Are Insects Heading Toward Their First Mass Extinction? Distinguishing Turnover From Crises in Their Fossil Record

Sandra R. Schachat1,5,6 and Conrad C. Labandeira2,3,4

1Department of Geological Sciences, Stanford University, Stanford, CA 94305, 2Department of Paleobiology, Smithsonian Institution, Washington, DC 20033, 3Department of Entomology, University of Maryland, College Park, MD 20742, 4College of Life Sciences, Capital Normal University, Beijing 100048, People’s Republic of China, and 5Corresponding author, email: schachat@stanford.edu

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Abstract

Time and again, over hundreds of millions of years, environmental disturbances have caused mass extinctions of animals ranging from reptiles to corals. The anthropogenic loss of species diversity happening now is often discussed as the ‘sixth mass extinction’ in light of the ‘Big Five’ mass extinctions in the fossil record. But insects, whose taxonomic diversity now appears to be threatened by human activity, have a unique extinction history. Prehistoric losses of insect diversity at the levels of order and family appear to have been driven by competition among insect lineages, with biotic replacement ensuring minimal net losses in taxonomic diversity. The end-Permian extinction, the ‘mother of mass extinctions’ in the seas, was more of a faunal turnover than a mass extinction for insects. Insects’ current biotic crisis has been measured in terms of the loss of abundance and biomass (rather than the loss of species, genera, or families) and these are essentially impossible to measure in the fossil record. However, should the ongoing loss of insect abundance and biomass cause the demise of many insect families, the current extinction event may well be the first sudden loss of higher-level insect diversity in our planet’s history. This is not insects’ sixth mass extinction—in fact, it may become their first.

Key words: biodiversity, Cretaceous, paleontology, paleoentomology, Permian

Insects have been largely neglected in studies of the current extinction crisis. Studies of extinction risk are overwhelmingly biased in favor of vertebrates, particularly birds and mammals (Ceballos et al. 2017). The current extinction crisis is often referred to as ‘the sixth extinction’ (Barnosky et al. 2011), a reference to the ‘Big Five’ mass extinctions that have been identified in animals’ fossil record: the end-Ordovician event at 444 million years ago (Ma), the Late Devonian event around 372 Ma, the end-Permian event at 252 Ma, the end-Ordovician event at 444 million years ago (Ma), the Late Devonian event around 372 Ma, the end-Permian event at 252 Ma, the end-Triassic event at 201 Ma, and the end-Cretaceous event at 66 Ma (Jablonski 1994, Raup 1994). Because the fossil record of animals is biased in favor of marine invertebrates with hard body parts, such as brachiopods, bivalves, and gastropods (Kidwell and Flessa 1996), studies that compare the current extinction crisis with the Big Five mass extinctions tend to focus on shelly marine invertebrates due to their extensive fossil record and on vertebrates due to the wealth of available data on extant lineages (Barnosky et al. 2011). Insects, which do not live on the ocean floor, do not have mineralized shells, and are not ‘charismatic megafauna’, do not lend themselves particularly well to comparisons between the current extinction crisis and the Big Five mass extinctions. However, insects’ tremendous ecological, economic, and aesthetic importance (Scudder 2017) means that their plight cannot be ignored.

As of July 2020, the Red List of Threatened Species maintained by the International Union for Conservation of Nature and Natural Resources contains evaluations for 91% of described mammal species, 100% of described bird species, and fewer than 1% of described insect species (IUCN 2020). While various studies have focused on genera (Salcido et al. 2020), families (Houghton and Holzenthal 2010), guilds (Lister and Garcia 2018), and communities (van Klink et al. 2020), studies and media coverage of insect decline often focus on individual species that are not representative of larger clades. The monarch butterfly Danaus plexippus (Linnaeus, 1758) (Lepidoptera: Nymphalidae) is well studied (Gustafsson et al. 2015, Thogmartin et al. 2017) but, as one of a handful of butterfly species that migrate across long distances (Gilbert and Singer 1975), offers few clues to the potential extinction risks that other butterflies face. The honey bee Apis mellifera Linnaeus, 1758 (Hymenoptera: Apidae) has also received tremendous attention (Suryanarayanan and Kleinman 2013, Staveley et al. 2014) but, as a domesticated eusocial species that is often transported by humans on a semiannual basis and has been introduced in much of its current range, does not necessarily represent other bee species. The cave beetle Anophthalmus hitleri Scheibel, 1937 (Coleoptera: Carabidae), named in honor of Adolf Hitler and
currently endangered because neo-Nazis pay large sums of money for poached specimens (Jóźwiak et al. 2015), provides no clues to the plight of other ground beetle species.

Because extinction history and extinction risk remain unknown for the vast majority of insect species (Dunn 2005, Sánchez-Bayo and Wyckhuys 2019, Didham et al. 2020), changes in abundance and biomass—rather than taxonomic diversity—are the most accessible clues to global patterns of insect decline (Shortall et al. 2009, Schuch et al. 2012, van Klink et al. 2020). Recent studies, primarily spanning temperate latitudes, have found precipitous declines in insect abundance and biomass, suggesting that insects are in the midst of an anthropogenic extinction crisis (Hallmann et al. 2017, Lister and Garcia 2018). Because a small fraction of species can dominate the abundance and biomass in their community, changes in the severity of extinction risk at the species level cannot be extrapolated from abundance and biomass data.

The sudden increase in concern about insect extinction raises the question of whether the current crisis can be compared to events in the fossil record, as has been done for many vertebrates and for marine invertebrates. Indeed, the fossil record of insects contains a cataclysmic extinction (of the paleopterous superorder Palaeodictyopteroidea) during one of the Big Five—a loss reminiscent of the extinctions of trilobites, ammonites, and nonavian dinosaurs (Labandeira 2005). At least one insect guild also experienced turnover during the most recent of the Big Five mass extinctions, the end-Cretaceous event (Donovan et al. 2014, Labandeira et al. 2016b).

However, three of the five largest extinctions identified in the fossil record of insects—at the Late Pennsylvanian (approximately 304 Ma), Late Jurassic (approximately 155 Ma), and later Early Cretaceous (approximately 113 Ma)—are uncorrelated with mass extinctions in other taxa (Labandeira 2005). The worst extinction events for clams, sharks, and tetrapods like us are not necessarily the worst events for insects, and vice-versa. Comparisons of the extant entomofauna with extinct entomofaunas should be made with caution, limited to inferences permitted by the data available from the fossil record.

**Strengths of the Insect Fossil Record**

The fossil record of insects provides considerably more information about insects’ evolutionary history than could be gleaned from inferences limited to extant taxa and their relationships. The earliest verified occurrences of relevant fossil insect taxa are used to time-calibrate divergences among extant lineages (Kohli et al. 2016, Evangelista et al. 2017). When incorporated as terminals, fossils can resolve conflicts among topologies generated from extant taxa alone (Engel 2001).

The fossil record sheds light on the timing of behavioral advances in addition to divergence times. For example, extant plant–insect interactions often occur between plant and insect lineages of very different ages, and insects can switch hosts over time (Vea and Grimaldi 2016). These phenomena raise the question of when those interactions originated—a question that only fossils can answer (Ren et al. 2009, Winkler et al. 2010, Schachat and Labandeira 2015, Peris et al. 2017). Eusociality provides another example of this type of insight: termites and ants are by far the two most speciose insect groups that are strictly eusocial, and they diversified around the same time despite having originated 30–40 Myr apart and belonging to very distantly related higher taxa (Engel et al. 2016, Barden 2017, Barden and Engel 2019). Other insect fossils demonstrate the ancient origins of behaviors ranging from camouflage (Pérez-de la Fuente et al. 2012, Wang et al. 2012, 2016a) to parental care (Laza 2006, Cai et al. 2014, Wang et al. 2015a; Gao et al. 2019).

Fossils also shed light on bizarre and fascinating episodes of insect history that have left no trace in the extant fauna. Over 100 million years ago, a number of insect groups—first Paleoptera, then neopterous Hemimetabola, then Holometabola—reached body sizes that exceed those of any extant insect (Grimaldi and Engel 2005). Early representatives of many insect groups, from ants (Barden and Grimaldi 2012) to Pterygota as a whole (Pecharová et al. 2015), did not resemble their extant relatives. Some extinct fossil groups also exhibit remarkable convergence with very distantly-related extant taxa (Labandeira et al. 2016c), raising the sorts of questions about contingency and inevitability that have long fascinated paleontologists (Sepkoski 2017).

