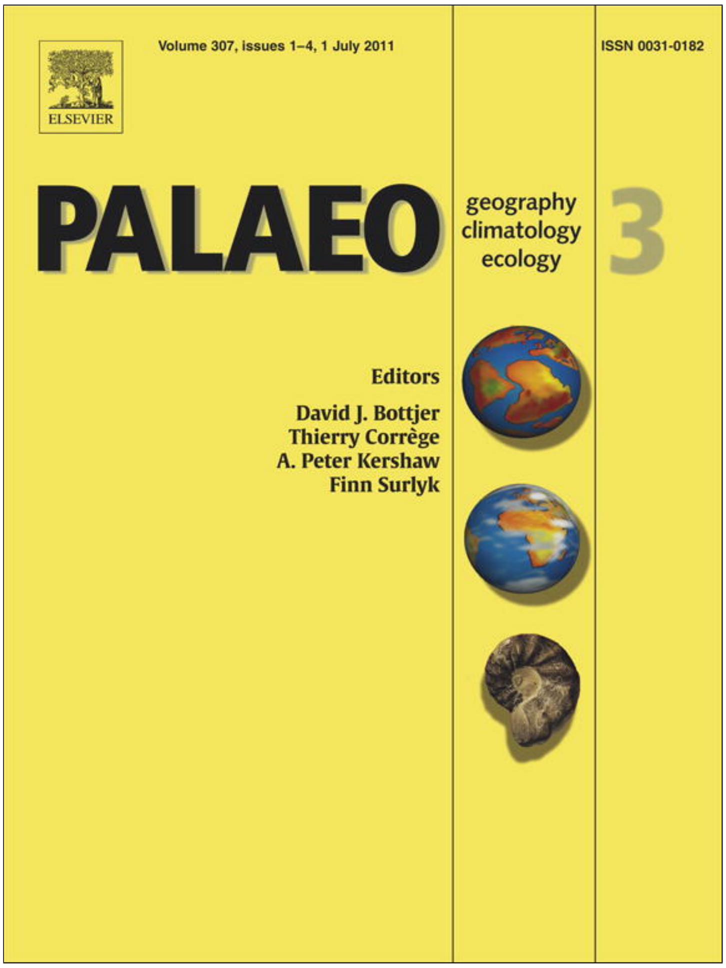

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Exceptional fossil preservation during CO_2 greenhouse crises?

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ABSTRACT

Exceptional fossil preservation may require not only exceptional places, but exceptional times, as demonstrated here by two distinct types of analysis. First, irregular stratigraphic spacing of horizons yielding articulated Triassic fishes and Cambrian trilobites is highly correlated in sequences in different parts of the world, as if there were short temporal intervals of exceptional preservation globally. Second, compilations of ages of well-dated fossil localities show spikes of abundance which coincide with stage boundaries, mass extinctions, oceanic anoxic events, carbon isotope anomalies, spikes of high atmospheric carbon dioxide, and transient warm-wet paleoclimates. Exceptional fossil preservation may have been promoted during unusual times, comparable with the present: CO_2 greenhouse crises of expanding marine dead zones, oceanic acidification, coral bleaching, wetland eutrophication, sea level rise, ice-cap melting, and biotic invasions.

1. Introduction

Commercial fossil collectors continue to produce beautifully prepared, fully articulated, complex fossils of scientific (Simmons et al., 2008), as well as market value (Forster, 2001). Such highly prized fossils of vertebrates, trilobites, crinoids and starfish are not unusual because commercially viable horizons yield them at a predictable low rate of return. Such predictably productive horizons are targeted for expensive and time consuming quarrying and preparation by academic paleontologists as well (Furrer, 1995). Commercially and scientifically valuable fossil localities are local feasts amid a general famine of poorly preserved fossils, and large volumes of unfossiliferous rock. A variety of factors create such local fossil bonanzas, widely known by the German *Konservat Lagerstätten* (preservational storage places, Seilacher et al., 1985): rapid burial (obrution), stagnation (eutrophic anoxia), fecal pollution (septic anoxia), bacterial sealing (microbial death masks), brine pickling (salinization), mineral infiltration (permineralization and nodule formation by authigenic cementation), incomplete combustion (charcoalification), desiccation (mummification) and freezing (Martin, 1999). The key to preserving articulated fossils is to prevent later disturbance of the corpse or exuviae by scavengers, burrowers, or sedimentary reworking. Even more paleobiological information is preserved if microbial decomposers are denied access to organic matter (Gaines et al., 2008). Preservation of decay-resistant lignin of wood and cuticle of plant leaves (van Bergen et al., 1995; Mösle et al., 1998; Barthel et al., 2002) is widespread, but exceptional preservation also extends to tissues that decay even more rapidly, such as muscle fiber (Schaal and Zeigler, 1992), sperm (Nishida et al., 2003), nuclei (Gould, 1971) and starch granules (Baxter, 1964). Taphonomic studies of such fossils have emphasized special places where fossils are exceptionally preserved (Martin, 1999; Bottjer et al., 2002).

This study tests the view that there may also have been special times of exceptional fossil preservation, on geological time scales intermediate between seasonal anoxia envisaged by Kauffman (1981) and extended periods of exceptional preservation (such as Cambrian and Jurassic) outlined by Allison and Briggs (1993). Thin intervals of fossil Lagerstätten are separated by enormous thickness of rock with disarticulated or poorly preserved fossils, much modified from the creatures that produced them by decay and disarticulation. In contrast to these background taphonomic processes, Lagerstätten represent distinctly different episodic taphonomic processes (Brett and Baird, 1997; Speyer and Brett, 1991). "In other words, the history of any one part of the earth, like the life of a soldier, consists of long periods of boredom and short periods of terror" (Ager, 1973, p. 100). Mass extinctions (Alvarez et al., 1980), oceanic anoxic events (Jenkyns, 2003) and chemostratigraphic anomalies (Retallack et al., 2006) also involved short-lived episodic environmental crises. The link between extraordinary global events and fossil preservation has been well expressed by Ager (1973, p. 49), with an archeological analogy. "It is only when the barbarian reduces the palace to a heap of stones in the desert and slaughters all the inhabitants, that the record of art and thought and everyday life is preserved for us." Do we similarly owe the most stunning records of life of the past to rare global crises? This study involves two distinct tests using graphic correlation and geochronological compilation to answer the following related questions. Were individual intervals of exceptional fossil preservation unevenly distributed through time? Were beds of exceptional fossil preservation globally correlative?

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Table 1
Modes of fossil preservation.

Mode	Fig.	Description	Examples	Example geological setting
Hard part	6B,G	Direct preservation of biominerals after decay of organic matrix	Bones, teeth, shells, carapaces, endocarps, phytoliths	Oxidizing paleosols, paleochannels, lakes, and sea floors
Mold (and cast)	4A–C, 6A	Empty (and filled) cavities of former hard parts	Cavities in rocks from dissolved bones or shells	Outcrops in humid forested areas where shells have dissolved in soil
Compression	1B–C, 6F	Cuticle, muscle fibers, organelles, or other oganic matter compressed within strata	Flattened fish, insects, leaves, flowers and fruits in shale	Anoxic to swampy lake and ocean deposits
Impression	1A, 6C, E	Outline of fossil within strata lacking organic remnants	Flattened fish, insects, leaves, flowers and fruits in shale	Anoxic to swampy lake and ocean shales oxidized in modern outcrop
Nodule (authigenic cementation)	1C, 4B, 6D	Fossil preserved within rounded, massive nodules (not concentrically banded like concretion or radially cracked like septarium), cemented by siderite, calcite, or pyrite	Nodules with leaves, cones, seeds and articulated trilobites, crabs, and shrimp	Swamp soils and shallow marine shales
Permineralization	6I	Cell walls remaining but cell lumens filled with cement of calcite, silica, pyrite or hematite	Silicified, calcified, pyritized and ferruginized wood	Marine and non-marine, volcaniclastic and non-volcanic sedimentary rocks
Petrifaction	6H	Fossil outline preserved in calcite, silica, pyrite or hematite, but cell structure obscured	Agatized wood	Volcaniclastic sediments
Charcoalification	6J	Compaction-resistant black plant debris without lamellae between cell walls	Charcoalified wood, leaves, fruits, seeds and flowers	Non-marine and marine sediments
Mummy		Dessicated corpse	Mainland Australian 4.6–4.7 Ka thylacine in cave	Desert caves and packrat middens
Frozen		Frozen corpse	"Ötzi", 5.3 Ka human from Italy; "Blue babe" 36 Ka bison from Alaska	Glacial and permafrost ice
Amber		Organisms embalmed in solidified plant resins	Termites in Dominican amber, wasps in Baltic amber	Non-marine and marine sediments

The working definition of exceptional preservation used in this paper corresponds more with the general concept of museum quality or fancy fossils (Schuchert, 1915) than *Konservat Lagerstätten* (Seilacher et al., 1985; Allison and Briggs, 1993). My database included all localities with articulation of complexly segmented fossil impressions, compressions, and nodule-encased fossils, as well as cellular permineralization of plants and soft-part preservation (Tables 1–2). This can be contrasted with the more common preservation of disarticulated hard parts, impressions, molds and casts (Schopf, 1975). Charcoalified, mummified, amber and frozen fossils, while noteworthy (Table 1), were not included in this compilation because they lack an extensive record in deep time. My working definition of exceptional preservation as the triad of articulation, permineralization or soft-part preservation means that thousands of localities for exceptional fossils are recognized by this study, rather than the usual handful of celebrated localities, such as the following: (1) Middle Cambrian Yuanshan Shale near Chengjiang, China; (2) Middle Cambrian Burgess Shale, near Field, British Columbia, Canada; (3) Pennsylvanian Francis Creek Shale near Mazon Creek, Illinois, U.S.A.; (4) Early Jurassic Posidonienschiefer near Holzmaden, Germany; (5) Late Jurassic Solnhofen Plattenkalk near Eichstatt,

Table 2
Exceptional versus normal fossil assemblages.

No.	Exceptional feature	Explanation of exception	Normal feature	Explanation of normal	References
1	Full articulation of insect, crustacean or trilobite exuviae, animal bones, echinoderm endoskeletons	Burial in anoxic or other unfavourable conditions excluding scavengers and decomposers	Disarticulated insect, crustacean or trilobite exuviae, animal bones, echinoderm endoskeleton	Decomposition and scavenging of dead organisms	Seilacher et al., 1985; Martin, 1999
2	Plant cell walls remaining, with cell lumens filled with cement of calcite, silica, pyrite or hematite	Mineral-rich fluid permeating fossil shortly after burial and before decay	Cell walls flattened or decayed	Cell contents and walls decayed then flattened by overburden	Schopf, 1975; Barthel et al., 2002
3	Preserved cuticle, muscle, or other non-mineralized organic matter	Burial in anoxic or other unfavourable conditions excluding scavengers and decomposers	Non-mineralized organic matter all decayed	Decomposition or scavenging of dead organisms	Schaal and Zeigler, 1992
4	Decalcified shell within periostracum	Lacustrine or oceanic acidification	Calcified shell	Neutral pH lake or ocean	Barthel et al., 1978; Kauffman, 1981
5	Active respirers such as molluscs or fish	Lacustrine or oceanic anoxia	Passive respirers such as corals or brachiopods	Oxygenated lake or ocean	Knoll et al., 2007
6	Back-arched and gaping fossil fish	Death by asphyxia or post-mortem desiccation	Fossil fish with mouth closed	Death by poison, disease, age or burial	Grogan and Lund, 2002
7	Crustaceans articulated at end of trail or burrow	Death in habitat	Crustaceans articulated on unbioturbated matrix	Death in water column	Seilacher, 2007
8	Locally common species that are rare regionally	Life assemblages of schooling groups	Rare fossils rare everywhere	Time averaged attritional assemblages	Gunther and Gunther, 1981
9	Lilliputian fossils	Reduced nutrients or oxygen	Normal size-ranges	Normal nutrients or oxygen	Twitchett, 2007
10	Cosmopolitan forms	Extinction or exclusion of endemic forms	Endemic forms	Adaptations to particular regions	Twitchett, 2007
11	Microbially induced clastic sedimentary structures	Extinction or exclusion of grazing macrobenthos	Trace fossils and bioturbation of clastic sediments	Diverse grazing, burrowing invertebrates	Furrer, 1995
12	Stromatolites	Extinction or exclusion of grazing macrobenthos	Marine algae, corals and bryozoans, reefs	Diverse calcite skeletonized invertebrates	Pruss and Bottjer, 2004

Germany; and (6) Early Cretaceous Jehol biota of the Yixian Formation near Sihetun, China (Bottjer et al., 2002). Soft-bodied preservation, the hallmark of the Burgess Shale, is now known also from many other localities and formations of the same age in Utah (Gunther and Gunther, 1981). Articulated and pyritized triarthrid trilobites are not unique to Beecher's trilobite bed (Frankfort Shale Member, Utica Formation) near Rome, New York, but found over a wide area of Pennsylvania and Ontario (Whiteley et al., 2002). The famous localities have been avidly collected and proven important for their wealth of information about life of the past, but they are not unique.

