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Margaret Yacobucci

Corresponding author:
Jonathan R. Hendricks;
Email: hendricksj@mpm.edu

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On the basis of stasis: documentation of taxon durations in paleontology and the necessity of museum voucher specimens

Jonathan R. Hendricks^{1,2}  and Bruce S. Lieberman³ 

¹Paleontological Research Institution, Ithaca, New York 14850, U.S.A.

²Milwaukee Public Museum, Milwaukee, Wisconsin 53233, U.S.A.

³Department of Ecology & Evolutionary Biology and Biodiversity Institute, University of Kansas, Lawrence, Kansas 66045, U.S.A.

Abstract

Most species exhibit morphological stasis following speciation, and this is a key feature of the concept of punctuated equilibria. Stasis results in species often having long durations on geological timescales. Durational data are fundamental to many types of paleobiological analyses and are ideally based on occurrence data represented by specimens in museum collections. Often, however, durational data are presented without supporting information about voucher specimens that document stratigraphic ranges, including first and last appearances. We use the iconic Devonian trilobite *Eldredgeops rana* to demonstrate that durational data can be challenging to determine at multiple taxonomic levels. Further, we show that different datasets—including Sepkoski's published databases, the Paleobiology Database, and iDigBio—give discordant results concerning first and last occurrences. We argue that paleontologists should adopt two general best practices to help address these problems. First, systematists should clearly identify voucher specimens that represent stratigraphic occurrences of species. Second, we recommend that high-quality photographs of occurrence vouchers be placed in open access websites and be assigned public domain licensing before being paywalled by journals. Such voucher images also have a role to play in training artificial intelligence (AI) systems that will be applied to future paleobiological questions.

Non-technical Summary

Most species exhibit little change (stasis) in form following speciation, and this is a key feature of the concept of punctuated equilibria. Stasis results in species often having durations that span millions of years. Durational data are fundamental to many types of paleobiological analyses and are ideally based on occurrence data represented by specimens in museum collections. Often, however, durational data are presented without supporting information about voucher specimens that document stratigraphic ranges, including first and last appearances. We use the iconic Devonian trilobite *Eldredgeops rana* to demonstrate that durational data can be challenging to determine at multiple taxonomic levels. Further, we show that different datasets derived from the published literature and museum collections give different results concerning the first and last appearances of species in the fossil record. We argue that paleontologists should adopt two general best practices to help address these problems. First, paleontologists should clearly identify voucher specimens that represent stratigraphic occurrences of species. Second, we recommend that high-quality photographs of occurrence vouchers be placed in open access websites and be assigned public domain licensing before being paywalled by journals. Such voucher images also have a role to play in training artificial intelligence (AI) systems that will be applied to future paleobiological questions.

What Every Paleontologist Knows, Revisited

The radical insight of Eldredge and Gould's (1972) concept of punctuated equilibria is not that morphological change is rapid on geological timescales, but rather that the forms of most species tend not to change much following speciation (see also Gould and Eldredge 1977; Gould 2002). That is, speciation does not tend to be characterized by a series of intermediate forms that link an ancestral species to its descendants (phyletic gradualism). Instead, morphological change typically occurs in a geological instant at the time of speciation (consistent with the allopatric model of Mayr 1963; see also Eldredge 1971) and this is often followed by subsequent morphological stability or stasis. This stability in form is one reason we can consider species as being analogous to organisms and having finite individuality (Hull 1980): they have a birth (speciation), a life span (duration), and a death (extinction). These features collectively make species the fundamental units of the study of macroevolution (Lieberman and Eldredge 2014).



The general stability of species over their life spans has practical utility and is the foundation of the science of biostratigraphy. Every biostratigraphic chart is an argument for the utility of species-level stasis for assigning ages to rocks. Eldredge and Gould (1977) recognized this and noted that “by the mere recognition of *any* nontrivial stratigraphic range of *any* morphologically defined taxon at near specific rank, we are necessarily implying a stability or stasis in species-specific *differentia*” (p. 29, italics in original). Gould (2002) characterized this as “What Every Paleontologist Knows” (p. 745) in a heading at the beginning of chapter 9 of his opus, explaining that “paleontologists have always recognized the long-term stability of most species, but we had become more than a bit ashamed by this strong and literal signal” (p. 749).

Our purpose here is not to review the strong evidence and general support for stasis, which has been provided elsewhere (e.g., Gould [2002] and Eldredge et al. [2005] and papers cited therein). Instead, we focus on the underlying data from specimens that support all accounts of species durations and examples of stasis. We are fundamentally interested in how durational data are generated in many modern analyses and present some suggestions for best practices in the future. If embraced, we think that these changes will facilitate prospecting for more examples of stasis in the age of “big data.”

Durational Data in Paleontology

Because of stasis, species often have long durations, sometimes spanning millions of years. Estimates vary considerably across different taxonomic groups and tend to be extrapolations from higher-level taxonomic data (Lamkin and Miller 2016). For example, Cambrian trilobites (1.5 Myr; Foote 1988), Mesozoic ammonoids (1–2 Myr; Kennedy 1977), and Cenozoic terrestrial mammals (1–2 Myr [Vrba 1985]; 2.4 Myr [Prothero and Heaton 1996]) have relatively shorter durations on geological timescales, although still tremendously long with respect to the predictions of phyletic gradualism. Animal groups with relatively longer durations on geological timescales include Devonian invertebrates from the Appalachian Basin (3–7 Myr; Brett et al. 1996) and Cenozoic bivalves (10 Myr; Raup and Stanley 1978: p. 323). Reported durations of some microfossil groups are sometimes much greater. For example, Buzas and Culver (1984) reported benthic foraminifera durations of 16–26 Myr (see also Strotz and Allen 2013). For additional summaries of typical species durations across other taxonomic groups, see Stanley (1979), Raup (1991), and May (2002). A general rule of thumb, however, is that “the average life span of a species in the fossil record ... is typically a few million years” (May 2002: p. 1328).

Such species durations are fundamental data in many paleobiological studies. This includes analyses conducted at the genus level (or above), because the geological duration of a genus reflects the combined durations of all its constituent species (Hendricks et al. 2014). A duration is determined by the first and last appearance of a species in the fossil record, and net stasis is demonstrated by minimal overall morphological change between those two end points, even if there are some oscillations in form in between. Quantitative examples of this were demonstrated in two Devonian brachiopods—*Athyris spiriferoides* (Eaton, 1831) and *Mediospirifer audaculus* (Conrad, 1842)—by Lieberman et al. (1995).