**Limitations of the Insect Fossil Record**

The fossil record of insects contains fewer genera and species than one might expect given their abundance and the hundreds of millions of years that have passed since they originated. Mineralized body parts, like shells and teeth, are most easily preserved as fossils. A typical insect exoskeleton is not nearly as thick or as durable as a clam’s shell or as a vertebrate’s tooth. Although insects have a far richer fossil record than, for example, earthworms—which lack mineralized body parts and do not live in microhabitats that facilitate fossilization—the fossil record of insects contains larger temporal and taxonomic gaps than the fossil records of vertebrates and of shelled, aquatic invertebrates (Benton and Simms 1995, Kidwell and Flessa 1996).

Barely 46,000 insect specimens have been described from the entire fossil record (Clapham et al. 2016), amounting to only 124 individuals per million years since the earliest evidence of winged insects (Pterygota) (Prokop et al. 2005, Haut and Haug 2017, Schachat et al. 2018). For a modern perspective, the 124 described fossil insects per million years from across the globe falls within the range of insect species diversity in a typical home in Raleigh, North Carolina (Bertone et al. 2016). Put another way, the less than 50,000 described insect specimens in the entire fossil record from the whole planet approximately equals the number of specimens collected by interception traps in a single study of modern arthropod diversity (Basset and Arthington 1992).

Due to the incompleteness of the insect fossil record, the lines of inquiry pursued with fossil marine invertebrates are not always feasible with fossil insects. The current decline of animal groups such as bivalves and vertebrates is typically compared to the Big Five mass extinctions with one of two goals. The first of these goals is to determine whether the current crisis could reach the severity of any of the Big Five mass extinctions (Barnosky et al. 2011). The second goal is to compare the patterns and causes inferred from the Big Five to the patterns and causes observed in the current crisis (Harnik et al. 2012, Payne and Clapham 2012, McCallum 2015). Neither of these goals can be achieved with the insect fossil record.

In addition to being sparse, the insect fossil record is fragmentary across space and in time. Most described insect fossils come from ‘konzentrat Lagerstätten’, or fossil assemblages where the depositional conditions permitted vast numbers of insects to be preserved. Here, we arbitrarily define konzentrat Lagerstätten as assemblages with 100 or more described insect specimens. Fossil insects have been described from approximately 2,500 assemblages and only 90 of these assemblages are konzentrat Lagerstätten (Fig. 1). However,
66% of all described insect occurrences in the fossil record come from these 90 konzentrat Lagerstätten.

The 90 konzentrat Lagerstätten in the insect fossil record cannot provide complete coverage of insect taxa for the past 320 million years. Konzentrat Lagerstätten are unevenly distributed in time: the longest gap between successive konzentrat Lagerstätten is 22 million years, between the 218-million-year-old Ipswich Lagerstätte and the 196-million-year-old Issyk-Kul Lagerstätte. In contrast, there are eight konzentrat Lagerstätten from the last 126,000 yr alone (Titusville (the United States), Omolon (Russia), Upton Warren (the United Kingdom), Malaya Konkovaya River (Russia), Thrupp House Farm (the United Kingdom), Magnolia Bluff (the United States), Ziegler Reservoir (the United States), Kalaloch (the United States)), encompassing the latest Pleistocene and Holocene epochs. These Lagerstätten occur within ‘unlithified’ sediments that have not hardened into rocks and that therefore have a low probability of persisting in the rock record millions into the future (Clapham et al. 2016). The Priabonian Stage of the Eocene Epoch, which lasted for four million years (37.8–33.9 Ma), also contains eight konzentrat Lagerstätten, due primarily to the preservation of amber near the Baltic Sea (Bembridge Marls (United Kingdom), Bitterfeld amber (Germany), Rovno amber (two Lagerstätten in Ukraine), Baltic amber (one Lagerstätte each in Russia, Poland, Lithuania, and Denmark)].

The distribution of konzentrat Lagerstätten is even more inconsistent across space than time. The vast majority of konzentrat Lagerstätten—90%—occur at paleolatitudes over 20° from the paleoequator, and over half of konzentrat Lagerstätten—52%—occur at paleolatitudes over 43° from the paleoequator (Fig. 1). Not a single konzentrat Lagerstätte occurs at paleolatitudes between 10° and 20° from the paleoequator. This overwhelmingly temperate distribution of fossil insects is comparable with that of fossil plants and contrasts with the primarily equatorial distribution of nonavian dinosaurs (Rees et al. 2004). The dearth of tropical and subtropical konzentrat Lagerstätten is troubling because the richness of extant insect species is highest, and disproportionately undescribed, in the tropics (Stork 2018).

Because fossil insects are relatively rare and occur so unevenly in time and space, the severity of insect extinctions in deep time is remarkably difficult to measure. This renders the timing of insect extinctions similarly difficult to constrain. These limitations preclude studies of whether the current insect decline is comparable in magnitude to any of the Big Five and prevent precise determinations of the causes of insect extinctions in the fossil record.

Abundance and biomass data are not available for fossil insects (Fig. 2). For marine animals that live in a circumscribed depositional setting, it is possible to measure changes in animal abundance through time. If animals become scarce or absent in such deposits, it can be inferred that these animals really were scarce or absent in the particular environment in which those deposits formed (Payne et al. 2006). The link between decreased abundance and increased extinction risk, central to many studies of the extinction crisis in living insects, has also been examined for marine animals in the fossil record (Payne et al. 2006, Simpson and Harms 2009). However, the fossil record of insects does not permit such inferences. This is not only because the fossil record of insects is relatively depauperate and uneven compared to that of many marine taxa, but also because insects overwhelmingly tend not to live in the sorts of settings, such as lake basins, where fossils most easily form. If a lake deposit containing insect fossils were studied in sufficient detail to determine changes in insect abundance through time, the apparent changes could reflect true changes in insect abundance near the lake but also could be confounded by abundance in nearby habitats. For example, if insects are typically swept into a lake by flash floods (Smith 2012), a decrease in flash flooding over time would cause a decrease in the number of insects brought into this depositional setting.

**Biases Inherent to the Insect Fossil Record**

The fossil record is biased toward certain orders and families, and thus to a lesser extent toward certain insect species (Smith 2012). The biases discussed in this section are inherent to the fossil record: there are biases as to which taxa are formally described in the fossil record. Since the fossil record is biased toward certain taxa, there are biases as to which taxa are formally described in the fossil record. Because the fossil record is biased toward certain taxa, there are biases as to which taxa are formally described in the fossil record. This is not only because the fossil record is biased toward certain taxa, but also because insects overwhelmingly tend not to live in the sorts of settings, such as lake basins, where fossils most easily form. If a lake deposit containing insect fossils were studied in sufficient detail to determine changes in insect abundance through time, the apparent changes could reflect true changes in insect abundance near the lake but also could be confounded by abundance in nearby habitats. For example, if insects are typically swept into a lake by flash floods (Smith 2012), a decrease in flash flooding over time would cause a decrease in the number of insects brought into this depositional setting.

**Fig. 1.** The ages and paleolatitudes of the 90 konzentrat Lagerstätten that contain at least 100 described insect occurrences. The points representing each Lagerstätte are semitransparent, such that darker points represent multiple Lagerstätten with nearly identical ages and paleolatitudes.
described, plus biases as to which taxonomic experts work on the material and which taxa journals are interested in publishing. One overarching question that arises from this series of biases is whether they cancel each other out, as was found to be the case in a canonical study of trilobites (Adrain and Westrop 2000), or reinforce each other. The answer to this question may vary with the taxonomic and temporal scale of the data considered.

The need for an insect to live near a body of water—or, alternatively, in a specific microhabitat such as a tree surface that exudes certain resins—causes a bias in the insect fossil record: habitat. Although a number of tree species exude resin that has been preserved as amber (Labandeira 2014a), many insect species do not live near these trees. The major amber deposits are formed from the resin of vastly different trees, ranging from gymnosperms to angiosperms, introducing another bias (Penney 2010). Because strata typically form in basins such as bodies of water, higher-altitude habitats and environments lacking internally drained ponds and lakes provide vanishingly few opportunities for fossilization. Paleobotanists have extensively discussed the role of upland and dryland habitats in plant evolution (Chaloner 1958, Falcon-Lang and Bashforth 2004, Thomas and Cleal 2017, Cleal and Cascales-Miñana 2019), but this topic is considered for insects only rarely (Shcherbakov 2008).

