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Research Article

Ichnological response of macrobenthic fauna to Late Devonian anoxic pulses: New evidence from North America and a global synthesis[☆]

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ABSTRACT

During the Late Devonian, several anoxic pulses triggered severe biotic crises such as the Kellwasser Event, profoundly affecting marine ecosystems. These episodes are well-documented in the North American Seaway (NAS), in which accumulated thick deposits of dark-gray/black shales generally lacking biogenic structures. This study applies an ichnological approach to assessing the impact of anoxic pulses on macrobenthic tracemakers at five sites in the NAS (one from the Anadarko Basin, three from the Illinois Basin, and one from the Appalachian Basin). The study sections consist of dark-gray to black shale beds interbedded with light-gray to greenish shale layers. Ichnological analysis identified five ichnoassemblages dominated by: (1) *Planolites*, (2) *Chondrites*, (3) *Planolites*, *Teichichnus*, and *Cylindrichnus*, (4) *Zoophycos*, *Chondrites*, and *Planolites*, and (5) vertical *spreiten*-bearing structures along with *Planolites*, *Teichichnus*, and *Cylindrichnus*. In the NAS, Givetian deposits exhibit the highest ichnodiversity (Ichnoassemblage 5). Stratigraphically upwards, several anoxic pulses are recorded by laminated black shale deposits, correlated with globally-recorded biological crises (e.g., Rhinestreet, Kellwasser, Dasberg): lower Frasnian sediments exhibit alternating unbioturbated/laminated intervals and Ichnoassemblages 1a and 1b along with mottled textures, whereas the Famennian is characterized by more persistent anoxia interrupted by oxic intervals with Ichnoassemblage 4 or 1 and common mottled textures. In contrast, the Anadarko Basin shows only mottled textures alternating with laminated facies in the Frasnian-Famennian transition, followed by a persistent decline in biogenic structures during the Famennian (only sparse records of Ichnoassemblages 1a and 2). Notably, in inner areas of the NAS, oxic conditions were prevalent during the Upper Kellwasser Event, characterized by Ichnoassemblage 3. Our ichnological study, compared with the global record, indicates that Late Devonian anoxic pulses had a greater impact on open-marine settings than on the restricted areas of the NAS, highlighting that regional features heavily conditioned global effects of the Late Devonian biocrises, leading to highly variable patterns in benthic recovery and oxygenation dynamics.

1. Introduction

Unlike the other "Big Five" mass extinctions, which were driven by abrupt catastrophic events such as large igneous province eruptions (e.g., end-Permian) or bolide impacts (e.g., end-Cretaceous), the Late Devonian biocrises consisted of multiple successive episodes of elevated extinction rates, especially at the Givetian-Frasnian Boundary (GFB; 382.3 Ma), the Frasnian-Famennian Boundary (FFB; 372.1 Ma), and the Devonian-Carboniferous Boundary (DCB; 358.8 Ma) (Algeo and Shen, 2024). Moreover, the true severity of this extinction event remains in debate, as some studies have inferred that it primarily reflects a decline in species origination rates rather than a sharp biodiversity loss,

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characterizing it as a "mass depletion" event (Bambach et al., 2004; Gereke and Schindler, 2012; Stanley, 2016). The Late Devonian mass extinction is arguably the least well understood of the "Big Five", as key factors such as paleoclimate dynamics, sea-level fluctuations, and the extent of marine anoxia remain poorly constrained (see reviews in Carmichael et al., 2019, and Qie et al., 2019).

The Late Devonian extinction episodes, particularly the Kellwasser and Hangenberg events (i.e., the classic designations for the FFB and DCB biocrises, respectively), had a profound impact on marine biota, primarily affecting shallow-water organisms such as coral-reef builders and pelagic taxa such as cephalopods and fish (House, 1985; Hallam and Wignall, 1999; Copper and Scotese, 2003; Sallan and Coates, 2010). Recently, the study of trace fossils has emerged as a critical tool for investigating both major mass extinctions ("Big Five") and smaller-scale events (e.g., oceanic anoxic events), particularly in cases where abrupt changes in benthic oxygenation occurred (e.g., Uchman et al., 2013; Rodríguez-Tovar and Uchman, 2017; Fernández-Martínez et al., 2021a, 2021b; Rodríguez-Tovar, 2021; Rodríguez-Tovar et al., 2022). The occurrence of black shales—typically deposited under anoxic conditions and frequently associated with these biocrises—combined with the analysis of their sedimentary structures and ichnological features, enables the assessment of benthic macrofaunal responses to changing bottom- and pore-water conditions. Ichnofossils record behavioral adaptations of macrobenthic tracemakers to redox fluctuations, among other paleoenvironmental changes, providing valuable insights into ecosystem dynamics during these extinction events.

Ichnological studies of the FFB are few in number, with the majority of research conducted in North America (Hannibal and Feldmann, 1983; Bezys, 1987; Boyer, 2007; Boyer and Droser, 2009, 2011; Boyer et al., 2014; Zou and Slatt, 2015; Boyer et al., 2021), although there are also studies from Eastern Europe (Stachacz et al., 2017) and China (Wang et al., 2006). In the present study, we review the existing literature and

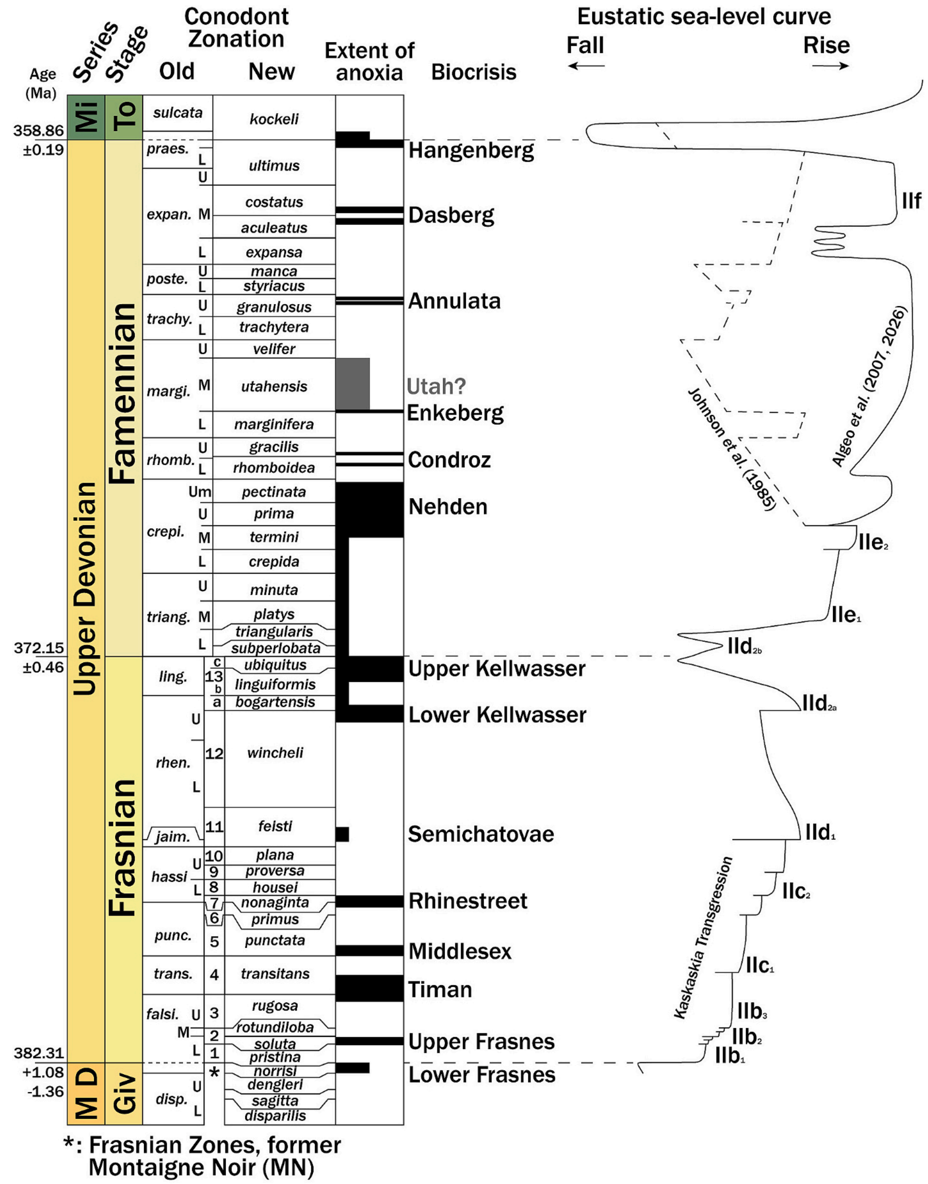

Fig. 1. Conodont biostratigraphy of the Frasnian and Famennian stages, indicating old (Ziegler and Sandberg, 1990) and new (Klapper and Kirchgasser, 2016; Corradini et al., 2017; Spalletta et al., 2017) conodont biozones, including the Frasnian Zones (FZ, former MN—Montaigne Noir), and the main biocrises (modified from figure 1 in Becker et al., 2016; and figures 1 and 2 in Brett et al., 2020). Sea-level curves are from Johnson et al. (1985), Algeo et al. (2007), as modified in Liu et al., 2025), and Algeo et al. (2026). The degree of shading within the anoxia column reflects the intensity and persistence of anoxic conditions. Ages follow Harrigan et al. (2022), their table 6. The thickness of zones is calibrated according to their inferred duration (after Spalletta et al., 2017). Gray shadowing indicates a possible anoxic event restricted to the North American Seaway. Abbreviations: MD, Middle Devonian; Gi, Givetian; Mi, Mississippian; To, Tournaisian.

analyze five new Upper Devonian sections (cores) from across the U.S.A. composed mainly of dark-gray/black and light-gray/greenish shales. Our focus is on the ichnological and sedimentological features of these sections. The objective of this research is to examine the spatio-temporal behavioral patterns of macrobenthic tracemaker communities and study their response to the anoxic pulses that characterized Late Devonian marine environments (Fig. 1).

2. Geological setting

The North American Seaway (NAS) was a vast epeiric sea that spanned much of North America during the Paleozoic, with its extent

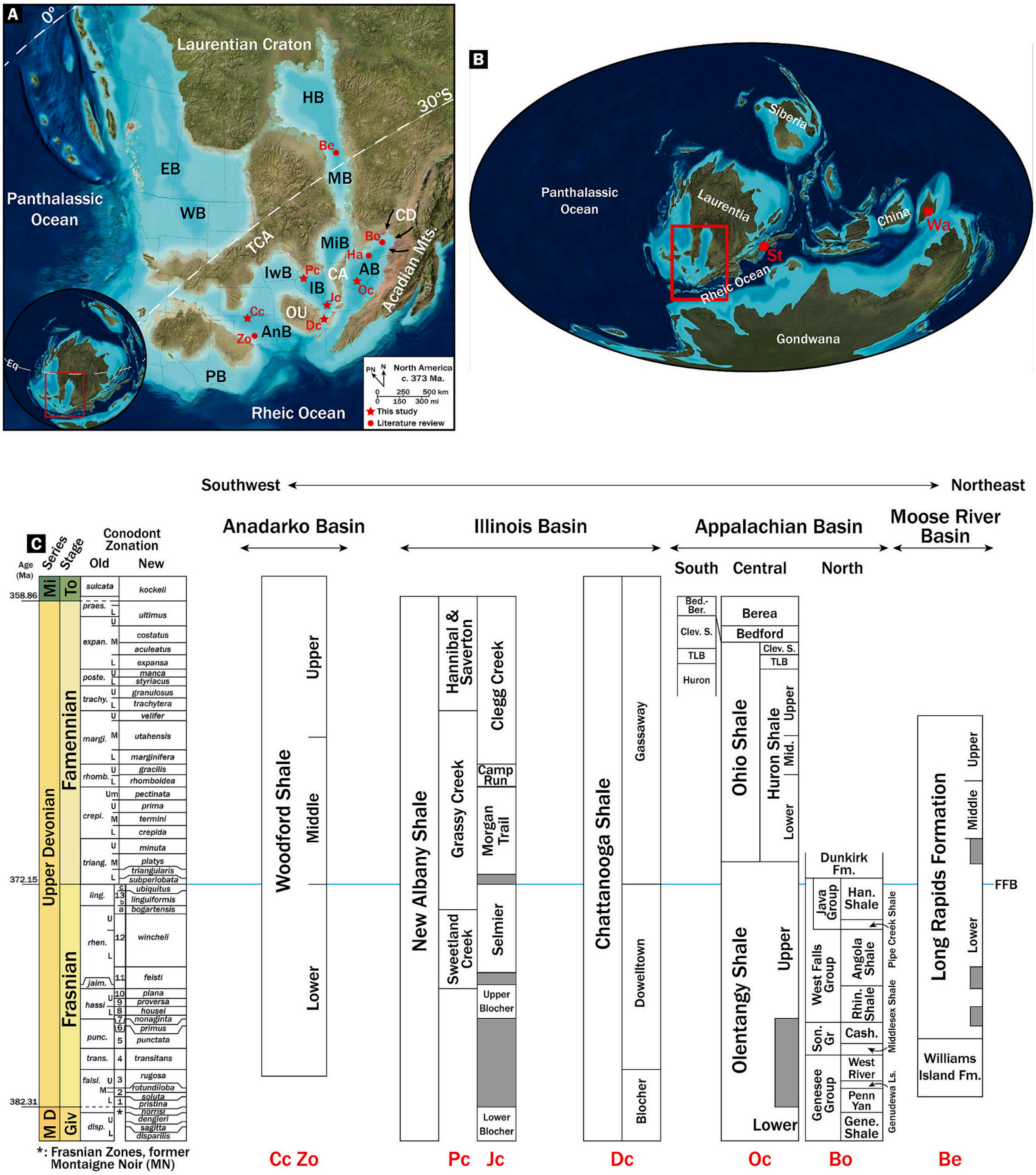

Fig. 2. A) Paleogeographic map during Late Devonian showing the location of the study cores and the main basins of the North American Seaway. The black arrows to the left of the Acadian Mountains indicate the input of terrigenous sediments linked to the Catskill Delta. Map modified from Deep Time Maps Inc. B) Global paleogeographic map indicating the study area (red rectangle) and global sections from the literature. Map modified from Deep Time Maps Inc. C) Correlation of the study units across the Anadarko, Illinois, Appalachian, and Moose River basins. Abbreviations: AB, Appalachian Basin; AnB, Anadarko Basin; Be, Bezys (1987); Bo, Boyer et al. (2014) and Haddad et al. (2018); CA, Cincinnati Arch; Cash., Cashaqua Shale; Cc, Current core; CD, Catskill Delta; Clev. S., Cleveland Shale; Dc, Dupont core; EB, Elk-Point Basin; FFB, Frasnian-Famennian Boundary; Gene. Shale, Geneseo Shale; Ha, Hannibal and Feldmann (1983); HB, Huron Bay Basin; Han. Shale, Hanover Shale; IB, Illinois Basin; IwB, Iowa Basin; Jc, Jackson core; Ls, Limestone; MB, Moose River Basin; MiB, Michigan Basin; Oc, OHRS-5 core; OU, Ozark Uplift; PB, Permian Basin; Pc, Palmer core; Rhin, Rhinestreet Shale; Son Gr, Sonyea Group; St, Stachacz et al. (2017); TCA, Trans-Continental Arch; TLB, Three Lick Bed; WB, Williston Basin; Wa, Wang et al. (2006); Zo, Zou and Slatt (2015).

and environmental conditions varying over time due to tectonic activity, paleoclimate changes, and sea-level fluctuations (Algeo et al., 2007). During the Late Devonian, the NAS reached its maximum expanse, covering much of present-day Canada and the United States (Fig. 2A). It was composed of a number of major basins (e.g., Appalachian, Illinois, Michigan, Moose River, Huron Bay, Iowa, and Anadarko), each exhibiting different depositional characteristics due to varying water depths, paleogeography, and connectivity to the global ocean.

The Appalachian and Illinois basins were surrounded by the Laurentian Craton to the north, the Acadian Orogen (precursor to the modern-day Appalachian Mountains) to the east, the Ozark Uplift to the southwest, and the Transcontinental Arch to the west. They were narrowly connected to the Rheic Ocean via the Cumberland Sill to the south and were partially separated from each other by the Cincinnati Arch (Fig. 2A). These basins experienced fluctuating environmental conditions, ranging from well-oxygenated shallow-marine settings to restricted deep-water regions severely affected by anoxia. The northern part of the Appalachian Basin was strongly influenced by the Catskill Delta (Algeo et al., 2026) (Fig. 2A), which increased water-column oxygenation and limited black shale accumulation in that area (Boyer et al., 2014).

Within this paleogeographic framework, sedimentation dynamics in the NAS during the Frasnian and Famennian stages were dominated by the deposition of thick black shales (up to 100 m) that serve as regional hydrocarbon source rocks (Barrows and Cluff, 1984; Higley et al., 2014; Cardott and Comer, 2021). The present research is focused on several of these units, from east to west (Fig. 2C): the Upper Olentangy and Ohio Shales in the Appalachian Basin; the Chattanooga Shale in the southern Appalachian and Illinois basins; the New Albany Shale in the Illinois Basin; and the Woodford Shale in the Anadarko Basin (see biostratigraphy and correlations in Fig. 2C). Although all of these units are generally considered to have been deposited under strongly anoxic conditions, sedimentological analysis reveals the presence of abundant thin, light-gray/greenish mudstone layers within the black shales that are indicative of transient oxygenation episodes.

