for minimizing environmental impact to Salmon Creek and Ludlowville Falls. Please be respectful of wildlife and private property, and leave no trace. As this is a site of active paleontological research, refrain from over-collecting and/or undercutting outcrop (creek walls).

Directions to Locality 1 Parking (Salmon Creek Lower Fishing Access Point) from Snee Hall (42°26'37.7"N 76°29'03.8"W).

- Take West Ave, University Ave and Lake St to E Shore Dr
- Continue onto E Shore Dr
- Continue on NY-34B N to your destination



**Appendix 3 Figure 2.** Physical map of Locality 1: Lower Salmon Creek (Lansing, NY), with all documented fossil occurrences colored by locality.

## Locality 1. Lower Salmon Creek

Spafford, Tichenor, “lower Moscow”, Deuel Road, and lower Windom members

Loc. 1 Parking Access: 42°32'23.3"N 76°32'42.1"W | Loc. 1a-1 Coords: 42°32'24.7"N 76°32'36.6"W | Loc. 1a-2 Coords: 42°32'26.9"N 76°32'35.8"W | Loc. 1a-T Coords: 42°32'29.4"N 76°32'35.5"W | Loc. 1b-T Coords: 42°32'33.7"N 76°32'27.5"W | Loc. 1b-1 Coords: 42°32'38.0"N 76°32'24.5"W

Directions to Locality 1a (Myers Road) from Locality 1 Parking.

- Walk from Locality 1 Parking east along the trail.
- Follow the western bank of Salmon Creek upstream, past the Myers Road Bridge, to the exposed platforms of the Spafford Member overlaid by the Tichenor and lower Moscow

members (Locality 1a-2: Main Outcrop). Note that the *Modiomorpha-Ancyrocrinus* Bed (Locality 1a-1) will be a small section of the lower Spafford Member exposed just before the Main Outcrop.

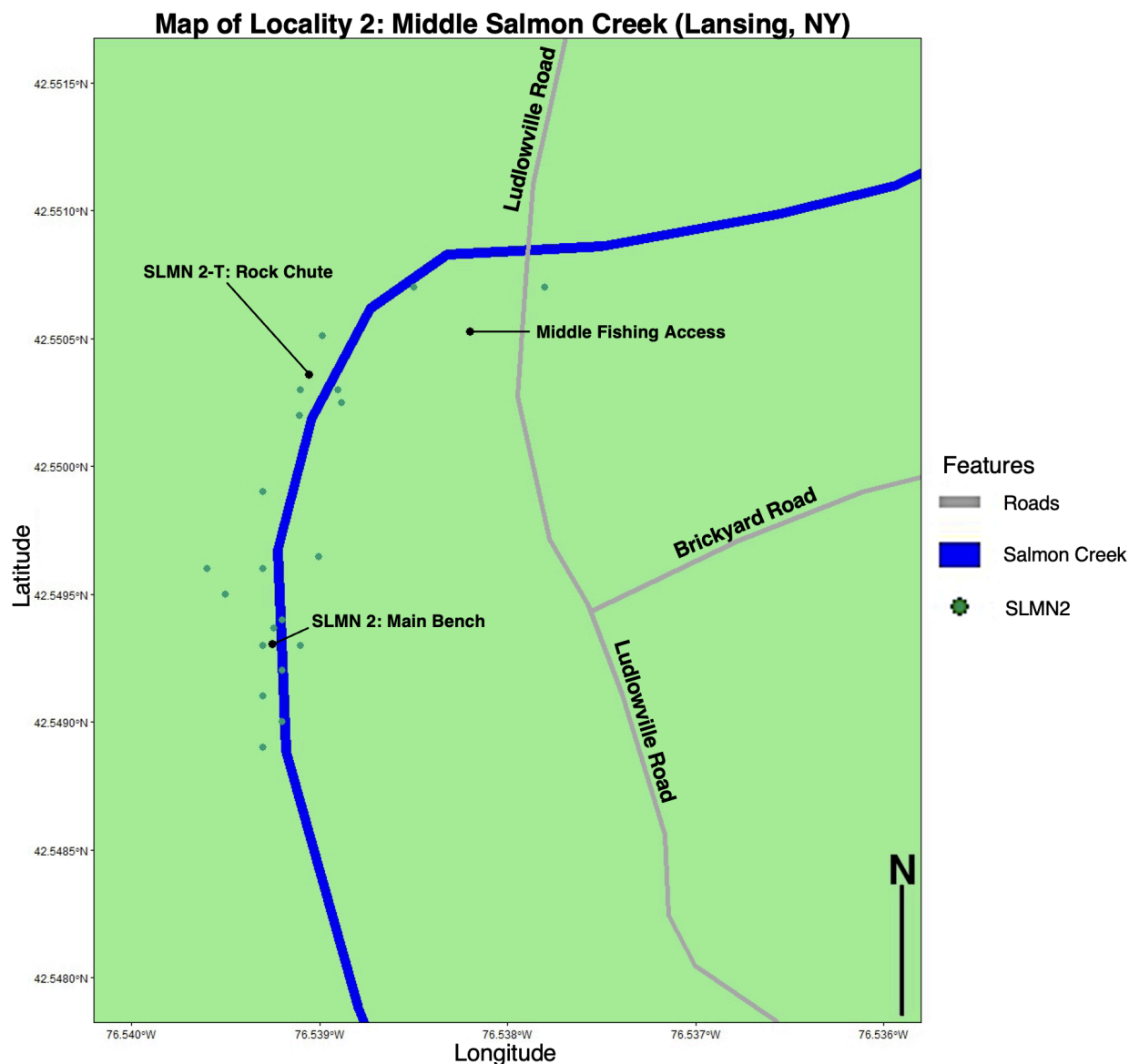
- Collect fossils in the Spafford Member (Localities 1a-1 and 1a-2). Note opportunities for talus collecting the Tichenor and lower Moscow members occur seasonally along the Spafford platforms at the northern end of the Main Outcrop (Locality 1a-T). If visited, take note of and avoid walking underneath the precarious overhangs of the Tichenor Member.