Within a given habitat, there are also biases in the body parts most likely to be preserved. The thorax, abdomen, antennae, legs, palps, and other structures consist of multiple segments that can easily become disarticulated in transit to a depositional setting that would permit fossilization (Smith 2000). Wings are the insect body part that fossilize most easily. Indeed, the two earliest definitive fossils of winged insects are isolated wings (Brauckmann and Schneider 1996, Prokop et al. 2005), as is common for many insect taxa throughout earth history.

Certain morphological features cause taxonomic biases. Lepidoptera (moths and butterflies) have a notoriously incomplete fossil record (Sohn et al. 2015), due in large part to their characteristic thickly scaled wings and delicate bodies. The scales cause wings to float, preventing them from sinking into sediments at the bottom of bodies of water where they can be buried and preserved. Lepidoptera are one of the five overwhelmingly speciose insect orders in the modern fauna (Grimaldi and Engel 2005), but their fossil record contains only 2.6% as many described specimens as that of Coleoptera (beetles), 4.5% as many described specimens as that of Diptera (true flies), 6.3% as many described specimens as that of Hymenoptera (sawflies, wasps, ants, and bees), and 6.8% as many described specimens as that of Hemiptera (aphids, whiteflies, scale insects, and bugs).

Because the smallest insect bodies and body parts are those that can most easily fit into a drop of tree resin or become completely buried in a body of water, the insect fossil record is overwhelmingly biased against large taxa (Labandeira 2014a). Gigantic dragonfly relatives such as the Meganisoptera and Palaeodictyopteroidea, present from the Middle Pennsylvanian to the Early Permian (315–272 Ma), are among the most spectacular of fossil insects but are extremely rare. Indeed, although paleopterous, orthopteroid, and holometabolous groups independently evolved to be larger than any insect alive today, there are only 54 wings known in the entire fossil record that are longer than those of any extant insect species (Clapham and Karr 2012). Furthermore, four described fossilized wings measure at least 30 cm but there are no described wings between 26 and 30 cm.

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**Fig. 2.** Data from the fossil record can only be compared at the coarser taxonomic scales of order and family, whereas modern ecological data allow comparisons at the genus, species, and especially the population scale. All icons are from PhyloPic.org. *Mantoida nitida* Newman, 1838 (Mantodea: Mantoididae), license at http://creativecommons.org/publicdomain/mark/1.0/. *Trachypachus gibbai* Leconte, 1861 (Coleoptera: Trachypachidae) by T. Michael Keesey and Yves Bousquet, and *Somatochlora tenebrosa* (Say, 1839) (Odonata: Corduliidae) and *Eristalis tenax* (Linnaeus, 1758) (Diptera: Syrphidae) by Gareth Monger, license at http://creativecommons.org/licenses/by/3.0/. *Hyalophora cecropia* (Linnaeus, 1758) (Lepidoptera: Saturniidae) by Mali'o Kodis and Jim Vargo, license at http://creativecommons.org/licenses/by-nc-sa/3.0/.
in length, although insects with 30-cm wings presumably had ancestors with wing lengths in this range.

**Publication Biases**

The smallest insects, which fossilize most easily (Smith 2012), are the most difficult to study, with minor exceptions of certain amber deposits (Labandeira 2014a) and compression–impression deposits occurring in unusual environments (Greenwalt et al. 2014). Their body size makes them difficult to notice, whether at a mountainside outcrop or in an amber specimen, and renders them difficult to view and image in a laboratory setting. The small size of a typical fossilized insect also reduces the number and quality of characters available for analysis in a taxonomic study. This ultimately leads to a bias toward medium-sized insects, which are small enough to fossilize relatively intact but large enough to be noticed by researchers and display an informative suite of apomorphies.

There also is a bias toward description of specimens that represent the first and last occurrences of higher-level taxa (Schachat et al. 2019). First occurrences are of unparalleled importance for time-calibration of divergences in phylogenies (Kohli et al. 2016, Evangelista et al. 2017) and last occurrences inform debates about when extinct taxa disappeared (Béthoux et al. 2010, Shcherbakov 2011). Because of this publication bias favoring first and last occurrences, the described fossil history of many groups contains large gaps between very early and very late occurrences. For example, the extinct family Lophioneuridae, related to Thysanoptera, has described fossil specimens from the first 32 million years of its known history and 11 described fossil specimens from the last 77 million years of its known history, but not a single described fossil specimen from the intervening 91 million years.

Because of the paleoentomological focus on systematics, few publications about fossil insects focus on faunas (Solórzano Kraemer 2007, Penney 2010, Guénard et al. 2015) rather than taxa. Publications typically describe new genera and species (Nel and Jarzembowski 2019, Zhao et al. 2019), or, less commonly, describe first occurrences of higher-level taxa (Haug et al. 2015, Zheng et al. 2018, Montagna et al. 2019). Only a handful of paleoentomological studies have quantified clades’ relative prevalence within a deposit (Solórzano Kraemer 2007, Grimaldi et al. 2010, Perrichot et al. 2010) as is often done for marine invertebrates (Hsieh et al. 2019). The commercial operations that mine amber from major deposits (Penney 2010) also obstruct the methods for conducting a paleontological census. As a result, only a small fraction of specimens from each deposit are mentioned in the published literature. Barely 5% of the fossil insects from the Late Jurassic Karatau deposit, for instance, have been formally described (Grimaldi and Engel 2005). Approximately 1,000 fossils insects have been excavated from each of the Obeschayushchiky, Kzyl-Zhar, and Orapa deposits (Zherikhin 2002), which date to the notoriously fossil-poor Late Cretaceous (100–66 Ma), but only 75, 57, and 38 specimens have been formally described from each of these deposits, respectively.

Investigator preference and expertise can also impact the emergent faunistic view of a Lagerstätte. For example, an examination of the tens of thousands of fossil insects collected from Daohugou (Jurassic) has shown that the three most abundant orders in this Lagerstätte are Orthoptera, Neuroptera, and Diptera (Huang et al. 2006). However, Hymenoptera dominate the small fraction of Daohugou insects that have been published. This anomaly may be attributable in large part to Alexandre Rasnitsyn, who became established as a preeminent expert in fossil Hymenoptera (Rasnitsyn 1967, 1988) long before the first description of fossils from Daohugou (Wang et al. 2000, Yuan 2000) and who has contributed to many publications describing fossil Hymenoptera from this Lagerstätte (Rasnitsyn and Zhang 2004a,b; Ansorge et al. 2006; Rasnitsyn et al. 2006; Rasnitsyn and Zhang 2007, 2010; Zhang and Rasnitsyn 2008; Li et al. 2013, 2015; Zhang et al. 2014; Wang et al. 2014, 2015b, 2016b, 2017; Kopylev et al. 2020; Rasnitsyn and Öhm-Kühnle 2020). The influence of investigator preference may depend on the amount of time that a Lagerstätte has been known, which can vary greatly. In Europe alone, Baltic amber has been known for centuries (Weitschat and Wichard 2010) whereas the amber deposits of Álava in Spain and Oise in France have been known for only a few decades (Nel et al. 1999, Alonso et al. 2000).

**Comparisons with Other Animals**

**Comparisons with Marine Invertebrates**

In general, shelled marine invertebrates have a far more complete fossil record than insects do (Foote and Sepkoski 1999). Marine groups such as bivalves, gastropods, and brachiopods have hard shells that facilitate fossilization, and these animals tend to spend their lives atop or within the layer of sediment where fossilization can occur (Kidwell and Flessa 1996).

The oxygen content of the oceans has decreased steadily for decades (Helm et al. 2011), increasing extinction risk for many marine animals (Keeling et al. 2010). From first principles one would expect insects to fare better than marine invertebrates during a biotic crisis caused by low oxygen concentrations. Seawater contains far less oxygen than the atmosphere (Vaquer-Sunyer and Duarte 2008). Furthermore, oxygen levels can fall in the ocean due to factors such as decreased solubility and increased stratification that are irrelevant in the atmosphere (Breitburg et al. 2018). Lastly, small molecules such as oxygen travel 10,000 times faster through air than water (Vogel 1994). For these reasons, breathing air is far easier than breathing water.