Articulation, permineralization and soft-part preservation are only three of the many intriguing features of exceptional fossil deposits (Table 2–3). Articulated xiphosurs and crustaceans dead at the end of their tracks (Seilacher, 2007), articulated parts of arthropods in molt configurations from animals that escaped preservation (Speyer, 1985), and finely interbedded, bioturbated and undisturbed beds (Kauffman, 1981), are evidence of life environments temporally or geographically close to the environment that killed and preserved the fossils. Other features such as preferential preservation of organisms with active respiratory ventilation (Knoll et al., 2007), or unusually small size (Lilliputian fossils of Twitchett, 2007) have been interpreted as indications of low oxygen, nutrients, or both. Fish with unnaturally arched backs and mouth open to expand branchiostegal rays (Fig. 1A–B) may also indicate anoxia as a cause of death (Grogan and Lund, 2002), although rigor mortis, desiccation, brine pickling and head-drag in a current may also explain fish back-arching (Maisey, 1991). Decalcified shells within their organic periostracum and lack of heavily calcified skeletons in many exceptional fossil deposits are evidence of unusually low oceanic pH (Barthel et al., 1978; Kauffman, 1981). Fine layering and microbially textured surfaces associated with exceptional fossil preservation (Furrer, 1995) are evidence of environmental stresses inimical to normal marine or lacustrine fauna, and perhaps also of microbial sealing, binding and cementation (Seilacher, 2008). Preservational environments inimical to microbial decomposers are suggested by preservation of organic residues of soft tissues (Gaines et al., 2008). Unusually fine-grained clays may preserve organic matter (Wollanke and Zimmerle, 1990), and be products of diagenetic or metamorphic alteration of organic matter (Page et al., 2008). Fossil Lagerstätten have an array of characteristic features distinct from normal fossil assemblages (Table 2).

2. Graphic correlation

2.1. Methods

Graphic correlation is a comparison of stratigraphic level of first and last appearances of fossils in an independent new section (y axis) compared with a reference measured section (x axis) for the purpose of demonstrating temporal equivalence of levels (Shaw, 1964). A good correlation should form a linear array of points with a high correlation coefficient and low probability of occurring by chance, as assessed by the various amenities of bivariate statistics. First and last appearances of fossils often define stages and biozones in correlative sections, but graphic correlation goes further than zonal correlation to establish equivalent stratigraphic levels. Although the method assumes continuous sedimentation as a proxy for time in each section, violation of this assumption is clear from disjunction of the trend in the case of unconformities (Sweet, 1979) or low coefficients of determination ($R^2<0.95$ of Fig. 2).

This study attempts graphic correlation, not of fossil ranges or stages, but of horizons of exceptional fossil preservation, here called taphostratigraphic correlation (Greek ταφος = burial, γραφω = to write, and

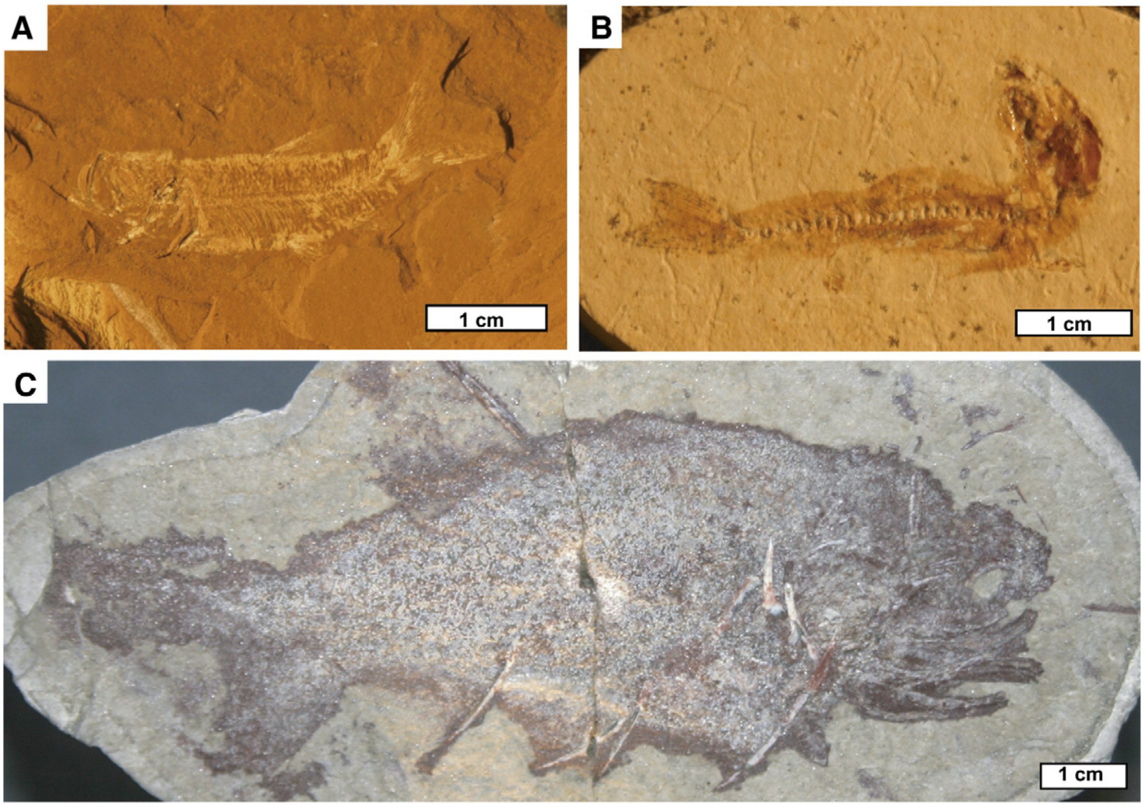

Fig. 1. Exceptional preservation of fossil fish: A, *Cavenderichthys talbragarensis* with mouth gape, skeletal impression in orange shale, from Purlawaugh Formation (Toarcian, late Early Jurassic), Farrs Hill, N.S.W., Australia: B, *Dastilbe elongatus* with strongly reflexed head, compression in limestone, from Crato Member, Santana Formation (Aptian, mid-Early Cretaceous) at Nova Olinda, Brazil; C, *Cheiracanthus latus* with preserved collagen endoskeleton, compression in calcite nodule, from Moray Firth Nodule Bed, Old Red Sandstone (upper Eifelian, late Early Devonian) in Tynet Burn, Scotland. Specimen numbers are F112464E (A), F111553A (B), F115286 (C), in Condon Collection, Museum of Natural and Cultural History, University of Oregon, Eugene (A–B) and Natural History Museum, Kensington, London (C).

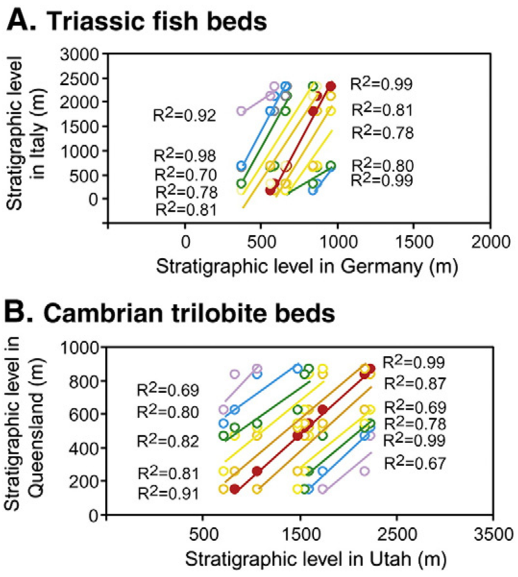

Fig. 2. Graphic correlation technique of Shaw (1964) applied to stratigraphic levels of exceptionally preserved Triassic fish in Germany and Italy (A) and trilobites in Utah and Queensland (B). The best correlation ($R^2 = 0.99$) considerably refines biostratigraphic correlation, and is statistically superior to other possible correlations of three or more successive localities.

Latin stratum = bed), comparable in concept with chemostratigraphic and magnetostratigraphic correlations (Retallack et al., 2006). This method takes stratigraphic levels of exceptional preservation for two stratigraphic sections and graphically compares these meter levels in different sections for possible discrepancies (Fig. 2). Any three successive stratigraphic levels can be compared from one section to another, effectively sliding them up and down with respect to each other to find the best fit. Correlations based on only two points are unusable because their R^2 is 1, and even correlations based on three or four points may not be statistically robust if equally spaced. Unlike paleontological and magnetostratigraphic correlation, taphostratigraphic correlations make no initial assumption of synchroneity of events, but test equivalence in stratigraphic level of particular beds.

In most cases the biostratigraphic zone of assemblages of exceptional preservation is known, but graphic correlation determines whether such assemblages are synchronous within biostratigraphic zones. Very high coefficients of variation ($R^2 > 0.99$ in Fig. 2) are indications that Carnian fish or Drumian trilobite localities were not only roughly contemporaneous, as already known from biostratigraphy (Table 4), but as synchronous as can be resolved with the rock record.

The examples given here of articulated Triassic fish and Cambrian trilobite localities are based on published measured sections, and on localities where articulated fossils have been reported (a full list of localities is presented in Supplemental Data online). Deep boreholes and mine shafts are ideal geological sections if sufficiently long, such as Newark Basin overlapping cores, U.S.A (Olsen et al., 1996), and Birthday Shaft near Sydney, Australia (Retallack, 1980). Other sections used here to order Triassic fish localities include composite sections of the southeastern European Alps (Furrer, 1995), and the central Germanic Basin (Simon, 1999). Scattered trilobite localities of southwest Queensland were all correlated locally to BMR Black Mountain #1 core (Smith, 1972), but composite sections were used to order trilobite localities of the House Range, Utah and nearby Pioche district, Nevada (Hintze and Robison, 1978), Dyfed coast of Wales (Williams and Stead, 1982; Allen and Jackson, 1985), and Brdy Mountains of the Czech Republic (Havlíček, 1971). Specific fossiliferous levels are represented by many localities, such as 22 localities with articulated trilobites in the *Goniagnostus nathorsti* zone of Queensland (Gravestock and Shergold, 2001), and 5 articulated fish localities in the lower Ashfield Shale near Sydney, Australia (Long, 1991). Fieldwork consisted of visiting and collecting from known localities, as well as reconnaissance of other stratigraphic levels where only disarticulated fossils were found. Like graphic correlation, taphostratigraphic correlation assumes constant sedimentation rate within individual sections, that existing biostratigraphic correlations are correct, and that collections of fossils are representative. Violation of these conditions is revealed by poor correlation (Fig. 2).