Durational data are fundamental to much of analytical paleobiology. For example, there is a general interest in the typical life spans of species from varied clades (see earlier examples), as

knowing this is key to calculating extinction rates. Durational data are also essential to the development of diversity curves across geological time, for example, the iconic depiction of Phanerozoic marine diversity presented by Sepkoski (1981: fig. 5). Such studies of past biodiversity have allowed paleontologists to quantify the scale of ancient extinction events and provide context for understanding modern biodiversity loss (e.g., Barnosky et al. 2011; Kiesling et al. 2019). Among other uses, durational data have also been used to investigate whether taxon attributes like geographic range confer resistance to extinction, resulting in longer durations (Jablonski and Hunt 2006; Payne and Finnegan 2007).

Ultimately, durational data are derived from fossil specimens, ideally housed in museum drawers that are accessible to paleontologists. In practice, however, durational data are usually presented without reference to voucher specimens and instead rely on earlier tabulations and summaries that may or may not be tied to actual vouchers. We illustrate this below with the example of the phacopid (Bault et al. 2023) trilobite *Eldredgeops rana* (Green, 1832) (formerly *Phacops rana*; Fig. 1), which featured prominently in Eldredge and Gould’s (1972) initial example of punctuated

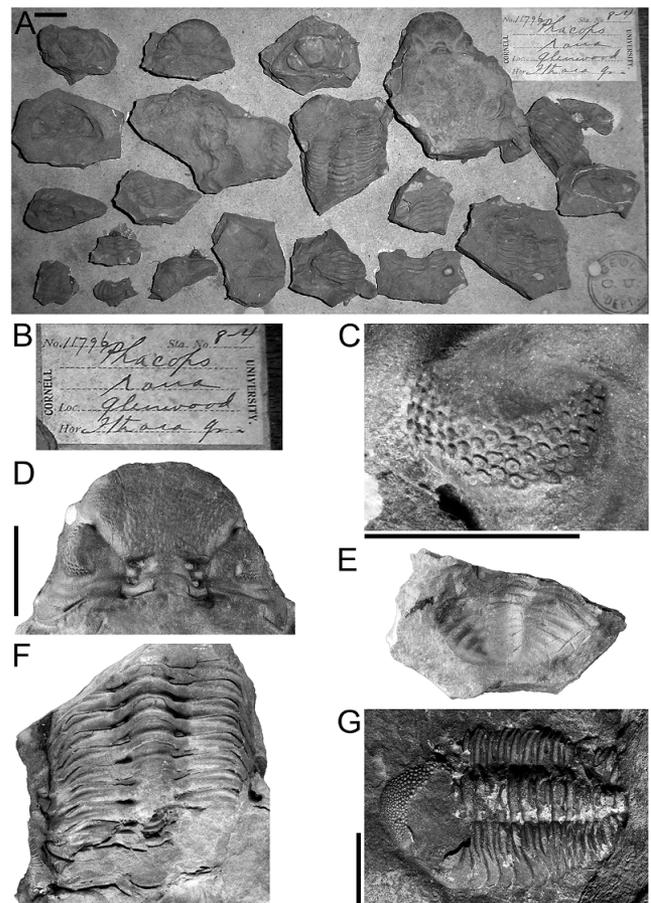


Figure 1. A–F, Specimens of Frasnian (likely Ithaca Formation) *Eldredgeops rana* from Tompkins County, New York (PRI 57222). **A**, Original sample from Kindle (1896) (originally catalogued as Cornell University 11796); scale bar, 1 cm; sample card is lost; image captured in 2006 provided by J. Zambito. **B**, Magnified view of label in **A**. **C**, **D**, Cephalon and magnified view of eye of one (specimen to left of label in **A**); scale bar below **C** pertains to that image and equals 5 mm. **E**, Pygidium of specimen on third row of card, second from the left. **F**, Thorax of specimen on second row of card, third from the left. Scale to left of **D** pertains to images **D–F** and equals 1 cm. **G**, Specimen of *E. rana* from the Pecksport Mbr. of the Oatka Creek Fm. (lower Givetian) Madison County, New York (KUMIP 419279); scale bar, 1 cm.

equilibria. Focusing mostly on purported first and last occurrences, we demonstrate that durational data can be challenging to pin down at multiple taxonomic levels, even for this classic example of morphological stasis.

The Example of *Eldredgeops rana* (Trilobita: Phacopidae)

Specimens of the “frog-eyed” phacopid trilobite *Eldredgeops rana* are very common in the Devonian Hamilton Group of New York State (Bartholomew and Ver Straeten 2023; Brett et al. 2023) and are much sought after by collectors, resulting in substantial representation of the species in museum collections, and undoubtedly even more in avocational collections. The most important systematic treatment of *E. rana* remains the monograph of Eldredge (1972), which provided the fundamental data in support of stasis in this species that was published by Eldredge and Gould (1972) the same year. The species is thus an apt subject for evaluating how durational data are underpinned in paleontological research. We consider this support at the family, genus, and species levels using data from the literature and online databases, with a focus on several large datasets (Sepkoski, 1982, 2002; Paleobiology Database [PBDB], <https://paleobiodb.org>) and museum collections (Integrated Digitized Biocollections [iDigBio] <https://www.idigbio.org>) that have provided key insights into the evolution of life. Given that most published and museum records of *E. rana* are attributed to *P. rana*, we included both genera in our investigation. Our attention is on how first and last appearances are underpinned and represented in these databases, as they determine total fossil durations in analyses.

Institutional Abbreviations

AMNH: American Museum of Natural History, New York; FHSM: Fort Hays State Museum (Sternberg Museum), Fort Hays, Kansas; HM: Hunterian Museum, London; KUMIP: Division of Invertebrate Paleontology, Biodiversity Institute, University of Kansas, Lawrence, Kansas; MNHN: Muséum National d'Histoire Naturelle, Paris; PRI: Paleontological Research Institution, Ithaca, New York; SDSM: South Dakota School of Mines, Rapid City, South Dakota; SMF: Senckenberg Museum Frankfurt, Germany; UF: Florida Museum of Natural History Division of Invertebrate Paleontology, University of Florida, Gainesville, Florida; YPM: Yale Peabody Museum, New Haven, Connecticut.