The Frasnian and Famennian stages are defined on the basis of conodont biozones (Over, 2002; Becker et al., 2016, cf. figure 9 in Algeo et al., 2007) and correlations based on gamma-ray logs and sequence stratigraphy (Lazar, 2007; Remírez et al., 2023) (see Section 4.4). The FFB is indicated by a regression during the *bogartensis-ubiquitus* zones (FZ 13a to 13c, former *linguliformis* Zone) linked to the FFB Glaciation (Algeo et al., 2026). This was followed by a rapid transgressive-regressive cycle during the *superlobata* and *triangularis* zones and then by a major transgression during the early Famennian (*triangularis-platys* zones) continuing until the *termini* Zone (Fig. 1).

3. Materials and methods

The five study cores were selected with the goal of achieving wide paleogeographic coverage of Upper Devonian black shale units in the eastern and central United States (Fig. 2): (1) the OHRS-5 core (central Appalachian Basin), (2) the Jackson core (central Illinois Basin), (3) the Palmer core (northern Illinois Basin), (4) the Dupont core (southern Illinois Basin), and (5) the Current core (Anadarko Basin), see Table 1 for location, curation site, study units, and more information. Some of the study cores have been the subject of earlier sedimentological and geochemical studies, e.g., the Dupont core (Over et al., 2019; Song et al., 2021), Jackson core (Chen et al., 2023; Remírez et al., 2023), and OHRS-5 core (Jaminski et al., 1998; Gilleaudeau et al., 2023; Liu et al., 2025).

For each core, we conducted an integrated sedimentological and ichnological analysis (see SM Figs. 1-5). We realized bed-by-bed descriptions, focusing on lithology and sedimentary structures and textures (such as lamination or mottling). The ichnological analysis focused on characterization of trace-fossil assemblages, including ichnological features such as trace size, distribution, abundance, infilling material, crosscutting relationships, orientation, internal structures, and penetration depths from the bed of origin. Detailed photographs were taken to illustrate both sedimentological texture and ichnological features (Figs. 3 and 4). Some photos were then treated using Adobe Photoshop CS6 to enhance visibility of selected features (as noted in the figure captions), following the methodology proposed by Dorador and Rodríguez-Tovar (2018).

4. Results

4.1. Synopsis of trace fossils

Our ichnological analysis led to the recognition of six well-characterized ichnogenera, along with several structures with uncertain taxonomic classification, and two types of biogenic structures (biodeformational and “mantle and swirl” structures) (Figs. 3 and 4). Overall, the distribution of trace fossils is highly variable among the study cores, varying in abundance, diversity, and infill type, thus reflecting lithological and paleoenvironmental constraints. A synopsis of the identified biogenic structures is presented below, highlighting their key diagnostic features for identification.

Light-gray and greenish shale beds are commonly characterized by a mottled texture (Figs. 3C-H and 4A-E, G-I, K). It is produced by benthic organisms “swimming” through a soft/soupy sediment near the sediment–water interface under well-oxygenated conditions. The soft consistency of the substrate prevented the preservation of primary sedimentary structures, which were obliterated by biogenic activity (i.e., resulting in a completely homogenized fabric), and produced non-diagnostic biodeformational structures (*sensu* Wetzel and Uchman, 1998; see also Uchman and Wetzel, 2011; Wetzel, 2025).

Chondrites von Šternberg (1833) is a common trace fossil observed in several intervals of the study cores. It occurs as small, unlined, dendritic burrow systems, typically 0.1–0.3 cm in diameter, appearing as flattened dots in vertical section (Figs. 3K–M and 4E, H). The burrows are filled with light-gray shale and may occur alone or in association with *Zoophycos*, only in dark sediments. Due to its complex morphology, *Chondrites* has been associated with several ethological interpretations

Table 1
Summary of the study cores, indicating location, curation site, study units, and driller.

Study core	Latitude (°N)	Longitude (°W)	Driller	County	State	Curation site	Study formations	SM Figure
Palmer	40°55'59.53"	90°15'19.18"	New Jersey Zinc Company	Knox	Illinois	Illinois State Geological Survey	Sweetland Creek Shale, Grassy Creek Shale	1
Jackson	37°24'56.39"	87°16'31.39"	CNX Gas Company, LLC.	McLean	Kentucky	Kentucky Geological Survey	New Albany Shale	2
Dupont	36°4'30.00"	87°29'42.00"	Dupont Chemical Corporation	Humphreys	Tennessee	Tennessee Geological Survey	Chattanooga Shale	3
OHRS-5	39°15'36.00"	83°4'48.00"	North American Exploration, INC.	Ross	Ohio	Ohio Geological Survey	Olentangy Shale, Ohio Shale	4
Current	37°1'35.52"	97°5'39.22"	M & S Drilling, INC.	Cowley	Kansas	Kansas Geological Survey	Woodford Shale	5

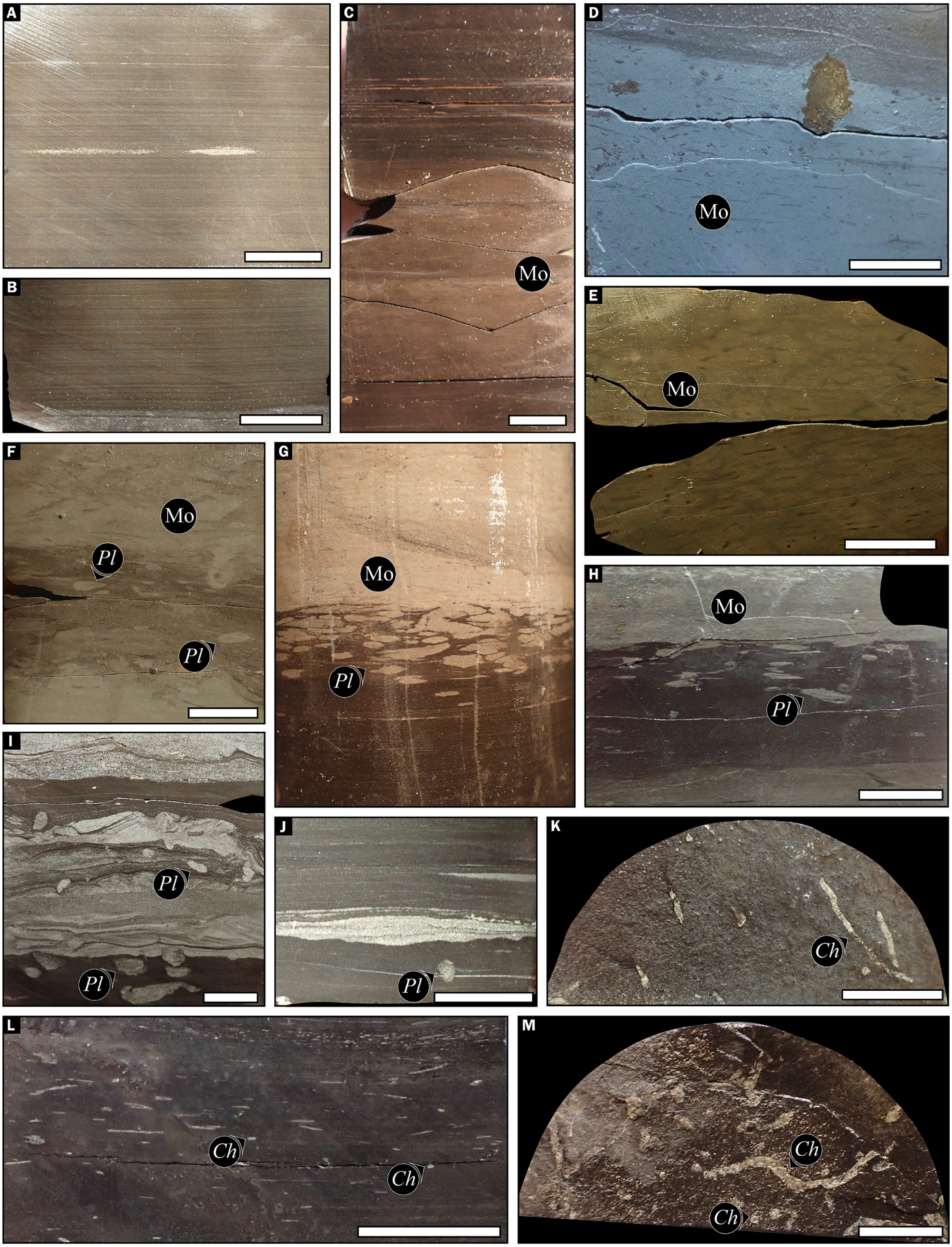

Fig. 3. A, B) Planar parallel lamination in black shale facies. C) From bottom to top, alternation of a black shale bed with massive texture, mottled light gray shale, and laminated black shale bed. Note the reddish color of the lamination, linked to siderite mineralization. D, E) Mottled texture in a light gray shale bed. F) Dark-gray shale layer with light-colored mud-filled *Planolites* (Ichnoassemblage 1a) interbedded within a mottled light-gray shale deposit. G) Laminated black shale bed with light-colored mud-filled *Planolites* (Ichnoassemblage 1a) bioturbating from the overlying mottled light-gray shale layer. H) Light-colored mud-filled *Planolites* in a black shale bed, penetrating from a mottled light shale bed (Ichnoassemblage 1a). I, J) fine-grained sandstone layers with cross-bedded lamination, showing sand-filled *Planolites* (Ichnoassemblage 1b), interbedded with black shale beds (with planar lamination in J). K-M) Tiny *Chondrites* in a black shale bed (Ichnoassemblage 2): vertical (L) and plain (K, M) views. Top is always upwards, except in K and M (plain view); each scale bar is 1 cm (0.4 inch). Abbreviations: *Ch*, *Chondrites*; Mo, mottled texture; *Pl*, *Planolites*. Panels C, E-G, and K-M were enhanced using Photoshop C6.

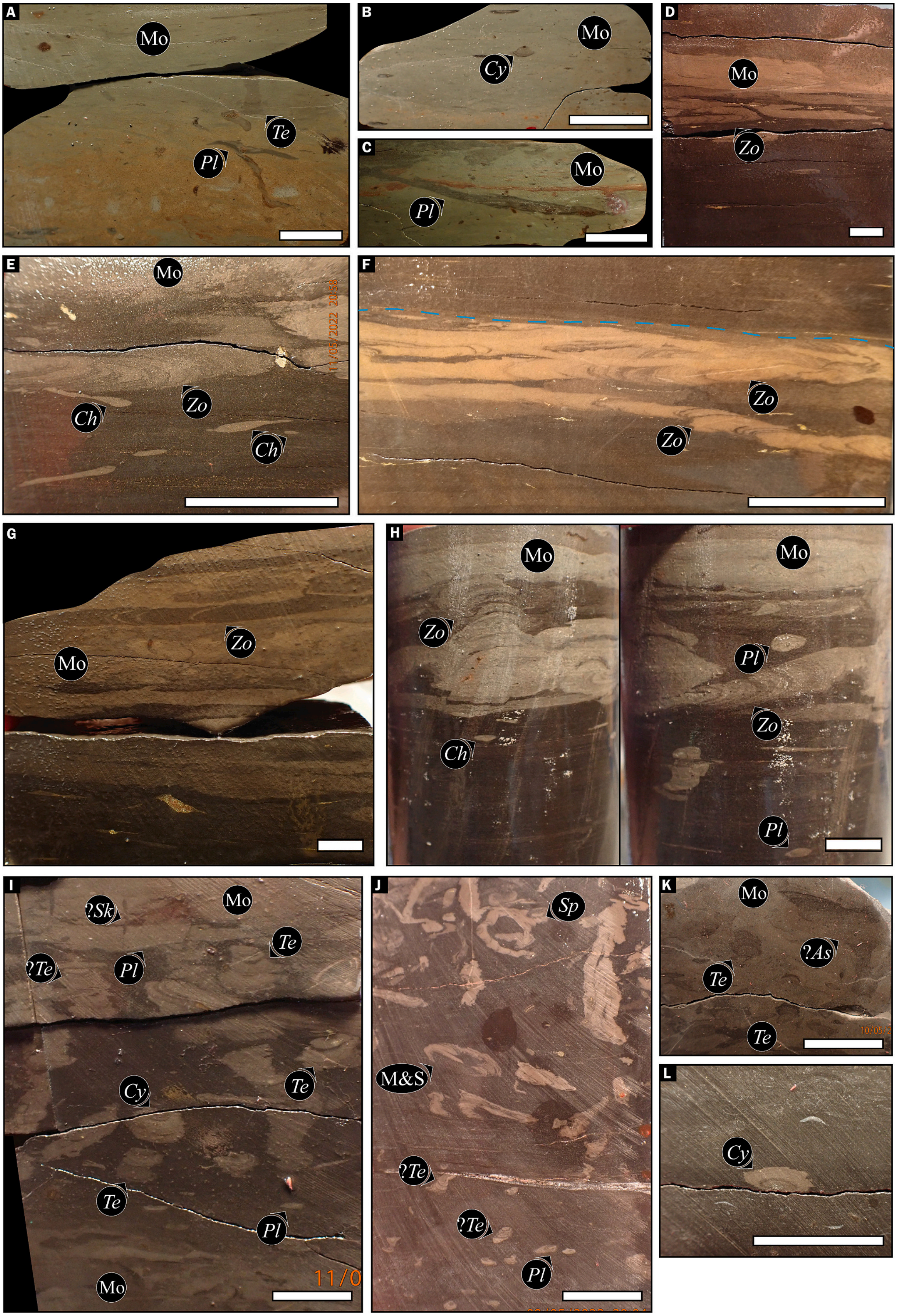

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Fig. 4. A-C) Dark-colored mud-filled *Planolites* and *Teichichnus* (A), *Cylindrichnus* (B) and *Planolites* (C) overprinting a mottled light-gray shale beds (Ichnoassemblage 3). D-H) Ichnoassemblage 4: light-colored mud-filled *Zoophycos* penetrating 1-2 cm into a black shale from a mottled light gray shale (D, F); note an erosive surface (dashed blue line) indicating the absence of the light bed from where *Zoophycos* originated (F), *Zoophycos* and *Chondrites* bioturbating a black shale bed from a mottled light bed (E), also with *Planolites* (H), dark-colored mud-filled *Zoophycos* within a mottled light shale bed (G). I-L) Dark gray shale bed bioturbated by light-colored mud-filled *Planolites*, *Cylindrichnus*, *Teichichnus*, *spreiten*-bearing trace fossils of varied morphologies and "mantle and swirl" structures (cf. figure 4 in Lobza and Schieber, 1999) (Ichnoassemblage 5), along with occasional dark-colored mud-filled ?*Skolithos* (I), ?*Asterosoma*-like structure with *Teichichnus* n a mottled light gray shale (K), *Cylindrichnus* with light-colored mud infill in a dark gray shale bed (L). Top is always upwards; each scale bar is 1 cm (0.4 inch). Abbreviations: ?*As*, *Asterosoma*; *Ch*, *Chondrites*; *Cy*, *Cylindrichnus*; Mo, mottled texture; M&S, mantle and swirl structures; *Pl*, *Planolites*; Sp: *spreiten*-bearing structures; *Te*, *Teichichnus*; *Zo*, *Zoophycos*. Panels D-G and I were enhanced using Photoshop C6.

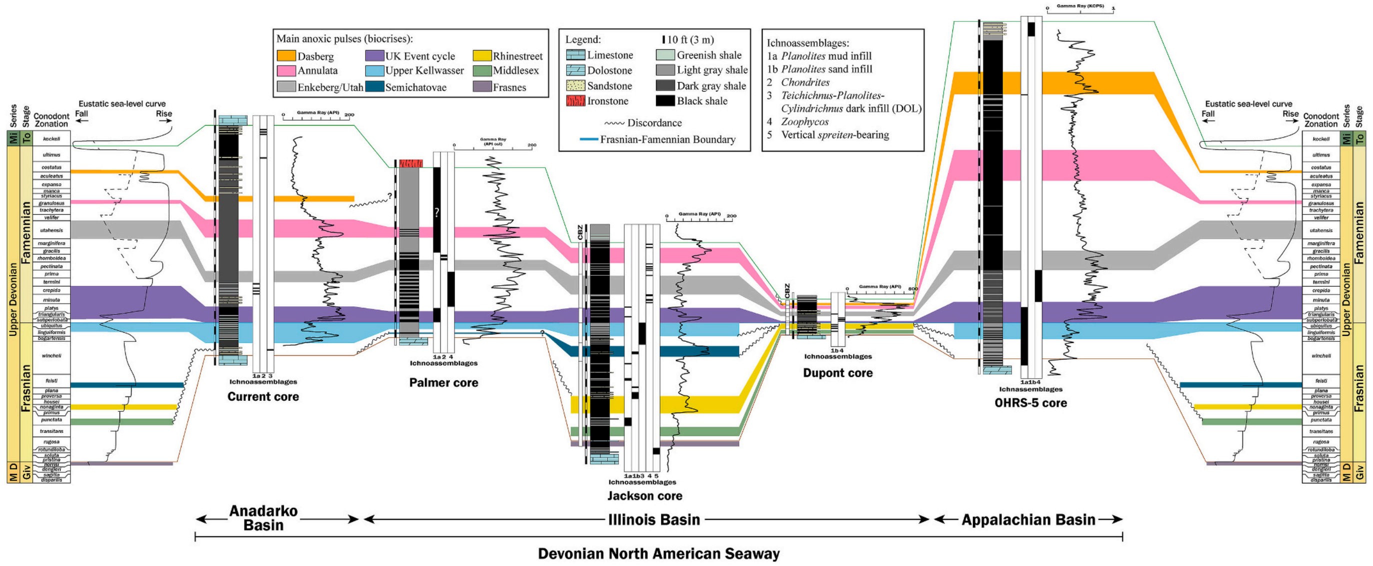

Fig. 5. Correlation of the study cores, using the Frasnian-Famennian boundary as datum (blue line). Stratigraphic columns, ichnoassemblages distribution, gamma-ray logs, and anoxic pulses (biocrises). Abbreviations: CBZ, conodont biozones; MD, Middle Devonian; Gi, Givetian; Mi, Mississippian; To, Tournaisian.

and potential producers, including fodinichnia (annelids engaged in deposit feeding), agrichnia (bivalves cultivating microbial "farms"), and chemichnia (chemosymbiotic thyasirid or lucinid bivalves hosting sulfur-reducing symbionts) (Simpson, 1956; Osgood Jr, 1970; Seilacher, 1990; Uchman et al., 2012; Baucon et al., 2020; Wetzel and Bojanowski, 2025).