Table 3
Exceptional versus normal sedimentary environments.

No.	Exceptional feature	Explanation of exception	Normal feature	Explanation of normal	Reference
1	Pyritic black shale	Lacustrine or oceanic anoxia	Gray to brown marine or lake shale	Oxygenated lake or ocean	Jenkyns et al., 2002, Jenkyns, 2003
2	Deep calcic horizon in paleosols	Humid climate	Shallow calcic horizon in paleosols	Semiarid climate	Retallack, 2009a
3	Extratropical laterites and bauxites	Warm–wet polar regions	Tropical laterites and bauxites	Warm-wet tropical regions	Retallack, 2008a
4	Siderite–berthierine paleosols	Unusually reducing wetland soils	Organic drab paleosols	Moderately reducing wetland soils	Retallack, 1997; Sheldon and Retallack, 2002
5	Marine–estuarine siderite nodular beds	Shallow marine alkalization cells	Dispersed carbonate cements and beds	Dispersed shallow marine alkalinity	Fara et al., 2005
6	Barite nodules and desert roses in paleosols	Acidification of aridland soils	Gypsum nodules and desert roses in paleosols	Alkaline aridland soils	Retallack and Kirby, 2007
7	Dolomitic caliche in paleosols	Acidification of aridland soils	Low Mg calcite caliche in paleosols	Alkaline aridland soils	Retallack and Mindszenty, 1993
8	Unusually fine grained clay	Neoformed colloids such as imogolite	Medium to coarse clay	Detrital clays such as illite	Wollanke and Zimmerle, 1990
9	Unusually low $\delta^{13}C$ of carbonate and organic matter	Atmospheric methane pollution from marine hydrates or igneous intrusion of coals	Normal value $\delta^{13}C$ of carbonate and organic matter	Unpolluted atmosphere	Retallack et al., 2006
10	Unusually low $\delta^{34}S$ of sulphate or pyrite	H_2S and S_o from marine euxinia	Normal value $\delta^{34}S$ of sulphate or pyrite	Dominantly aerobic sulfur cycle	Riccardi et al., 2006
11	Thin marine beds among non-marine	High sea level	Non-marine beds thick and long duration	Low sea level	Retallack, 2009a
12	Low stomatal index of fossil plants	High atmospheric CO_2	High stomatal index of fossil plants	Low atmospheric CO_2	Retallack, 2009a

Table 4
Exceptional fossil levels of the past 600 Ma.

Ma	Locality	Rock unit	Stage and biostratigraphic zone	Reference
7	Lompoc, USA	Monterey Formation	Messenian (middle planktonic foram zone N17)	Isaacs, 1989
16	Clarkia, USA	Columbia River Basalt	Base Langhian (middle planktonic foram zone N8)	Smiley, 1985
19	Río Rubielos, Spain	Río Rubielos beds, Unit C	Middle Burdigalian (middle planktonic foram zone N5)	Peñalver and Baena, 2000
30	Bechlejovice, Czech Republic	Děčin Formation	Upper Rupelian (base planktonic foram zone P21)	Spinar, 1972
35	Florissant, USA	Florissant Formation	Priabonian (base planktonic foram zone P16)	Meyer, 2003
39	Chapelcorner, England	Chapelcorner Fish Bed	Lower Bartonian (base planktonic form zone P13)	Gaudant and Quayle, 1988
49	Messel, Germany	Messel Ölschiefer	Base Lutetian (base planktonic foram zone P10)	Schaal and Zeigler, 1992
55	Fur Island, Denmark	Mo Clay	Base Ypresian (middle planktonic foram zone P5)	Bonde, 2008
66	Worli Hill, India	Deccan Intertrappean	Base Danian (base planktonic foram zone P1)	Ribiero, 1921
84	Elkader, USA	Smoky Hill Chalk	Middle Santonian *Clioscaphites choteauensis* zone	Bottjer et al., 2002
93	Quero, Italy	Scaglia Bianca	Base Turonian (Bonarelli event base *Watinoceras devonense* zone)	Gomez et al., 2002
100	Haqel, Lebanon	Hajoula Limestone	Base Cenomanian (Breitstoffer event *Stolickzkaia dispar* zone)	Poyato-Ariza and Wenz, 2005
104	Tlayúa, Mexico	Tlayúa Formation	Upper Albian (Toolebuc event FAD *Hysteroceras varicosum*)	Gonzalez-Rodriguez et al., 2004
111	Santana, Brazil	Romualdo Member	Lower Albian (Urbino event FAD *Douvilleiceras mammillatum*)	Fara et al. 2005
112	Crato, Brazil	Crato Member	Base Albian (Paquier event FAD *Leymeriella tardefurcata*)	Fara et al. 2005
113	Xiaomidian, China	Jiufotang Formation	Upper Aptian (Jacob event *Nolaniceras jacobi* zone)	Zhou et al., 2003
124	Sihetun, China	Yixian Formation	Lower Aptian (Selli event FAD *Deshayesites weissi*)	Zhou et al., 2003
130	Las Hoyas, Spain	Calizas de la Huergina	Upper Hauterivian (Faraoni event FAD *Simbirskites variabilis*)	Poyato-Ariza and Wenz, 2002
137	Montsec, Spain	Montsec Formation	Upper Valanginian (Weissert event *Eleniceras paucinodum* zone)	Poyato-Ariza and Wenz, 2002
145	Portland, England	Lulworth Formation	Base Berriasian (FAD *Berriasiella jacobi*)	Grande and Bemis, 1998
150	Solnhofen, Germany	Solnhofen Plattenkalk	Early Tithonian (*Hybonoticeras hybonotum* zone)	Barthel et al., 1978
152	Cerin, France	Calc. Lithograph. de Cerin	Late Kimmeridgian (*Hybonoticeras beckeri* zone)	Poyato-Ariza and Wenz, 2002
165	la Voulte-sur-Rhône, France	Callovian Stage	Callovian *Macrocephalites gracilis* zone	Bottjer et al., 2002
170	Schinznach, Switzerland	Hauptrogenstein	Middle Bajocian *Stephanoceras humphriesianum* zone	Hess et al., 1999
182	Holzmaden, Germany	Posidonienschiefer	Lower Toarcian *Harpoceras serpentinum* zone	Kauffman, 1981
193	Osteno, Italy	Lombardische Kieselkalk	Lower Sinemurian *Coroniceras bucklandi* zone	Bottjer et al., 2002
200	Lyme Regis, England	lower Blue Lias	Base Hettangian (FAD *Psiloceras planorbis*)	Grande and Bemis, 1998
210	Bergamo, Italy	Argilliti di Riva di Solto	Late Norian (FAD *Sagenites reticulatus*)	Bottjer et al., 2002
217	Solite, USA	Cow Branch Formation	Base Norian (FAD *Guembelites jandianus*)	Grimaldi et al., 2004
219	Lunz, Austria	Lunzer Sandstein	Mid Carnian (FAD *Austrotrachyceras austriacum*)	Dobruskina, 1998
228	Wayao, China	Xiaowa Formation	Base Carnian (FAD *Trachyceras aon*)	Hagdorn et al., 2007
230	Meride, Switzerland	Kalkschieferzone Member	Upper Ladinian (FAD *Protrachyceras regelodanus*)	Furrer, 1995
235	Perledo, Italy	Calcare di Perledo Member	Lower Ladinian (FAD *Protrachyceras margaritosum*)	Furrer, 1995
237	Besano, Italy	Grenzbitumenzone	Base Ladinian (FAD *Eoprotrachyceras curionii*)	Bottjer et al., 2002
240	Xinmin, China	Guanling Formation	Middle Anisian (FAD *Balatonites*)	Jiang et al., 2005
245	Hangviller, France	Grès á Voltzia	Base Anisian (FAD *Paracrochordiceras*)	Gall and Grauvogel-Stamm, 1999
249	Wapiti Lake, Canada	Vega-Phroso Siltstone Mbr	Lower Smithian (*Meekoceras gracilitatus* zone)	Mutter and Neuman, 2008
251	Ambilobe, Madagascar	Couches á poissons et *Claraia*	Basal Griesbachian (FAD *Hindeodus parvus*)	Beltan, 1996
259	Bad Sachsa, Germany	Kupferschiefer	Lower Wuchaipingian (FAD *Clarkina postbittneri*)	Malzahn, 1968
270	Koštálov, Czech Republic	Libštát Formation	Basal Roadian (FAD *Jinogondolella nankingensis*)	Dietze, 2000
272	Tschekarda, Russia	Koshelevka Formation	Basal Kungurian (*Neostreptogranuths prayi* zone)	Prokofiev, 2005
280	Calvinia, South Africa	Whitehill Formation	Middle Artinskian (zone of *Sweetognathus whitei*)	MacRae, 1999
292	Elmo, USA	Carlton Limestone Member	Lower Sakmarian (zone of *Sweetognathus merrilli*)	Durden, 1977
297	Odernheim, Germany	Odernheimschichten	Middle Asselian (zone of *Streptognathodus fusus*)	Witzmann and Pfritzschner, 2003
300	Gottlob, Germany	Goldlauterschichten	Base Asselian (FAD *Streptognathodus isolatus*)	Werneburg and Schneider, 2006
308	Mazon Creek, USA	Francis Creek Shale	Mid-Desmoinesian	Shabica and Hay, 1997
320	Bear Gulch, USA	Heath Formation	Base Morrowan (FAD *Declinognathus noduliferus*)	Poplin and Lund, 2000
332	Bearsden, Scotland	Manse Burn Formation	Base Namurian (FAD *Lochriea cruciformis*)	Coates and Sequeira, 2001
359	Grahamstown, South Africa	Witpoort Formation	Base Tournaisian (Hangenberg event FAD *Siphonodella sulcata*)	MacRae, 1999
366	Hyner, USA	Duncannon Member	Middle Famennian (Annulata events FAD *Palmatolepis postera*)	Retallack et al., 2009
375	Canowindra, Australia	Mandagery Formation	Base Famennian (Kellwassser events *Palmatolepis rhenana* zone)	Johanson et al., 2003
380	Naples, USA	Grimes Sandstone	Middle Frasnian (Rhinestreet event *Palmatolepis haasi* zone)	McIntosh, 2001
382	Nora Springs, USA	Mason City Member	Middle Frasnian (Middlesex event FAD *Palmatolepis punctata*)	Strimple and Levorson, 1973
384	Miguasha, Canada	Escuminac Formation	Lower Frasnian (Genundewa event *Palmatolepis falsiovalis* zone)	Schultze and Cloutier, 1996
392	Achanarras, Scotland	Achanarras Limestone	Upper Eifelian (Kačák event, *Polygnathus xylus ensensis* zone)	Newman and Trewin, 2001
395	Koneprusy, Czech Republic	Acanthopgye Limestone	Lower Eifelian (Chotec event, *Polygnathus partitus* zone)	Snajdr, 1990
400	Jebel Issoumour, Morocco	Formation El Remlia	Upper Emsian (Daleje event, *Polygnathus serotinus* zone)	Morzadec, 2001
407	Bundenbach, Germany	Hünsruckschiefer	Lower Emsian (Zlichov event, FAD *Polygnathus gronbergi*)	Bottjer et al., 2002
411	Tillywhandland, Scotland	Dundee Formation	Lower Pragian (Prague event, FAD *Monograptus hercynicus*)	Turner, 1982
416	Ledbury, England	Passage Beds	Base Lochkovian (Klonk event, FAD *Monograptus uniformis*)	Woodward, 1947
420	Leintwardine, England	Leintwardine Beds	Upper Ludlovian (Lau event FAD *Neocucullograptus kozlowski*)	Siveter, 1983
424	Lesmahagow, Scotland	Slot Burn Formation	Upper Wenlockian (Mulde event FAD *Colonograptus praedeubeli*)	Bluck, 1973
428	Götland, Sweden	uppermost Visby Bed	Lower Wenlockian (Ireviken event FAD *Cyrtograptus centrifugus*)	Ramsköld, 1984
437	Waukesha, USA	Brandon Bridge Formation	Middle Llandoverian (Sandvika event FAD *Stimulograptus sedgwicki*)	Mikulic et al., 1985
444	Anticosti Island, Canada	Becsie Formation	Base Landoverian (FAD *Akidograptus ascensus*)	Chatterton et al., 2003
450	Clanwilliam, South Africa	Soom Shale Member	Mid Katian (FAD *Dicellograptus complanatus*)	MacRae, 1999
456	Cañon City, USA	Harding Sandstone	Base Katian (FAD *Diplacanthograptus caudatus*)	Sansom et al., 1997
461	Winneshiek, USA	St Peter Sandstone	Base Sandbian (FAD *Nemagraptus gracilis*)	Liu et al., 2006
472	Volkhov, Russia	Volkhov Horizont	Base Dapingian (FAD *Isograptus victoriae*)	Ivantsov, 2003
479	Changsa, China	Fenxiang Formation	Base Floian (FAD *Tetragraptus approximatus*)	Yang et al., 1986
488	Shineton Brook, England	Shineton Shales	Base Tremadocian (FAD *Iapetognathus fluctivagus*)	Donovan and Paul, 1985
496	Bryn-Llin-Fawr, Wales	Cwmshesgen Formation	Late Cambrian, *Parabolina spinulosa* zone	Allen and Jackson, 1985
503	Chopko River, Russia	Chopko Formation	Lower Paibian, *Erixanium sentum* zone	Varlamov et al., 2006
504	Weeks Canyon, USA	Weeks Formation	Base Paibian FAD *Glyptagnostus reticulatus*	Gunther and Gunther, 1981