These are major reasons why deoxygenation of the ocean is a major concern in the context of anthropogenic global warming (Keeling et al. 2010) whereas deoxygenation of the atmosphere is not. Furthermore, the atmosphere is sufficiently well mixed that atmospheric oxygen levels do not vary geographically in the absence of a large change in altitude. In contrast, the ocean is poorly mixed (Paulmier and Ruiz-Pino 2009). The ocean appears to have contained anoxic regions throughout earth history (Meyer and Kump 2008) and has occasionally contained massive anoxic zones during intervals that may (Lau et al. 2016) or may not (Jenkyns 1980) be associated with the Big Five mass extinctions.

Other consequences of increased $pCO_2$ and the resulting global warming can cause extinction in the oceans but not on land. Ocean acidification makes it more difficult for animals such as corals to produce calcium carbonate for their skeletons (Andersson and Gledhill 2013). Warming also changes the distribution of salinity in the ocean (Durack and Wijffels 2010). Deoxygenation, acidification, and changes in salinity caused by increased $pCO_2$ are not new problems: all of these have been implicated in at least one of the Big Five (Kiessling and Simpson 2011, van Soelen et al. 2018, Zhang et al. 2018).

To put it simply, environmental changes can cause more physiological stress for animals in the ocean than on land. An increase in $pCO_2$ large enough to prevent clams from breathing and constructing their shells might not pose any challenge to insect physiology.

**Comparisons with Tetrapods**

On land, tetrapods are one of the few groups that predominate in terms of biomass, although their biomass pales in comparison to
that of insects (Bar-On et al. 2018). Because tetrapods have a far more complete fossil record than insects, it is tempting to look to the tetrapod fossil record for clues as to how insects may have fared during mass extinctions.

Several differences limit the relevance of the tetrapod fossil record to that of insects. Perhaps, the most obvious is the minimum overlap in body size between insects and tetrapods. Currently, most insects are smaller than the smallest living tetrapod (Finlay et al. 2006, Rittmeyer et al. 2012). Insects’ smaller body size makes it easier for them to hide and to survive on limited quantities of food. Insects’ small size also allows them to occur at higher abundances within a community (Finlay et al. 2006) and to reach reproductive maturity quicker, which leaves insects with shorter generation times. During brief environmental disturbances such as drought, extreme heat, or the aftermath of an asteroid impact, insects’ small body size may allow them to take refuge in microhabitats that are not available to tetrapods. Arthropod faunas in modern forests can contain just as many species and genera in leaf litter as on vegetation (Brühl et al. 1998), but this is not the case for tetrapods (Gardner et al. 2007).

Within a given timespan in a particular habitat, the average insect species can adapt to changing environmental conditions faster than the average tetrapod species. Insects occur at higher densities, providing more variation on which natural selection can act, and insects’ greater number of generations per unit of time allows evolution to happen faster. The frequency with which insects enter diapause also has been invoked as a mechanism through which they manage to survive environmental crises, particularly those of limited durations (Whalley 1987, Tuljapurkar and Istock 1993). Consequently, an environmental crisis that causes a mass extinction of tetrapods need not cause a mass extinction of insects.

Data, Methods, and Terminology

Extinctions in deep time will be discussed here in terms of the geological periods of the Phanerozoic Eon (541 Ma to the present), which are from oldest to youngest: the Cambrian (541–485 Ma), Ordovician (485–444 Ma), Silurian (444–419 Ma), Devonian (419–359 Ma), Mississippian (359–323 Ma), Pennsylvanian (323–299 Ma), Permian (299–252 Ma), Triassic (252–201 Ma), Jurassic (201–145 Ma), Cretaceous (145–66 Ma), Paleogene (66–23 Ma), Neogene (23–2.6 Ma), and Quaternary (2.6 Ma to the present) Periods. Of note, some authors denote the interval from 359 to 299 Ma as the Carboniferous Period and many others divide the Carboniferous into two Periods, the Mississippian and the Pennsylvanian. Here, the Mississippian and the Pennsylvanian are treated as separate periods rather than subperiods in accordance with the latest geochronology (Walker et al. 2013) and because the Pennsylvanian contains definitive insect body fossils whereas the only fossil insects that might be Mississippian in age occur in very close proximity to the Mississippian/Pennsylvanian boundary (Brauckmann and Schneider 1996, Prokop et al. 2005).

Subordinate intervals are discussed here as belonging to the early, middle, or late portions of their respective periods. For example, all fossils and events from the Changhsingian Age of the Lopingian Epoch will be discussed here as part of the Late Permian. The early, middle, and late intervals within each geologic period were designated long before the advent of reliable absolute dating methods, such as uranium-lead dating, and are not necessarily of equal length. For example, the Early Permian lasts for more than half of the Permian, and the Middle Triassic begins and ends within the earliest third of the Triassic. The Cretaceous consists of an early and a late interval with no formal Middle. The early, middle, and late intervals within each period are demarcated just below the period designations in Fig. 1.

The concept of a ‘stem’ and ‘crown’ group within each clade is illustrated in Fig. 3. Crown representatives of many extant orders appeared during the Triassic, but stem groups typically extend back to the Paleozoic (Grimaldi and Engel 2005, Labandeira 2006).

Some of the figures presented here include insect occurrence data from the fossil record. These figures were generated with data downloaded...
from the Paleobiology Database on 22 March 2020, compiled primarily by Clapham et al. (2016). To visualize family-level relationships among insect communities before and after mass extinction boundaries, we conducted nonmetric multidimensional scaling (NMDS) of insect Lagerstätten using vegan (Oksanen et al. 2019) version 2.5–6 in R (R Development Core Team 2020) version 3.6.2. Because Lagerstätten contain varying numbers of described occurrences, we subsampled each Lagerstätte down to 100 occurrences and iterated this procedure 100 times. We generated plots of our NMDS results in ggplot2 version 3.2.1 (Wickham 2009) illustrating each subsampled insect community and an 84% confidence ellipse for each Lagerstätte, following the methods outlined by Schachat et al. (2020).

The Meaning of a Mass Extinction

The insect fossil record contains major insect extinctions that do not overlap with the Big Five. Labandeira (2005) identified insect extinctions at the Late Pennsylvanian, Late Jurassic, and later Early Cretaceous. The Late Pennsylvanian insect extinction (Labandeira and Phillips 2002) occurred as the world became warmer and dryer (Joeckel 1999) and coal swamps shrank (DiMichele et al. 2006), causing rapid turnover (DiMichele et al. 2001) in which approximately two-thirds of all coal-swamp plant species disappeared (DiMichele and Phillips 1996). The Late Jurassic and later Early Cretaceous extinctions are the two main pulses in the long decline of several major insect lineages, particularly Neuroptera and Mecoptera, and other lineages such as certain odonate families and bizarre, flea-like insects (Labandeira and Sepkoski 1993, Bechly et al. 2001, Ren et al. 2009, Gao et al. 2013, Lin et al. 2019). Although Neuroptera and Mecoptera have not gone extinct, their current diversity is considerably less than what it was during the Mesozoic (Labandeira 2010), and entire suborders or superfamilies have gone extinct within both orders (Yang et al. 2014, Lin et al. 2019).

The difference between a mass extinction and turnover is the key to understanding these three events. Changes in taxonomic diversity in deep time are measured by changes in extinction rates, origination rates, and total taxonomic diversity (Alroy and Hunt 2010). The extinction rate is the proportion of taxa within an interval that do not survive into the next interval. The origination rate is the proportion of taxa within an interval that were not present in the previous interval.

One of the two things can happen when extinction rates increase. If origination rates do not rise along with extinction rates, total taxonomic diversity will drop. Under this scenario, many taxa have gone extinct with insufficient new taxa to replace them. If extinction rates are high enough and total taxonomic diversity decreases sharply enough, a mass extinction occurs.

Alternatively, origination rates can increase alongside extinction rates. Under this scenario, many taxa have gone extinct but many new taxa have originated at approximate replacement levels, causing total taxonomic diversity to remain relatively stable. Such an extinction event occurs within the context of biotic replacement and is not a mass extinction. The term ‘turnover’ conveys an increase in origination that compensates for the increase in extinction.