Family Phacopidae

Sepkoski Database. The underlying family-level durational data analyzed by Sepkoski (1981) are largely derived from the *Treatise on Invertebrate Paleontology* (numerous volumes and authors), Harland et al. (1967), and Romer (1966). This database was published by Sepkoski (1982) and consists of times (mostly stage level) of first and last appearances for each family. Sepkoski (1982) reported, based on Harland et al. (1967), that the trilobite family Phacopidae Hawle and Corda, 1847 first appeared in the lower Silurian (Llandoveryan Series) and last appeared in the Upper Devonian (Famennian). The record in Harland et al. (1967: p. 491) for Phacopidae presents a first occurrence in the Ordovician Ashgillian (contra Sepkoski 1982) based on Cooper's (1930) record of *Phacops primaevus* Clarke, 1908 from the Upper Ordovician of Percé, Quebec, Canada (as *Portlockia primaeva* (Clarke) in Cooper; this species has also been assigned to *Eophacops* Delo, 1935 and *Acernaspis* Campbell, 1967, both phacopids). This record is

supported by figured specimens in the collection of the YPM (see White and Lieberman 1998). The last occurrence of Phacopidae, according to Harland et al. (1967), is based on Devonian Famennian occurrences of *Cryphops* Richter and Richter, 1926, *Dianops* Richter and Richter, 1923, and species of *Phacops* Emmrich, 1839, including *Phacops accipitrinus* (Phillips, 1841) from Europe. Harland et al. (1967) cited Richter and Richter (1926, 1951) and Goldring (1955) in support of the Famennian occurrences of *P. accipitrinus*, although Richter and Richter (1926, 1951) do not mention it and Goldring (1955) did not figure or refer to any specimens of it.

PBDB Records. We downloaded all PBDB records assigned to Phacopidae, resulting in 1283 occurrences (Supplementary Table 1; accessed 4 January 2024). The oldest record of Phacopidae is assigned to the Middle Ordovician for an occurrence (PBDB 3414) of Phacopidae indet. reported in an unpublished Ph.D. dissertation by Parker (1983). We could find no reference, however, to Phacopidae or its constituent taxa in Parker's dissertation. The youngest record of Phacopidae is assigned to the beginning of the Carboniferous for an occurrence (PBDB 402531) of *Phacops* (*Omegops* Struve, 1976) sp. attributed to Brauckmann et al. (1993). However, Brauckmann et al. (1993) note (p. 513) that “the local overlap of *Ph. (Omegops)* in the lowest Carboniferous bed at La Serre (Flajs and Feist, 1988) is exceptional and possibly caused by transport and redeposition from the older beds.” Flajs and Feist (1988) did figure (plate 11, fig. 15) the “fragmentary cephalon” (p. 76) that is the ultimate basis of this record (SMF 49449).

iDigBio Records. We downloaded all iDigBio specimen records assigned to Phacopidae, resulting in records for 4866 lots, 917 of which have associated photographs (Supplementary Table 2; accessed 8 January 2024). Of these, 4131 are attributed to the Devonian Period. The two oldest lots are assigned to the Cambrian Period and are represented by SDSM 2658 (purportedly *Phacops rana* from Millard County, Utah, which we presume is a misidentification or other type of error) and MNHN A44830 (“*Lamanaspis nyx*” from Seville, Spain, although this taxon name may not be available). The youngest records (13 lots) are attributed to the Pleistocene (all *P. rana*), which we presume are a result of data entry error.

Genera *Phacops* and *Eldredgeops*

Sepkoski Database. Sepkoski's “A Compendium of Fossil Marine Animal Genera” was published posthumously in 2002 (edited by D. Jablonski and M. Foote) and provided the underlying data for his earlier tabulation of genus-level marine animal diversity (Sepkoski 1997: fig. 1.1). Sepkoski (2002: p. 192) reported the first occurrence of *Phacops* as Siegenian (now Pragian, Lower Devonian) and last appearance as Famennian (Upper Devonian), supported by Harland et al. (1967) and Chlupáč (1994). The supporting records from Harland et al. (1967) are those presented earlier for the family Phacopidae. Chlupáč (1994) reported lower Emsian (Zlichovian; Lower Devonian) *Phacops degener* Barrande, 1852 as “the first known link” of the lineage of large-eyed phacopids and Famennian *Phacops granulatus* Münster, 1840 and *P. accipitrinus* as among the last lineages of *Phacops*; Chlupáč (1994) did not provide information about voucher specimens for these earliest and latest records of *Phacops*.

Sepkoski (2002: p. 191) reported the first occurrence of *Eldredgeops* Struve, 1990 as occurring in the Eifelian (Middle Devonian) and last occurrence in the *varcus-cristatus* Zones of the Givetian

(Middle Devonian), both derived from Struve (1992). Struve (1992) reported *Eldredgeops* as ranging from the “Eifelium bis Ober-Givetium” (p. 532; Eifelium to upper Givetian, Middle Devonian), but did not provide information about voucher specimens.

PBDB Records. We downloaded all PBDB records assigned to *Phacops*, resulting in 362 occurrences (Supplementary Table 3; accessed 18 January 2024). Of these, 1 is assigned to the Ordovician, 19 to the Silurian, 341 to the Devonian, and 1 to the Mississippian. The oldest record (PBDB 725769) is *Phacops (Calliops) jukesi* Salter, 1853 from the Burrellian (Middle to Upper Ordovician) Balclatchie Beds of Girvan, derived from Reed’s (1945) variety *Phacops (Calliops) jukesi* var. *vicina*. Clarkson and Tripp (1982) synonymized this record (HM A 5370) with *Calyptaulax brongniartii* (Portlock, 1843), negating its relevance as a first occurrence of *Phacops*. The youngest record (PBDB 402531) is from the Hastarian (Lower Mississippian) and comes from the report by Brauckmann et al. (1993) of *Phacops (Omegops)* sp. discussed earlier for the youngest record of Phacopidae, which, as mentioned, may be a reworked, older specimen.

There are 241 PBDB records assigned to *Eldredgeops*, and all but one are assigned to the Middle Devonian (Supplementary Table 4; accessed 18 January 2024). The oldest record (PBDB 414107) comes from a Lower Devonian record from the Stooping River Formation of Ontario published by Sanford and Norris (1975) as “*Phacops* cf. *P. rana* Green”; this record is based on a taxon list in Sanford and Norris (1975) and no voucher specimen is identified. Numerous published references in the PBDB dataset support last occurrences of *Eldredgeops* during the Givetian (Middle Devonian), all represented by *E. rana* or its subspecies.

iDigBio Records. We downloaded all iDigBio specimen records assigned to *Phacops*, resulting in records for 3666 lots, 533 of which have associated photographs (Supplementary Table 5; accessed 19 January 2024). The oldest record is SDSM 2658, identified as *P. rana*, from the Middle Cambrian of Utah; this same record is the basis of the oldest occurrence of Phacopidae in the iDigBio database (see “Family Phacopidae”). The iDigBio dataset includes other Cambrian records, however, including specimens identified as *Phacops enceutra* [sic] (= *eucentra*) Angelin, 1851 from the Upper Cambrian of Sweden (YPM 74803–74808); see remarks by Temple (1952) concerning the problematic nature of this taxon, which may be an Upper Ordovician dalmanitid trilobite. Records of *Phacops* from the Ordovician and Silurian are also present. The youngest records for *Phacops* in the iDigBio dataset are from the Pleistocene (FHSM collection).