Cylindrichnus Toots (in Howard, 1966) exhibits a flabellate to oblate morphology with concentric lining, typically 0.4–0.8 cm in width. They commonly occur with light infill within dark beds, although dark-colored mud-filled *Cylindrichnus* are also reported within mottled greenish shales (Fig. 4B). They may occur alone, associated with mottled beds, but are more frequently found with *Planolites*, *Teichichnus*, and non-classified *spreiten*-bearing burrows (Fig. 4I–L). *Cylindrichnus* is commonly interpreted as a domichnion produced by suspension-feeding polychaete worms (Belaústegui and de Gibert, 2013).

Planolites Nicholson (1873) is among the most common ichnogenera in the study cores. These occur as unlined, cylindrical, straight to slightly curved burrows, ranging from 0.3 to 0.5 cm in diameter. They are also reported as flattened, unlined circles in vertical section. They exhibit dark- and light-colored mud and sand infills (Figs. 3F-J and 4A, C, H-J). *Planolites* are commonly found alone or associated with bio-deformational structures, and they may also co-occur with other trace fossils such as *Zoophycos* or *Teichichnus*. They are present in all lithologies of the study cores. *Planolites* is interpreted as a fodinichnion (deposit-feeding structure). Owing to its simple morphology, it is potentially produced by a wide range of organisms, mostly vermiform animals (e.g., annelids, priapulids), although bivalves and arthropods are also plausible tracemakers (Pemberton and Frey, 1982; Knaust, 2017).

Teichichnus Seilacher (1955) occurs as vertical to oblique, unbranched, unlined *spreiten* burrows, commonly with stacked convex-down laminae, although convex-up stacks are also observed in some intervals (Fig. 4K). Diameters commonly range between 0.3 and 0.6 cm. The burrows may be filled with dark- or light-gray mud and are commonly associated with mottled beds. *Teichichnus* frequently co-occurs with *Planolites*, *Cylindrichnus*, and non-classified *spreiten*-bearing burrows (Fig. 4A, I-K). Similar to *Planolites*, *Teichichnus* is commonly interpreted as a deposit-feeding trace (fodinichnion), produced while the tracemaker adjusted the vertical position of its burrow in response to sedimentation (i.e., equilibrichnion). It was likely produced by vermiform organisms such as annelids, though arthropods are also possible tracemakers (Seilacher, 1955).

Thalassinoides Ehrenberg (1944) is rare in the study cores, occurring as unlined circular burrows with light-colored mud infill, penetrating dark beds. They are commonly associated with mottled beds and may occur alone or in association with *Planolites*. *Thalassinoides* is interpreted as a domichnion produced primarily by arthropods such as callianassids (thalassinidean shrimp) since the Permian. However, Paleozoic *Thalassinoides* were likely produced by other arthropods, including trilobites, or even by enteropneust worms, depending on the morphology of the burrow systems (Fürsich, 1973; Ekdale, 1992; Myrow, 1995; Ekdale and Bromley, 2003).

Zoophycos Massalongo (1855) is also common in the study sections, observed as subhorizontal *spreiten* laminae, generally ranging from 0.3 to 0.8 cm in diameter. They are mostly filled with light mud and penetrate dark beds, although a case of dark-colored mud-filled *Zoophycos* is reported from a gray shale bed (Fig. 4G). In the study cores, *Zoophycos* represents shallow-tier structures, penetrating only ~5 cm into the sediment and comprising one or two lamina stacks, in agreement with previous reports (e.g., figure 3 in Zhang et al., 2015). They commonly originate from mottled light beds and are found alone or in association with *Chondrites* and *Planolites* (Fig. 4D-H). Due to its complex and variable morphology, *Zoophycos* has been attributed to several potential producers, although vermiform organisms (e.g., polychaetes, echiurans, sipunculans) are generally considered the most likely candidates. Its ethological interpretation also remains in debate: while the *spreiten* are commonly viewed as the product of deposit-feeding activity (fodinichnion), *Zoophycos* has alternatively been interpreted as a domichnion or agrichnion (Bromley et al., 1999; Olivero, 2007; Olivero and Gaillard, 2007; Knaust, 2009; Rodríguez-Tovar et al., 2009; Zhang et al., 2015). Both *Zoophycos* and *Chondrites* are widely—though not exclusively—associated with organic-rich sediments such as those characterizing the study units, as well as with the availability of organic matter within the substrate (Löwemark et al., 2005, 2007; Löwemark, 2011).

Finally, a restricted interval of dark-gray shale beds exhibits the highest ichnodiversity and contains several biogenic structures of uncertain taxonomic classification (see Ichnoassemblage 5, Section 4.2). The latter include: a) tiny vertical, unlined burrows with dark-colored mud infill (0.1 cm in diameter, 0.5 cm in length) (Fig. 4I), tentatively attributed to *Skolithos* Haldeman (1840), which is interpreted as a domichnion produced by a wide variety of suspension-feeding organisms, including vermiform taxa (e.g., priapulids, polychaetes), amphipod crustaceans, and sea anemones (actinians) (Knaust, 2017); and b) *spreiten*-bearing burrows of various morphologies, whose features do not allow precise taxonomic classification (e.g., ?*Daedalichnus*, ?*Paradyctiodora*, ?*Asterosoma*, etc.), sometimes resembling “mantle and swirl” structures (Fig. 4I and J; *sensu* Lobza and Schieber, 1999, cf. their figure 4).

4.2. Ichnoassemblages

Our ichnological analysis revealed the presence of five ichnoassemblages, which exhibit variable distribution among the study cores, both in abundance and diversity, reflecting lithological and paleoenvironmental controls. Ichnoassemblages have been described based exclusively on discrete trace fossils, which are commonly associated with light-gray to greenish shale beds characterized by a mottled texture.

Most identified ichnoassemblages are composed of shallow- to middle-tier trace fossils (except for *Chondrites*). They generally reflect similar behavioral patterns, with fodinichnial behavior being the most common. Overall, trace-fossil abundance and diversity are low in ichnoassemblages 1, 2, and 4, indicating mostly stressful conditions for benthic tracemakers, whereas ichnoassemblages 3 and 5 record higher abundance and diversity, reflecting more favorable conditions for benthic communities. Their distribution among the study units is highly variable, alternating with unbioturbated black facies (see Section 4.3), reflecting volatile redox and paleoenvironmental conditions in benthic settings of the North American Seaway (see Discussion).

Ichnoassemblage 1 consists only of *Planolites* and is subdivided into 1a (mud infill) (Fig. 3F–H) and 1b (sand infill), the latter always linked to thin, fine-grained sandstone layers (Fig. 3I–J). More rarely, and only in the OHRS-5 core, Ichnoassemblage 1a may include sparse *Teichichnus* and *Chondrites*. Thus, this ichnoassemblage is composed mostly of simple, shallow-tier fodinichnial structures.

Ichnoassemblage 2 is composed solely of *Chondrites*, which can occur as scattered light-colored mud-filled burrows in the black shale facies (Fig. 3K-M), or, more rarely, just below a mottled shale bed. This corresponds to the only ichnoassemblage of deep-tier structures, linked to the availability of organic matter within the sediment (thus likely fodinichnia).

Ichnoassemblage 3 is dominated by dark-colored mud-filled trace fossils in greenish/light gray shale beds (i.e., dark-on-light trace fossils—DOL—*sensu* Locklair and Savrda, 1998), including *Planolites*, *Teichichnus*, and *Cylindrichnus* (Fig. 4A-C). Sometimes, these DOL trace fossils occur together with light-colored mud-filled burrows bioturbating the underlying dark beds (i.e., light-on-dark trace fossils—LOD), including common *Planolites*, sparse *Chondrites* and rare *Thalassinoides*. This ichnoassemblage is composed of shallow- to middle-tier structures associated with fodinichnial and domichnial behaviors. Its abundance and relative diversity, along with the presence of DOL structures, indicate optimal conditions for benthic fauna.

Ichnoassemblage 4 is characterized by *Zoophycos*, commonly accompanied by *Chondrites* and sparse *Planolites* (Fig. 4D-H). This ichnoassemblage is varied, comprising simple shallow (*Planolites*), complex shallow (*Zoophycos*), and complex deep-tier (*Chondrites*) trace fossils. Occasionally, *Chondrites* crosscuts both *Zoophycos* and *Planolites* (e.g., Fig. 4E), indicating the sequential development of the traces: *Planolites* first, followed by *Zoophycos* and then *Chondrites*, suggesting exploitation of organic matter within preexisting burrows. Overall, this ichnoassemblage consists mainly of fodinichnial traces linked to resource exploitation.

Ichnoassemblage 5 is restricted to the Blocher Member of the New Albany Shale (Jackson core). It includes shallow- to middle-tier structures: *Cylindrichnus*, *Teichichnus*, *Planolites*, ?*Skolithos*, and non-classified subvertical *spreiten*-bearing structures (Fig. 4I-L), representing the most complex ichnological association identified in the study sections. Its high abundance and relative diversity indicate that it developed under highly favorable conditions for benthic communities.

4.3. Distribution of trace fossils

The study cores are dominated by thick black shale deposits (~13–85 m), intercalated with thin (cm-scale) light-gray or greenish shale and sandstone layers. Black shales may display planar-parallel lamination or a massive texture (Figs. 3 and 4). All sections contain basal carbonates (limestones or dolostones) of Silurian to Middle Devonian age, overlain by Frasnian–Famennian shale deposits. Detailed stratigraphic columns, including the distribution of each ichnotaxon, are provided in the Supplementary Material (SM Figs. 1–5). Ichnodiversity is notably higher in the Illinois and Appalachian basins, which were partially restricted watermasses, than in the open-marine Anadarko Basin (Figs. 2A and 5). In the following subsections, we describe the sedimentological characteristics of the study intervals and detail the distribution of the ichnoassemblages among the cores.

4.3.1. The Illinois Basin

Three cores from the Illinois Basin were examined. The Palmer core (Pc), located in the northern depocenter, and the Jackson core (Jc), near the central depocenter (e.g., figure 1 from Remírez et al., 2023), record the New Albany Shale, whereas the Dupont core (Dc), situated in the southern part of the basin (e.g., figure 1 from Song et al., 2021), consists of the Chattanooga Shale (Fig. 2A for locations; Fig. 2C for correlation of local subdivisions).

Upper Devonian deposits in the Palmer core overlie the Middle Devonian Lime Creek Dolostone (SM Fig. 1). The Frasnian is represented by the Sweetland Creek Shale, a 7 m-thick light-gray shale with a single intercalated black shale bed. Discrete trace fossils are largely absent in this interval, except for a single occurrence of ?*Thalassinoides* with light-colored mud infill. The FFB is recorded as a disconformity, separating the Sweetland Creek Shale from the overlying Grassy Creek Shale (299 ft in SM Fig. 1). The uppermost Frasnian is marked by mottled gray shale, while the lowermost Famennian is represented by laminated black shale.

The Grassy Creek Shale comprises 27 m of black shale with thin (cm-scale) interbedded light-gray layers. Its basal interval records low ichnodiversity, with only *Planolites* and rare *Chondrites* (Ichnoassemblage 1a). Upsection, *Zoophycos* becomes common (Ichnoassemblage 4), occurring with abundant *Planolites* and *Chondrites*, and rare ?*Palaeophycus* and ?*Teichichnus*. Notably, *Chondrites* frequently reworks *Planolites*, indicating that it was the last trace-making activity, most likely exploiting the organic matter within preexisting structures (see Section 4.2). The uppermost 4 m of the Grassy Creek Shale is characterized by the exclusive occurrence of *Chondrites* (Ichnoassemblage 2). Above this interval, the upper Famennian Saverton Shale consists of 40 m of light-gray shale with interbedded black layers; this interval is highly fractured, preventing detailed ichnological analysis. The section is capped by an ironstone of undefined Pennsylvanian age, indicating a major discordance.

The central Illinois Basin is represented by the Jackson core (SM Fig. 2). Upper Devonian deposits overlie the Eifelian Jeffersonville Limestone, characterized by an abundant and diverse body-fossil assemblage, including corals, crinoids, and chonitid brachiopods (Stumm, 1964; Droste and Shaver, 1975). The Frasnian Blocher Member can be divided into two parts. The lowermost interval, corresponding to the uppermost Givetian, consists of alternating dark- to light-gray and black shales with abundant brachiopods, ichnofossils, and phosphate nodules, containing Ichnoassemblage 5. This interval is overlain by thick, unbioturbated black shale deposits with planar-parallel lamination or a massive texture, which dominates the remainder of the Blocher Member, recording the Givetian-Frasnian transition. These black shales contain sparse interbeds of light-gray shale and thin sandstone layers hosting *Planolites* (Ichnoassemblages 1a and 1b, respectively). This pattern also characterizes the lower part of the Selmier Member, which corresponds to the uppermost Frasnian (FZ 10 to 12).

The Selmier Member (~15 m thick) overlies the Blocher Member along a discordant contact. As mentioned, the lower interval contains black shale deposits with thin interbeds of sandstone, characterized by Ichnoassemblage 1, whereas the upper interval comprises light-gray to greenish shales alternating with cm-scale black shale beds and occasional thin sandy layers and sideritic red beds showing planar lamination. This part of the Selmier Member is characterized by Ichnoassemblage 3 (dark-colored mud-filled *Planolites* with scarce *Teichichnus* and *Cylindrichnus*), alternating with commonly bioturbated dark beds. *Planolites* frequently overprint the lamination of the black shales. Abundant light-colored mud-filled *Chondrites* are also present, along with rare *Thalassinoides*. The FFB is present at the top of the Selmier Member (3707 ft in SM Fig. 2), based on conodont biostratigraphy (Chen et al., 2023).

The Famennian succession of the Jackson core is represented by the Morgan Trail (6 m), Camp Run (12 m), and Clegg Creek (15 m) members, consisting predominantly of thick black shales with common pyrite nodules or layers, sporadically interrupted by thin light-gray shale beds. In the Morgan Trail Member, light shale interbeds display a mottled texture and contain light-colored mud-filled *Planolites* (Ichnoassemblage 1a). Upsection, in the Camp Run and Clegg Creek Members, light-gray shale interbeds are associated with Ichnoassemblage 4, dominated by *Zoophycos*, accompanied by common *Chondrites* and sparse *Planolites*, which penetrate 3–7 cm into the underlying black beds. *Chondrites* typically extend 2–5 cm deeper than *Zoophycos*, with a single example of *Chondrites* crosscutting *Zoophycos* (Fig. 4E). The DCB is represented by an unconformity, as biostratigraphy indicates the lack of the uppermost Famennian (above the *styriacus* Zone). The uppermost 10 m of the core contain the New Providence Shale (Tournaisian, lowermost Mississippian), consisting of greenish to light-gray shales with abundant pyrite nodules and plant remains, characterized by pyritized *Planolites*.

The southern Illinois Basin, represented by the Dupont core (SM Fig. 3), records a condensed Upper Devonian interval compared to other areas of the basin (approximately 14 m vs. ~100 m). Located on the Cumberland Sill between the Ozark Uplift and the Cincinnati Arch, near the connection of the NAS with the Rheic Ocean (Fig. 2A), this core records unique sedimentological and ichnological features, with bioturbation mainly linked to thin sandstone layers—contrary to other cores, where trace fossils are associated mainly with light-gray to greenish shales. Upper Devonian deposits overlie the Givetian Selmier Limestone, with the contact characterized by a discordance recorded as a breccia.

The Frasnian Dowelltown Member consists of alternating fine-grained cross-bedded sandstone and black shale beds exhibiting planar-parallel lamination and abundant pyrite nodules. Bioturbation is mostly linked to thin sandstone layers that host *Planolites* with sand infill; these burrows frequently extend downward from sandstone layers several centimeters into the underlying black shale (Ichnoassemblage 1b). The FFB is present as a condensed interval just below a thick sandstone bed at 291 ft (SM Fig. 3; Over et al., 2019), at the contact between the Dowelltown and Gassaway Members.

The Famennian Gassaway Member is also condensed and characterized by several discordances. Its lowermost interval consists of alternating dm- to cm-scale laminated black and gray shale beds containing abundant *Zoophycos* and *Chondrites* (Ichnoassemblage 4). Upsection, the unit is dominated by laminated black shales with sparse sandstone interbeds, which contain only rare sand-filled *Planolites* (Ichnoassemblage 1b). The uppermost Famennian is missing (above the *aculeatus* Zone), marked by a discordance with the overlying Tournaisian Maury Formation (Over et al., 2019).

4.3.2. *The Appalachian Basin*

The Appalachian Basin is represented in its central sector by the OHRS-5 core (SM Fig. 4). Upper Devonian deposits overlie the Silurian Peeble and Greenfield dolostones. The Lower (Givetian) and Upper (Frasnian) Olentangy Shales, separated by a disconformity, share a similar lithology of alternating cm- to dm-scale light-gray and black shale beds. In the Lower Olentangy, black beds dominate, whereas in the Upper Olentangy light beds are more abundant in the lower part, with black beds predominating again in the upper part. The uppermost part of the unit, known as the "False Olentangy" (C. Brett, pers. comm., 2022), is separated by a further disconformity and dominated by light shale beds. Ichnodiversity in the Olentangy Shale is low, with Ichnoassemblage 1a dominating and uncommon occurrences of *Teichichnus* and *Chondrites* in some beds. Rare examples of DOL *Planolites* are also recorded in the Upper and "False" Olentangy (cf. Ichnoassemblage 3).