(continued on next page)

Table 4 ***(continued)***

Ma	Locality	Rock unit	Stage and biostratigraphic zone	Reference
505	Cedar Bluff, USA	Conosauga Formation	Base Guzhangian FAD *Leiopyge laevigata*	Schwimmer and Montante, 2007
506	Marjum Pass, USA	Marjum Formation	Middle Drumian FAD *Goniagnostus nathorsti*	Gunther and Gunther, 1981
507	Jince, Czech Republic	Jince Formation	Lower Drumian FAD *Ptychagnostus punctuosus*	Fatka and Kordule, 1992
508	Field, Canada	Burgess Shale	Base Drumian FAD *Acidusus atavus*	Briggs et al., 1994
510	Beetle Creek, Australia	Beetle Creek Formation	Middle stage 5 FAD *Ptychagnostus gibbus*	Öpik, 1967
512	Balang, China	lower Kaili Formation	Lower stage 5 FAD *Peronopsis bonnerensis*	McNamara et al., 2003
515	Ruin Wash, USA	upper Pioche Shale	Base stage 5 FAD *Oryctocephalus indicus*	Webster et al., 2008
518	Chengjiang, China	Yu'anshan Shale Member	Base stage 4 FAD *Hebediscus attleborensis*	Hou et al., 2004
524	Amouslek, Morocco	Issaten Formation	Base stage 3 FAD *Parabadiella yunnanensis*	Geyer and Palmer, 1995
535	Kuanchanpu, China	upper Denying Formation	Base stage 2 FAD *Skolithos linearis*	Bengtson and Zhao, 1997
542	Swartpunt farm, Namibia	Spitzkopf Formation	Base Fortunian and Cambrian FAD *Manykodes pedum*	Narbonne et al., 1997
555	Ediacara Hills, Australia	Ediacara Member	Upper Ediacaran with *Dickinsonia costata*	Fedonkin et al., 2007
565	Mistaken Point, Canada	Mistaken Point Formation	Upper middle Ediacaran with *Fractofusus misrai*	Fedonkin et al., 2007
575	Vinnitsa, Ukraine	Redkino Horizont	Lower middle Ediacaran with *Beltanelliformis brunsae*	Fedonkin et al., 2007
600	Miaohe, China	upper Doushantuo Form.	Lower Ediacaran with *Doushantouphyton lineare*	Xiao and Knoll, 1999

Numerical time scale used throughout this paper is from Gradstein et al. (2004).

2.2. Correlation of Triassic fish beds

An initial puzzle that stimulated this study was articulated Triassic fish preserved in non-pyritic light-gray to red-green mottled shales of the Grès á Voltzia of France and upper Buntsandstein of Germany (Schultze and Kriwet, 1999). These fluviodeltaic facies include paleosol evidence for neither excessively arid nor saline conditions (Weber, 1994), and are far removed from euxinic marine facies that characterize many fossil fish beds (Furrer, 1995). Similar fluvial facies, including non-arid, well drained paleosols (Retallack, 1997), yield fossil fish of very similar age (Table 4) in the Terrigal and Newport Formations of Australia (Woodward, 1890). If these non-marine fish beds were generally comparable in biostratigraphic age, could they have been more precisely correlative?

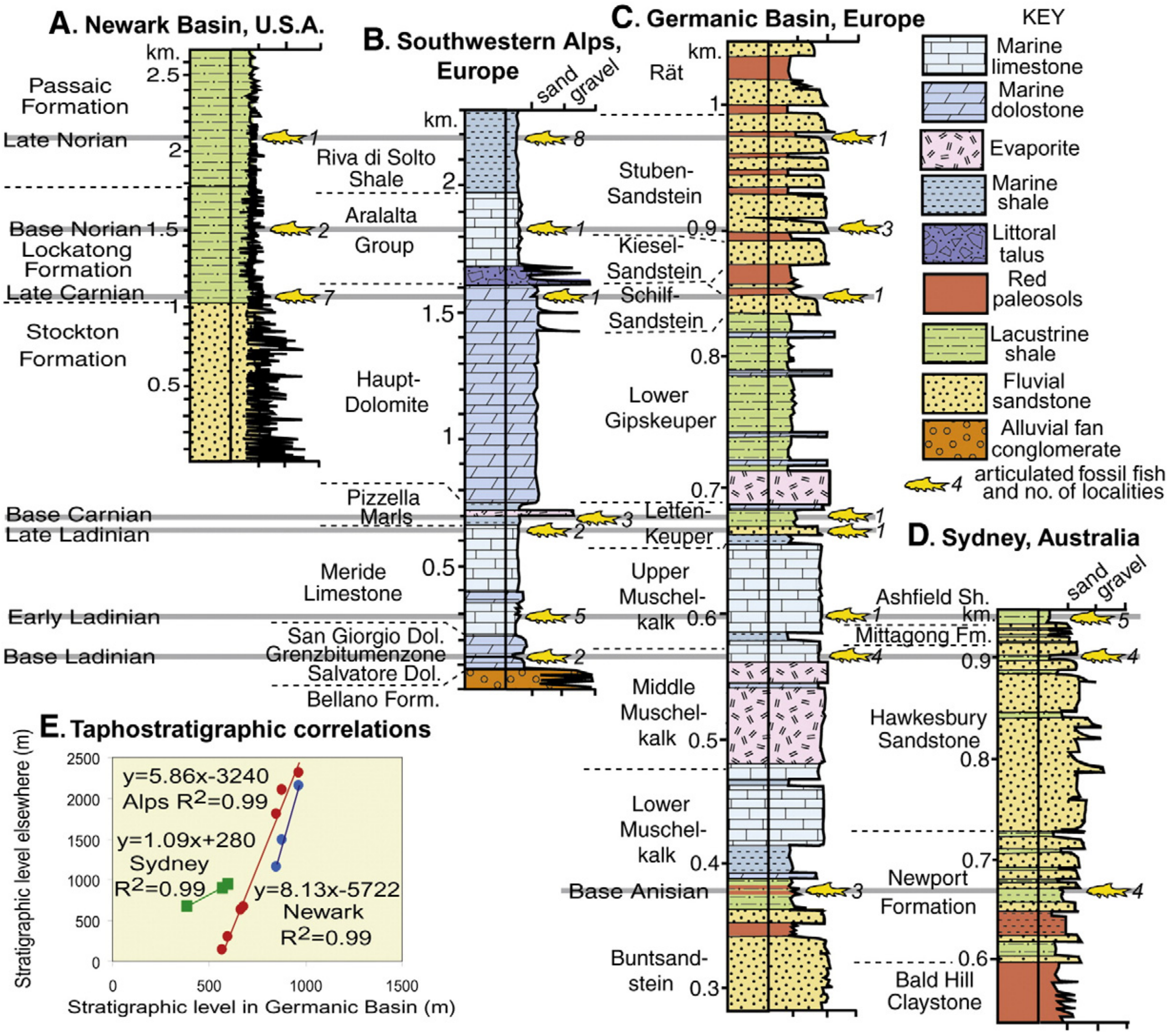

Fig. 3. Taphostratigraphic correlations of Triassic fossil fish beds. The geological sections are from Newark basin core (Olsen et al., 1996), southeastern Alps composite (Furrer, 1995), Germanic Basin composite (Simon, 1999), and Birthday Shaft (Retallack, 1980), but fossil occurrences are correlated from nearby localities (for other sources and localities see Supplementary Material).

Complete fossil fish are found in a wide range of lithologies. Newark Supergroup fish are in laminated black shales of large Rift Valley Lakes (Olsen et al., 1996), whereas those of the Alpine Triassic are from marine pyritic, black shales (Furrer, 1995), and other German fish are from light gray, shallow marine limestones (Schultze and Kriwet, 1999). Non-marine fossil fish from the Hawkesbury Sandstone include some in extraordinarily fine-grained shales (Brookvale), whereas other fish localities (Somersby) are in silty matrix (Vickers-Rich and Rich, 1993). In my collecting experience, no particular lithology is indicative of articulated fossil fish, nor is the presence of fish scales, centra, otoliths or ribs an indication that complete fish will be found by more strenuous effort. Localities most likely to yield complete fossil fish are those where one has already been found: articulated fish commonly are preserved as concentrations of many individuals, and this is widely interpreted as due to schooling behavior (Boucot, 1990).

Taphostratigraphic correlation requires sequences with several fish-bearing horizons, such as the Sydney and Germanic Basins (Fig. 3). Non-linear sedimentation and erosional disconformities would be readily apparent in such correlations between sections (Sweet, 1979), but was not found in these cases of fish-bearing sequences around the world (Fig. 3). High coefficients of variation for such correlation are not statistically remarkable if three or fewer localities are correlated (Fig. 1), or if localities are spaced at regular stratigraphic intervals. Although Sydney and Newark successions have only three fish bearing horizons, they are at unequal intervals (Fig. 3). This is especially remarkable because measured stratigraphic levels are different in each basin, in proportion to different rates of sediment accumulation and different sedimentary environments. Taphostratigraphic correlation of the Sydney, Germanic and other fish-bearing sequences is statistically significant: F-test probabilities of ANOVA regressions are 0.0005 for Newark/Germany, 0.000009 for Italy/Germany, and 0.009 for Sydney/Germany. These correlations are not just confirmation of common knowledge that upper Carnian to lowest Norian rocks, for example, have widespread fossil fish beds, but indicate that particular fossil fish beds around the world formed within very limited intervals of time.