Surveying iDigBio for *Eldredgeops* resulted in records for 495 lots, 350 of which have associated photographs (Supplementary Table 6; accessed 19 January 2024). All lots with age determinations ($n = 451$) are assigned to either the Devonian or Middle Devonian.

Species *Phacops/Eldredgeops rana*

PBDB Records. We downloaded all PBDB records assigned to *P. rana/E. rana*, resulting in 241 occurrences (Supplementary Tables 7, 8, which contain the same records; accessed 19 January 2024). The oldest is the Early Devonian record of Sanford and Norris (1975) addressed earlier. Numerous published references supported a latest occurrence of this species in the Givetian (Middle Devonian). Among records from New York State, the youngest specimens come from the Genesee Formation of Chenango County, supported by data obtained from the Thayer Collection at the YPM (PBDB collection 86241). We note that an earlier

download of this PBDB dataset (accessed 15 August 2022) included a Frasnian (Upper Devonian) record of *P. rana* (PBDB occurrence 1197130, part of collection 154838) published by Clarke and Swartz (1913) that is no longer in the PBDB. Clarke and Swartz briefly described (p. 699) and figured (plate 72, fig. 8) a partial cephalon and pygidium from the “Jennings Fm.” (abandoned) of Allegany County, Maryland.

iDigBio Records. We downloaded all 1077 records of *P. rana* (Supplementary Table 9; accessed 19 January 2024) and 480 records of *E. rana* (Supplementary Table 10; accessed 19 January 2024) from iDigBio; 782 of these have associated photographs. The oldest (middle Cambrian) and youngest (Quaternary) records are the same as those described earlier at the genus level. Among records from New York State, the oldest are from the Silurian Niagara Formation of Niagara County and are represented by SDSM 423 and SDSM 424; we presume that these are misidentifications. The youngest records are from the Frasnian (Upper Devonian) Ithaca Formation of Tompkins County and are represented by PRI 57221 and PRI 57222; see additional discussion of one of these lots in “Species *Phacops/Eldredgeops rana*.”

Summary

Our purpose here is not to provide a definitive accounting of the first and last appearances of *E. rana* and its parent genus and family ranks. The data we present are based solely on the literature- and specimen-based datasets that we analyzed and do not include unpublished or undigitized museum records. We anticipate that additional records may become available that will impact the durations that we have presented. Instead, our goal here is to demonstrate that our understanding of the duration of the species-, genus-, and family-level taxonomic ranks associated with *E. rana* is little connected to tangible specimen-based support and that different datasets give inconsistent results.

Family Phacopidae

The literature tree associated with the Sepkoski (1982) family-level database supports a first appearance in the Upper Ordovician based on specimens published in Cooper (1930) of *Phacops primaevus*; the last appearance during the Upper Devonian is not supported by specimen evidence in the cited references. The PBDB dataset suggests a first appearance of Phacopidae in the Middle Ordovician, but this is not supported by the underlying reference; the last appearance at the beginning of the Carboniferous is supported by specimen data, but may be a result of redeposited sediments. The iDigBio dataset suggests a first appearance in the Cambrian and a last appearance in the Pleistocene, both of which are likely a result of specimen misidentification or data entry error.

Genera *Phacops* and *Eldredgeops*

The reference trees associated with Sepkoski’s (2002) genus-level database for *Phacops* (Lower to Upper Devonian) do not provide specimen support for reported durations; this is also the case for *Eldredgeops* (Middle Devonian). The PBDB supports a Middle/Upper Ordovician to Mississippian range for *Phacops*, with both end points associated with published specimens (although the supporting record for the Middle/Upper Ordovician is no longer attributed to *Phacops*); a suggested first appearance of *Eldredgeops* in the Lower Devonian is not supported by specimen data, and

numerous references support a Middle Devonian last appearance. Specimen data from iDigBio suggest a first appearance of *Phacops* in the Cambrian and a last appearance in the Pleistocene, both of which are doubtful; *Eldredgeops* specimens with age determinations are all assigned to the Devonian or Middle Devonian.

Species *Phacops/Eldredgeops rana*

Setting aside the conferred record of Sanford and Norris (1975), data from the PBDB suggest that *E. rana* is restricted to the Givetian (Middle Devonian). iDigBio records, taken at face value, suggest that *E. rana* spans most of the Phanerozoic; this is, of course, incorrect and most iDigBio records support a Middle Devonian fossil record.

While robust, the PBDB and iDigBio databases are not comprehensive and many literature sources and most museum collections have not yet been entered into them. What do published sources beyond those included in the PBDB suggest about the fossil record of *E. rana*? Eldredge (1972) reported *E. rana* as coming from “the ‘Hamilton’ (comprising the Marcellus, Skaneateles, Ludlowville, and Moscow formations ...) and the overlying Tully and ‘Chemung’ formations and their lateral equivalents” (p. 53) and the oldest occurrences of *E. rana* from the Cardiff Formation of New York, now recognized as a member of the Oatka Creek Formation (Givetian) (see Ver Straeten et al. 2023); however, supporting specimens were not identified. That said, additional specimens from the similarly aged Pecksport Member of the Oatka Creek Formation that were collected by Eldredge are deposited in the collections of the KUMIP (KUMIP 419280, KUMIP 419281, and KUMIP 419279 [Fig. 1G]; originally labeled as Solsville Mbr., but the Swamp Road locality in Madison County, New York—where they were collected—is now known to instead expose the overlying Pecksport Mbr.; see Ver Straeten et al. 2023). The youngest occurrence of *E. rana* reported by Eldredge (1972) may be of “Chemung age” and was supported in part by a “poorly preserved” specimen (AMNH 496911). The stratigraphic meaning of “Chemung” is nebulous but is applied to a sequence of Frasnian rocks in New York (see text-fig. 1 in Ver Straeten [2023] and text-fig. 1 in Over et al. [2023]). Did *E. rana* indeed persist from the Givetian into the Frasnian? Cr n ier and Fran ois (2014), citing a personal communication, stated that *Eldredgeops* (presumably related to records of *E. rana*) did survive into the Frasnian in “Northeast America” (p. 14). Feist and Klapper (2022) criticized the “Chemung” occurrence of Eldredge (1972), noting that it is probably from “the Ithaca Sandstone” and “led to the assumption that *Eldredgeops* persisted into the Late Devonian” (p. 3). They further noted that the Chemung specimens were “neither figured nor described” and thus the record “remains doubtful and it is not considered here” (p. 3).