The distinction between turnover and a mass extinction shows why the Late Pennsylvanian, Late Jurassic, and later Early Cretaceous insect extinction events identified by Labandeira (2005) are not analogous to the current insect extinction crisis. The Late Pennsylvanian extinction of insects that lived in coal swamps and adjacent humid habitats was part of a transition in which other insect groups diversified in more xeric habitats (Labandeira 2006), a pattern also seen in the plant and tetrapod records from this interval (DiMichele and Aronson 1992, Huttenlocker et al. 2018). The insect extinction event of the Late Jurassic is overshadowed by many contemporaneous diversification events, such as the mid-Mesozoic family-level radiation of parasitoid wasps (Labandeira 2018, Schachat et al. 2019). The insect extinction event of the later Early Cretaceous occurred during one of the most spectacular diversification events in insect history (Labandeira 2014b) when total insect diversity reached one of its highest peaks (Schachat et al. 2019).

The ‘Big Five’ Mass Extinctions in Deep Time

The End-Ordovician Event

The first of the Big Five mass extinctions, the end-Ordovician event, occurred 444 million years ago (Sheehan 2001). This event is known entirely from the marine realm and predates all putative fossil insect occurrences by tens of millions of years. In addition to the lack of fossil evidence of any insects before this extinction, there are also no fossils of vascular plants or tetrapods. Bryophytes are inferred to have diversified before this extinction but their depauperate fossil record does not contain any macroscopic remains (Taylor et al. 2009). The end-Ordovician event is of no relevance to insects.

The Late Devonian Event

Controversy surrounds the timing, magnitude, and duration of the Late Devonian event (McGhee Jr 2013). Extinctions have been noted near the beginning of the Givetian Stage at 388 Ma (Bosetti et al. 2011); later in the Givetian, approximately 384 Ma (Aboussalam and Becker 2011, Marshall et al. 2011); at the Frasnian/Famennian boundary, 372 Ma (McGhee 1996); and at the end of the Devonian, 359 Ma (Kaiser et al. 2016). This loss of biodiversity may in fact be

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**Fig. 4.** Variations in origination and extinction rates, and the resulting changes in total taxonomic diversity. In (a), extinction and origination both increased: the extinction that occurred is not immediately obvious in the diversity curve because the extinction event happened within the context of evolutionary turnover. In (b), extinction increased while origination decreased, causing a net loss of taxonomic diversity as seen in the diversity curve: a true biotic crisis, or mass extinction. In (c), total taxonomic diversity has decreased, but not due to an increase in extinction: extinction decreased, rather than increased, but origination decreased even more than extinction, causing a ‘mass depletion’ sensu Bambach et al. (2004).
more of a ‘depletion’, caused in large part by low origination rates (Fig. 4), than a true mass extinction (Bambach et al. 2004).

During the approximately 75 million years that passed between the end-Ordovician event and the Late Devonian event, terrestrial ecosystems changed dramatically: in many habitats, microbial soil crusts seemingly devoid of macroscopic animal life were replaced by forests with 30-m-tall trees (McGhee Jr 2013). Early tetrapods ambled through shallow bodies of water, perhaps occasionally venturing onto land (Ahlberg and Clack 2006). Though vertebrates may not have been terrestrial by this time, Middle-to-Late Devonian landscapes were unquestionably home to a wide range of terrestrial arthropod groups including early centipedes, scorpions, and springtails, extinct groups such as trigonotarbids and arthropleurans—and most likely to primitives wingless insects as well (Shear et al. 1984).

The fossil record of insects before the Late Devonian event is minimally informative: the one and only insect fossil from this interval whose affinity and age have not been questioned is a small fragment assigned to Archaeognatha (Shear et al. 1984), a primitively wingless order that is widely agreed to represent the most early-diverging known branch of Insecta (Misof et al. 2014). The presence of Archaeognatha in Middle Devonian landscapes is unsurprising, given the presence of a collemboolan in the Early Devonian (Whalley and Jarzembowski 1981). In addition to this probable Devonian archaeognathan fragment, there is another possible Devonian archaeognathan fragment (Labandeira et al. 1998) whose antiquity was questioned by authors who did not examine the original material (Jeram et al. 1990) and a headless fragment of an animal that appears to belong to either Archaeognatha or Zygentoma (Fayers and Trewin 2005). Regardless of whether these additional fragments represent Devonian insects, they do not change the emergent view of Devonian insect life.

Until recently, the Late Devonian event was considered by some authors to have occurred within a biotic crisis that suppressed insect abundance for tens of millions of years. A 407-million-year-old mandible was interpreted, controversially, as belonging to a winged insect (Engel and Grimaldi 2004). The next known fossils of winged insects are approximately 80 million years younger than this mandible (Brauckmann and Schneider 1996, Prokop et al. 2003), raising the question of why Pterygota are absent from the fossil record for several tens of millions of years of their supposed history. Shortly after the 407-million-year-old mandible was attributed to a winged insect, estimates of atmospheric oxygen in Earth’s deep past showed that the gap in the insect fossil record coincides with reduced pO2 (Berner 2006). These findings suggest that the Late Devonian event occurred near the midpoint of a long interval in which reduced oxygen availability suppressed insect abundance (Ward et al. 2006).

More recently, the 407-million-year-old mandible was redescribed as belonging to a centipede (Haug and Haug 2017). In a relevant development, the same model that reconstructed low oxygen levels near the Late Devonian event was re-run with updated input of isotopic data and estimates of low oxygen were not recovered at or near the Late Devonian (Schachat et al. 2018). Estimates of unremarkable oxygen levels are consistent with the various described occurrences of arachnids throughout this interval (Shear 2000, Gess 2013) which suggest that winged insects could have become abundant on the landscape and could have been preserved in the Devonian rock record if they had already originated (Schachat et al. 2018). An environmental crisis no longer explains why Pterygota are not known within 45 million years of the Late Devonian event, but an explanation is no longer needed because there is no evidence that Pterygota existed at that time.

Like Collembola, Archaeognatha appear to have originated before the Late Devonian event. Accordingly, Archaeognatha could not have gone extinct during the Late Devonian, because they still exist today. That Archaeognatha survived is all that can be confidently said about how insects fared during the Late Devonian event.

### The End-Permian Event

The end-Permian event at 252 million years ago was the most severe extinction crisis in the history of life (Raup and Sepkoski 1982) and the most ecologically impactful (McGhee et al. 2004, 2012; Wagner et al. 2006). Over 80% of all marine genera are estimated to have perished (Stanley 2016). The end-Permian was also the only time when a supraregional clade of insects went extinct (Labandeira and Sepkoski 1993). This has led certain paleontologists to communicate the unique severity of the end-Permian event by describing it as the only extinction event that was severe enough to extinguish insects (Bowring et al. 1998). Indeed, all methods used to estimate insect diversity in deep time show a major loss of family-level diversity at the end-Permian (Labandeira and Sepkoski 1993, Jarzembowski and Ross 1996, Scherbakov 2008, Clapham et al. 2016, Dmitriev et al. 2018, Schachat et al. 2019). However, the attribution of this loss of insect diversity to environmental causes, rather than evolutionary dynamics unique to the Insecta, is questionable.

Two paleopterous groups appear to have gone extinct near the end-Permian. These contain the majority of the paleopterous orders that ever existed; their disappearance constitutes a major loss of morphological diversity and evolutionary history. The order Meganisoptera, also known as Protodonata, is widely agreed to form the stem-group (Fig. 3) to crown Odonata (Nel et al. 2001, Grimaldi and Engel 2005). The superorder Paleodictyopteroidea contains four extinct orders—Palaeodictyoptera, Permothemistida, Megasecoptera, and Diaphanopteroidea—and its relationships with other lineages of Paleoptera are still in dispute (Béthoux 2008).

Meganisoptera and Paleodictyopteroidea are the two lineages whose representatives reached the largest body sizes in insect history: Meganisoptera reached wing lengths of at least 33 cm and Paleodictyopteroidea reached wing lengths of at least 22.6 cm, whereas the longest insect wing length known after the Permian/Triassic boundary is merely 18 cm. But not all Paleodictyopteroidea were gigantic, and certain lineages evolved progressively smaller body sizes throughout the Permian with some reaching the size of a mosquito (Woottton 1981, Van Dijk and Geertsema 1999).

Meganisoptera and Paleadictyopteroidea are also known for their feeding strategies. Meganisoptera were specialized hawk predators whose visual acuity allowed them to patrol ancient forests (Nel et al. 2018a) and Palaeodictyopteroidea had piercing-and-sucking mouthparts that are structurally reminiscent of Hemiptera but evolved independently (Labandeira 1997, 2019; Pecharóvá et al. 2015). During the Pennsylvanian Period (323–299 Ma), the first geologic period with definitive evidence of insects, Palaeodictyopteroidea were abundant and diverse, comprising appropriately half of the described insect species from this time (Carpenter 1971).