Some of these fish-bearing intervals in exceptionally thick sequences, such as the 2.7 km thick Newark Supergroup, have multiple fish beds in as much as 100 m of lower Lockatong Formation in New Jersey, USA. The fish beds are cued to paleoclimatic fluctuations on annual to supra-Milankovitch scales, and represent as much as 413 kyr of recurrent fish-preserving conditions (Olsen et al., 1996). Even in this case, this thick bundle of articulated-fish-bearing beds is separated from other fish-bearing units by 0.5 km of rock with no fish, or with only disarticulated fish. In other cases of German, Australian and Alpine Triassic fish beds, productive fish beds are less than 1 m thick and separated by hundreds of meters (Retallack, 1980; Furrer, 1995; Schultze and Kriwet, 1999; Simon, 1999).

2.3. Correlation of Cambrian trilobite quarries

Trilobite fossils are most prized when articulated and unusually complete (Fig. 4A) rather than molts (Fig. 4B–D). Commercial and amateur quarries for Cambrian trilobites are widespread in the House Range of Utah and nearby Pioche mining district of Nevada (Hintze and Robison, 1978; Gunther and Gunther, 1981). In this desert region of excellent exposure articulated trilobites come from a limited number of thin (<2 m) intervals marked by lines of active quarries and separated by hundreds of meters of comparable shales with disarticulated trilobites or barren of fossils. The same pattern of limited horizons of articulated trilobites in sequences of few or disarticulated fossils is clear from excellent outcrops in the desert of western Queensland (Smith, 1972), and also demonstrated in scattered outcrops of forested Wales and Bohemia (Havlíček, 1971; Williams and Stead, 1982; Allen and Jackson, 1985). No particular lithology is unique to articulated trilobites. Bohemian and Welsh Cambrian trilobites come from gray shales (Snajdr, 1990), but these are not

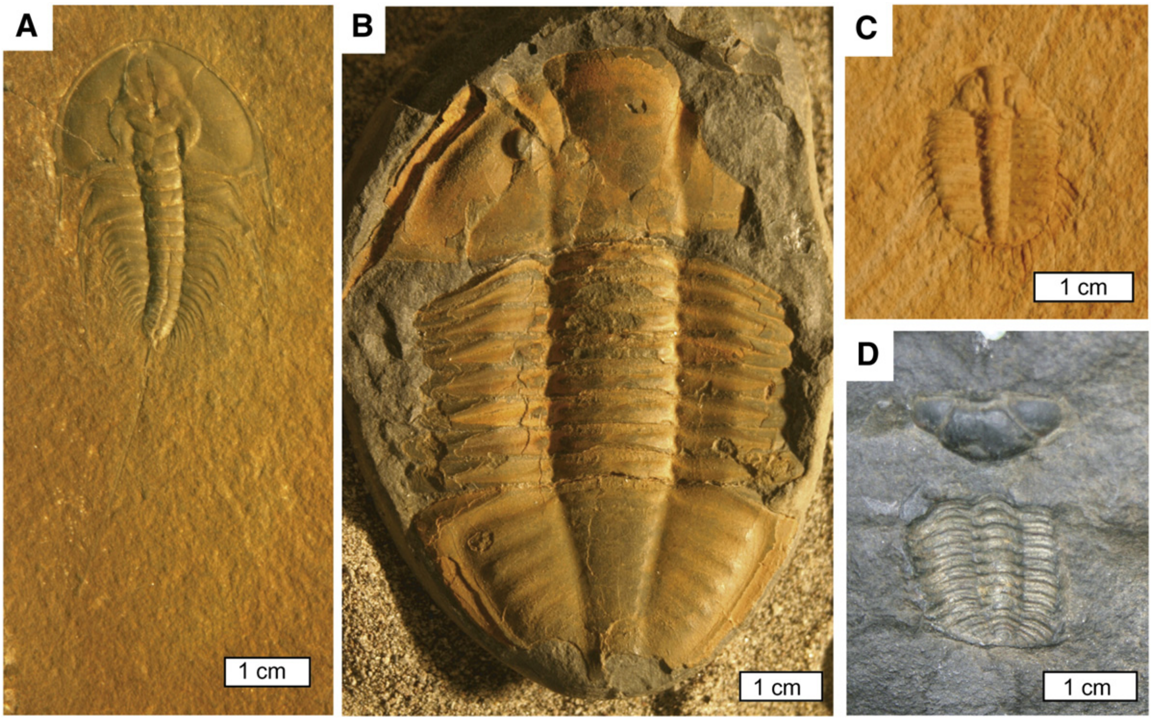

Fig. 4. Exceptional preservation of fossil trilobites: A, *Olenellus* sp. aff. *O. gilberti* complete with pleural spines and flexuous telson, oxidized internal mold, from Eager Formation (late Early Cambrian) near Cranbrook, British Columbia, Canada: B, *Hoekaspis matacensis* molt with displaced free cheeks, oxidized internal mold in siderite nodule, from San Luis Ocuri Formation (lower Dapingian, early Middle Ordovician) near Camargo, Bolivia: C, *Sinespinaspis markhami* molt without free cheeks, oxidized internal mold, from Cotton Beds (upper Telychian, late Early Silurian) near Forbes, N.S.W., Australia: D, *Trimerocephalus mastopthalmus* molt of Salterian mode (with reversed cephalon), compression in shale, from Ostracod Slate (late Frasnian, mid-Late Devonian) near Newton Abbott, England. Specimen numbers are F112142A (A), F108966 (B), F113639A (C), and P13132 (D), in Condon Collection, Museum of Natural and Cultural History, University of Oregon, Eugene (A–C) and Natural History Museum, Kensington, London (D).

exceptionally black with organic matter or fine in grain size, and include burrows and other fossil fauna (Havlíček, 1971; Williams and Stead, 1982; Allen and Jackson, 1985). Articulated Cambrian trilobites from Queensland (Öpik, 1967) are in cherty black shales (Inca Formation), gray limestones (V-Creek Limestone, lateral to Devoncourt Limestone), siderite nodules (Pomegranate Limestone), and silty to sandy pelletoidal phosphorites (Beetle Creek Formation). Utah Cambrian trilobites (Gunther and Gunther 1981; Gaines et al., 2005) include remarkable expansion of the middle lamella of the exoskeleton by early diagenetic calcite (Wheeler Shale), as well as black shale compressions with soft-body preservation (Marjum Formation), and compressions in shaley oxidized partings within flaggy coarse limestone (Weeks Formation). These same lithologies are barren or have disarticulated trilobites elsewhere in the same formations. In all 41 trilobite localities collected by me, layers with disarticulated pleurae yielded fully articulated trilobites on further focused excavation (in some cases for an additional 12 h), whereas layers with only isolated glabellae and pygidia failed to yield articulated trilobites. Reasons for this field rule of thumb are uncertain. Elongate pleurae would be sorted by currents differently than rounded glabellae and pygidia, but there is little evidence of currents in most trilobite beds. Or perhaps trilobites ate less sclerotized parts of their exuviae, like some (Eriksson and Baden, 1998), but not all (Greenway, 1985), living crustaceans.

Taphostratigraphic correlations of quarries for articulated trilobites with levels of comparable preservation in Utah, Queensland, Wales and Bohemia are highly significant (Fig. 5): F-test probabilities from ANOVA regressions are $4 \cdot 10^{-10}$ for Queensland/Utah, $3 \cdot 10^{-5}$ for Wales/Utah, and 0.002 for Bohemia/Utah. Furthermore, the best of alternative sliding correlations (Fig. 2B) confirms biostratigraphic correlations already demonstrated. Within the *Acidusus atavus* zone, localities with *Elrathia kingi* in Utah (Gaines et al., 2005, 2008) were correlative with localities with *Penarosa elaticeps* in Queensland (Gravestock and Shergold, 2001). Articulated trilobite horizons in these various sequences around the world are notable for their irregular distribution through time, with an earliest Middle Cambrian pair of horizons, four mid-Middle Cambrian horizons, and an earliest Late Cambrian pair of closely spaced horizons. This pattern for correlation is analogous to a bar code, reflecting events at irregularly spaced intervals. In this case, the events are not coded bars of uneven thickness and spacing, but events in time recorded in basins of very different sediment accumulation rate (represented by slopes in Figs. 3E and 5E). This episodic pattern in space and time is a statistical advantage, because periodic patterns would have problems of autocorrelation.

Trilobites were obligate marine organisms. Remarkably, articulated remains of the aglaspid *Kodymirus vagans* have never been found with other marine fossils so are presumed non-marine (Gray, 1988), yet were found at 3 localities in the Paseky Shale Member of Bohemia (Havlíček, 1971) correlative with articulated trilobite beds containing *Redlichia*

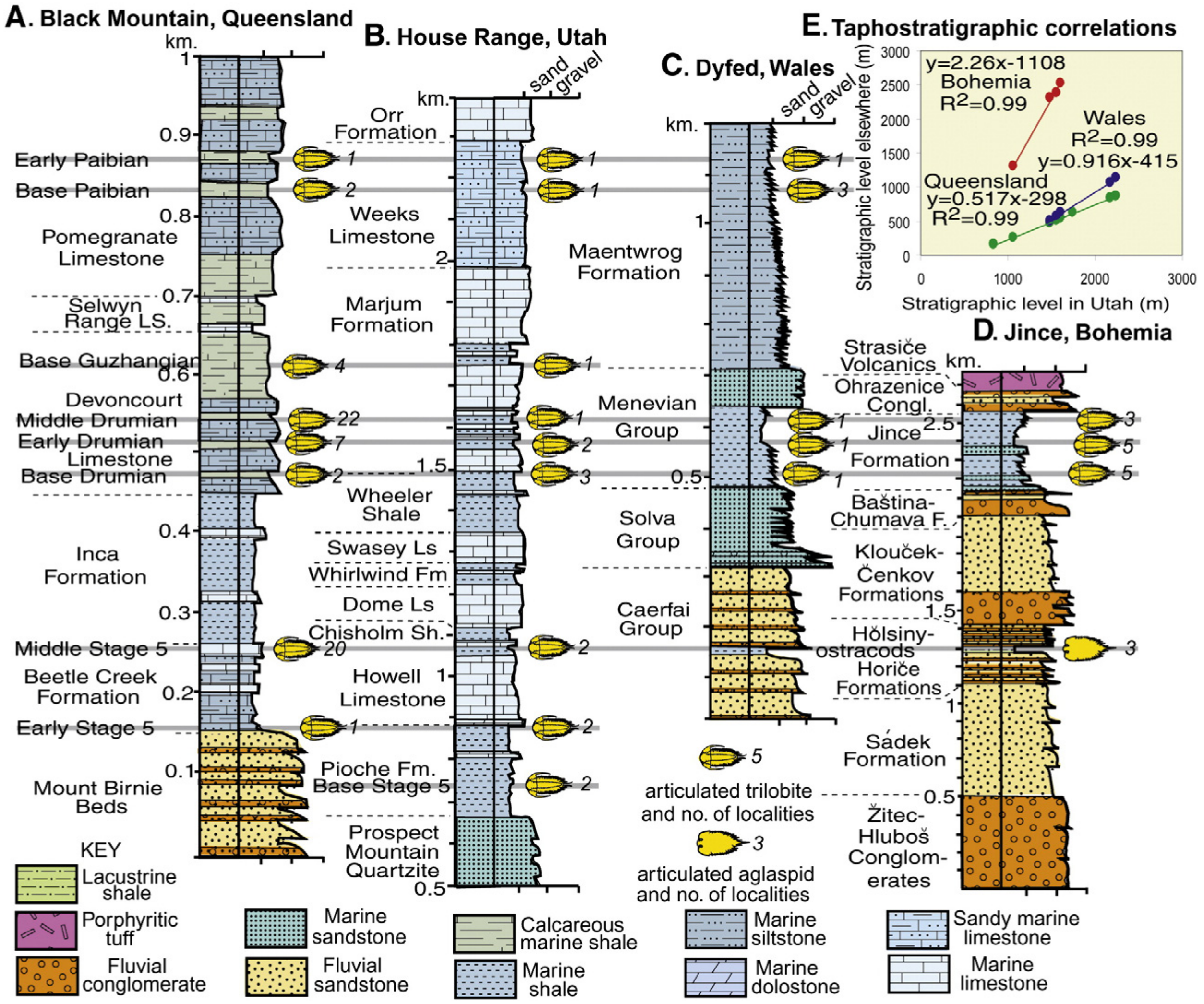

Fig. 5. Taphostratigraphic correlations of Cambrian fossil trilobite beds. The geological sections are respectively from BMR Black Mountain #1 core (Smith, 1972), House Range composite (Hintze and Robison, 1978), Dyfed coast of Wales (Williams and Stead, 1982; Allen and Jackson, 1985), Brdy Mountains composite (Havlíček, 1971: for other sources and localities see Supplementary Material).