The FFB is recorded as a disconformity separating the Olentangy and Huron Shales (587 ft in SM Fig. 4) (Over, 2002; Liu et al., 2025). Famennian deposits are represented by the Ohio Shale, which is subdivided into the Huron Shale, Three Lick Bed, and Cleveland Shale members (Fig. 2C). The basal interval of the Lower Huron Shale consists of alternating laminated dark-gray shales and mottled light-gray beds, containing Ichnoassemblage 1a very rarely accompanied by dark-colored mud-filled *Zoophycos* (Fig. 4G). Upsection, thicker dark beds dominate, while interbedded light shales contain Ichnoassemblage 4, characterized by abundant *Zoophycos*, *Planolites*, and rare *Chondrites*. The Middle and Upper Huron Shales consist predominantly of thick, unbioturbated, massive-texture black shale deposits, interrupted only by sparse, cm-scale light-gray shale interbeds with mottled texture (lacking discrete trace fossils), especially toward the top. The Three Lick Bed consists of alternating dm-thick black and light-gray shale beds, with discrete trace fossils being rare, as only isolated *Planolites* (Ichnoassemblage 1a) are recorded in the upper part. The Cleveland Shale is represented by a thick, unbioturbated black shale interval characterized by planar parallel lamination, with a single mottled light-gray shale bed. The Ohio Shale is bounded above by a discordance, which separates it from the Bedford and Berea Formations representing the DCB interval (Fig. 2C). These units consist of gray shale and sandstone beds, with the lower part exhibiting mottled textures and the upper part sand-filled *Planolites* (Ichnoassemblage 1b).

4.3.3. *The Anadarko Basin*

The Anadarko Basin is represented by the Current Core (SM Fig. 5), which records an open-marine setting well connected to the Rheic Ocean. The base of the core consists of the Lower Devonian (Emsian) Hunton Limestone, overlain by the Frasnian–Famennian Woodford Shale. The Woodford Shale is subdivided into Lower, Middle, and Upper members. Frasnian deposits correspond to the Lower Woodford Shale. Its basal interval is characterized by dark-gray shales with interbeds of sandstone and greenish shale layers. Trace fossils in this interval are scarce, with only dark-colored mud-filled *Planolites* and ?*Chondrites* recorded in the mottled greenish shales (Ichnoassemblage 3). Upsection, the Lower Woodford contains an alternation of cm-scale beds, consisting of faintly laminated dark-gray shales and mottled greenish shales in which discrete trace fossils are absent. The FFB is present as a disconformity at 555 ft (SM Fig. 5) (cf. Watney et al., 2013).

Famennian deposits are represented by the Middle and Upper members of the Woodford Formation. The basal interval of the Middle Member (lowermost Famennian) consists of black shales alternating with cm-thick greenish shale layers, transitioning upsection into a thick dark-gray shale deposit with sandstone and greenish shale interbeds in the lower part. Most of the Famennian is barren of trace fossils, and only the lower part of the interval records mottled greenish shales, sometimes yielding light-colored mud-filled *Planolites* (Ichnoassemblage 1a). The Upper Member includes a lower interval of dm-thick dark-gray shales with sparse thin sandstone beds, and an upper interval of thick laminated black shales with occasional sandstone beds and lenses. Trace fossils are restricted to the uppermost part, where light-colored mud-filled *Chondrites* occur rarely. These structures largely overprint, but do not deform, the planar-parallel lamination (Ichnoassemblage 2). The Woodford Shale is overlain by the Tournaisian (Mississippian) Welden Limestone.

4.4. *Correlation and identification of major biological crises*

Several works have addressed the correlation and dating of the units recorded in the study cores (Fig. 2C), based on conodont zonation (Over, 1990, 1992, 2002, 2007, 2021; Over and Rhodes, 2000; Levman and Bitter, 2002; Klapper et al., 2004; Klapper and Kirchgasser, 2016; Over et al., 2019; Chen et al., 2023; Over and Mason, 2024) and/or integration of lithostratigraphy, gamma-ray logs, sequence stratigraphy, and geochemistry (Schieber, 1994; Ettensohn, 1998; Schieber, 1998a, 1998b; Lazar, 2007; Watney et al., 2013; Zou and Slatt, 2015; Lazar and Schieber, 2022; Remírez et al., 2023; Liu et al., 2025). Based on these studies, two of the cores have robust age constraints derived from conodont biozonation (Dupont core: Over et al., 2019; Jackson core: Chen et al., 2023). The remaining three cores have been dated by extrapolation from equivalent units in other cores or outcrops (OHRS-5 core: Over and Rhodes, 2000; Over, 2021; Over and Mason, 2024; Liu et al., 2025; Current core: Watney et al., 2013; Zou and Slatt, 2015; Palmer core: Day and Witzke, 2017) (see Figs. 2C and 5; SM Figs. 1–5). Additionally, gamma-ray logs are available for all cores (provided by the curators of the respective USGS repositories), which, when combined with the sedimentological and ichnological analyses, allow detailed correlation and age assessment of the study units. Here, we address the correlation of the cores and the relationship of the recorded units with the major biological crises of the Frasnian and Famennian stages (Fig. 1).

Black shales lacking bioturbation and typically exhibiting planar-parallel lamination are interpreted as deposits formed under anoxic conditions in benthic settings of the North American Seaway. These anoxic intervals were frequently interrupted by relatively short oxic or dysoxic pulses, expressed as light-gray and greenish shale beds. However, some anoxic pulses were more persistent, generating thicker stratigraphic successions and exerting a stronger impact on benthic tracemaker communities. Such intervals are commonly marked by thick black shale deposits with elevated TOC contents, positive excursions in gamma-ray logs, and anomalous enrichments of redox-sensitive trace elements (e.g., Mo and U), and they are often linked to abrupt sea-level changes, primarily transgressions. Regionally, these intervals can be correlated by integrating these features with conodont zonation, allowing their connection to globally recognized biological crises such as the Middlesex, Kellwasser, and Dasberg events as well as to regional events like the Rhinestreet crisis (Figs. 1 and 5).

Based on conodont biostratigraphy, lower to middle Frasnian deposits in the study cores are generally condensed, with most conodont zones of this stage absent (Fig. 5), and the successions characterized by multiple disconformities (Fig. 5; SM Figs. 1–5) (Over et al., 2019; Liu et al., 2025). The Illinois Basin preserves the most complete Givetian-Frasnian record, particularly in the Jackson core (SM Fig. 2). The lower interval of the Blocher Member encompasses the uppermost Givetian (*disparilis* to *norrisi* zones; Chen et al., 2023). The contact with the Frasnian is probably represented by a disconformity at the top of a grainstone limestone bed overlain by a black shale unit, likely reflecting the Givetian–Frasnian Boundary transgression (Fig. 5, SM Fig. 2). A comparable pattern occurs in the nearby Dupont core, where the Frasnian-Givetian boundary is recorded as a breccia (Over et al., 2019). In the Palmer core, Frasnian deposits rest directly upon an undifferentiated Middle Devonian limestone. In the Appalachian Basin, the Givetian Lower Olentangy Shale is separated from the Frasnian Upper Olentangy by a disconformity (Liu et al., 2025). In contrast, the Current core (Anadarko Basin) records only a restricted Frasnian succession (Lower Woodford), spanning the *bogartensis* to *ubiquitus* zones (FZ 13a–b) (Fig. 5), as reported by Watney et al. (2013) and Zou and Slatt (2015).

The remainder of the Blocher Member in the Jackson core records the lower Frasnian, spanning the *pristina* to *plana* zones (FZ 1–10), whereas the overlying Selmier Member corresponds to the *feisti* to *ubiquitus* zones (FZ 11–13) (Fig. 5; SM Fig. 2; Chen et al., 2023). This succession is equivalent to the Dowelltown Member in the Dupont core, which encompasses the interval from the *punctata* to *ubiquitus* zones (FZ 5–13) (Fig. 5, SM Fig. 3; Over et al., 2019). In both members, thick black shale intervals, locally interbedded with thin sandstone beds, can be correlated by distinct positive gamma-ray peaks within the *punctata* and *nonaginta* zones (FZ 5 and 7, respectively). These intervals correspond to the global Middlesex Event and the regional Rhinestreet biocrisis (Figs. 1 and 5) (Becker et al., 2016; Brett et al., 2020; equivalent with the Anoxic Pulse I in Remírez et al., 2023). In the Palmer core, lower Frasnian deposits are absent, with the onset of Sweetland Creek Shale deposition occurring during FZ 11 (Day and Witzke, 2017) (Fig. 5). In the Appalachian Basin, these intervals may correspond to the boundary between the Lower and Upper Olentangy Shale, which is marked by a disconformity and/or highly condensed deposits (Fig. 5; SM Fig. 5) (Liu et al., 2025). In the Anadarko Basin, the lowermost Frasnian is also missing, as deposition of the Lower Woodford began at FZ 13 (Watney et al., 2013; Zou and Slatt, 2015). Consequently, the lower–middle Frasnian events (Middlesex and Rhinestreet) are only recorded in the central and southern Illinois Basin (Fig. 5). Notably, just below the Givetian–Frasnian boundary in the Jackson core, a positive gamma-ray peak coincides with a 2 m-thick laminated black shale bed and a slight increase in Mo_{EF} (Remírez et al., 2023). This interval may represent a local expression of the Frasnes Event and could be correlated with the thin black shale beds recorded in the Lower Olentangy Shale of the OHRS-5 core (Appalachian Basin) (Fig. 5).

Upper Frasnian deposits are better represented in the study cores, although they are also marked by several disconformities (Over et al., 2019; Liu et al., 2025). In the Jackson core, the Selmier Member can be subdivided into a lower interval (FZ 11–12) and an upper interval (FZ 13). The lower interval consists of a thick, laminated black shale unit, coinciding with a gamma-ray peak and increased Mo_{EF} and U_{EF} values (Anoxic Pulse II of Remírez et al., 2023). This interval correlates with an unbioturbated black shale in the Palmer core, also characterized by a pronounced gamma-ray peak. Based on conodont zonation, this anoxic pulse most likely corresponds to the Semichatovae Event (FZ 11; Fig. 1). However, because the Lower Kellwasser Event begins in the upper FZ 12, a potential relationship with this crisis cannot be excluded. No equivalent has been identified in the other study cores, where the interval is highly condensed in the Dupont core (SM Fig. 3; Over et al., 2019), and where the Upper Olentangy and Lower Woodford Shales record only FZ 13 and/or younger intervals (Fig. 2C; Over and Rhodes, 2000; Watney et al., 2013; Zou and Slatt, 2015; Liu et al., 2025). Notably, Remírez et al. (2023) correlated this interval across the main depocenter of the Illinois Basin (see their figs. 1, 8, and 9), and, based on data from the Palmer core, it also affected the northwest depocenter, albeit to a lesser extent (Fig. 5).

The Frasnian–Famennian boundary interval represents a special case within the study sections, as discussed below. This interval is highly condensed (virtually absent) in the southern Illinois Basin (Dupont core; Over et al., 2019), whereas in the other cores it is represented mainly by light-gray to greenish shales with mottled textures, alternating with thin, commonly bioturbated black shale beds. These intervals correspond to a general trend of low gamma-ray values punctuated by several minor positive peaks (SM Figs. 1-5). In the Jackson core, it corresponds to the upper interval of the Selmier Member (FZ 13); in the Palmer core, to the upper Sweetland Creek Shale; in the Appalachian Basin (OHRS-5 core), to the Upper and "False" Olentangy Shales; and in the Anadarko Basin (Current core), to the upper interval of the Lower Woodford (Fig. 5; SM Figs. 1–5) (cf. Over and Rhodes, 2000; Watney et al., 2013; Zou and Slatt, 2015; Day and Witzke, 2017; Chen et al., 2023; Liu et al., 2025). Thus, in contrast to its global expression as relatively thick, unbioturbated black shale intervals, the Upper Kellwasser Event in the North American Seaway is recorded in a markedly different manner (see discussion below).

The Famennian stage is well recorded in the study cores. The lowermost Famennian is represented by the Morgan Trail Member in the Jackson core (*triangularis* to *crepida* zones; Chen et al., 2023) and the lowermost Dowelltown Member in the Dupont core (*crepida* zone; note that the *subperlobata* to *minuta* zones—i.e., older *triangularis*—are absent; Over et al., 2019). This interval consists of unbioturbated black shales, corresponding to a positive gamma-ray peak and elevated Mo_{EF} and U_{EF} values (Remírez et al., 2023; their Anoxic Pulse III). In the Palmer core, it correlates with thick black shales in the lower Grassy Creek Shale exhibiting a positive gamma-ray excursion (Fig. 5), and in the Appalachian Basin it corresponds to the lower interval of the Lower Huron Shale, recorded as an alternation of dark-gray and thin light-gray shale beds coinciding with gamma-ray peaks. In the Current core (Anadarko Basin), it is represented by black shales alternating with thin greenish shale beds, also associated with a positive gamma-ray excursion. Based on conodont zonation in the Jackson and Dupont cores, this interval corresponds to the aftermath of the Upper Kellwasser event ("Upper Kellwasser Event cycle" *sensu* Algeo et al., 2026), when anoxic conditions persisted to a moderate extent, and preludes the strongly anoxic Nehden event (Fig. 1; cf. Becker et al., 2016).

The lower Camp Run Member of the Jackson core records the *prima* to ?*marginifera* conodont zones (Chen et al., 2023), equivalent to the middle Dowelltown Member of the Dupont core (*prima* to *gracilis* zones; Over et al., 2019) (Fig. 5; SM Figs. 2 and 3). It consists of dm-scale black shale beds alternating with thin light-gray shale layers, characterized by the presence of *Zoophycos*. The gamma-ray signal shows an initial positive peak followed by lower values, mirroring the geochemical record, which exhibits alternating high and low Mo_{EF} and U_{EF} values (Remírez et al., 2023). This interval is correlated across the study area based on similar lithological, ichnological, and gamma-ray data, corresponding to the middle part of the Grassy Creek Shale in the Palmer core and the upper Lower Huron Shale in the Appalachian Basin. In the Anadarko Basin, it is represented by gray shales alternating with sandstone and greenish shale layers, associated with variable gamma-ray values. Based on conodont zonation, this interval records a condensed section of the middle Famennian, corresponding to the globally recognized Nehden and Condroz events.

The upper Camp Run Member records the ?*marginifera* to *utahensis* conodont zones, equivalent to the middle Dowelltown Member spanning the *marginifera* and *utahensis* to *trachytera* zones (Over et al., 2019; Chen et al., 2023). This interval is characterized by unbioturbated black shales, with elevated gamma-ray, Mo_{EF}, and U_{EF} values. It is correlated with the uppermost Grassy Creek Shale in the Palmer core and the lower part of the Middle Huron Shale in the Appalachian Basin, both of which consist of thick, unbioturbated black shale deposits exhibiting positive gamma-ray peaks. In the Anadarko Basin, it corresponds to the termination of bioturbated intervals, represented by the lower portion of a thick dark-gray shale in the Middle Woodford Shale, which also shows a positive gamma-ray peak. Based on conodont zonation, this interval corresponds to the Enkeberg Event, or a local expression of its aftermath, spanning at least the entire *utahensis* Zone (i.e., the older middle *marginifera*) (Fig. 1; cf. Brett et al., 2020).

The Upper Famennian is well constrained in all of the Illinois Basin study cores. In the Jackson core, the Clegg Creek Member corresponds to the *granulosus* conodont Zone, characterized in its upper interval by unbioturbated black shales and positive excursions in gamma-ray, Mo_{EF}, and U_{EF} values (Remírez et al., 2023; their Anoxic Pulse IV). It is correlated with the *granulosus* Zone within the Dowelltown Member of the Dupont core, which is likewise characterized by unbioturbated black shales and high gamma-ray values (Over et al., 2019), and with the black shale beds of the Saverton Shale (Palmer core), which display higher gamma-ray values than the rest of the unit. This interval correlates with unbioturbated black shales of the Upper Huron Shale in the Appalachian Basin (Fig. 5). In the Anadarko Basin, it is marked by a positive gamma-ray peak within the unbioturbated gray shales of the upper interval of the Middle Woodford Shale. Based on conodont zonation, this interval is equivalent to the globally recorded Annulata Event (Fig. 1).

Finally, the uppermost Famennian is absent in some sections, probably eroded during the Devonian–Carboniferous Boundary regression (cf. Remírez et al., 2023). In the Jackson core, this interval is not recorded, representing a major disconformity with the overlying Tournaisian New Providence Shale. In the Dupont core, the uppermost Dowelltown Member records the *aculeatus* Zone, represented by unbioturbated black shales, and is overlain by a disconformity with the Maury Formation, where the Devonian–Carboniferous Boundary is placed (Over et al., 2019; Song et al., 2021). In the Appalachian Basin, the Three Lick Bed spans the *expansa* to lower *aculeatus* zones, whereas the Cleveland Shale corresponds to the upper *aculeatus* to ?*costatus* interval (Over, 2021; Liu et al., 2025); the Devonian–Carboniferous Boundary is recorded within the Bedford and Berea Formations (Over, 2021). In the Anadarko Basin, the Upper Woodford Shale is characterized by a positive gamma-ray peak correlated with the transgression across the *aculeatus*–*costatus* zonal boundary (Zou and Slatt, 2015), and the Devonian–Carboniferous Boundary is likely located at its discordant contact with the Welden Limestone. The interval of unbioturbated black shales from the *aculeatus*–*costatus* zones is correlated with the Dasberg Event (cf. Hartenfels, 2011), representing a fourth-order biological crisis (Becker et al., 2016).