The end-Permian marks the disappearance of insect groups that had previously been abundant and diverse. However, Meganisoptera and Palaeodictyopteroidea were in decline throughout the Permian (Fig. 5). In some regions, Paleoptera became rare before the Permian began (Rasnitsyn et al. 2004, Schneider et al. 2004, Scherbakov 2008). The Palaeodictyopteroidea are inferred to have been outcompeted by the Hemiptera due to the similarity of their mouthparts and feeding strategies (Labandeira 1997, Grimaldi and Engel 2005, Schachat and Labandeira 2015). The extinction of the Meganisoptera
The current consensus is that the end-Permian event was caused by the Siberian Traps, a massive ‘large igneous province’ whose magma burned through overlying coal deposits, releasing CO₂ into the atmosphere from both lava and coal (Ganino and Arndt 2009, Svensen et al. 2009, Ogden and Sleep 2012). The geographic ranges of many groups, including insects, shifted poleward in an apparent response to global warming (Shcherbakov 2008). Changing environmental conditions would have posed many challenges to animal physiology at this time. And yet, controversy continues to surround the chemical composition of the atmosphere and the timing of the environmental perturbations (Cui and Kump 2015, Shen et al. 2019).

The fossil records of plants and tetrapods, which are more complete than that of insects, show evidence of widespread ‘disaster forms’ or ‘disaster taxa’ during the Early Triassic. Disaster taxa include the small pole-like tree Pleuro menia Corda, (1852) (Pleuro meziales: Pleuro mezaceae), a lycopod whose closest living relative is the diminutive quillwort Isoetes Linnaeus, 1715 (Isoetales: Isoetaceae), and the tetrapod Lystrosaurus Cope, 1870 (Anomodontia: Lystrosauridae), a therapsid whose closest living relatives are mammals. These became widespread after the extinction event (Benton 1983, Grauvogel-Stamm and Ash 2005, Looy et al. 2005). Disaster taxa are emblematic of the low alpha, beta, and gamma diversity that characterized plant and tetrapod communities for several million years after the end-Permian event (Benton and Newell 2014). A debate persists, however, as to whether plants experienced a mass extinction at the end-Permian (Cascales-Miñana and Cleal 2014, Nowak et al. 2019) as tetrapods did (Maxwell 1992), with doubts surrounding the geographic scale of the purported plant extinction (Rees 2002). Nevertheless, the end-Permian event depressed plant and tetrapod diversity for an extended interval and fundamentally different communities emerged in its wake.

The relevance of plants and especially tetrapods to insects at the end-Permian event is tenuous. The number of described insect species that exist today vastly exceeds the number of described and estimated total species of plants and tetrapods (Mora et al. 2011), and there is no reason to doubt that insects were already far more diverse than plants and tetrapods at the end of the Permian. The number of described insect species from each of the nine Permian konzentrat Lagerstätten exceeds the global estimated tetrapod diversity for the entire Permian (Benson and Upchurch 2013). The highest number of estimated plant species from all Permian stages is approximately equal to the number of insect species described thus far from the Elmo Lagerstätte of the Early Permian of Kansas (Nowak et al. 2019). Because insects already were relatively diverse at the end-Permian, an insect community would have had to lose far more species, genera, and families than a plant or tetrapod community in order to become dominated by a single ‘disaster taxon’.

The Lagerstätte-driven nature of the insect fossil record precludes definitive statements about the dominance of ‘weedy’ disaster taxa after the end-Permian event. Disaster taxa are defined by their occurrence across multiple assemblages and in multiple environments. The Madygen assemblage from southwestern Kyrgyzstan is the oldest insect konzentrat Lagerstätte that follows the end-Permian event and was deposited approximately 20 million years after the extinction boundary (Fig. 1), when terrestrial ecosystems are believed to have recovered (Chen and Benton 2012). Along with the Ipswich assemblage from northeastern Australia, Madygen is one of only two insect konzentrat Lagerstätten from the entirety of the Triassic. The occurrence of the same species at both Triassic Lagerstätten would be unlikely due to the 14.25 million years and over 100° of paleolatitude that separate these assemblages. In the event that co-occurrence of insect taxa were elevated between these
Lagerstätten, the two assemblages are insufficient to establish a global pattern. Finally, insects’ poleward range shifts occurred on a timescale that, in geochronological terms, was essentially instantaneous (Schcherbakov 2008). Consequently, differences among Lagerstätten probably reflect shorter-term climatic fluctuations as much as they reflect biogeography and long-term changes in gamma diversity.

Like the Triassic, the Late Permian contains two insect konzentrat Lagerstätten. These intervals contain one Lagerstätte each from the Northern and Southern Hemispheres, from relatively similar paleolatitudes: 40.05° to 40.26° north of the equator and 60.76° to 78.65° south of the equator (Fig. 1).

The NMDS plot comparing described insect communities of Late Permian and Triassic Lagerstätten does not suggest a major family-level extinction at the Permian/Triassic boundary: the Lagerstätten are not arranged chronologically, nor are the Permian Lagerstätten clearly separated from the Triassic Lagerstätten (Fig. 6). The Permian Isady Lagerstätte is closer to the three other Lagerstätten than any of these are to each other.

When the prevalence of different insect orders is visualized for the Late Permian and the Triassic, no clear differences emerge (Fig. 6). The clearest differences correspond not with time but with geography. Various polyneopteran orders—the extinct order Reculida, and the extant orders Plecoptera, Blattodea, Grylloblattodea, and Phasmatodea—are better-represented among described occurrences from the Northern Hemisphere Lagerstätten of Isady and Madgveny than would be expected from extant diversity. In contrast, Belmont and Ipswich, the Lagerstätten from the Southern Hemisphere, contain far more described occurrences of Hemiptera.

Any pattern gleaned from a comparison of these Lagerstätten should be treated with great caution. The four available Lagerstätten represent a small fraction of insect diversity—especially for nearly 40 million years of evolutionary history. The limitations of the fossil record for quantifying the impact of the end-Permian event on insect diversity are exacerbated by the finding that insects from this interval appear to have been most diverse, and most modern, at tropical latitudes where they had the lowest probability of preservation (Schcherbakov 2008). Debate continues as to whether observed changes in Permian insect assemblages are better ascribed to a decline in diversity or a change in habitat types where preservation occurred (Schcherbakov 2008).

Plant-insect interactions provide a record of insect ecological diversity from habitats and intervals in which insect body parts are not preserved (Labandeira 2013). Insect herbivory on fossilized plants from the Late Permian through Middle Triassic has been documented only rarely (Scott et al. 2004, Krassilov and Karasev 2008, Prevec et al. 2009, McNelis 2011, Kustatscher et al. 2014, Wüppler et al. 2015, Bernardi et al. 2017, Cariglino 2020), and remarkably few localities contain plants from both the Permian and Triassic. A recent study conducted with plants from the same geographic region found no decrease in Middle Triassic herbivory compared to the Late Permian (Labandeira et al. 2016a). However, the absence of Early Triassic (252–247 Ma) fossils from this region precludes strong conclusions about how its herbivores fared during the end-Permian event.

Given the dearth of Late Permian Lagerstätten and the absence of any Lagerstätten from the Early–Middle Triassic, insect diversity in the aftermath of the world’s greatest extinction event remains poorly known. Nevertheless, the similarities between Late Permian and Late Triassic insect communities—and the absence of Palaeodictyopteroidea and Meganisoptera from both intervals—suggests that the loss of insect diversity by the end of the Permian was due to earlier biotic replacement.

For insects, the end-Permian event is best conceptualized as a turnover event rather than a mass extinction (Fig. 7), analogous to the late Trempealeauan eclipse at the end of the Cambrian Period (Jun-yuan and Teichert 1983). The fossil record indicates that many animal phyla originated in rapid succession around 540 million years ago during the ‘Cambrian Explosion’ (Marshall 2006). For decades, it was believed that early representatives of many phyla were lost in a mass extinction at the end-Cambrian (Newell 1967). However, as additional research was conducted with more precise stratigraphic correlations (Palmer 1965) and abandonment of the layer-cake stratigraphic concept (Labandeira 1986), it was realized that these taxa went extinct slowly over many millions of years, not suddenly in a single catastrophic event. The concept of a mass extinction therefore holds limited relevance to species loss toward the end of the Cambrian because these losses occurred as a series
of smaller extinctions (Palmer 1984, Westrop 1988, Rieboldt 2005, Taylor 2006). Many other taxa that appeared to have gone extinct at the end of the Cambrian were later found to have persisted into the Ordovician for tens of millions of years after the presumed extinction event (Van Roy et al. 2010). This slow loss of ancient lineages, barely 50 million years after their phyla originated, is now known as the ‘late Trempealeauan eclipse’ (Fang et al. 2019).