idonea in Queensland and *Zacanthoides typicalis* in Nevada (Fig. 3). Paseky-correlative rocks in Wales are a thin bed of red shale with bradoriid crustacea and brachiopods, unusual within this sandstone-dominated marginal-marine sequence (Williams and Stead, 1982). Localities in the Beetle Creek Formation (Queensland: Öpik, 1967), Wheeler Shale (Utah: Gaines et al., 2005) and Jince Formation (Bohemia: Fatka and Kordule, 1992) have multiple horizons of articulated trilobites, often nearly monospecific, within individual layers, through a thickness of at least 2 m, indicating return of conditions preserving articulated fossils through intervals of several tens of thousands of years. As for fossil fish, horizons of articulated trilobites and aglaspids are limited in vertical stratigraphic distribution, and were correlative in both marine and non-marine environments.

3. Age compilation

3.1. Methods

A literature compilation was made of the geological age, representative taxa and geological details of thousands of fossil sites, not only for articulated fish (Fig. 1) and trilobites (Fig. 4), but for starfish and crinoids with arms, articulated insects and small animals, as well as cuticular preservation of plants, other kinds of soft body preservation, and cellular permineralization by silica, calcite and pyrite–hematite (Fig. 6). A full list of all localities of this compilation, together with example taxa and references is presented in Supplemental Data online. Like fish and trilobites, starfish (Fig. 6A), crinoids (Fig. 6B), insects (Fig. 6C) and small animals (Fig. 6F–G) have many individual skeletal elements, prone to disarticulation and scattering upon decay, transport and bioturbation. The few known conodont animal compressions (but not isolated conodonts) were included in the compilation of fish, because these extinct marine animals were non-tetrapod chordates like hagfish (*Myxine*) and lancelets (*Branchiostoma*), which also are "fish" in common parlance. My compilation did not include calyces of crinoids, tests of echinoids, or skulls of animals because these are compact and transportable, with sutured or closely fitting connections. Separate compilations were also made of exceptional preservation of soft tissues, such as skin and muscles of animals (Fig. 6D,F), and the enigmatic unskeletonized integuments of Ediacaran and other Precambrian problematica (Fig. 6E). Additional compilations were made of plants

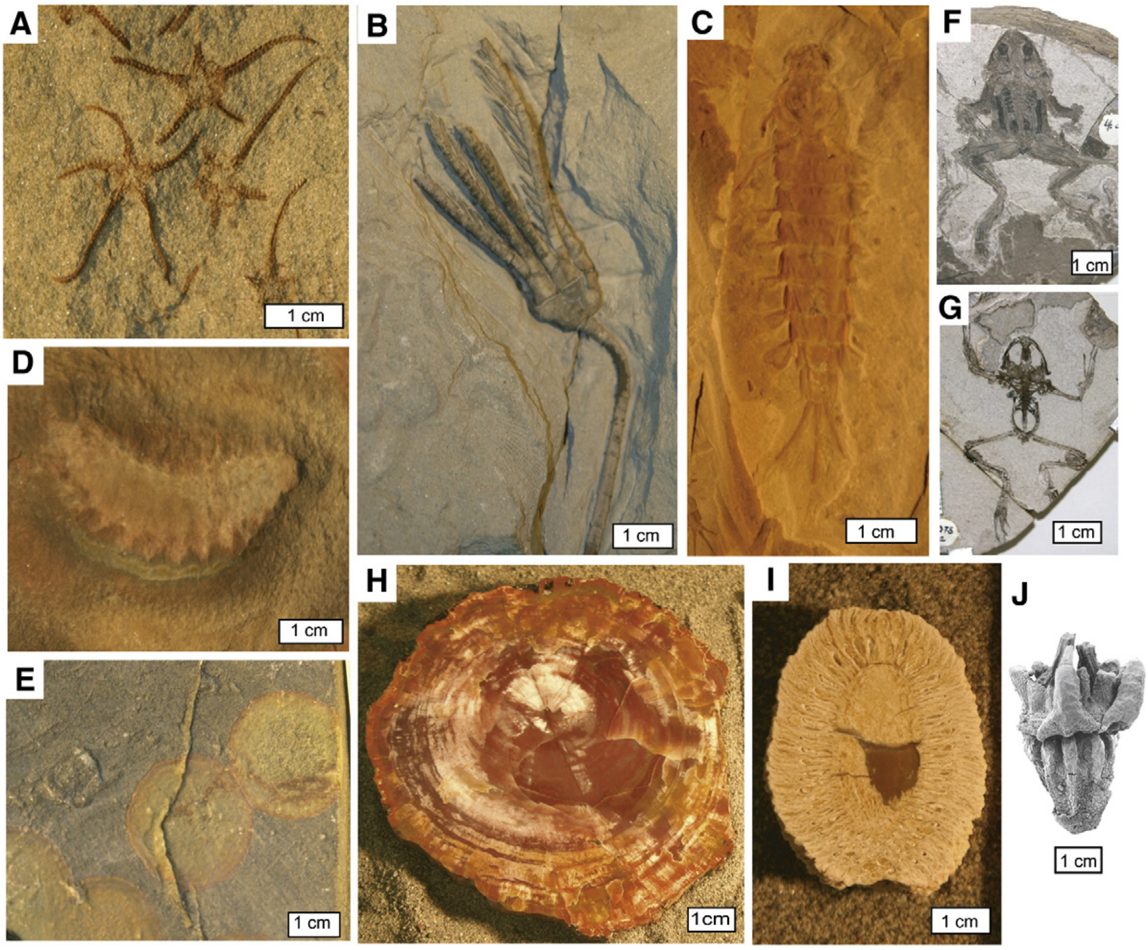

Fig. 6. Other forms of exceptional fossil preservation: A, *Ophiocrossota baconi*, external mold of brittle stars, from Middle Coaledo Formation (early Lutetian, middle Eocene) at Shore Acres, Oregon, U.S.A.; B, *Scytalocrinus disparilis* crinoid with arms and column firmly attached, hard-part preservation, from Ramp Creek Formation (mid-Visean, Early Carboniferous) near Crawfordsville, Indiana, U.S.A.; C, *Ephemeropsis trisetalis* aquatic nymph of mayfly, compression, from Jiufotang Formation (late Aptian, mid-Early Cretaceous) near Chaomidian, China; D, *Helenodora inopinata* onychophoran (velvet worm), compression in siderite nodule, from Francis Creek Shale (middle Moscovian, mid Pennsylvanian) near Essex, Illinois, U.S.A. ; E, *Aspidella* sp. indet., a problematic discoid fossil (dark) from the Cambridge Argillite (early Ediacaran) at low tide level near Hewitts Cove, Massachusetts, U.S.A., with encrustation by discoid, crustose, living, green, marine lichens *Verrucaria mucosa* (light): F–G, *Palaeobatrachus grandipes* frog compressions with varied amounts of soft part preservation from diatomites (middle Aquitanian, early Miocene) of Bechlejovice and Březiny (respectively), Czech Republic; H, *Araucarioxylon arizonicum* polished round of petrified (agatized) conifer wood from lower Chinle Formation (lower Carnian, early Late Triassic) near St Johns, Arizona, U.S.A.; I, *Araucaria mirabilis* silica-permineralized conifer cone, from La Matilda Formation (late Bajocian, Middle Jurassic), Cerro Quadrado, Argentina: J, *Scandianthus costatus*, charcoalified flower Santonian–Campanian (Late Cretaceous), from Åsen, Sweden. Specimen numbers are F109501 (A), F106381 (B), F113021 (C), F111064A (D), F114497 (E), Pb01691 (F), Pb01693 (G), F111197 (H), F111552 (I) and SEM142 (J) in Condon Collection, Museum of Natural and Cultural History, University of Oregon, Eugene (A–E, H), Narodni Muzeum, Prague, Czech Republic (F–G), and Swedish National Museum (J). Image J is courtesy of Else-Marie Friis.

preserved with cuticles, and permineralized with silica (Fig. 6I), calcite (including coal balls) and pyrite. Phosphorite permineralization is remarkably effective in the case of Cambrian crustaceans (Müller et al., 1995) and Precambrian cells (Xiao and Knoll, 1999), but the numbers of such occurrences so far reported do not allow robust statistical analysis. For the same reason, localities of frozen fossils (Guthrie, 1990), charcoalified fossils (Friis et al., 2006) and fossils in amber (Poinar and Poinar, 1995) are not tabulated here. For the same reasons of low numbers, region-specific histograms of fossil occurrences were not compiled. New sites of exceptional preservation continue to be reported from China at such a high rate, that this region is probably still under-reported. The compilations presented here are all global.

The particular species and assemblages of fossils found at the various localities are not relevant to this study, but example species following the taxonomy of cited authors are listed in Supplemental Data online for the following reasons. Many localities are known best for particular fossils, and these lists are a guide to sources of commercially traded fossils. Not all exceptionally preserved fossils were attributed to species for a variety of reasons: juveniles such as tadpoles lacking diagnostic adult characters, skin impressions or feathers not associated with diagnostic bones, permineralized wood or coal balls not yet studied microscopically, or fossils illustrated but not yet studied in detail. Also included in the database are specimens collected by the author and housed in the Condon Fossil Collection of the Museum of Natural and Cultural History, University of Oregon, Eugene.

A locality for the purpose of this compilation covers the area of a small European village or large quarry (ca. 1 km^2), and does not include finer scale lateral subdivision of quarries and cliffs. Precision of the Phanerozoic time scale used here (Gradstein et al., 2004) is ±2 myr. Thus data was binned by 4 myr increments, even though this procedure glosses over known horizons more closely spaced in time (Figs. 3 and 5; Table 4) and does not do justice to finer temporal resolution of Neogene localities. Only localities whose age was known within the limits of ±2 Ma, in most cases a third or quarter of a stage, are reported for the Phanerozoic (0–542 Ma), but age constraints were relaxed (±10 Ma) in order to capture a selection of Neoproterozoic (542–600 Ma) localities. A large number of localities were not tabulated because their age is unknown within these specified limits. Numerical ages of the Gradstein et al. (2004) time scale are used consistently in the large databases supporting this work, despite subsequent numerical revisions (Kaufmann, 2006; Ovtcharova et al., 2006), but this account does use subsequently adopted international period and stage names (Knoll et al., 2006; Landing et al., 2007; Peng et al., 2008; Sadler et al., 2009). Supplemental Data online lists mainly local age constraints, which also are tabulated by Gradstein et al. (2004).