Directions to Locality 1b (Ridge Road) from Locality 1a.

- Follow the western bank of Salmon Creek upstream until directly opposite to Locality 1b Talus. Be aware of private property and do not trespass.
- Cross to the eastern bank of Salmon Creek to the Rock Fall (Locality 1b-T). Only cross Salmon Creek in safe conditions during low stream flow and stage. If safe to cross, be aware of strong currents, deeper pockets of water, and slippery algae on the stream bed. Note opportunities for talus collecting the lower Moscow occur seasonally at the Rock Fall. If visited, take note of and avoid walking underneath the precarious overhangs of the Tichenor Member.
- Follow the eastern bank of Salmon Creek upstream until immediately below the Ridge Road Bridge.
- Collect fossils in the Lower *Ambocoelia* Beds (Locality 1b).
- Return to Locality 1 Parking.

Directions to Locality 2 Parking (Salmon Creek Ludlowville Road Fishing Access Point) from Locality 1 Parking.

- Head east
- Turn left toward Myers Rd
- Merge onto Myers Rd
- Turn left onto NY-34B N
- Turn right onto Ludlowville Rd
- Turn right to stay on Ludlowville Rd
- Destination will be on the right



**Appendix 3 Figure 3.** Physical map of Locality 2: Middle Salmon Creek (Lansing, NY), with all documented fossil occurrences colored by locality.

## Locality 2. Middle Salmon Creek (Ludlowville Road)

Upper Cuylerville, Big Tree, and Bear Swamp submembers

Loc. 2 Parking Access: 42°33'02.2"N 76°32'17.7"W | Loc. 2-T Coords: 42°33'01.3"N 76°32'20.6"W | Loc. 2-1

Coords: 42°32'57.5"N 76°32'21.3"W

Directions to Locality 2 (Ludlowville Road) from Locality 2 Parking.