5. Discussion

The ichnological and sedimentological analysis of the study cores provides key insights into the response of benthic fauna to Late Devonian environmental changes across a spectrum of paleogeographic settings within the North American Seaway. The observed patterns in trace fossil distribution, abundance, and ichnodiversity suggest a close relationship with redox fluctuations and sedimentary dynamics, which are commonly associated with globally recorded biological crises (Section 5.1). This pattern is also evident when comparing the study sections with other settings within the North American Seaway (in Canada and the northeastern U.S.A.) and with carbonate platforms from eastern Laurasia (in Poland) and Panthalassan islands (in China) (Section 5.2). Given the limited ichnological information available for the Late Devonian biocrises relative to other paleontological records, we compile and synthesize the evidence presented in the previous sections to establish a broad framework that may serve as a basis for future studies (Section 5.3).

5.1. Benthic response to Late Devonian anoxic pulses in the North American Seaway

5.1.1. Upper Givetian

Givetian sediments are only recorded in the Jackson core (central

Illinois Basin) and the OHRS-5 core (central Appalachian Basin) (Fig. 5). In the Illinois Basin, this interval displays the highest ichnodiversity (Ichnoassemblage 5) (SM Fig. 2), a pattern also inferred in other areas of the basin based on Remírez et al. (2023); (their figs. 2 [Kavanaugh core], 3 [Chinn core], and 4 [Storey core]). This indicates well-ventilated conditions in benthic settings prior to the initial flooding of the basin (Remírez et al., 2023), associated with the Kaskaskia Transgression (Fig. 1). Trace fossils abruptly disappear upwards, giving way to unbioturbated black shales towards the Givetian–Frasnian boundary, suggesting that benthic tracemaker communities were forced to migrate shoreward within the North American Seaway—likely recording the effects of the Frasnes Event. However, the lack of sedimentary record in these shallower areas (cf. Remírez et al., 2023) prevents a clear assessment of whether this initial flooding event caused a true extinction of the benthic fauna or merely a displacement within the basins.

In the Appalachian Basin, anoxic pulses (i.e., black shales) and oxic intervals (i.e., bioturbated light shales) alternate throughout the upper Givetian (Lower Olentangy Shale) (Fig. 5, SM Fig. 4). In this setting, ichnodiversity is lower (Ichnoassemblage 1a with scarce *Teichichnus*), and anoxic–oxic shifts were more frequent and shorter. This is reflected both in the lower ichnodiversity and in the simpler biogenic structures recorded (*Planolites* and scarce *Teichichnus*) compared to the more complex *spreiten*-bearing structures of the Illinois Basin, which require longer and more stable colonization intervals to develop.

The contrasting redox conditions and benthic behavior between the inner Illinois Basin and the central Appalachian Basin are linked to the hydrographic patterns of both basins. As shown by Algeo et al. (2007, their fig. 9), the Blocher Member was deposited under more restricted conditions than the Lower Olentangy Shale; that is, bottom waters in the Appalachian Basin were more frequently renewed than in the Illinois Basin, as the former maintained a better connection with the Rheic Ocean. A stronger connection to the open ocean favored water-mass exchange and inhibited strong stratification, leading to more frequent oxic–anoxic fluctuations in the Appalachian Basin compared to the inner Illinois Basin (see the “reservoir effect” defined by Algeo and Lyons, 2006). Consequently, late Givetian conditions were more stable in the Illinois Basin, resulting in longer-lasting anoxic intervals during the initial flooding of the NAS (possibly corresponding to the Frasnes Event). Simpler and less diverse ichnoassemblages in the Appalachian Basin reflect more volatile redox conditions and the prevalence of opportunistic tracemaker communities, whereas climax communities were established in the Illinois Basin before flooding, producing thicker bioturbated intervals characterized by more complex structures, which disappeared due to widespread anoxic conditions.

5.1.2. Lower and middle Frasnian

Lower and middle Frasnian deposits are better recorded within the Illinois Basin, where several globally recognized biological crises are well constrained. Following the initial flooding of the basin during the upper Givetian, anoxic conditions persisted, recorded in the central and southern areas (Jackson and Dupont cores) as thick, unbioturbated black shale intervals. These deposits are linked to short-term transgressions or highstand periods during the major Kaskaskia Transgression (Lazar and Schieber, 2022) and are characterized by elevated Mo_{EF} and U_{EF} values indicating pervasive anoxia (Remírez et al., 2023). Based on conodont zonation, these intervals are associated with the Middlesex and Rhinestreet events.

Benthic biological activity during this interval was limited to short colonization windows. In inner areas of the Illinois Basin (Jackson core), benthic communities partially recovered after the Middlesex Event, as evidenced by thin light-gray shale beds with mottled textures and Ichnoassemblage 1a (light-colored mud-filled *Planolites*, rarely accompanied by *Chondrites*), occurring just below a limestone bed. In contrast, in the shallower southern part of the basin (Dupont core), only Ichnoassemblage 1b (*Planolites* with sand infill) is recorded, linked to thin sandstone layers interbedded within black shales. A similar pattern is observed during the Rhinestreet Event, with anoxic intervals punctuated by sandstone layers associated with Ichnoassemblage 1b.

These observations indicate that the Kaskaskia Transgression led to pervasive anoxic conditions in the Illinois Basin, which were briefly interrupted in inner (distal) areas, likely linked to short-term sea-level falls (as indicated by the presence of limestone beds), a feature absent in shallower areas. The dominance of Ichnoassemblage 1b suggests that benthic activity was largely restricted to short-lived hyperpycnal flows, recorded as thin sandstone layers with cross-bedded lamination (cf. Wilson and Schieber, 2015, 2017). Thus, although geochemical and sedimentological data indicate highly restricted and anoxic conditions in the Illinois Basin (Algeo et al., 2007; Remírez et al., 2023) (Fig. 5, SM Figs. 2–3), brief colonization windows allowed the establishment of opportunistic tracemaker communities immediately following the Middlesex Event. In contrast, the Rhinestreet Event is characterized by more persistent anoxia, only interrupted by terrigenous input (i.e., hyperpycnal flows). Ichnoassemblages 1a and 1b, therefore, document the activity of opportunistic benthic communities during major anoxic intervals in the Illinois Basin.

5.1.3. Upper Frasnian

Anoxic conditions prevailed during the upper Frasnian in most of the North American Seaway. In the central Illinois Basin (Jackson core), black shales are sparsely interbedded with light-gray shale and sandstone layers, characterized by Ichnoassemblages 1a and 1b, respectively, indicating pervasive anoxic conditions intermittently interrupted by short oxic pulses (linked to hyperpycnal flows in the case of the sandstone layers). In the northwestern depocenter of the basin (Palmer core), although sedimentation is dominated by light-gray shales, bioturbation remains scarce. Upsection, the Selmier Member (Jackson core) is recorded as unbioturbated black shales, interrupted only by sandstone layers containing Ichnoassemblage 1b. This interval of pervasive anoxia is associated with the Semichatovae Event, and its effects on benthic fauna are comparable to those of the Middlesex and Rhinestreet Events: only thin colonization windows occur, mostly linked to hyperpycnal flows.

In the Appalachian Basin, although the lack of a robust biostratigraphic framework prevents a direct correlation of the Upper Olentangy Shale to the Semichatovae Event, a similar pattern to the upper Givetian is observed. Unbioturbated black shales alternate with mottled light-gray shale beds containing Ichnoassemblage 1a, indicating more frequent oxic-anoxic shifts in this sector of the North American Seaway.

The record from the Anadarko Basin also indicates pervasive anoxic conditions during the upper Frasnian, recorded by unbioturbated black shales and sparse trace fossils associated with greenish shale beds. Notably, sandstone layers occur, though lacking bioturbation, likely reflecting higher terrigenous input rather than processes that enhanced oxygenation of the water column.

Thus, the upper Frasnian records a pattern similar to that of the Givetian–Frasnian transition, with hydrographic restriction more pronounced in the inner areas of the North American Seaway (Algeo et al., 2007), leaving only short windows for benthic activity, mostly linked to hyperpycnal flows (Ichnoassemblage 1b). In contrast, more frequent water-mass exchange with the Rheic Ocean in the Appalachian Basin allowed for more frequent and longer-lasting oxic pulses, as evidenced by the presence of scarce *Teichichnus* in the Upper Olentangy Shale. The Anadarko Basin, on the other hand, exhibited paleoenvironmental conditions comparable to the inner Illinois Basin.

5.1.4. The Frasnian-Famennian Boundary

Contrary to the global record of the Frasnian-Famennian Boundary, characterized by the Kellwasser Event, anoxic conditions were not dominant in the North American Seaway at this time. In the Illinois Basin, light-gray shales with abundant bioturbation are common in FZ 13 in both the central (Jackson core, Ichnoassemblage 3) and northwestern (Palmer core, mottled textures) depocenters. Note that this interval is highly condensed in the southern part of the basin (Dupont core) (Fig. 5). In the Appalachian Basin, light-gray shale beds also dominate, characterized by mottled textures and sparse *Planolites* (Ichnoassemblage 1a). In contrast, in the Anadarko Basin, black shale beds are more frequent, although they also alternate with mottled greenish shale layers. Therefore, trace fossils indicate well-ventilated conditions during the Upper Kellwasser Event within the North American Seaway. This is also supported by lower Mo_{EF} and U_{EF} values (Remírez et al., 2023), despite hydrographic conditions being relatively restricted, similar to those during the middle Frasnian (Algeo et al., 2007, 2026).

Notably, ichnodiversity is higher in inner areas of the Illinois Basin compared with the Appalachian and Anadarko Basins, which were better connected to the Rheic Ocean. Furthermore, Ichnoassemblage 3, characteristic of the FZ 13 sediments in the Jackson core, includes DOL trace fossils, indicating that even the scarce dark sediments were deposited under oxic conditions. This pattern suggests that anoxic conditions linked to the Upper Kellwasser Event were buffered in the inner regions of the epeiric North American Seaway—that is, anoxia was more pervasive in open settings (the Rheic Ocean?) than in more restricted basins.

Overall, the main regression at the Frasnian–Famennian Boundary appears to have allowed more prolonged oxic conditions in restricted/inner settings, whereas in more open settings (i.e., the Appalachian and, especially, the Anadarko Basin), oxic pulses were shorter, permitting benthic communities to develop only simpler structures (Ichnoassemblage 1a) or to bioturbate primarily the sediment–water interface—albeit profusely. This highlights the stronger impact of the Kellwasser Event on benthic communities in open-marine settings.

5.1.5. *Lower Famennian*

Contrary to what occurred during the Upper Kellwasser Event, anoxic conditions became widespread again immediately after the Frasnian–Famennian Boundary, within the lowermost interval of the Famennian (*triangularis* to *crepida* zones), as indicated by sedimentological, geochemical, and ichnological evidence. Furthermore, this interval can be correlated across all of the study cores (Fig. 5).

It is recorded as alternating black and light/greenish shales, characterized by Ichnoassemblage 1a and/or mottled textures. This pattern indicates abrupt oxic–anoxic fluctuations, resulting in unstable benthic habitability, where tracemakers were only able to colonize the sediment–water interface and produce simple structures. Based on conodont zonation, this interval corresponds to the aftermath of the Kellwasser Event, immediately preceding the Nehden biocrisis (Anoxic Pulse III in Remírez et al., 2023). In all basins, hydrographic restriction was moderate (Algeo et al., 2007), consistent with the ichnological evidence, suggesting that water exchange with the Rheic Ocean was similar in all the basins, thereby producing these repeated anoxic–oxic shifts and resulting in generally unfavorable conditions for benthic communities.

The abrupt shift from well-ventilated benthic conditions below the FFB to strong anoxia immediately above it is associated with the end of the FFB Glaciation and the subsequent sharp transgression (*triangularis–platys* zones), representing the “Upper Kellwasser Event Cycle” (Algeo et al., 2026). Thus, during the Frasnian–Famennian transition in the North American Seaway, favorable conditions for benthic communities were linked to periods of greater continental ice volume, drier climates, lower sea-level, and lower-salinity watermasses (although fully freshwater conditions likely did not affect the study sections, i.e., the inner and deeper areas of the NAS; Algeo et al., 2026). The melting of continental icesheets triggered a rapid transgression, a more humid climate, and enhanced organic matter accumulation, which led to the extinction or migration of benthic tracemaker communities toward more shoreward regions within the NAS.

5.1.6. *Middle and upper Famennian*

This interval represents the highest variability within the Illinois, Appalachian, and Anadarko Basins. In the Illinois Basin, the occurrence of *Zoophycos* (Ichnoassemblage 4) became common, associated with light-gray shales interbedded within unbioturbated black or dark-gray shales. A similar pattern is recorded across the Appalachian Basin, whereas trace fossils remain scarce in the Anadarko Basin. Based on conodont zonation, three major biological crises are recognized within this interval—the Enkeberg (*marginifera–utahensis* zones), Annulata (*granulosus* zone), and Dasberg (*expansa–aculeatus* zones) events—defining a highly unstable interval for benthic communities.

In the Illinois Basin, ichnological distribution varies widely depending on the area. Although Ichnoassemblage 4 is common in the central part of the basin during oxic intervals (i.e., light-gray shale beds) of the middle and upper Famennian, this pattern is restricted to the interval below the *marginifera–utahensis* zones in both the southern and northern areas (Figs. 2A and 5). A similar situation occurs in the Appalachian Basin, where Ichnoassemblage 4 is confined to the Lower Huron Shale, corresponding to a comparable age (i.e., below *marginifera*). Above this interval, a thick black shale deposit can be correlated across all of the study cores (Fig. 5), representing a major anoxic pulse that caused the extinction or migration of the benthic fauna responsible for Ichnoassemblage 4 in all areas except the central Illinois Basin (i.e., the Jackson core).

Based on conodont biozonation, this interval corresponds to the Enkeberg Crisis or its aftermath during the *utahensis* Zone—although detailed biostratigraphy is needed to determine whether the observed shift toward anoxic facies relates directly to the Enkeberg Event, its aftermath, or a separate, regionally recorded biocrisis (in which case, we propose the name “Utah Event”) (Figs. 1 and 5). In any case, higher Mo_{EF} and U_{EF} values (Remírez et al., 2023) together with moderate to high hydrographic restriction (Algeo et al., 2007) support the ichnological evidence, indicating unfavorable conditions for benthic tracemaker communities during this interval.

The dominance of complex structures such as *Zoophycos* and *Chondrites* indicates that oxic pulses were longer than during the Frasnian and lower Famennian. Simple structures like *Planolites* require only weeks to colonize the substrate following anoxic conditions (Barrett and Schieber, 1999). In contrast, *Zoophycos* and *Chondrites* reflect prolonged benthic stability, as these traces record long-term colonization phases, likely spanning the entire lifespan of the tracemaker. Moreover, both *Zoophycos* and *Chondrites* have been widely associated with the availability of organic matter within the sediment (Löwemark et al., 2005, 2007; Löwemark, 2011).

Therefore, this interval is characterized by a marked behavioral change in the benthic tracemaker communities during the anoxic–oxic shifts, evolving from opportunistic behavior during the Frasnian and lowermost Famennian—represented by the simpler structures of Ichnoassemblage 1—to more specialized–opportunistic communities represented by Ichnoassemblage 4. Notably, the Anadarko Basin during this interval is characterized by Ichnoassemblage 1a, indicating that oxic pulses were shorter and, consequently, benthic habitability was poorer in open settings than in the epeiric basins—similar to conditions during the Frasnian–Famennian transition.

In any case, Ichnoassemblage 4 disappears after the Enkeberg/Utah biocrisis in all study areas except for the central Illinois Basin. In the southern Illinois, central Appalachian, and Anadarko basins, unbioturbated black to dark-gray shale deposits dominate the remainder of the Famennian, corresponding to the Dasberg and Annulata events. This interval represents a barren phase for macrobenthic tracemaker communities across most parts of the North American Seaway, where benthic activity was virtually absent during the middle and upper Famennian—only sparse *Chondrites* are recorded in the Anadarko Basin in the uppermost Famennian, following the Dasberg Event. In this case, although hydrographic restriction varied from moderate to high (Algeo et al., 2007), the tracemaker response to anoxic pulses remained similar. This suggests that paleoenvironmental conditions were not the main driver of the extinction or migration of benthic communities. Instead, the prolonged anoxic conditions throughout the Frasnian and Famennian likely led to progressively impoverished benthic faunas that became increasingly vulnerable to subsequent oxygen depletion (cf. Boyer et al., 2021).

However, Ichnoassemblage 4 is consistently present in light shale interbeds throughout the entire recorded Famennian succession in the Jackson core (i.e., both before and after the Enkeberg/Utah and Annulata biocrises) (Fig. 5). This contrasts with other regions of the North American Seaway and indicates that the central Illinois Basin functioned as a refuge for benthic communities, mirroring the pattern observed in the uppermost Frasnian during the Kellwasser Event, when Ichnoassemblage 3 likewise reflects well-developed benthic tracemaker communities in this area. Therefore, these observations support a "refuge scenario" in which inner, restricted parts of the North American Seaway buffered benthic communities during widespread anoxic intervals, permitting colonization windows.

Notably, based on conodont zonation, the Hangenberg Event is not present in the study sections. Only the Appalachian Basin (Bedford–Berea Formations) preserves the *costatus–ultimus–?kockeli* zones, which are characterized by Ichnoassemblage 1a and mottled textures. This suggests that the Devonian–Carboniferous regression did not lead to widespread anoxia in that area.

5.2. *Comparative analysis*

5.2.1. *The northern NAS: Appalachian Basin and Moose River Basin*

Although ichnological studies of the Frasnian-Famennian Boundary remain relatively scarce, several investigations have been conducted in the North American Seaway, especially in the northern region of the Appalachian Basin (the states of New York and Pennsylvania) and the Moose River Basin (Ontario, Canada).