Contrary to Feist and Klapper (2022), there is acceptable, if sparse, evidence that *E. rana* survived the Givetian into Frasnian time. Kindle (1896) described a section of “Ithaca Group” strata at a section exposed at Glenwood Creek, on the western shore of Cayuga Lake in Tompkins County, New York (Kindle station 8-4, “360 feet above the lake,” p. 30). Kindle remarked that “this station is above the Ithaca shale in the lower part of the Ithaca group. It is remarkable for the great abundance of the species which occur in the sandy shales, and for the presence of *Phacops rana* in abundance in a single layer” (p. 30). He described *E. rana* as “abundant” at station 8-4 (p. 46) and notes the significance of *E. rana* (as well as several other species) as “recurrent Hamilton fossils” (p. 48; see also Williams 1913). The stratigraphic samples

collected by Kindle (1896) reside in the PRI collections and include 19 specimens of *E. rana* collected at station 8-4 (PRI 57222; Fig. 1A–F). Exposures at Glenwood Creek (42.495°N, 76.543°W) are important reference sections for the Sherburne (Givetian) and Renwick (Frasnian) formations (see Over et al. 2023). Kindle (1896) reported “the upper *Spirifer laevis* zone” at 210 feet in the Glenwood Creek section at station 8-4 (p. 30). The abundant occurrence of this brachiopod, now recognized as *Warrenella laevis* (Hall, 1843), indicates the base of the Renwick Formation (Cornell Member) (see Zambito et al. 2007, 2009; Over et al. 2023). De Witt and Colton (1978: plate 3) published a section (I-1) for Glenwood Creek that reported a 25–30 ft thickness for the Renwick. The presence of *E. rana* 150 feet higher yet in the section strongly suggests that it is from the overlying Ithaca Formation and leaves no doubt about its Frasnian assignment. Frasnian occurrences are also supported by records in Williams (1913), although these were not associated with specimens.

Based on this evidence, we agree with Eldredge (1972) that *E. rana* persisted into the Frasnian and aberrant records past the Givetian “simply represent a greatly diminished population near extinction” (p. 93). We conclude, based on cataloged specimens, that *E. rana* persisted in stasis for 6 Myr or more—from ca. 386 Ma (near the top of the Oatka Creek Fm.) to ca. 380 Ma (base Ithaca Fm.) (ages from text-fig. 1 in Ver Straeten 2023)—and perhaps even longer if the “Chemung” occurrences are truly from higher in the sequence than the Ithaca Formation specimens. The establishment of *E. rana* in the Frasnian also confirms the persistence of *Eldredgeops* as well into the Late Devonian.

Toward a Systematic Paleontology

Linnaean taxonomy is underpinned by the concept of voucher types: species are tied to type specimens, genera to type species, and families to type genera. Species may shift between higher taxa according to the whims of systematists, but concepts and definitions of higher taxa—as well as their properties—are ultimately circumscribed by the features of real specimens (see also Hendricks et al. 2014). However, the properties of ancient taxa that are of greatest interest in studies of macroevolution—especially duration over geological time, but also including geographic range and morphological trait data—tend not to be explicitly tied to voucher specimens. This makes verification impossible and contributes to the inconsistency of results, including for taxa as well sampled and documented as *Eldredgeops rana*.

The PBDB has facilitated important contributions to our understanding of ancient life and has made it simple for anyone to attain durational data for species and higher taxa, democratizing a process that previously required years of research in the library (e.g., Sepkoski 1993). The records in the PBDB, which is largely built from the literature, are often estranged from specimens in museum collections. Verifying stratigraphic occurrences for individual taxa often leads one down a proverbial rabbit hole, sometimes with no cataloged specimen at the end of the tunnel. When durational data are not tied to corresponding specimen data, users of these data have limited means to verify taxonomic assignments or independently evaluate reported durations or stasis. The iDigBio database provides the opposite: all records are inherently tied to cataloged museum specimens, but taxa may be misidentified, or there may be data entry errors that distort temporal and geographic occurrences. Obvious errors are simple to recognize and discard from downloaded datasets (e.g., Pleistocene records of *E. rana*). But what about records that are not altogether unreasonable? Would someone who

does not have expertise on phacopid trilobites immediately discard Lower Devonian or Lower Mississippian records of *E. rana*? In general, as is almost certainly the case for *E. rana*, establishment of voucher specimens will have the likely effect of reducing durations of taxa relative to reports or data compilations that have not been critically evaluated.

For the sake of verification, quality of analysis, and reproducibility of results, paleontology needs a better way to document occurrences and tie such records to voucher specimens, just as it needs a better system for recognizing the scientists who make these associations (Smith et al. 2023). We have two general recommendations to address this issue. First, as a matter of best practice, systematists should publish museum catalog numbers for voucher specimens that represent stratigraphic occurrences when they summarize the durations of species, whether newly described, revised, or comprehensively monographed. First and last appearances are especially important to document, because they set the boundaries for studies of morphological evolution (or stasis) in the fossil record, as well as provide core data for biostratigraphic analysis. It is also useful to directly document with vouchers all of the stratigraphic units (formations or members) from which a species has been found. This is simple for a taxonomist to do in the systematics portions of a manuscript. For example, where Hendricks (2009) reported the occurrence of *Conus marylandicus* Green, 1830 (now *Conasprella (Ximeniconus) marylandica* (Green), n. comb.) as “Virginia (Yorktown Formation), North Carolina (Duplin Formation), and Florida (Tamiami and Jackson Bluff formations)” (p. 23), it would have been better practice to present this as “Virginia (Yorktown Formation; PRI 52915), North Carolina (Duplin Formation; PRI 82912), and Florida (Tamiami [PRI 53183] and Jackson Bluff formations [UF 78488]).” Although our focus is on documentation of stratigraphic occurrences, vouchers are also useful for formally documenting specimens found at extremes of a geographic range or representing morphological end-members. In addition to being formally recognized in the literature, established voucher specimens should also be incorporated into online databases like the PBDB. Occurrences that are supported by taxonomist-approved vouchers should be clearly identified as such. It is also critical that—just like type specimens—occurrence voucher specimens be deposited in museum collections where they can be accessed and evaluated by the research community.