- Walk from Locality 2 Parking north to Salmon Creek.
- Cross Salmon Creek at its shallowest and least turbid point, typically below the Ludlowville Road Bridge. Only cross Salmon Creek in safe conditions during low stream flow and stage. If safe to cross, be aware of strong currents, deeper pockets of water, and slippery algae on the stream bed.
- Be aware of private property and do not trespass once across Salmon Creek.

- Follow the creek downstream along the western bank. Note opportunities for talus collecting the upper Moscow Formation occur seasonally at the Rock Chute (Locality 1b-T). If visited, take note of and avoid walking underneath jointed sections of the upper Moscow Formation.
- Collect fossils in the upper Cuylerville and Big Tree submembers (Locality 2).
- Return to Locality 2 Parking.

Directions to Locality 3a Parking (Salmon Creek Upper Fishing Access Point) from Locality 2 Parking. Note that additional parking is available at Ludlowville Park; Locality 3 can be accessed in the reverse direction from Locality 3c (Ludlowville Falls) to Locality 3a (Green Road).

- Head west on Mill St toward Ludlowville Rd
- Turn left onto Ludlowville Rd
- Destination will be on the right



**Appendix 3 Figure 4.** Physical map of Locality 3: Upper Salmon Creek (Lansing, NY), with all documented fossil occurrences colored by locality.

### Locality 3. Upper Salmon Creek

Upper Windom, Garrattsville, Labrador Valley, Upperville, and Long Hill members

Loc. 3a Parking Access: 42°33'08.5"N 76°32'04.0"W | Loc. 3a Coords: 42°33'11.2"N 76°31'59.6"W | Loc. 3b Coords: 42°33'13.4"N 76°32'03.1"W | Loc. 3c Parking Access: 42°33'13.3"N 76°32'13.7"W | Loc. 3c-1 Coords: 42°33'17.2"N 76°32'10.8"W | Loc. 3c-2 Coords: 42°33'17.5"N 76°32'14.5"W

Directions to Locality 3a from Locality 3a Parking.

- Cross to the eastern bank of Salmon Creek immediately from Locality 3a Parking. Only cross Salmon Creek in safe conditions during low stream flow and stage. If safe to cross, be aware of strong currents, deeper pockets of water, and slippery algae on the stream bed.
- Follow the eastern bank of Salmon Creek upstream to Locality 3a.
- Collect fossils in the Fisher Gully Submember.

Directions to Locality 3b (Dug Road) from Locality 3a.

- Follow the eastern bank of Salmon Creek north until reaching the stream mouth. Be aware of private property and do not trespass.
- Cross to the southern bank of Salmon Creek at the stream mouth. Only cross Salmon Creek in safe conditions during low stream flow and stage. If safe to cross, be aware of strong currents, deeper pockets of water, and slippery algae on the stream bed.
- Follow the southern bank of Salmon Creek upstream to Locality 3b.
- Collect fossils in the Taunton Submember lower Fall Brook Bed equivalent.

Directions to Locality 3c from Locality 3b.

- Follow the southern bank of Salmon Creek upstream until immediately across from Locality 3c.
- Cross to the northern bank of Salmon Creek. Only cross Salmon Creek in safe conditions during low stream flow and stage. If safe to cross, be aware of strong currents, deeper pockets of water, and slippery algae on the stream bed.
- Collect fossils in the Taunton Submember *Ambocoelia*-rich Fall Brook Bed equivalent (Locality 3c-1: Upper *Ambocoelia* Lags).
- Cross to the southern bank of Salmon Creek. Only cross Salmon Creek in safe conditions during low stream flow and stage. If safe to cross, be aware of strong currents, deeper pockets of water, and slippery algae on the stream bed.
- Follow the southern bank of Salmon Creek upstream until reaching Ludlowville Falls (Locality 3c-2). Enjoy the view!
- Return to Locality 3a Parking by following the trail from Ludlowville Falls to Ludlowville Park, and then following Mill St east to Green Rd.

Directions from Locality 3c Parking back to Snee Hall.

- Take Brickyard Rd and NY-34B S to NY-34 S/E Shore Dr
- Turn right onto NY-34 S/E Shore Dr
- Continue on Lake St to your destination

**End of Field Trip.**