Insect diversity near the end-Permian recapitulates the sequence of events documented for the late Cambrian and can therefore be described as a turnover event. Just as many animal phyla originated in a geologic instant during the Cambrian, many orders of winged insects appeared in quick succession around 320 million years ago (Brauckmann and Schneider 1996, Prokop et al. 2005, Nel et al. 2013, Schachat et al. 2018, Haug et al. 2015). Less than 75 million years after these first appearances, entire orders, some comprising stem representatives of higher taxa—from Paleoptera to Orthopteroidea to Hemipteroidea to some Holometabola (Labandeira and Sepkoski 1993, Labandeira 2011, Prokop et al. 2017)—went extinct while the Modern Insect Fauna came to overshadow the Paleozoic Insect Fauna. As additional stratigraphic and paleontological data become available, it becomes even more clear that these extinctions of the Paleozoic Insect Fauna occurred as the culmination of long declines, with some taxa restricted to marginal habitats before going extinct (Shcherbakov 2008). These extinctions were neither simultaneous nor sudden.

The word ‘turnover’ conveys the slow twilight of the Paleozoic Insect Fauna as analogous to the range shifts that occurred within Miocene and Pliocene plant communities as C 4 grasslands expanded and subsequently migrated in synchrony with glacial–interglacial cycles (Lindström 2016). On land, tetrapods are the group whose fate during the end-Triassic event has been most intensely studied. Controversy remains as to whether dinosaurs gradually outcompeted non-ornithodiran archosaurs throughout the Triassic or diversified during the Jurassic as to whether dinosaurs gradually outcompeted non-ornithodiran archosaurs throughout the Triassic or diversified during the Jurassic (Brusatte et al. 2010, Irmis 2010). A clearer consensus has emerged for plants.

It appears that plants did not experience a mass extinction at the end-Triassic. Plant communities changed drastically shortly before the end of the Triassic (Lindström 2016)—most likely due to the environmental perturbations caused by volcanism—but these changes appear transient, with no corresponding mass extinction at higher taxonomic levels (Kürschner and Herngreen 2010, Bonis and Kürschner 2012, Lucas and Tanner 2015). The severity of genus- and species-level plant extinction at the end-Triassic varies greatly with latitude (Lindström 2016). Acute, global ‘fern spikes’ indicate severe disruption of plant communities at the end-Permian and end-Cretaceous. In contrast, the ‘fern spikes’ near the end-Triassic are patchy, and variable in duration (Lindström 2016). Plant communities changed near the end-Triassic, but not nearly as severely as they did at the end-Permian or end-Cretaceous.

Migrating end-Triassic plant communities may have little in common with the extinction that ravaged marine ecosystems at that time. End-Triassic plant migrations are perhaps better understood as analogous to the range shifts that occurred within Miocene and Pliocene plant communities as C 4 grasslands expanded and subsequently migrated in synchrony with glacial–interglacial cycles (Edwards et al. 2010). Climate change caused certain biomes to expand and others to contract but caused no increase in the family-level extinction rate (McElwain and Punyasena 2007, Cascales-Miñana and Cleal 2014).
These Triassic shifts in plant communities caused by climate change may be responsible for turnover among herbivorous tetrapods (Bond and Grasby 2017). Insects, however, appear to have been less impacted by these shifts: previous paleoentomological studies have not noted any mass extinction of insects at or near the end-Triassic (Zherikhin 2002, Nel et al. 2018b).

When family-level similarities between described insect communities of Triassic and Early Jurassic konzentrat Lagerstätten are visualized in an NMDS plot, the Triassic Lagerstätten are easily distinguishable from the Jurassic Lagerstätten (Fig. 8). However, both Triassic Lagerstätten are more similar to the Jurassic Sai-Sagul Lagerstätte than they are to each other. As was the case for the end-Permian event (Fig. 6), the severity of the end-Triassic event is obscured by the dearth of Triassic Lagerstätten. Nevertheless, the NMDS plot suggests that the differences that accumulated in insect communities before and after the extinction event are no greater than would be expected given the tens of millions of years that separate them.

At the level of the insect order, one of the most noticeable differences between the Triassic and Early Jurassic is that Diptera are more prevalent among the described occurrences from all six Early Jurassic konzentrat Lagerstätten than from either Triassic Lagerstätte (Fig. 8). However, the Ipswich Lagerstätte of the Triassic is the only assemblage with a described beetle fauna whose prevalence approaches that seen today. The Jurassic Lagerstätten contain fewer described beetle occurrences than Ipswich and the younger faunas. The extinct order Reculida is better-documented in the Posidonia Lagerstätte from the Jurassic than in either of the Triassic Lagerstätten. It is not immediately clear whether Jurassic entomofaunas are taxonomically more modern than those of the Triassic.

The End-Cretaceous Event

The end-Cretaceous event, occurring at 66 Ma, perhaps is best known for the extinction of nonavian dinosaurs. The event was triggered by an asteroid impact whose environmental fallout would have made life difficult for insects and plants as well as dinosaurs (Alvarez et al. 1980, Schulte et al. 2010, Hull et al. 2020). However, insects seem not to have struggled as mightily as dinosaurs and other tetrapods.

Tetrapods with larger body sizes had the greatest risk of extinction during the end-Cretaceous event (Archibald 1996). Individuals who survived the event may have had to seek shelter from environmental hazards such as fire (Wolbach et al. 1988), acid rain (Ohno et al. 2014), and extreme temperatures (Schulte et al. 2010). If primary productivity collapsed during an ‘impact winter’ scenario immediately after the asteroid impact (Vellekoop et al. 2016), detritivorous insects would have been the most reliable food source for tetrapods (Sheehan and Fastovsky 1992), and insectivorous tetrapods tend to have smaller body sizes than co-occurring herbivorous, omnivorous, and carnivorous tetrapods (Pineda-Munoz et al. 2016).

This trend of increased extinction risk for larger taxa at the end-Cretaceous also holds for relatively small-bodied tetrapod groups such as snakes and lizards. The largest body size for both of these groups shifted across the boundary from multiple kilogrammes to approximately 300 g (Longrich et al. 2012). However, the largest insect that ever lived had an estimated body mass more than ten times smaller than this, below 50 g (Dorrington 2016).

The small body size of insects as compared to tetrapods leaves no reason to expect that larger-than-average insects would have faced the elevated extinction risk that larger-than-average snakes and lizards did. Any habitat that would provide sufficient shelter to smaller snakes and lizards should also provide sufficient shelter to insects of all sizes. And because detritivorous insects vary greatly in body size (Ruesink and Srivastava 2001), a collapse of primary productivity that favors smaller tetrapods for their insectivorous diet need not favor smaller insects.

Heterotrophs of all sizes, from gigantic to unicellular, suffered from elevated extinction rates at the end-Cretaceous (Hull et al. 2011). Ecosystems recovered from the end-Cretaceous event much faster on land than in the oceans (Beering et al. 2001). Terrestrial ecosystems were, nevertheless, impacted by the end-Cretaceous event. In addition to the loss of large vertebrates, a ‘fern spike’ epitomizes an abrupt and dramatic shift in dominance of plant communities from angiosperms to ferns as terrestrial ecosystems collapsed (Beering et al. 2001). Nevertheless, the end-Cretaceous does not mark a regime shift in plant communities as it does for tetrapods and marine organisms. Although plant communities changed at the end-Cretaceous (Fastovsky and Bercovici 2016), such as the replacement of mesic communities by mire communities on well-drained substrates in North America (Tschny et al. 1984), losses of higher
taxa were strictly local and not a single plant family went extinct (Cascales-Miñana and Cleal 2014).

Insects likely experienced the end-Cretaceous event similarly to plants, with a momentary drop in alpha and beta diversity that did not impact higher-level taxonomic diversity (Labandeira et al. 2002). Unfortunately, the insect fossil record preserves minimal evidence of insect diversity shortly before, during, and after the end-Cretaceous. Canadian amber deposits from the provinces of Alberta and Manitoba, the last insect konzentrat Lagerstätten that predate the end-Cretaceous event, formed approximately ten million years before the Cretaceous ended, and Menat, the first insect konzentrat Lagerstätte that postdates the end-Cretaceous event, formed over five million years after the Cretaceous ended (Fig. 1). By this time, plant communities and many plant–insect interactions had unquestionably recovered (McElwain and Punyasena 2007, Wappler et al. 2009).