Our second recommendation is that high-quality photographs of occurrence voucher specimens be placed in established open access websites (e.g., GBIF, MorphoSource, or FigShare) and be assigned public domain licensing. This should be done before publication so that images of significant specimens (including future types, but also occurrence vouchers) cannot become “paywalled” later by journal copyright restrictions. To our knowledge, no study has investigated the number of fossil species whose type specimens (as well as descriptions) are only represented by single images locked behind journal paywalls, but we anticipate that it is a significant percentage; the same likely applies to extant taxa. Organizations such as the Biodiversity Heritage Library have commendably liberated such data from articles whose copyrights have expired, as well as through partnerships with society journals that have made the decision to make available some or most of their holdings. But, much literature—including from the Paleontological Society’s own flagship systematics journal—remains “paywalled” and this is ultimately a detriment to the advancement of our understanding of ancient life, especially for researchers who do not have access to large academic research libraries. (Note that the *Treatise on Invertebrate Paleontology*, which contains numerous images of invertebrate fossil type specimens, is now open access.) Fortunately, authors now have much more control

over the scientific content that they generate and how it is shared. Releasing images of important specimens into the public domain before copyright is transferred to a journal removes barriers for future workers. If such images are assigned their own stable web addresses (e.g., a digital object identifier, or DOI), it also becomes possible to link them to other online records, for example, in the PBDB. Depending on journal requirements, an alternative approach is to place images of stratigraphic voucher specimens in supplementary material associated with a paper, although such repositories are not always easy to find or can be overlooked.

Novel methodological approaches, for example, ecological niche modeling in combination with newly digitized specimens, have renewed the importance of museum collections for addressing questions that are broader than systematic studies of individual species or clades (e.g., Lieberman and Kimmig 2018). Further, it is likely that the millions of specimens that reside in museum collections—once digitized—will provide the fuel for paleontology’s big data future (e.g., Allmon et al. 2018). The success of these approaches rests upon the underlying data being sound, and we have argued here that the establishment of expert-vetted voucher specimens is important for both modern and future workers. We have no doubt that artificial intelligence (AI) will soon play a role in taxonomic work in ways that have yet to be determined (or perhaps even imagined). Such AI systems will need to be trained, however, and voucher specimens will and should play an important part in this process. Paleontologists should not fear or delay this future, for it will allow us to prospect for stasis and other features of macroevolutionary history in new ways, as well as spur the research questions that will occupy our field for the next 50 years.

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Literature Cited

- Allmon, W. D., G. P. Dietl, J. R. Hendricks, and R. M. Ross. 2018. Bridging the two fossil records: paleontology’s “big data” future resides in museum collections. Pp. 35–44 in G. D. Rosenberg and R. M. Clary, eds. *Museums at the forefront of the history and philosophy of geology: history made, history in the making*, Vol. 535. Geological Society of America, Boulder, Colo.
- Angelin, N. P. 1851. *Palaeontologia Scandinavica, P. I. Crustacea formationis transitionis*. Fasciculi I & II. Apud Samson & Wallin, Stockholm.
- Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, et al. 2011. Has the Earth’s sixth mass extinction already arrived? *Nature* 471:51–57.
- Barrande, J. 1852. *Système silurien du centre de la Bohême: 1ère partie, Recherches paléontologiques. I, Crustacés; Trilobites*. Prague-Paris.