In the northern Appalachian Basin (Fig. 2C), Boyer et al. (2014) described the effects of the Upper Kellwasser Event on benthic fauna (see also Boyer, 2007; Boyer and Droser, 2009, 2011; Boyer et al., 2021). In contrast to the central region of the basin (i.e., OHRS-5 core), where the Upper Kellwasser Event is recorded by alternating black and light shale beds, black shale deposits in the northern sections are limited to two thin (cm-scale) intervals: the precursor black shale bed (PBSB) and the Upper Kellwasser interval. These black shale beds are interbedded within a light gray shale (mudstone) succession. According to the authors, the study sections exhibit an ichnoassemblage dominated by *Skolithos*, with sparse occurrences of *Chondrites*, *Planolites*, and *Thalassinoides* in the lower unit, beneath the PBSB. Upwards, the PBSB is laminated and mostly unbioturbated, whereas the overlying light shale interval is completely bioturbated by *Chondrites* with light mud infill, which penetrates into the uppermost part of the PBSB. Above this, the black shale marking the Upper Kellwasser Event remains largely laminated, with only sporadic small burrows (?*Planolites*). In the upper portion of this black shale bed, large *Thalassinoides* burrows extend approximately 5 cm downward from the overlying light mudstone.

Additional sections in the northern Appalachian Basin were examined by Haddad et al. (2018), who documented ichnoassemblages similar to those reported by Boyer et al. (2014). These assemblages are dominated by *Planolites*, accompanied by *Skolithos*, *Chondrites*, and *Thalassinoides* below the laminated PBSB. Between the PBSB and the black shale recording the Upper Kellwasser Event, a mottled gray shale with large burrows is present. Within the Kellwasser event bed, Haddad et al. (2018) identified planar-parallel lamination alternating with ?*Planolites*, as well as large *Thalassinoides* burrows penetrating up to 5 cm into the uppermost part of the black shale, which is overlain by a greenish shale bed. *Planolites* within the Kellwasser event bed are associated with cm-scale greenish shale beds containing abundant silt laminae and ripples, interpreted as evidence of increased bottom-current energy. In a nearby area of the northern Appalachian Basin (Fig. 2C), Hannibal and Feldmann (1983) documented several arthropod trackways (aff. *Rusophycus*) and "*Zoophycoid*" traces in the Chagrin Formation (lateral equivalent of the Three Lick Bed), just below the Cleveland Shale.

According to the above, a similar pattern is observed in the study sections of the northern (more shoreward) part of the Appalachian Basin, which contrasts with that of the more distal (inner) regions, represented here by the OHRS-5 core. During the Kellwasser Event, anoxic conditions were common in the inner regions of the basin, recorded as frequent black shale beds alternating with lighter shale intervals. In contrast, in the northern area, anoxic conditions were restricted, represented by two discrete black shale beds. Furthermore, both ichnodiversity and trace-fossil abundance are higher in the shoreward regions (*Planolites*, *Chondrites*, *Skolithos*, and *Thalassinoides* vs Ichnoassemblage 1a). Thus, in these proximal settings, anoxic episodes were shorter, while oxic conditions prevailed for longer periods, allowing more stable benthic colonization by tracemaker communities. The influence of the nearby Catskill Delta likely played a major role in mitigating the development of pervasive anoxia in these shallow environments by reducing watermass stratification.

Northward, in the Moose River Basin (Fig. 2C), Bezys (1987) studied the Long Rapids Formation, where black shales are mostly unbioturbated, whereas light-gray to greenish mudstones and carbonate beds contain relatively diverse ichnoassemblages similar to those from the study cores (i.e., *Planolites*, *Chondrites*, *Zoophycos*, and rare *Teichichnus*). Klapper et al. (2004) later proposed a detailed biostratigraphic framework for the OGS Onakawana B borehole, previously examined by Bezys (1987) (Fig. 2C). An ichnoassemblage composed of *Planolites*, *Teichichnus*, and *Chondrites*, associated with greenish mudstone and limestone beds showing mottled textures, is recorded in the upper interval of the Williams Island Formation, corresponding to the FZ 2 to FZ 4. Overall, this interval of the early Frasnian is characterized by favorable and relatively stable conditions for benthic tracemaker communities.

Upsection, black shale deposits dominate the FZ 4 to FZ 10 interval (corresponding to the effects of the Middlesex and Rhinestreet biocrises), where trace fossils are limited to scarce *Planolites* and *Chondrites* restricted to greenish shale beds (cf. Ichnoassemblage 1a), recording a pattern similar to that observed in the inner areas of the Illinois Basin. The remainder of the Frasnian (FZ 11 to FZ 13) is dominated by greenish to light-gray shale deposits with abundant unclassified burrows, *Chondrites*, and *Planolites*, with interbedded black shale beds within FZ 12 (possibly corresponding to the Semichatovae or Lower Kellwasser crises), characterized by light-colored mud–filled *Chondrites* in the upper part. Just above the Frasnian–Famennian boundary, black shale beds prevail up to the *termini* Zone, again interbedded with greenish to light-gray shale beds bearing *Chondrites*. Therefore, the ichnological pattern closely resembles that documented in the study cores from the present work, where the interval corresponding to FZ 13 is dominated by relatively oxic conditions, whereas the lowermost Famennian records renewed anoxic conditions. Ichnodiversity appears to be lower in the Moose River Basin than in the Illinois Basin, instead showing stronger similarities to the pattern recorded in the Appalachian Basin.

Notably, the occurrence of *Zoophycos* in the Long Rapids Formation is dated to the upper *termini* to *pectinata* zones, exactly the same age as Ichnoassemblage 4 in the Illinois and Appalachian Basins. In this case, *Zoophycos* occurs in association with *Chondrites* and rare ?*Teichichnus* (i.e., a similar record to Ichnoassemblage 4). This ichnoassemblage disappears before the *rhomboidea* Zone, and trace fossils become scarce upwards to the *velifer* Zone, where the record ends. Thus, the pattern of ichnological distribution is again comparable to that of the Appalachian and southern Illinois basins (OHRS-5 and Dupont cores, respectively), indicating that the Moose River Basin experienced similar paleoenvironmental conditions to those prevailing in the southern areas of the North American Seaway during the Famennian.

5.2.2. *Open-marine settings: the Anadarko Basin and carbonate platforms*

In the Anadarko Basin of southern Oklahoma, Zou and Slatt (2015) studied the ichnology of the Woodford Shale (Fig. 2C). They identified abundant *Chondrites* in the Middle and Upper Members of the formation, accompanied by *Paleodictyon* and sparse *Planolites*. In the Lower Member, bioturbation is scarce, similar to what was here recorded in the Current core. Bioturbation remains limited in the interval corresponding to the FFB and lower Famennian, whereas the Upper Member exhibits the highest degree of bioturbation.

The ichnological distribution described by Zou and Slatt (2015) aligns with the patterns observed in this study. Notably, the presence of *Paleodictyon* (identified using 3D micro-CT) is consistent with the findings of Wilson et al. (2021) in the Williston and Illinois Basins. *Palaeodictyon* is a graphoglyptid interpreted as an agrichnial trace produced by a worm-like organism, mostly in deep-water settings but also in shallower environments such as prodelta or mid-to-deep shelf areas (Ekdale et al., 1984; Seilacher, 2007; Fürsich et al., 2007; Metz, 2012). The occurrence of *Paleodictyon* within Upper Devonian black shale units in North America demonstrates that anoxia was not permanent during their deposition, and that intermittent oxygenation events—although not reflected by lithological changes—allowed the establishment of complex biogenic structures.

Finally, two studies have examined the ichnology of the Frasnian and Famennian stages outside North America. Wang et al. (2006) investigated the Yaosu, Zhewang, Kolaohe, and Tangbagou formations in the Dushan area (Guizhou Province, China), which represent a shallow marine basin dominated by platform carbonates. The uppermost Frasnian is described as an "ecologically barren area" linked to the Upper Kellwasser Event. Following the FFB, trace fossils appear before the recovery of body fossils, with deposit feeders (*Planolites* and *Palaeophycus*) first recorded in the lower Famennian. Upwards in the section, *Planolites* and *Palaeophycus* are accompanied by *Skolithos*, *Chondrites*, and small *Thalassinoides*, coinciding with the first appearance of body fossils such as ostracods, gastropods, and brachiopods. The upper Famennian is characterized by a highly diverse ichnoassemblage, including *Planolites*, *Palaeophycus*, *Skolithos*, *Chondrites*, *Thalassinoides*, *Rhizocorallium*, *Teichichnus*, and *Cochlichnus*, indicating the full recovery of benthic communities. Similarly, Stachacz et al. (2017) analyzed two sections (Kowala and Płucki) in the Holy Cross Mountains (Góry Świętokrzyskie, Poland). The Frasnian deposits consist of shallow-marine stromatoporoid-coral reef carbonates, which were flooded during the earliest Famennian, transitioning to pelagic limestones, marlstones, and shales.

Lower Frasnian carbonates are dominated by stromatoporoids and corals, indicating well-ventilated benthic conditions. Below the FFB, the shallower Kowala section exhibits fluctuations between oxic and anoxic conditions, recorded as alternating abundant laminated, unbioturbated intervals and *Trichichnus* (a commonly unbranched, wire-like structure with a mostly vertical orientation, typically associated with poorly oxygenated benthic settings; McBride and Picard, 1991; Uchman, 1995; Kędzierski et al., 2015). In contrast, the deeper Płucki section shows more diverse and abundant trace fossils, including *Trichichnus* and undetermined burrows, interbedded with fewer and thinner unbioturbated layers. Across the Frasnian–Famennian Boundary, both sections generally lack trace fossils, reflecting anoxic conditions during the Kellwasser Event. During the Famennian, tracemaker communities recovered earlier in the Kowala section, indicating a faster return to oxygenated conditions compared to the Płucki section. Moreover, ichnodiversity is higher in Kowala, with *Multina* and ?*Planolites*, whereas at Płucki, the presence of *Trichichnus* and undetermined burrows suggests more persistently anoxic conditions.

The ichnological analysis of Stachacz et al. (2017) indicates that the deterioration of benthic settings occurred earlier in shallower areas (Kowala section) than in deeper settings (Płucki section). This is evidenced by the dominant occurrence of *Trichichnus*, commonly linked to poorly oxygenated benthic settings. Notably, the recovery of oxic conditions was also faster in shallow areas, whereas anoxic conditions persisted longer in deeper settings during the early Famennian. Overall, this pattern is similar to that observed in the Appalachian Basin, where shoreward areas (e.g., Boyer et al., 2014) experienced shorter and less intense anoxic pulses associated with the Kellwasser Event, while deeper settings were characterized by more frequent fluctuations among anoxic, dysoxic, and oxic conditions.

5.3. Synthesis: Global patterns in Frasnian and Famennian ichnology

Based on the ichnological analyses discussed above, this section integrates all available data on macrobenthic tracemaker communities and their response to the complex redox fluctuations that characterize the Late Devonian, aiming to develop a comprehensive framework for future ichnological studies of globally distributed Frasnian and Famennian deposits.

Overall, three main types of tracemaker communities can be recognized based on their behavioral strategies, which, according to the study of the North American Seaway, can be correlated globally: (a) climax communities, (b) opportunistic communities, and (c) opportunistic–-specialized communities.

Notably, tracemaker communities (b) and (c) are composed almost exclusively of shallow-tier structures, predominantly fodinichnia, with occurrences of specific behaviors such as agrichnia or chemichnia. This suggests that widespread anoxia restricted benthic activity to exploiting detritus within the substrate—either through direct consumption or by leveraging microbial metabolisms—regardless of the tracemakers' level of specialization (e.g., *Zoophycos* versus *Planolites* producers). In contrast, climax communities (a) are characterized by higher diversity and abundance (i.e., higher bioturbation index), including both fodinichnia and domichnia produced by suspension feeders or arthropods, whereas highly specialized behaviors are less common. These patterns indicate that benthic communities are closely linked to discrete redox conditions: (a) climax communities developed in well-ventilated, oxic settings over prolonged periods, allowing the development of diverse and abundant trace fossils; (b) opportunistic communities, characterized by simple structures (mostly *Planolites*), reflect detritus feeding at or close to the sediment-water interface during brief oxic pulses interrupting generally anoxic conditions; and (c) opportunistic–specialized communities, characterized by complex trace fossils, indicate more specialized behaviors such as systematic detritus feeding (indicated by *spreiten*), agrichnia (e.g., *Palaeodictyon*, and possibly *Zoophycos* and *Chondrites*), or even chemichnia. These communities formed during relatively longer oxic intervals than those generating type-(b) opportunistic communities, as indicated by the higher complexity of trace fossils and behaviors.

During the upper Givetian and uppermost Frasnian, climax tracemaker communities produced complex and abundant trace fossils (Ichnoassemblages 3 and 5) within the inner regions of the North American Seaway, associated with well-ventilated benthic environments both prior to the onset of the Kaskaskia Transgression and again toward its end, during the Kellwasser interval (FZ 13). Similar communities are observed in the shoreward sections of the Appalachian Basin, where well-established benthic communities developed complex ichnoassemblages just before and after the Kellwasser Event, including *Skolithos*, *Planolites*, *Thalassinoides*, and *Chondrites*. Therefore, the development of these communities was not necessarily controlled by sea-level fluctuations, but rather by the establishment of sustained oxic conditions in benthic settings—conditions that primarily occurred in restricted areas acting as refuges (e.g., the inner Illinois Basin) or regions influenced by continental input (e.g., the Catskill Delta), where the effects of anoxia were buffered.

Notably, the middle and upper Famennian of China also record the onset of climax communities after a barren interval linked to the Kellwasser Event, characterized by a diverse ichnoassemblage (*Planolites*, *Palaeophycus*, *Skolithos*, *Chondrites*, *Thalassinoides*, *Rhizocorallium*, *Teichichnus*, and *Cochlichnus*), indicating that open, shoreward settings were less affected by widespread anoxia during the middle and upper Famennian, evidencing faster recolonizations. This is also consistent with observations from the Polish carbonate platforms, where anoxic conditions were more persistent in deeper areas (i.e., the Płucki section) during the Kellwasser Event.

In contrast, during most of the Frasnian and especially the Famennian, anoxic pulses associated with globally recorded biocrises such as the Middlesex and Dasberg events led to a marked impoverishment of benthic communities. During these intervals, only brief oxic pulses occurred, allowing short colonization windows when opportunistic tracemakers inhabited the sediment–water interface, producing simple structures (Ichnoassemblage 1) that sometimes intensely bioturbated the substrate, generating mottled textures. These communities are comparable to those from the Anadarko Basin (characterized mainly by *Planolites* and *Palaeophycus*), most of the Polish carbonate platforms (characterized by *Trichichnus*), and the lowermost Famennian of China (dominated by absence of trace fossils, and later *Planolites* and *Palaeophycus*). Thus, although the response of the benthic fauna may vary regionally, the highly stressful conditions associated with these biocrises produced similar behavioral patterns regardless of paleogeographic or depositional setting, as comparable simple ichnoassemblages (fodinichnia produced by opportunistic tracemakers) are recorded in restricted basins, open-marine environments, and shallow carbonate platforms.

Finally, the presence of Ichnoassemblage 4 in the Famennian of the North American Seaway shows that regional features strongly modulated the benthic response to these anoxic pulses, overprinting the global triggers. This ichnoassemblage is interpreted as the product of opportunistic yet highly specialized tracemakers that occupied the benthos for longer intervals than typical opportunistic communities, but whose development was still linked to abrupt shifts between anoxic and oxic conditions and to the availability of organic matter within the sediment. The persistent presence of *Zoophycos* in the inner areas of the Illinois Basin, compared with its disappearance from the southern Illinois, central Appalachian, and Moose River Basins after the Enkeberg/Utah Event, indicates that anoxic conditions were buffered in restricted settings. This pattern suggests the existence of a corridor of anoxic-watermass exchange during the Famennian between the Moose River–central Appalachian–southern Illinois Basins and the Rheic Ocean, which did not affect cratonward regions of the Appalachian Basin and the inner, restricted parts of the Illinois Basin.

Overall, the Kellwasser Event and other Late Devonian biocrises profoundly impacted benthic communities, yet their effects were strongly modulated by regional factors (cf. other minor biocrises such as the Toarcian Oceanic Anoxic Event, e.g., Fernández-Martínez et al., 2023). Opportunistic tracemakers dominated open, well-connected settings, commonly characterized by frequent oxic–anoxic shifts. In contrast, inner and shoreward areas of the North American Seaway (i.e., epeiric settings) and restricted carbonate platforms often acted as refuges, buffering widespread anoxia. Although the Kellwasser Event affected both deep and shallow settings, its intensity on macrobenthic communities was attenuated in these refugial regions. The variable development of anoxic conditions and the tracemaker response during the Famennian highlights how local and regional hydrography and environmental constraints frequently overrode global triggers during these biocrises, shaping benthic fauna resilience and behaviors. Further integration of ichnological, sedimentological, and geochemical data is encouraged to more precisely assess the causes of Late Devonian biological crises and their effects on benthic tracemaker communities.

6. Conclusions

An integrated ichnological and sedimentological analysis was conducted on Upper Devonian shale units from North America. The correlation of gamma-ray logs, conodont biostratigraphy, and geochemical proxies allowed the identification of several strong anoxic pulses, corresponding to globally recorded biotic crises that affected marine ecosystems during the Late Devonian.

Within the North American Seaway, anoxic pulses profoundly affected benthic tracemaker communities, promoting opportunistic behavior (Ichnoassemblage 1) throughout most of the Frasnian and Famennian in all depositional settings. This pattern is even more pronounced in the open-marine Anadarko Basin, where only mottled intervals and sparse occurrences of *Planolites* or *Chondrites* are recorded.

Notably, the impact of the Kellwasser Event was less pronounced in the inner regions of the North American Seaway, where highly diverse ichnotaxa (Ichnoassemblage 3) characterize the inner Illinois Basin. In contrast, areas with better connection to the Rheic Ocean are marked by reduced ichnodiversity (Ichnoassemblage 1) and more frequent redox shifts. In the Anadarko Basin, this pattern is even more pronounced, as only mottled textures are recorded during brief oxic pulses. A similar pattern to that of the inner Illinois Basin is observed in shoreward regions of the Appalachian Basin, where anoxic pulses linked to the Kellwasser Event were restricted to short intervals (recorded as thin black shale beds), and ichnodiversity was higher than in other parts of the North American Seaway.