The Phanerozoic time scale of this analysis can not only reveal whether exceptional fossil preservation was evenly distributed in time, but also reveal general correlation with independent lithological indications of exceptional times. Exceptional strata (Table 3) in marine rocks include pyritic black shales taken as evidence of widespread marine anoxic events (Jenkyns et al., 2002; Jenkyns, 2003). Nodular beds with crabs and trilobites in marine sequences (Schweitzer and Feldmann, 2000) or with crustaceans and fish in estuarine to freshwater sequences (Maisey, 1991; Fara et al., 2005) also are restricted in stratigraphic distribution, and like pyritic black shales, yield exceptionally preserved fossils (Bottjer et al., 2002). Long sequences of paleosols are punctuated by narrow intervals of unusual paleosols as indicators of global change events: deep-calcic versus shallow-calcic Aridisols (Retallack, 2009a), extratropical laterites and bauxites (Retallack, 2008a), dolomitic versus calcitic caliche (Retallack and Mindszenty, 1993), baritic versus gypsic Aridosols (Retallack and Kirby, 2007), siderite or berthierine versus ferrihydritic or pyritic wetland paleosols (Retallack, 1997; Sheldon and Retallack, 2002), and thin transgressive marine limestones within paleosol-sequences (Retallack, 2009a). Finally both marine and non-marine sequences are punctuated by carbon (Retallack et al., 2006) and sulfur isotopic excursions (Riccardi et al., 2006). Black shales, nodule beds and anomalous paleosols and isotopic signatures are associated with mass extinctions (Alvarez et al., 1980; Retallack et al., 2006), other significant biotic overturns (Talent et al., 1993), pronounced paleoclimatic spikes (Retallack, 2009a,b), and oceanic anoxic events (Jenkyns, 2003). Was exceptional fossil preservation also more common at these lithologically defined times of exceptional paleoenvironments?

3.2. Global preservational events

The result of this large compilation of fossil locality ages is a very uneven distribution through time of localities for exceptional fossil preservation (Fig. 7). Peaks in locality abundance are very different from the null hypothesis of even distribution through time: χ^2 probabilities of observed occurrences versus expected equal numbers per 4-m.-yr bin over observed geological ranges are less than 10^{-10} for each group tabulated. The abundance of exceptional preservation varied considerably through time. The record is best known for fossil fish and trilobites, and confirmed by synchronous peaks in that long stretch of geological time when trilobites and fish coexisted. Exceptional fossil preservation was widespread during the Middle Cambrian, Late Ordovician, late Middle Silurian, earliest Triassic, early Aptian, earliest Eocene, latest Eocene and middle Miocene. Many of these peaks in the fossil compilation with bin resolution of 4 Ma (Fig. 7) are compounded from successive fossil beds separated by less time (Figs. 3 and 5, Table 4). Only graphic correlation can show synchrony at resolution of less than 4 Ma.

Less surprising is the temporal coincidence of modes of the various categories of fossils compiled: many exceptional fossil beds yield a variety of fossil taxa (Fig. 7). It is a rare quarry for articulated trilobites that does not also have a few articulated merostomes or crustaceans (Gunther and Gunther, 1981). Many articulated crinoid beds often

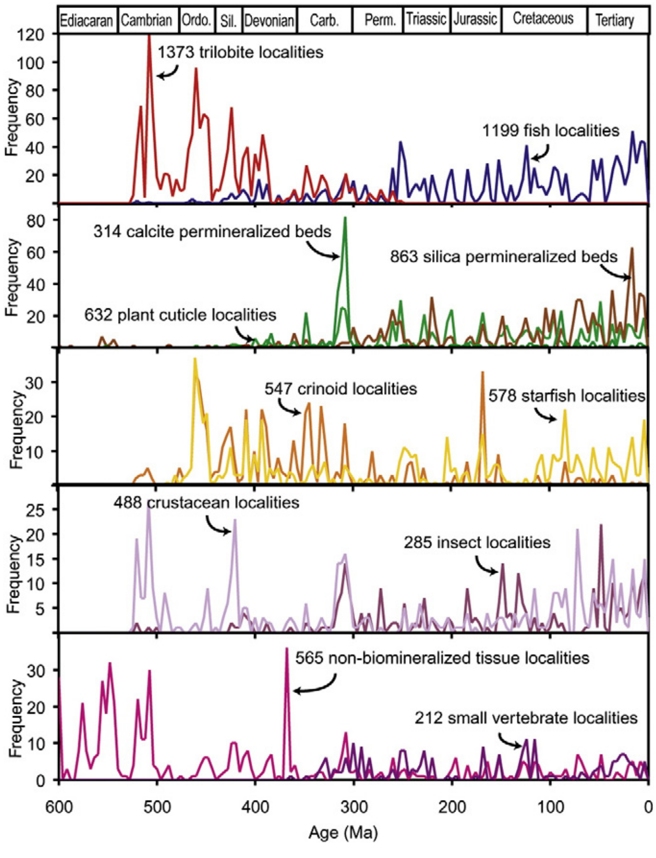

Fig. 7. Geological ages of exceptionally preserved fossils. Bin interval is 4 m yr (for sources, example taxa, and localities see Supplementary Material).

also contain articulated starfish (Hess et al., 1999). As for taphostratigraphic correlation of Triassic marine and non-marine fish (Fig. 3) and Cambrian marine trilobites and non-marine aglaspids (Fig. 5), entirely non-marine insect and plant modes overlap with entirely marine echinoderm and trilobite modes. Each mode represents many localities around the world, formed both on land and in the sea, and thus records a spike in global fossil preservation.

Horizons of exceptional fossil preservation (Table 4) correspond well with global events independently indicated by lithological and geochemical evidence (Table 3). Many of the exceptional fossil levels are close to stage boundaries. For example, the Grenzbitumenzone is a Swiss-Italian black shale with articulated fossil fish and crustaceans at the boundary (*Grenz*) of the Anisian and Ladinian stages (Furrer, 1995). The big five mass extinctions of late Ordovician, Frasnian–Famennian, Permian–Triassic, Triassic–Jurassic, and Cretaceous–Tertiary (Peters and Foote, 2002) are all represented with localities of exceptional preservation (Table 4). Lesser extinction events of the Paleozoic, such as the Kačák event, are also represented (Talent et al., 1993; Retallack et al., 2006). All Cretaceous oceanic anoxic events (Gradstein et al., 2004) are represented, including the Aptian *Selli* event (Table 4). Some exceptional fossil preservation peaks are coincident with carbon isotope anomalies, and interpreted as evidence of global redox crises (Talent et al., 1993; Zhou et al., 2003; Retallack et al., 2006). Exceptional fossil preservation also coincides with spikes of atmospheric CO_2 significantly higher than now, as estimated from stomatal index of fossil leaves, with the *caveat* that cuticular preservation of plants is required for such estimates. All 20 episodes of transient CO_2 spikes within the last 300 myr recognized from evidence of stomatal index by Retallack (2009a) are listed in Table 4. Thus global greenhouse crises may have included other environmental changes that expanded opportunities for exceptional preservation of fossils.

All 40 transient spikes of warm-wet paleoclimates in aridlands over the past 300 myr, apparent from degree of weathering and depth of carbonate in calcareous paleosols (Retallack, 2009a,c), also are listed in Table 4 and cross-correlated with spikes of exceptional fossil preservation in Fig. 8. Thick sequences of calcareous paleosols provide suitable long-term paleoclimatic records to compare with compilations of exceptional fossil localities, because they include thousands of paleosols with sufficient temporal resolution to detect abrupt increases in rainfall, temperature and CO_2 levels. Temperature and CO_2 estimates are known from only dozens of paleosols because of the expense of analysis (Retallack, 2009c; Retallack et al., 2009), but time series for depth to calcareous nodules (Bk horizon) in paleosols is available for the past 300 Ma from 3718 paleosols in Utah and Montana, USA (Retallack, 2009a), and for 405–542 Ma from 1086 paleosols in Australia (Retallack, 2009b). Depth to Bk shows numerous anomalies of unusually deep carbonate reflecting transient spikes in soil respiration (Retallack, 2009c) and mean annual precipitation (Retallack, 2005a) in aridlands, and these spikes have been correlated explicitly with times of widespread exceptional fossil preservation (Retallack, 2009a,b). The list of such times presented here (Table 4) will not be the last word on such events, because paleosol studies (Retallack, 2009a,b) fail to reveal some events apparent now from taphostratigraphy (Figs. 3 and 5). Like geological time scales (Gradstein et al., 2004, already supplanted by Ovtcharova et al. 2006; Kaufmann, 2006; Sadler et al. 2009) the schedule and definition of unusually widespread preservational events will require continuing refinement.

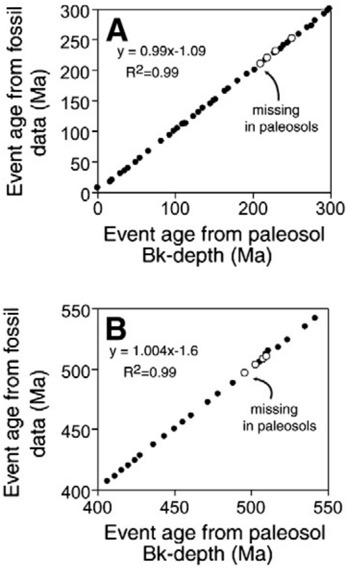

Fig. 8. Correlations between event ages determined in this study from biostratigraphic and taphostratigraphic data (y-axes) and event ages determined from local age models of paleosols (x axes) in Utah and Montana (A, after Retallack 2009a) and in Australia (B, after Retallack 2009b).

Other global change indicators also show peaks comparable with those of the preservation record documented here (Fig. 7), but require further development before comparison. Comprehensive isotopic data (for example Veizer et al., 2000) are currently tied to outdated time scales and binned to an average geological age for a formation, rather than exact stratigraphic level and explicit age models like Cenozoic records (Zachos et al., 2001). Mass balance models of atmospheric CO_2 and O_2 through the last 500 Ma have temporal steps of 10 m yr (Berner, 2006) and can be matched by degrading records similar to those shown here with 10 point running means (Retallack, 2001).

4. Greenhouse preservation hypothesis

The pronounced alignment of times of exceptional preservation (Table 4), atmospheric CO_2 and warm-wet paleoclimatic spikes (Fig. 8) is unlikely to be a coincidence. A greenhouse preservation hypothesis is now proposed in which spikes in atmospheric CO_2 coincide with widespread exceptional preservation, and both are consequences of transient global perturbations such as massive flood basalt eruptions, methane outbursts, and large extraterrestrial impacts (Retallack, 2001). Environmental changes observed with ongoing global crisis of greenhouse warming due to human burning of fossil fuels (Solomon et al., 2007) are remarkably similar to paleoenvironmental perturbations inferred from exceptional fossil deposits (Table 3). Is modern global greenhouse warming an analog for episodes of widespread exceptional fossil preservation in the past? The following paragraphs discuss environmental consequences of global warming and comparable features of exceptional fossil deposits in more detail. The possibility that the divergent phenomena of exceptional fossil sites could have a common cause in greenhouse crises of the past is a new hypothesis worthy of further attention, because past events could be a key to understanding future climate change.