- Bartholomew, A. J., and C. A. Ver Straeten.** 2023. Marine strata of the middle to upper Hamilton Group (Middle Devonian, lower Givetian), eastern outcrop belt in New York State. In C. A. Ver Straeten, D. J. Over, and D. Woodrow, eds. *Devonian of New York*, Vol. 2. *Bulletins of American Paleontology* 405–406: 197–258.
- Bault, V., C. Crônier, C. Monnet, D. Balseiro, F. Serra, B. Waisfeld, A. Bignon, and J. J. Rustán.** 2023. Rise and fall of the phacopids: the morphological history of a successful trilobite family. *Palaeontology* 66:e12673.
- Brauckmann, C., I. Chlupáč, and R. Feist.** 1993. Trilobites at the Devonian–Carboniferous boundary. *Annales de la Société Géologique de Belgique* 115: 507–518.
- Brett, C. E., L. C. Ivany, and K. M. Schopf.** 1996. Coordinated stasis: an overview. *Palaeogeography, Palaeoclimatology, Palaeoecology* 127:1–20.
- Brett, C. E., G. C. Baird, J. J. Zambito IV, and A. J. Bartholomew.** 2023. Stratigraphy and facies of the middle and upper Hamilton Group (Middle Devonian; Givetian) in New York State and adjacent areas. In C. A. Ver Straeten, D. J. Over, and D. Woodrow, eds. *Devonian of New York*, Vol. 2. *Bulletins of American Paleontology* 405–406:1–195.
- Buzas, M. A., and S. J. Culver.** 1984. Species duration and evolution: benthic foraminifera on the Atlantic continental margin of North America. *Science* 225:829–830.
- Campbell, K. S. W.** 1967. Trilobites of the Henryhouse Formation (Silurian) in Oklahoma. *Oklahoma Geological Survey Bulletin* 115:1–68.
- Chlupáč, I.** 1994. Devonian trilobites—evolution and events. *Geobios* 27:487–505.
- Clarke, J. M.** 1908. Early Devonian history of New York and eastern North America. *New York State Museum Annual Report, Memoir* 9:1–366.
- Clarke, J. M., and C. K. Swartz.** 1913. Trilobita. P. 699 in C. S. Prosser and C. K. Swartz, eds. *The Upper Devonian deposits of Maryland*. Maryland Geological Survey: Middle and Upper Devonian. Johns Hopkins Press, Baltimore, Md.
- Clarkson, E. N. K., and R. P. Tripp.** 1982. The Ordovician trilobite *Calyptaulax bronniartii* (Portlock). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 72:287–294.
- Conrad, T. A.** 1842. Observations on the Silurian and Devonian systems of the United States, with descriptions of new organic remains. *Journal of the Academy of Natural Sciences of Philadelphia* 8:228–280.
- Cooper, G. A.** 1930. Upper Ordovician and Lower Devonian stratigraphy and paleontology of Percé, Quebec. Part II. New species from the Upper Ordovician of Percé. *American Journal of Science*, 5th series 20:265–288.
- Crônier, C., and A. François.** 2014. Distribution patterns of Upper Devonian phacopid trilobites: paleobiogeographical and paleoenvironmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 404:12–23.
- Delo, D. M.** 1935. A revision of the phacopid trilobites. *Journal of Paleontology* 9:402–420.
- de Witt, W., Jr., and G. W. Colton.** 1978. Physical stratigraphy of the Genesee Formation (Devonian) in western and central New York. *U.S. Geological Survey Professional Paper* 1032-A:22.
- Eaton, A.** 1831. Geological equivalents. *American Journal of Science and Arts* 21: 132–138.
- Eldredge, N.** 1971. The allopatric model and phylogeny in Paleozoic invertebrates. *Evolution* 25:156–167.
- Eldredge, N.** 1972. Systematics and evolution of *Phacops rana* (Green, 1832) and *Phacops iowensis* Delo, 1935 (Trilobita) from the Middle Devonian of North America. *Bulletin of the American Museum of Natural History* 147: 45–114.
- Eldredge, N., and S. J. Gould.** 1972. Punctuated equilibria: an alternative to phyletic gradualism. Pp. 82–115 in T. J. M. Schopf, ed. *Models in paleobiology*. Freeman, Cooper, San Francisco.
- Eldredge, N., and S. J. Gould.** 1977. Evolutionary models and biostratigraphic strategies. Pp. 25–40 in E. G. Kauffman, J. E. Hazel, and B. D. Heffernan, eds. *Concepts and methods of biostratigraphy*. Dowden, Hutchinson & Ross, Stroudsburg, Penn.
- Eldredge, N., J. N. Thompson, P. M. Brakefield, S. Gavrillets, D. Jablonski, J. B. C. Jackson, R. E. Lenski, B. S. Lieberman, M. A. McPeck, and W. Miller.** 2005. The dynamics of evolutionary stasis. *Paleobiology* 31:133–145.
- Emmrich, H. F.** 1839. De trilobitis. *Dissertatio petrefactologica quam consensu et auctoritate amplissimi philosophorum ordinis in alma litterarum universitate Friderica Guilelma pro summis in philisophia honoribus*. Thesis, Friderica Guilelma, Berlin.
- Feist, R., and G. Klapper.** 2022. Phacopid trilobites in post-Taghanic Givetian through Frasnian cephalopod limestones, Montagne Noire (France) and related areas (Thuringia, Morocco). *Bulletin of Geosciences* 97:1–32.
- Flajs, G., and R. Feist.** 1988. Index conodonts, trilobites and environment of the Devonian–Carboniferous Boundary beds at La Serre (Montagne Noire, France). *Courier Forschungsinstitut Senckenberg* 100:53–107.
- Foote, M.** 1988. Survivorship analysis of Cambrian and Ordovician trilobites. *Paleobiology* 14:258–271.
- Goldring, R.** 1955. The Upper Devonian and Lower Carboniferous trilobites of the Pilton Beds in N. Devon, with an appendix on goniatites of the Pilton Beds. *Senckenbergiana Lethaea* 36:27–48.
- Gould, S. J.** 2002. *The structure of evolutionary theory*. Harvard University Press, Cambridge, Mass.
- Gould, S. J., and N. Eldredge.** 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* 3:115–151.
- Green, J.** 1830. Monograph of the cones of North America, including three new species. *Transactions of the Albany Institute* 1:121–125.
- Green, J.** 1832. *A monograph of the trilobites of North America with coloured models of the species*. Joseph Brano, Philadelphia.
- Hall, J.** 1843. *Geology of New-York. Part IV. Comprising the Survey of the Fourth Geological District*. Carroll and Cook, Printers to the Assembly, Albany.
- Harland, W. B., C. H. Holland, N. F. House, N. F. Hughes, A. B. Reynolds, M. J. S. Rudwick, G. E. Satterthwaite, L. B. H. Tarlo, and E. C. Willey,** eds. 1967. *The fossil record*. Geological Society of London, London.
- Hawle, L., and A. J. C. Corda.** 1847. *Prodrom einer monographie der böhmischen trilobiten*. J. G. Calvesche Buchhandlung, Prag.
- Hendricks, J. R.** 2009. The genus *Conus* (Mollusca: Neogastropoda) in the Plio-Pleistocene of the southeastern United States. *Bulletins of American Paleontology* 375:1–178.
- Hendricks, J. R., E. E. Saupe, C. E. Myers, E. J. Hermesen, and W. D. Allmon.** 2014. The genericification of the fossil record. *Paleobiology* 40:511–528.
- Hull, D. L.** 1980. Individuality and selection. *Annual Review of Ecology and Systematics* 11:311–332.
- Jablonski, D., and G. Hunt.** 2006. Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: organismic versus species-level explanations. *American Naturalist* 168:556–564.
- Kennedy, W. J.** 1977. Ammonite evolution. Pp. 251–304 in A. Hallam, ed. *Developments in palaeontology and stratigraphy*, Vol. 5. Elsevier, Amsterdam.
- Kiessling, W., N. B. Raja, V. J. Roden, S. T. Turvey, and E. E. Saupe.** 2019. Addressing priority questions of conservation science with palaeontological data. *Philosophical Transactions of the Royal Society B* 374(1788):20190222.
- Kindle, E. M.** 1896. The relation of the fauna of the Ithaca Group to the faunas of the Portage and Chemung. *Bulletins of American Paleontology* 2:1–57.
- Lamkin, M., and A. I. Miller.** 2016. On the challenge of comparing contemporary and deep-time biological-extinction rates. *BioScience* 66:785–789.
- Lieberman, B. S., and N. Eldredge.** 2014. What is punctuated equilibrium? What is macroevolution? *Trends in Ecology and Evolution* 29:185–186.
- Lieberman, B. S., and J. Kimmig.** 2018. Museums, paleontology, and a biodiversity science–based approach. Pp. 335–348 in G. D. Rosenberg and R. M. Clary, eds. *Museums at the forefront of the history and philosophy of geology: history made, history in the making*, Vol. 535. Geological Society of America, Boulder, Colo.
- Lieberman, B. S., C. E. Brett, and N. Eldredge.** 1995. A study of stasis and change in two species lineages from the Middle Devonian of New York State. *Paleobiology* 21:15–27.
- May, R. M.** 2002. The future of biological diversity in a crowded world. *Current Science* 82:1325–1331.
- Mayr, E.** 1963. *Animal species and evolution*. Harvard University Press, Cambridge, Mass.
- Münster, G.** 1840. Die versteinungen des uebergangskalkes mit clymenien und orthoceratiten von Oberfranken. *Beiträge zur Petrefaktenkunde* 3(7):33–121.
- Over, D. J., G. C. Baird, and W. T. Kirchgasser.** 2023. The Frasnian strata—lower Upper Devonian—of New York State. In C. A. Ver Straeten, D. J. Over, and D. Woodrow, eds. *Devonian of New York*, Vol. 3. *Bulletins of American Paleontology* 407–408:1–28
- Parker, W. C.** 1983. Fossil ecological successions in Paleozoic level bottom brachiopod-bryozoan communities. Ph.D. dissertation. University of Chicago, Chicago.