During the Famennian, trace fossil distribution was highly variable, but characterized by the presence of *Zoophycos* and *Chondrites* (Ichnoassemblage 4). These taxa appear following a strong anoxic pulse in the lowermost Famennian and disappear in most regions during the remainder of this stage. Notably, the inner Illinois Basin acted as a refuge for benthic communities, as Ichnoassemblage 4 persisted in these areas throughout the Famennian despite widespread anoxia.

At a global scale, crises such as the Upper Kellwasser Event profoundly impacted benthic tracemaker communities, although regional factors strongly modulated their effects. During anoxic episodes, most regions were dominated by simple structures produced by opportunistic tracemakers. In contrast, inner-restricted and shoreward areas, such as the Illinois Basin or shallow carbonate platforms, usually acted as refuges for benthic communities, buffering the effects of widespread anoxia. Continued integration of ichnological, sedimentological, and geochemical datasets will help further refine our understanding of the controls and consequences of these Late Devonian biocrises on benthic ecosystems.

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CRediT authorship contribution statement

Javier Fernández-Martínez: Investigation, Writing – original draft. **Francisco J. Rodríguez-Tovar:** Funding acquisition, Writing – review & editing. **Francisca Martínez-Ruiz:** Writing – review & editing. **Thomas Algeo:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

References

Algeo, T.J., Lyons, T.W., 2006. Mo–total organic carbon covariation in modern anoxic marine environments: Implications for analysis of paleoredox and paleohydrographic conditions. Paleoceanography 21 (1). https://doi.org/10.1029/2004PA001112.

Algeo, T.J., Shen, J., 2024. Theory and classification of mass extinction causation. Natl. Sci. Rev. 11 (1). https://doi.org/10.1093/nsr/nwad237 nwad237.

Algeo, T.J., Lyons, T.W., Blakey, R.C., Over, D.J., 2007. Hydrographic conditions of the Devono–Carboniferous North American Seaway inferred from sedimentary Mo–TOC relationships. Palaeogeogr. Palaeoclimatol. Palaeoecol. 256 (3–4), 204–230. https://doi.org/10.1016/j.palaeo.2007.02.035.

Algeo, T.J., Remírez, M.N., Zhao, H., Schwark, L., Gordon, G., Anbar, A., Bates, S., Lyons, T.W., Over, J., Sageman, B., 2026. Transient glacio-eustatic fall and its climato-environmental effects during the Frasnian Famennian transition. Glob. Planet. Chang. 256, 105135. https://doi.org/10.1016/j.gloplacha.2025.105135.

Bambach, R.K., Knoll, A.H., Wang, S.C., 2004. Origination, extinction, and mass depletions of marine diversity. Paleobiology 30 (4), 522–542. https://doi.org/10.1666/0094-8373(2004)030<0522:OEAMDO>2.0.CO;2.

Barrows, M.H., Cluff, R.M., 1984. New Albany Shale Group (Devonian-Mississippian) source rocks and hydrocarbon generation in the Illinois basin. In: Demaison, G., Murris, R.J. (Eds.), Petroleum Geochemistry and Basin Evaluation, AAPG Memoir, Vol. 35. https://doi.org/10.1306/M35439C7.

Barrett, T., Schieber, J., 1999. Experiments on the Self-Compaction of Fresh Muds: Implications for Interpreting the Rock Record. Geological Society of America Abstracts with Programs 31–7, A282.

Baucon, A., Bednarz, M., Dufour, S., Felletti, F., Malgesini, G., De Carvalho, C.N., Niklas, K.J., Wehrmann, A., Batstone, R., Bernardini, F., Briguglio, A., Cabella, R., Cavalazzi, B., Ferretti, A., Zanzerl, H., McIlroy, D., 2020. Ethology of the trace fossil Chondrites: form, function and environment. Earth Sci. Rev. 202, 102989. https://doi.org/10.1016/j.earscirev.2019.102989.

Becker, R.T., Königshof, P., Brett, C.E., 2016. Devonian climate, sea level and evolutionary events: an introduction. In: Becker, R.T., Königshof, P., Brett, C.E. (Eds.), Devonian Climate, Sea Level and Evolutionary Events, Vol. 423. Geological Society of London, Special Publication, pp. 1–10. https://doi.org/10.1144/SP423.15.

Belaústegui, Z., de Gibert, J.M., 2013. Bow-shaped, concentrically laminated polychaete burrows: A *Cylindrichnus concentricus* ichnofabric from the Miocene of Tarragona, NE Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 381, 119–127. https://doi.org/10.1016/j.palaeo.2013.04.021.

Bezys, R.K.A., 1987. An ichnological and sedimentological study of Devonian black shales from the Long Rapids Formation, Moose River Basin, Northern Ontario. M.Sc. Thesis. McMaster University, p. 255.

Boyer, D.L., 2007. Microstratigraphic Resolution of Devonian Black Shales: A Combined Paleoecological, Ichnological, and Geochemical Approach. Ph.D. Thesis. University of California Riverside, p. 245.

Boyer, D.L., Droser, M.L., 2009. Palaeoecological patterns within the dysaerobic biofacies: Examples from Devonian black shales of New York state. Palaeogeogr. Palaeoclimatol. Palaeoecol. 276 (1-4), 206–216. https://doi.org/10.1016/j.palaeo.2009.03.014.

Boyer, D.L., Droser, M.L., 2011. A combined trace- and body-fossil approach reveals high-resolution record of oxygen fluctuations in Devonian seas. Palaios 26 (8), 500–508. https://doi.org/10.2110/palo.2010.p10-073r.

Boyer, D.L., Haddad, E.E., Seeger, E.S., 2014. The last gasp: trace fossils track deoxygenation leading into the Frasnian–Famennian extinction event. Palaios 29 (12), 646–651. https://doi.org/10.2110/palo.2014.049.

Boyer, D.L., Martinez, A.M., Evans, S.D., Cohen, P.A., Haddad, E.E., Pippenger, K.H., Love, G.D., Droser, M.L., 2021. Living on the edge: the impact of protracted oxygen stress on life in the Late Devonian. Palaeogeogr. Palaeoclimatol. Palaeoecol. 566, 110226. https://doi.org/10.1016/j.palaeo.2021.110226.

Brett, C.E., Zambito IV, J.J., McLaughlin, P.I., Emsbo, P., 2020. Revised perspectives on Devonian biozonation and environmental volatility in the wake of recent time-scale revisions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 549, 108843. https://doi.org/10.1016/j.palaeo.2018.06.037.

Bromley, R.G., Ekdale, A.A., Asgaard, U., 1999. *Zoophycos* in the Upper Cretaceous chalk of Denmark and Sweden. Greifswalder Geowiss. Beitr. 6, 133–142.

Cardott, B.J., Comer, J.B., 2021. Woodford Shale (Upper Devonian to Lower Mississippian): From hydrocarbon source rock to reservoir. Oklahoma Geol. Surv. Bull. 152.

Carmichael, S.K., Waters, J.A., Königshof, P., Suttner, T.J., Kido, E., 2019. Paleogeography and paleoenvironments of the Late Devonian Kellwasser event: A review of its sedimentological and geochemical expression. Glob. Planet. Chang. 183, 102984. https://doi.org/10.1016/j.gloplacha.2019.102984.

Chen, J., Hogancamp, N., Lu, M., Ikejiri, T., Malina, N., Ojeda, A., Sun, Y., Lu, Y., 2023. Lipid biomarkers recording marine microbial community structure changes through the Frasnian-Famennian mass extinction event. Geobiology 21 (6), 725–742. https://doi.org/10.1111/gbi.12568.

Copper, P., Scotese, C.R., 2003. Megareefs in Middle Devonian supergreenhouse climates. In: Chan, M.A., Archer, A.W. (Eds.), Extreme Depositional Environments: Mega End Members in Geologic Time, Geological Society of America, Special Paper 370, pp. 209–230. https://doi.org/10.1130/0-8137-2370-1.209.

Corradini, C., Spalletta, C., Mossoni, A., Matyja, H., Over, D.J., 2017. Conodonts across the Devonian/Carboniferous boundary: a review and implication for the redefinition of the boundary and a proposal for an updated conodont zonation. Geol. Mag. 154 (4), 888–902. https://doi.org/10.1017/S001675681600039X.

Day, J., Witzke, B.J., 2017. Upper Devonian biostratigraphy, event stratigraphy, and Late Frasnian Kellwasser extinction bioevents in the Iowa Basin: western Euramerica. In: Montenari, M., Wade, B., Steffensen, J.P., Singer, B., Erba, E., Raymo, M., Barker, S. (Eds.), Stratigraphy & Timescales, Vol. 2. Academic Press, pp. 243–332. https://doi.org/10.1016/bs.sats.2017.08.002.

Dorador, J., Rodríguez-Tovar, F.J., 2018. High-resolution image treatment in ichnological core analysis: Initial steps, advances and prospects. Earth Sci. Rev. 177, 226–237. https://doi.org/10.1016/j.earscirev.2017.11.020.

Droste, J.B., Shaver, R.H., 1975. Jeffersonville Limestone (Middle Devonian) of Indiana: stratigraphy, sedimentation, and relation to Silurian reef-bearing rocks. AAPG Bull. 59 (3), 393–412. https://doi.org/10.1306/83D91C9F-16C7-11D7-8645000102C1865D.

Ehrenberg, K., 1944. Ergänzende Bemerkungen zu den seinerzeit aus dem Miozän von Burgschleinitz beschriebenen Gangkernen und Bauten dekapoder Krebse. Paläontol. Z. 23, 354–359.

Ekdale, A.A., 1992. Muckraking and mudslinging: the joys of deposit-feeding. Short Courses Paleontol. 5, 145–171.

Ekdale, A.A., Bromley, R.G., 2003. Paleoethologic interpretation of complex *Thalassinoides* in shallow-marine limestones, Lower Ordovician, southern Sweden. Palaeogeogr. Palaeoclimatol. Palaeoecol. 192 (1-4), 221–227. https://doi.org/10.1016/S0031-0182(02)00686-7.

Ekdale, A.A., Bromley, R.G., Pemberton, S.G., 1984. Ichnology: the use of trace fossils in sedimentology and stratigraphy. In: SEPM Society for Sedimentary Geology, Vol. 15, p. 317. https://doi.org/10.2110/scn.84.15.

Ettensohn, F.R., 1998. Compressional tectonic controls in epicontinental black-shale deposition: Devonian-Mississippian examples from North America. In: Schieber, J., Zimmerle, W., Sethi, P. (Eds.), Shales and Mudrocks, I. Schweizerbart'sche, Stuttgart, Germany, pp. 351–369.

Fernández-Martínez, J., Rodríguez-Tovar, F.J., Piñuela, L., Martínez-Ruiz, F., García-Ramos, J.C., 2021a. Bottom- and porewater oxygenation during the early Toarcian Oceanic Anoxic Event (T-OAE) in the Asturian Basin (N Spain): Ichnological information to improve facies analysis. Sediment. Geol. 419, 105909. https://doi.org/10.1016/j.sedgeo.2021.105909.

Fernández-Martínez, J., Rodríguez-Tovar, F.J., Piñuela, L., Martínez-Ruiz, F., García-Ramos, J.C., 2021b. The Halimedides record in the Asturian Basin (northern Spain): supporting the Toarcian Oceanic Anoxic Event relationship. In: Reolid, M., Duarte, L. V., Mattioli, E., Ruebsam, W. (Eds.), Carbon Cycle and Ecosystem Response to the Jenkyns Event in the Early Toarcian (Jurassic), Vol. 514. Geological Society of London, Special Publication, pp. 173–184. https://doi.org/10.1144/SP514-2020-156.

Fernández-Martínez, J., Ruíz, F.M., Rodríguez-Tovar, F.J., Piñuela, L., García-Ramos, J. C., Algeo, T.J., 2023. Euxinia and hydrographic restriction in the Tethys Ocean: Reassessing global oceanic anoxia during the early Toarcian. Glob. Planet. Chang. 221, 104026. https://doi.org/10.1016/j.gloplacha.2022.104026.

Fürsich, F.T., 1973. A revision of the trace fossils *Spongeliomorpha*, *Ophiomorpha* and *Thalassinoides*. N. Jb. Geol. Paläont. 12, 719–735.

Fürsich, F.T., Taheri, J., Wilmsen, M., 2007. New occurrences of the trace fossil Paleodictyon in shallow marine environments: examples from the Triassic–Jurassic of Iran. Palaios 22 (4), 408–416. https://doi.org/10.2110/palo.2006.p06-041r.

Gereke, M., Schindler, E., 2012. "Time-Specific Facies" and biological crises — The Kellwasser Event interval near the Frasnian/Famennian boundary (Late Devonian). Palaeogeogr. Palaeoclimatol. Palaeoecol. 367-368 (2012), 19–29. https://doi.org/10.1016/j.palaeo.2011.11.024.

Gilleaudeau, G.J., Wei, W., Remírez, M.N., Song, Y., Lyons, T.W., Bates, S., Anbar, A.D., Algeo, T.J., 2023. Geochemical and hydrographic evolution of the Late Devonian Appalachian Seaway: linking sedimentation, redox, and salinity across time and space. Geochem. Geophys. Geosyst. 24 (8). https://doi.org/10.1029/2023GC010973 e2023GC010973.

Haddad, E.E., Boyer, D.L., Droser, M.L., Lee, B.K., Lyons, T.W., Love, G.D., 2018. Ichnofabrics and chemostratigraphy argue against persistent anoxia during the Upper Kellwasser Event in New York State. Palaeogeogr. Palaeoclimatol. Palaeoecol. 490, 178–190. https://doi.org/10.1016/j.palaeo.2017.10.025.

Haldeman, S.S., 1840. Supplement to number one of "A monograph of the *Limniades*, and other freshwater univalve shells of North America," containing descriptions of apparently new animals in different classes, and the names and characters of the subgenera in *Paludina* and *Anculosa*. J. Dobson, Philadelphia 3.

Hallam, A., Wignall, P.B., 1999. Mass extinctions and sea-level changes. Earth Sci. Rev. 48 (4), 217–250. https://doi.org/10.1016/S0012-8252(99)00055-0.

Hannibal, J.T., Feldmann, R.M., 1983. Arthropod trace fossils, interpreted as echinocarid escape burrows, from the Chagrin Shale (Late Devonian) of Ohio. J. Paleontol. 5 (4), 705–716. jstor.org/stable/1304943.

Harrigan, C.O., Schmitz, M.D., Over, D.J., Trayler, R.B., Davydov, V.I., 2022. Recalibrating the Devonian time scale: A new method for integrating radioisotopic and astrochronologic ages in a Bayesian framework. Geol. Soc. Am. Bull. 134 (7-8), 1931–1948. https://doi.org/10.1130/B36128.1.

Hartenfels, S., 2011. Die globalen Annulata-Events und die Dasberg-Krise (Famennium, Oberdevon) in Europa und Nord-Afrika: hochauflösende Conodonten-Stratigraphie, Karbonat-Mikrofazies, Paläoökologie und Paläodiversität. Verlagshaus Monsenstein und Vannerdat. Münster. Forsch. Geol. Paläontol. 105, 17–383.

Higley, D.K., Gaswirth, S.B., Abbott, M.M., Charpentier, R.R., Cook, T.A., Ellis, G.S., Gianoutsos, N.J., Hatch, J.R., Klett, T.R., Nelson, P.H., Pawlewicz, M.J., Pearson, O. N., Pollastro, R.M., Schenk, C.J., 2014. Assessment of undiscovered oil and gas resources of the Anadarko Basin Province of Oklahoma, Kansas, Texas, and Colorado, 2010. In: Higley, D.K. (Ed.), Petroleum Systems and Assessment of Undiscovered Oil and Gas in the Anadarko Basin Province, Colorado, Kansas, Oklahoma, and Texas—USGS Province 58. U.S. Geological Survey Digital Data, Series DDS–69–EE. https://doi.org/10.3133/ds69EE.

House, M.R., 1985. Correlation of mid-Palaeozoic ammonoid evolutionary events with global sedimentary perturbations. Nature 313 (5997), 17–22. https://doi.org/10.1038/313017a0.

Howard, J.D., 1966. Characteristic trace fossils in Upper Cretaceous sandstones of the Book Cliffs and Wasatch Plateau. Bull. Utah Geol. Min. Surv. 80, 35–53.

Jaminski, J., Algeo, T.J., Maynard, J.B., Hower, J.C., 1998. Climatic origin of dm-scale compositional cyclicity in the Cleveland Member of the Ohio Shale (Upper Devonian), Central Appalachian Basin, USA. In: Schieber, J., Zimmerle, W., Sethi, P. (Eds.), Shales and Mudstones, 1. Schweizerbart'sche, Stuttgart, Germany, pp. 217–242.

Johnson, J.G., Klapper, G., Sandberg, C.A., 1985. Devonian eustatic fluctuations in Euramerica. Geol. Soc. Am. Bull. 96 (5), 567–587. https://doi.org/10.1130/0016-7606(1985)96%3C567:DEFIE%3E2.0.CO;2.

Kędzierski, M., Uchman, A., Sawlowicz, Z., Briguglio, A., 2015. Fossilized bioelectric wire–the trace fossil *Trichichnus*. Biogeosciences 12 (8), 2301–2309. https://doi.org/10.5194/bg-12-2301-2015.

Klapper, G., Kirchgasser, W.T., 2016. Frasnian Late Devonian conodont biostratigraphy in New York: graphic correlation and taxonomy. J. Paleontol. 90 (3), 525–554. https://doi.org/10.1017/jpa.2015.70.