4.1. Ocean anoxia

Global warming and other human modifications of the environment are considered partly responsible for the current spread of marine dead zones of mass mortality (Diaz and Rosenberg, 2008). Unprecedented upwelling due to unusually warm water and strong seasonal onshore breezes since 2002 have brought dead zones into shallow water three or four times each summer in Oregon, USA (Hales et al., 2006; Pierce et al., 2006; Barth et al., 2007). During these summer anoxic events, waves swashing onto central Oregon beaches are extraordinarily green with phytoplankton blooms, and deliver dead and dying crabs, rather than the usual molted carapaces. Underwater cameras revealed dead fish and crabs over a wide area of the central Oregon continental shelf (Grantham et al., 2004), but during intervening weeks and winter months the anoxic zone retreats to deeper water allowing biological recolonization (Barth et al., 2007).

Similar hypoxia in lakes, and estuaries is blamed on eutrophication induced by human pollution of phosphates, nitrates and organic matter (Breitburg et al., 2009).

Pyritic black shales (Furrer, 1995), gaping and back-arched fossil fish (Grogan and Lund, 2002), and dysaerobic invertebrate fossils (Knoll et al., 2007; Twitchett, 2007) in many exceptionally preserved fossil assemblages are evidence of similar past ocean anoxic events. Milankovitch time scales of recurrence of anoxia are indicated by cyclical sediments (Furrer, 1995; Olsen et al., 1996), and intraseasonal recurrence is recorded by exceptional fossils of different age cohorts of articulated fossils in the same beds (Hughes and Chapman, 1995). In the past as well as the present, lethal conditions of mass mortality recurred on seasonal and astronomical time scales.

4.2. Ocean acidification

Another environmental problem attributed to current rise of atmospheric CO_2 is oceanic acidification, which is considered responsible for a 14.2% decline in Australian coral calcification between 1990 and 2005, a decline unprecedented in at least the past 400 yr (De'ath et al., 2009). Acidification is not the only agent of coral demise, because temperature, irradiance, and perhaps infection, have led to expulsion of zooxanthellae (coral bleaching) and even death of coral polyps (Brown, 1997). Nevertheless, average ocean water pH has dropped from 8.2 to 8.1 since preindustrial times, and is expected to decline to 7.7 or 7.8 under projected atmospheric CO_2 of about 800 ppmv expected by 2100 (Orr et al., 2005). Aragonite is approximately 50% more soluble than calcite, and may become undersaturated in the surface ocean by 2100, with profound consequences for aragonite corals and molluscs, but with significant effects also on calcite nannoplankton and coralline algae (Doney et al., 2009).

Direct evidence of past oceanic decalcification comes from two German Lagerstätten, Solnhofen (Barthel et al., 1978) and Holzmaden (Kauffman, 1981), which both yield ammonites with shells completely dissolved within their preserved organic periostracum. These flattened ghosts of uncracked shells lie within single laminae, with no mold or mineral (calcite or pyrite) fill of the formerly inflated shell, so were dissolved in the sea floor before the next seasonal lamina was deposited. Marine acidification is a potential mechanism of mass mortality not only at Solnhofen and Holzmaden, but in numerous Lagerstätten (Seilacher et al., 1985; Mikulic et al., 1985). Coral reefs show a remarkably punctuated fossil record, disappearing at numerous times of life crisis and exceptional preservation (Table 4), only to be reconstituted anew, sometimes from unskeletonized ancestors (Copper, 2002; Stanley, 2003). Reefs at times of life crisis and exceptional preservation are dominated by stromatolites, thrombolites (Pruss and Bottjer, 2004), or sponges (Barthel et al., 1978).

4.3. Sea level rise and melting ice caps

Retreating glaciers (Moore et al., 2009), melting permafrost (Froese et al., 2008), Arctic ice thinning (Perovich and Richter-Menge, 2009), and calving Antarctic ice shelves (Braun et al., 2009) are the most persuasive evidence of current global warming expected from the rise of anthropogenic CO_2 in the atmosphere. Water now stored in continental ice as well as thermal expansion of the ocean is expected to bring rising sea levels in the near future, although that signal is difficult to detect among tidal, current and climatic oscillations. Measured sea-level rise from January 1870 to December 2004 was 195 mm, for a twentieth century rate of 1.7 ± 0.3 mm yr^{-1} and acceleration of sea level rise of 0.013 ± 0.006 mm.yr^{-2}. Extrapolated to 2100 this will give 0.28–0.34 m rise (Church and White, 2006), consistent with model projections (Solomon et al., 2007).

To paraphrase Miall's (1992) facetious comment on correlation using sequence-stratigraphic sea-level curves, there does seem to be a sea level rise for every occasion, that is, for every event of exceptional fossil preservation (Retallack, 2009a). The logical difficulty of foolproof correlation of isolated cases is obviated here by correlation of multiple examples (Figs. 3E and 5E). Independent lithological evidence has long indicated that both Jurassic German Lagerstätten of Solnhofen (Barthel et al., 1978) and Holzmaden (Kauffman, 1981) are at the peak of local marine transgression. Assemblages of articulated crinoids and starfish in the Permian of the Sydney Basin (Willink, 1979, 1980) are lower Wuchaipingian (259 Ma), upper Kungurian (272 Ma), and middle Artinskian (280 Ma), which were times of elevated CO_2, high temperature, humid climate, and glacial retreat judging from independent evidence of stomatal index, paleosols, glendonites and glacial sediments (Retallack, 2005b).

4.4. Increased storm and drought magnitude

Between 1981 and 2006 the intensity of the strongest (above 70th percentile) tropical winds increased (Eisner et al., 2008), as did the magnitude of tropical rainfall events (Allan and Soden, 2008). Models confirm that the magnitude, if not frequency (Knutson et al., 2008), of storms is expected to increase in a more active hydrological cycle of coming anthropogenic greenhouse, along with heightened local seasonality, droughts and fire (Solomon et al., 2007).

Storm intensity is a key variable in burial of exceptional fossils to depths where subsequent aerobic decomposers and burrows cannot reach them, and storm deposits are recognized in many obrution Lagerstätten (Seilacher et al., 1985). Seasonal drought is also a common precondition for extensive wildfires, which can produce beautifully charcoalified flowers (Friis et al., 2006) and leaves (Plotnick et al., 2009). Seasonal drought has been inferred for duckbill dinosaur mummies (Carpenter, 2007), but the famous thylacine mummy (Partridge, 1967) found in a cave in the Nullarbor Plain was always in a dry climate. The Neolithic iceman “Otzi” has been called a “mummy” (Rollo et al., 2002), but was not dried, rather frozen like Pleistocene bison (Guthrie, 1990) and mammoth (Bocherens et al., 1996). Thus whether these creatures succumbed to hypothermia in a perennially frigid climate or were caught in a freezing storm is uncertain (Guthrie, 1990). Mummified and frozen fossils are uncommon and were not tabulated here.

4.5. Intensified chemical weathering

Chemical weathering increases with global warming have not yet been observed because measurable changes in weathering take more than a few decades. Nevertheless, increased chemical weathering with ongoing anthropogenic global warming has been predicted from comparisons of soils at different altitudes, and thus different temperatures, within North Carolina (Velbel, 1993) and Iceland (Gislason et al., 2009). The Iceland study for example, predicts a 4–14% increase in chemical weathering for every degree Celsius of temperature increase.

Studies of paleosols in high paleolatitude sequences of Permian age near Sydney (Retallack, 2005a), and Early Eocene age near Canberra, Australia (Retallack, 2008a), reveal transient increases in base depletion, clay formation and other indices of chemical weathering at times of exceptional fossil preservation recognized here. Furthermore, these were times when temperate soils (Ultisols) and tropical soils (Oxisols) spread north and south to the polar circles, greatly expanding land area under intense chemical weathering. These well drained kaolinitic and clayey paleosols are anomalous for their sequences (Retallack, 1997, 2008a). Intensified weathering on land delivers cationic nutrients to the sea, which in turn feed plankton blooms and hypoxia in lakes and seas, creating black shales that host exceptional fossil beds (Algeo et al., 1995). Human nitrogenous, phosphatic and organic pollution (Breitburg et al., 2009) is not the only mechanism for aquatic eutrophication and hypoxia. In addition, increased silica, bicarbonate, phosphate and sulfate in solution would have promoted cellular permineralization and nodularization of fossils (Martin, 1999; Gaines et al., 2005).

4.6. Biotic invasions and biodiversity loss

Humans have assisted biotic invasions deliberately in the case of European agroecosystems imposed on Australia (Flannery, 1994), and accidently in the case of Russian zebra mussels (*Dreissenia polymorpha*) in the Great Lakes, USA (Sousa et al., 2009), with consequent loss of endemic biodiversity. The Balkan region of Europe is the source of many cosmopolitan agricultural weed species now dispersed as far afield as Australia, New Zealand and Oregon (Retallack, 2008b). With ongoing global warming, poleward migrations are already apparent in the Arctic, and include microbial pathogens (Mulder et al., 2008), plant species (Alsos et al., 2007), and biomes (MacDonald et al., 2008).

Fish beds (Bonde 2008) and extraordinary pyritized floras (Collinson, 1983) of the Paleocene–Eocene (55 Ma) thermal maximum and CO_2 greenhouse (Retallack, 2008a) formed at a time of notable biotic invasions broadly similar to modern trends. Artiodactyl and primate mammals migrated from Asia to North America via warm Arctic regions (Clyde et al., 2003). Subtropical plants migrated northward into Wyoming temperate floras (Wing et al., 2005), and their leaves show increased insect damage (Currano, 2009). Comparable invasions at other times of warm-wet climate may explain such extraordinarily cosmopolitan taxa as the Cambrian trilobite *Leiopyge laevigata* (504 Ma) and Ordovician graptolite *Nemagraptus gracilis* (461 Ma), which allow international biostratigaphic correlation because they appear among faunas of endemic taxa (Retallack, 2009b).

5. Conclusions

Graphic correlation of horizons of exceptional preservation of fish and trilobites in different parts of the world indicate that such preservation can be correlated over wide areas and was irregularly spaced in time (Figs. 3 and 5). Compilation of geological ages of exceptional fossil deposits also reveals a highly uneven distribution of these remarkable assemblages through time (Fig. 7). These data suggest that certain times, as well as places, were conducive to exceptional preservation of fossils.

Times of especially widespread exceptional fossil preservation were also times of stage boundaries, mass extinctions, oceanic anoxic events (Table 4), carbon isotope anomalies, spikes of high atmospheric CO_2, and transient warm-wet paleoclimates in aridlands (Retallack, 2009a). The ongoing greenhouse crisis is a useful analog for past episodes of exceptional fossil preservation, bringing a constellation of factors that promote exceptional fossil preservation: obrution, eutrophic and septic anoxia, microbial sealing, salinization, permineralization, authigenic cementation, and mummification (Martin, 1999). Transient greenhouse crises of the geological past were not human induced, and have been blamed on bolide impact, giant volcanic eruptions and large igneous intrusions (Retallack, 2009a), but entailed many environmental changes similar to those now in the news. Warmer and more nutrient rich waters supplied by deep chemical weathering may have led to eutrophication and anoxia of aquatic ecosystems (Algeo et al., 1995). Warmer and wetter air created more severe storms (Seilacher et al., 1985), droughts and fires (Plotnick et al., 2009), and enabled the poleward spread of plants and animals (Clyde et al., 2003; Wing et al., 2005). Increased acidity of natural waters from high atmospheric CO_2 may have curtailed growth of aragonitic shells and corals (Doney et al., 2009). Widespread biotic disruptions may have led to more cosmopolitan biota of reduced biodiversity (Retallack et al., 2006). From such episodes of greenhouse crisis may have come our most stunning visions of ancient life. Furthermore, greenhouse transients of the past may have more to tell us about the future.

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