- Payne, J. L., and S. Finnegan. 2007. The effect of geographic range on extinction risk during background and mass extinction. *Proceedings of the National Academy of Sciences USA* **104**:10506–10511.
- Phillips, J. 1841. Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon, and West Somerset; observed in the course of the Ordinance Geological Survey of that district. *Geological Society of London*.
- Portlock, J. E. 1843. *Report on the geology of Londonderry and parts of Tyrone and Fermanagh*. Andrew Milliken, Dublin.
- Prothero, D. R., and T. H. Heaton. 1996. Faunal stability during the Early Oligocene climatic crash. *Palaeogeography, Palaeoclimatology, Palaeoecology* **127**:257–283.
- Raup, D. M. 1991. A kill curve for Phanerozoic marine species. *Paleobiology* **17**:37–48.
- Raup, D. M., and S. M. Stanley. 1978. *Principles of paleontology*, 2nd ed. Freeman, New York.
- Reed, F. R. C. 1945. XXVIII.—Notes on some Ordovician brachiopods and a trilobite from the Balclatchie Beds of Girvan. *Annals and Magazine of Natural History* **12**:309–316.
- Richter, R., and E. Richter. 1923. Systematik und stratigraphie der Oberdevon-Trilobiten des Ostthüringischen Schiefergebirges. *Senckenbergiana* **5**:59–76.
- Richter, R., and E. Richter. 1926. *Die Trilobiten des Oberdevons*. Beiträge zur Kenntnis Devonischer Trilobiten. IV. Preußischen Geologischen Landesanstalt, Berlin.
- Richter, R., and E. Richter. 1951. Der beginn des Karbons im wechsel der trilobiten. *Senckenbergiana* **32**:219–266.
- Romer, A. S. 1966. *Vertebrate paleontology*, 3rd ed. University of Chicago Press, Chicago.
- Salter, J. W. 1853. Figures and descriptions illustrative of British organic remains. *Memoir of the Geological Survey of Great Britain* **7**.
- Sanford, B. V., and A. W. Norris. 1975. Devonian stratigraphy of the Hudson Platform. Part 1: Stratigraphy and economic geology. *Geological Survey of Canada Memoir* **379**:1–124.
- Sepkoski, J. J. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* **7**:36–53.
- Sepkoski, J. J. 1982. A compendium of fossil marine families. *Milwaukee Public Museum Contributions in Biology and Geology* **51**.
- Sepkoski, J. J. 1993. Ten years in the library: new data confirm paleontological patterns. *Paleobiology* **19**:43–51.
- Sepkoski, J. J. 1997. Biodiversity: past, present, and future. *Journal of Paleontology* **71**:533–539.
- Sepkoski, J. J. 2002. A compendium of fossil marine animal genera. *Bulletins of American Paleontology* **363**.
- Smith, J. A., N. B. Raja, T. Clements, D. Dimitrijević, E. M. Dowding, E. M. Dunne, B. M. Gee, et al. 2023. Increasing the equitability of data citation in paleontology: capacity building for the big data future. *Paleobiology* **50**:165–176.
- Stanley, S. M. 1979. *Macroevolution: pattern and process*. Freeman, San Francisco.
- Strotz, L. C., and A. P. Allen. 2013. Assessing the role of cladogenesis in macroevolution by integrating fossil and molecular evidence. *Proceedings of the National Academy of Sciences USA* **110**:2904–2909.
- Struve, W. 1976. Beiträge zur Kenntnis der Phacopina (Trilobita), 9: *Phacops (Omegops)* n. sg. (Trilobita; Ober-Devon). *Senckenbergiana Lethaea* **56**:429–451.
- Struve, W. 1990. Paläozoologie III (1986–1990). *Courier Forschungsinstitut Senckenberg* **127**:251–279.
- Struve, W. 1992. Neues zur stratigraphie und fauna des rhenotypen Mittle-Devon. *Senckenbergiana Lethaea* **71**:503–624.
- Temple, J. T. 1952. A revision of the trilobite *Dalmanitina mucronata* (Brongniart) and related species. *Lunds Universitets Årsskrift N. F. Avd. 2* **48**(1):1–33.
- Ver Straeten, C. A. 2023. An introduction to the Devonian Period, and the Devonian in New York State and North America. In C. A. Ver Straeten, D. J. Over, and D. Woodrow, eds. *Devonian of New York*, Vol. 1. *Bulletins of American Paleontology* **403–404**:11–102.
- Ver Straeten, C. A., C. E. Brett, G. C. Baird, A. J. Bartholomew, and D. J. Over. 2023. Lower Middle Devonian (Eifelian–lower Givetian) strata of New York State: the Onondaga Formation and Marcellus Subgroup. In C. A. Ver Straeten, D. J. Over, and D. Woodrow, eds. *Devonian of New York*, Vol. 1. *Bulletins of American Paleontology* **403–404**:205–280.
- Vrba, E. S. 1985. Environment and evolution: alternative causes of the temporal distribution of evolutionary events. *South African Journal of Science* **81**:229–236.
- White, R. D., and B. S. Lieberman. 1998. A type catalog of fossil invertebrates (Arthropoda: Trilobita) in the Yale Peabody Museum. *Postilla* **214**:151.
- Williams, H. S. 1913. Recurrent *Tropidoleptus* zones of the Upper Devonian in New York. *U.S. Geological Survey Professional Paper* **79**.
- Zambito, J. J., IV, G. C. Baird, C. E. Brett, and A. J. Bartholomew. 2007. Re-examination of the type Ithaca Formation: correlations with sections in western New York. Pp. 83–106 in C. A. McRoberts, ed. *New York State Geological Association 79th Annual Meeting, Field Trip Guidebook*.
- Zambito, J. J., IV, G. C. Baird, C. E. Brett, and A. J. Bartholomew. 2009. Depositional sequences and paleontology of the Middle–Upper Devonian transition (Genesee Group) at Ithaca, New York: a revised lithostratigraphy for the northern Appalachian Basin. Pp. 49–69 in D. J. Over, ed. *Studies in Devonian stratigraphy: Proceedings of the 2007 International Meeting of the Subcommission on Devonian Stratigraphy and IGCP 499*. *Palaeontologica Americana* **63**.