Klapper, G., Uyeno, T.T., Armstrong, D.K., Telford, P.G., 2004. Conodonts of the Williams Island and Long Rapids formations (Upper Devonian, Frasnian-Famennian) of the Onakawana B Drillhole, Moose River Basin, northern Ontario, with a revision of Lower Famennian species. J. Paleontol. 78 (2), 371–387. https://doi.org/10.1666/0022-3360(2004)0782.0.CO;2.

Knaust, D., 2009. Complex behavioural pattern as an aid to identify the producer of *Zoophycos* from the Middle Permian of Oman. Lethaia 42 (2), 146–154. https://doi.org/10.1111/j.1502-3931.2008.0012.

Knaust, D., 2017. Atlas of trace fossils in well core: appearance, taxonomy and interpretation. Springer, Cham, p. 219.

Lazar, O.R., 2007. Redefinition of the New Albany Shale of the Illinois Basin: an integrated stratigraphic, sedimentologic, and geochemical study. Ph.D. Thesis. Indiana University, p. 363.

Lazar, O.R., Schieber, J., 2022. New Albany Shale, Illinois Basin, USA—Devonian carbonaceous mudstone accumulation in an epicratonic sea: Stratigraphic insights from outcrop and subsurface data. In: Bohacs, K.M., Lazar, R.O. (Eds.), Sequence Stratigraphy: Applications to Fine-Grained Rocks. AAPG Memoir, Vol. 126. https://doi.org/10.1306/137123043860.

Levman, B.G., Bitter, P.H.V., 2002. The Frasnian-Famennian (mid-Late Devonian) boundary in the type section of the Long Rapids Formation, James Bay Lowlands, northern Ontario, Canada. Can. J. Earth Sci. 39 (12), 1795–1818. https://doi.org/10.1139/e02-073.

Liu, J., Algeo, T.J., Hinnov, L.A., 2025. Identifying and quantifying stratigraphic disconformities in shale: An example from the Upper Devonian of the Appalachian Basin. Geol. Soc. Am. Bull. 137. https://doi.org/10.1130/B38148.1.

Lobza, V., Schieber, J., 1999. Biogenic sedimentary structures produced by worms in soupy, soft muds; observations from the Chattanooga Shale (Upper Devonian) and experiments. J. Sediment. Res. 69 (5), 1041–1049. https://doi.org/10.2110/jsr.69.1041.

Locklair, R.E., Savrda, C.E., 1998. Ichnofossil tiering analysis of a rhythmically bedded chalk-marl sequence in the Upper Cretaceous of Alabama. Lethaia 31 (4), 311–321. https://doi.org/10.1111/j.1502-3931.1998.tb00521.x.

Löwemark, L., 2011. Ethological analysis of the trace fossil *Zoophycos*: hints from the Arctic Ocean. Lethaia 45 (2), 290–298. https://doi.org/10.1111/j.1502-3931.2011.00282.x.

Löwemark, L., Lin, H.L., Sarnthein, M., 2005. Temporal variations of the trace fossil Zoophycos in a 425 ka long sediment record from the South China Sea: implications for the ethology of the *Zoophycos* producer. Geol. Mag. 143 (1), 105–114. https://doi.org/10.1017/S0016756805001408.

Löwemark, L., Lin, I.T., Wang, C.H., Schönfeld, J., 2007. A test of the gardening hypothesis for the trace fossil *Zoophycos*. In: Bromley, R.G., Buatois, L.A., Mángano, M.G., Genise, J.F., Melchor, R.N. (Eds.), Sediment-Organism Interactions: A Multifaceted Ichnology, Vol. 88. SEPM Special Publication. https://doi.org/10.2110/pec.07.88.0079.

Massalongo, A., 1855. *Zoophycos, novum genus plantarum fossilium*. Monographia, Typis Antonellianis, Veronae, pp. 45–52.

McBride, E.F., Picard, M.D., 1991. Facies implications of *Trichichnus* and *Chondrites* in turbidites and hemipelagites, Marnoso-arenacea formation (Miocene), Northern Apennines, Italy. Palaios 281-290. https://doi.org/10.2307/3514908.

Metz, R., 2012. The trace fossil *Paleodictyon* within the *Cruziana* ichnofacies: first record from the Devonian in Pennsylvania. Ichnos 19 (4), 190–193. https://doi.org/10.1080/10420940.2012.733320.

Myrow, P.M., 1995. *Thalassinoides* and the enigma of Early Paleozoic open-framework burrow systems. Palaios 58-74. https://doi.org/10.2307/3515007.

Nicholson, H.A., 1873. Contributions to the study of the errant annelids of the older Palaeozoic rocks. In: Proceedings of the Royal Society of London, 21, pp. 288–290 (also Geological Magazine 10, 309-310).

Olivero, D., 2007. *Zoophycos* and the role of type specimens in ichnotaxonomy. In: Miller III, W. (Ed.), Trace Fossils, Concepts, Problems. Prospects. Elsevier, Amsterdam, pp. 219–230.

Olivero, D., Gaillard, C., 2007. A constructionalmodel for *Zoophycos*. In: Miller III, W. (Ed.), Trace Fossils, Concepts, Problems. Prospects. Elsevier, Amsterdam, pp. 466–476.

Osgood Jr., R.G., 1970. Trace fossils of the Cincinnati area. Paleontogr. Am. 6 (41).

Over, D.J., 1990. Conodont biostratigraphy of the Woodford Shale (Late Devonian—Early Carboniferous) in the Arbuckle Mountains, South-Central Oklahoma. Ph.D. Thesis. Texas Tech University, p. 186.

Over, D.J., 1992. Conodonts and the Devonian–Carboniferous boundary in the upper Woodford Shale, Arbuckle Mountains, south-central Oklahoma. J. Paleontol. 66 (2), 293–311. https://doi.org/10.1017/S0022336000033801.

Over, D.J., 2002. The Frasnian-Famennian Boundary in the Appalachian Basin, Michigan Basin, Illinois Basin, and southern continental margin, central and eastern United States. Palaeogeogr. Palaeoclimatol. Palaeoecol. 181, 153–170. https://doi.org/10.1016/S0031-0182(01)00477-1.

Over, D.J., 2007. Conodont biostratigraphy of the Chattanooga Shale, Middle and Upper Devonian, southern Appalachian Basin, eastern United States. J. Paleontol. 81 (6), 1194–1217. https://doi.org/10.1666/06-056R.1.

Over, D.J., 2021. The Devonian-Carboniferous boundary in the United States. Palaeobiodiv. Palaeoenviron. 101 (2), 529–540. https://doi.org/10.1007/s12549-020-00428-1.

Over, D.J., Mason, C.E., 2024. *Palmatolepis gracilis expansa* Zone and *Bispathodus aculeatus aculeatus* Zone conodonts from the Three Lick Bed at the type locality, Ohio Shale, Upper Devonian, eastern Kentucky. J. Geol. Soc. Lond. 182 (1). https://doi.org/10.1144/jgs2024-125 jgs2024-125.

Over, D.J., Rhodes, M.K., 2000. Conodonts from the upper Olentangy Shale (Upper Devonian, central Ohio) and stratigraphy across the Frasnian-Famennian boundary. J. Paleontol. 74 (1), 101–112. https://doi.org/10.1666/0022-3360(2000)0742.0.CO;2.

Over, D.J., Hauf, E., Wallace, J., Chiarello, J., Over, J.S., Gilleaudeau, G.J., Son, Y., Algeo, T.J., 2019. Conodont biostratigraphy and magnetic susceptibility of Upper Devonian Chattanooga Shale, eastern United States: Evidence for episodic deposition and disconformities. Palaeogeogr. Palaeoclimatol. Palaeoecol. 524, 137–149. https://doi.org/10.1016/j.palaeo.2019.03.017.

Pemberton, S.G., Frey, R.W., 1982. Trace fossil nomenclature and the *Planolites-Palaeophycus* dilemma. J. Paleontol. 56 (4), 843–881. jstor.org/stable/1304706.

Qie, W., Algeo, T.J., Luo, G., Herrmann, A., 2019. Global events of the late Paleozoic (early Devonian to Middle Permian): a review. Palaeogeogr. Palaeoclimatol. Palaeoecol. 531, 109259. https://doi.org/10.1016/j.palaeo.2019.109259.

Remírez, M.N., Gilleaudeau, G.J., Elrick, M., Henderson, M.A., Over, D.J., Willette, D.C., Algeo, T.J., 2023. Linking anoxia, biotic events, and basin evolution in the Late Devonian Illinois Basin, North America: A geochemical approach. Mar. Pet. Geol. 158, 106556. https://doi.org/10.1016/j.marpetgeo.2023.106556.

Rodríguez-Tovar, F.J., 2021. Ichnology of the Toarcian Oceanic Anoxic Event: An underestimated tool to assess palaeoenvironmental interpretations. Earth-Sci. Rev. 216, 103579. https://doi.org/10.1016/j.earscirev.2021.103579.

Rodríguez-Tovar, F.J., Uchman, A., 2017. The Faraoni event (latest Hauterivian) in ichnological record: The Río Argos section of southern Spain. Cretac. Res. 79, 109–121. https://doi.org/10.1016/j.cretres.2017.07.018.

Rodríguez-Tovar, F.J., Uchman, A., Martín-Algarra, A., 2009. Oceanic Anoxic Event at the Cenomanian–Turonian boundary interval (OAE-2): ichnological approach from the Betic Cordillera, southern Spain. Lethaia 42 (4), 407–417. https://doi.org/10.1111/j.1502-3931.2009.00159.

Rodríguez-Tovar, F.J., Kaskes, P., Ormö, J., Gulick, S.P., Whalen, M.T., Jones, H.L., Lowery, C.M., Bralower, T.J., Smit, J., King Jr., D.T., Goderis, S., Claeys, P., 2022. Life before impact in the Chicxulub area: unique marine ichnological signatures preserved in crater suevite. Sci. Rep. 12 (1), 11376. https://doi.org/10.1038/s41598-022-15566-z.

Sallan, L.C., Coates, M.I., 2010. End-Devonian extinction and a bottleneck in the early evolution of modern jawed vertebrates. Proc. Nat. Acad. Sci. (U.S.A.) 107 (22). https://doi.org/10.1073/pnas.0914000107, 10131-10135.

Schieber, J., 1994. Evidence for high-energy events and shallow-water deposition in the Chattanooga Shale, Devonian, central Tennessee, USA. Sediment. Geol. 93 (3-4), 193–208. https://doi.org/10.1016/0037-0738(94)90005-1.

Schieber, J., 1998a. Sedimentary features indicating erosion, condensation, and hiatuses in the Chattanooga Shale of Central Tennessee: Relevance for sedimentary and stratigraphic evolution. In: Schieber, J., Zimmerle, W., Sethi, P. (Eds.), Shales and Mudstones, 1. Schweizerbart'sche, Stuttgart, Germany, pp. 187–215.

Schieber, J., 1998b. Developing a sequence stratigraphic framework for the Late Devonian Chattanooga Shale of the southeastern USA.: Relevance for the Bakken Shale. In: Christopher, J.E., Gilboy, C.F., Paterson, D.F., Bend, S.L. (Eds.), Eighth International Williston Basin Symposium, Vol. 13. Saskatchewan Geological Society Special Publication, pp. 58–68.

Seilacher, A., 1955. Spuren und Fazies im Unterkambrium. In: Schindewolf, O.H., Seilacher, A. (Eds.), Beiträge zur Kenntnis des Kambriums in der Salt Range (Pakistan). Akademie der Wissenschaften und der Literatur zu Mainz, Abhandlung Mathematisch-Naturwissenschaftliche Klasse 1955, pp. 373–399.

Seilacher, A., 1990. Aberrations in bivalve evolution related to photo-and chemosymbiosis. Hist. Biol. 3 (4), 289–311. https://doi.org/10.1080/08912969009386528.

Seilacher, A., 2007. Trace Fossil Analysis. Springer, Berlin, p. 226.

Simpson, S., 1956. On the trace-fossil *Chondrites*. Q. J. Geol. Soc. 112 (1-4), 475–499. https://doi.org/10.1144/GSL.JGS.1956.112.01-04.23.

Song, Y., Gilleaudeau, G.J., Algeo, T.J., Over, D.J., Lyons, T.W., Anbar, A.D., Xie, S., 2021. Biomarker evidence of algal-microbial community changes linked to redox and salinity variation, Upper Devonian Chattanooga Shale (Tennessee, USA). Bulletin 133 (1-2), 409–424. https://doi.org/10.1130/B35543.1.

Spalletta, C., Perri, M.C., Over, D.J., Corradini, C., 2017. Famennian (Upper Devonian) conodont zonation: revised global standard. Bull. Geosci. 92 (1), 31–57. https://doi.org/10.3140/bull.geosci.1623.

Stachacz, M., Uchman, A., Rodríguez-Tovar, F.J., 2017. Ichnological record of the Frasnian–Famennian boundary interval: two examples from the Holy Cross Mts (Central Poland). Int. J. Earth Sci. 106, 157–170. https://doi.org/10.1007/s00531-016-1308-1.

Stanley, S.M., 2016. Estimates of the magnitudes of major marine mass extinctions in earth history. Proc. Nat. Acad. Sci. (U.S.A.) 113 (42). https://doi.org/10.1073/pnas.1613094113. E6325-E6334.

Stumm, E.C., 1964. Silurian and Devonian corals of the Falls of the Ohio, Vol. 93. Geological Society of America. https://doi.org/10.1130/MEM93-p1.

Uchman, A., 1995. Taxonomy and palaeoecology of flysch trace fossils: The Marnoso-arenacea Formation and associated facies (Miocene, Northern Apennines, Italy). Beringeria 15, 3.

Uchman, A., Wetzel, A., 2011. Deep-sea ichnology: the relationships between depositional environment and endobenthic organisms. In: Hüneke, H., Mulder, T. (Eds.), Developments in Sedimentology, Vol. 63, pp. 517–556.

Uchman, A., Caruso, C., Sonnino, M., 2012. Taxonomic Review of *Chondrites affinis* (Šternberg, 1833) from Cretaceous-Neogene Offshore-Deep-Sea Tethyan Sediments and Recommendation for its Further Use. https://doi.org/10.13130/2039-4942/6008.

Uchman, A., Rodríguez-Tovar, F.J., Oszczypko, N., 2013. Exceptionally favourable life conditions for macrobenthos during the Late Cenomanian OAE-2 event: Ichnological record from the Bonarelli Level in the Grajcarek Unit, Polish Carpathians. Cretac. Res. 46, 1–10. https://doi.org/10.1016/j.cretres.2013.08.007.

von Šternberg, G.K., 1833. Versuch einer geognostisch botanischen Darstellung der Flora der Vorwelt. In: Kommission im Deutschen Museum. https://doi.org/10.5962/bhl.title.154066.

Wang, Y., Wang, X., Shi, X., 2006. Pioneer organisms after F-F mass extinction in Dushan region, Guizhou Province, and their significance in establishing new ecosystem. Sci. China Ser. D Earth Sci. 49 (5), 449–460. https://doi.org/10.1007/s11430-006-0449-7.

Watney, W.L., Boardman, D.R., Puckette, J.O., Victorine, J.R., Doveton, J.H., Cruse, A., Suneson, N., 2013. Analysis of the Upper Devonian to Lower Carboniferous (Frasnian-Tournaisian) Woodford Shale in the KGS-OGS Current #1, Southwestern Arkoma Basin. AAPG Woodford Shale Forum.

Wetzel, A., 2025. Ichnofabrics without trace fossils – interpretation and significance of biodeformational structures. In: Dorador, J., Rodríguez-Tovar, F.J. (Eds.), Abstracts Volume of the XVIII International Ichnofabric Workshop, Granada (Spain), p. 114.

Wetzel, A., Bojanowski, M., 2025. 'Resurrected'concretions–resumed cementation after exhumation, transport, re-deposition and exploitation by producers of the trace fossil *Chondrites* when still being soft. Mar. Pet. Geol. 107576. https://doi.org/10.1016/j.marpetgeo.2025.107576.

Wetzel, A., Uchman, A., 1998. Biogenic sedimentary structures in mudrocks—an overview. In: Schieber, J., Zimmerle, W., Sethi, P. (Eds.), Shales and Mudrocks, Vol. I. Schweizerbart'sche, Stuttgart,]Germany, pp. 351–369.

Wilson, R.D., Schieber, J., 2015. Sedimentary facies and depositional environment of the Middle Devonian Geneseo Formation of New York, USA. J. Sediment. Res. 85 (11), 1393–1415. https://doi.org/10.2110/jsr.2015.88.

Wilson, R.D., Schieber, J., 2017. Association between wave-and current-aided hyperpycnites and flooding surfaces in shelfal mudstones: An integrated sedimentologic, sequence stratigraphic, and geochemical approach. J. Sediment. Res. 87 (11), 1143–1155. https://doi.org/10.2110/jsr.2017.62.

Wilson, R.D., Schieber, J., Stewart, C.J., 2021. The discovery of widespread agrichnia traces in Devonian black shales of North America: another chapter in the evolving understanding of a "not so anoxic" ancient sea. Paläontol. Z. 95, 661–681. https://doi.org/10.1007/s12542-021-00599-y.

Zhang, L.J., Fan, R.Y., Gong, Y.M., 2015. *Zoophycos* macroevolution since 541 Ma. Sci. Rep. 5 (1), 14954. https://doi.org/10.1038/srep14954.

Ziegler, W., Sandberg, C.S., 1990. The Late Devonian standard conodont zonation. Cour. Forsch. Senckenberg 121.

Zou, F., Slatt, R.M., 2015. Relationships between bioturbation, microfacies and chemostratigraphy and their implication to the sequence stratigraphic framework of the Woodford Shale in Anadarko Basin, Oklahoma, USA. In: Unconventional Resources Technology Conference, San Antonio, Texas, 20-22 July 2015, pp. 1620–1638.