Because the temporal distribution of konzentrat Lagerstätten precludes estimates of insect diversity for the time when plants and tetrapods reeled from the end-Cretaceous event, the next best exercise would be to compare insect communities from Lagerstätten on either side of the end-Cretaceous. Due to the nature of the insect fossil record, this is not advisable either. The end-Cretaceous occurs near the midpoint of a 16-million-year gap in the insect fossil record.

Another approach would be to calculate the average rate of insect community turnover per 16 million years for the Late Cretaceous and then compare this to the rate of turnover between the last Cretaceous Lagerstätte and the first Paleogene Lagerstätte. However, here the preservational modes of Lagerstätten would cause a significant problem. All five of the Late Cretaceous Lagerstätten are amber deposits whereas Menat is an adpression deposit consisting of rocks formed at the bottom of a body of water (Fig. 1). Insects preserved in adpression deposits such as Menat tend to be less complete than those preserved in amber; fewer visible body parts result in fewer taxonomic characters, which results in fewer opportunities to identify a specimen’s affinities (Karr and Clapham 2015). This taphonomic bias can cause insect communities preserved in adpression deposits to appear less diverse than they really were (Karr and Clapham 2015). Furthermore, amber deposits come from tree resin and adpression deposits come from aquatic settings, such that these two types of deposits represent fundamentally different habitats (Martínez-Delclós et al. 2004, Labandeira 2014a). Lastly, amber deposits tend to preserve smaller insects than adpression deposits (Martínez-Delclós et al. 2004, Labandeira 2014a).

In lieu of insect body fossils, the fossil record of plants is the only direct source of information about how insects fared before, during, and after the end-Cretaceous event. Analyses of insect herbivory on leaves from various Cretaceous–Paleogene assemblages have shown that specialized modes of herbivory, especially piercing and sucking, mining, and galling, led to an increased risk of extirpation (Labandeira et al. 2016b). Plant–herbivore interactions recovered on different timescales in different regions (Labandeira et al. 2002, Wilf et al. 2006, Wappler et al. 2009, Donovan et al. 2014), with insect herbivores at localities more distant from the Chicxulub impact crater faring better (Wappler et al. 2009, Donovan et al. 2017). Where specialized herbivores appear to have been extirpated at the end-Cretaceous, new herbivores with convergent feeding habits colonized localities within the same region on varying timescales (Wilf et al. 2006, Donovan et al. 2014).

To summarize, not a single insect Lagerstätte from before the end-Cretaceous can provide a meaningful comparison to Menat, the only available insect Lagerstätte deposited within ten million years of the end-Cretaceous event. Because entomofaunas changed substantially during the Late Cretaceous, as insects adapted to radiating angiosperm taxa that took over plant communities (Zherikhin 2002), the only insect Lagerstätte deposited within ten million years of the end-Cretaceous event cannot be meaningfully compared with any Cretaceous adpression Lagerstätten, which all predate the ecological expansion of angiosperms (Fig. 1).

### The End-Cretaceous Event as a Template for a Future Insect Extinction

Various methods for estimating insect diversity in deep time have reconstructed a massive loss of family-level diversity near the end-Cretaceous (Clapham et al. 2016, Schachat et al. 2019). However, this apparent mass extinction is better attributed to the complete absence of adpression konzentrat Lagerstätten from the entire Late Cretaceous (100–66 Ma) fossil record of insects. The insect families that had their last known appearance during the Early Cretaceous (145–100 Ma) and those that had their first known appearance during the Paleogene may well have coexisted. But if these families have a low potential of being preserved in amber due to their habitat preferences or a large body size, the fossil record will obscure their coexistence—with an apparent extinction resulting as an artifact of this gap in our knowledge.

An NMDS comparison of described insect communities of Lagerstätten from the Late Cretaceous through early-Middle Paleogene (Fig. 9) supports the consensus in the paleoentomological literature that the end-Cretaceous was hardly catastrophic for insects (Whalley 1987, Labandeira and Sepkoski 1993, Jarzembowski and Ross 1996, Zherikhin 2002, Labandeira 2005). The clusters of Late Cretaceous and Paleogene Lagerstätten (Fig. 9) do not suggest a fundamental change in insect community composition at the end-Cretaceous. For example, the Fushun amber Lagerstätte from the Paleogene of eastern China is nearly indistinguishable from the Oise amber Lagerstätte from France in terms of both age and paleolatitude (Fig. 1), but the insect community described thus far at Fushun is noticeably more similar to that of the Cretaceous amber Lagerstätte from Manitoba, Canada than to that of Oise (Fig. 9).

The documented prevalence of particular insect orders within konzentrat Lagerstätten does not change meaningfully from the Late Cretaceous to early-Middle Paleogene (Fig. 9). The insect orders Hemiptera, Hymenoptera, Coleoptera, and Diptera consistently dominate these faunas. Along with Lepidoptera, which have an inordinately depauperate fossil record (Sohn et al. 2015), these four orders are by far the most diverse in modern ecosystems (Grimaldi and Engel 2005). The clearest shift in the ordinal-level composition of these Lagerstätten is the decline of Neuroptera at approximately 90 million years before the present. This is a well-documented phenomenon that has not been linked to an environmental crisis or to species loss in any other taxon (Labandeira and Sepkoski 1993, Grimaldi and Engel 2005).

There is little a priori reason to suspect that insects would suffer a mass extinction during an event such as the end-Cretaceous, in which not a single plant family went extinct (Cascales-Miñana and Cleal 2014). Herbivorous insects that lived in distant habitats from the impact crater, in places such as Patagonia, Argentina and Menat, France, appear to have re-populated the communities that suffered during the end-Cretaceous. Although Pangaea began to split apart long before this time, the continents were not as widely dispersed across the planet as they are now (Barron 1987) and latitudinal temperature gradients were much gentler than they are today (Sewall
1. Changes in the fossil record of insect diversity are currently understood only at the levels of family and order. This lack of genus- and species-level resolution can be attributed to several factors. First is insufficient support for taxonomic studies of fossil insects. Second is the difficulty of tracking a single genus through time, caused by the infrequency with which insects are preserved as fossils. Third is the rarity and inaccessibility of insect morphological characters, such as genitalia, used to distinguish genera and species.

2. It is safe to assume that numerous families of insects would have to go extinct for the anthropogenic biodiversity crisis to leave its mark in the fossil record. The current decline of insects is primarily measured by the loss of abundance and biomass. Because the insect fossil record is unsuited to estimates of these two metrics, it is essentially impossible to compare the current plight of insects with mass insect extinctions in deep time.

3. The five major extinction events identified in the fossil record of insects—the Late Pennsylvanian, end-Permian, Late Jurassic, later Early Cretaceous, and end-Cretaceous—are best understood as examples of turnover, rather than as mass extinction events. Major groups of insects went extinct during each of these events, but these events were not sudden, and replacement of the extinct insect groups occurred quickly. Two major insect losses overlap with Big Five mass extinctions, the end-Permian and end-Cretaceous, but both commenced well before the environmental crises associated with these extinctions. The other Big Five mass extinction that occurred after the origin of winged insects, the end-Triassic, is long recognized to have no association with any large-scale change in the entomofauna.

4. Insects fare better than tetrapods and marine invertebrates during mass extinctions. The small body size of insects, their unparalleled abundance, and their ability to enter diapause may give them an advantage over tetrapods during environmental crises. The relatively mild effects of increased $\rho CO_2$ and decreased $\rho O_2$ in the atmosphere, compared to the oceans, shield insects from many of the physiological challenges that marine invertebrates face during catastrophic climate change. The extinction history of insects is most comparable to that of plants. The end-Permain is the only one of the Big Five mass extinctions that coincides with global losses at or above the level of family; all other extinction events appear to have been local or restricted to lower taxonomic levels.

5. Insects do not appear to have ever suffered a sudden mass extinction. If the current biodiversity crisis extinguishes diverse higher-level clades, then perhaps humans will have caused insects’ first true mass extinction. However, at present, there are no indications that we are anywhere near a crisis of this severity.

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