Chapter 13
Why Did Terrestrial Insect Diversity Not Increase During the Angiosperm Radiation? Mid-Mesozoic, Plant-Associated Insect Lineages Harbor Clues

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Abstract Several studies provided evidence that family-level insect diversity remained flat throughout the initial mid-Cretaceous angiosperm radiation 125–90 million years ago. As this result has engendered considerable commentary, a reanalysis was done of a new dataset of 280 plant-associated insect families spanning the 174 million year interval of the Jurassic–Paleogene periods from 201 to 23 million years ago. Lineage geochronologic ranges were determined, and feeding attributes were characterized by: (i) dominant feeding guild (herbivore, pollinator, herbivore–pollinator, pollinator–mimic, xylophage); (ii) membership in one of eight functional feeding groups; and (iii) dominant plant host or host transition (cryptogam/fern only, cryptogam/fern → angiosperm, gymnosperm only, gymnosperm → angiosperm, angiosperm only). A time-series plot of insect lineages and their dominant plant–host affiliations resulted in four conclusions. First, insect lineages with dominant gymnosperm hosts reached a level of 95 families in the 35 million years preceding the initial angiosperm radiation. Second, earlier insect lineages with gymnosperm → angiosperm host transitions and newly originated insect lineages that developed dominant associations with emerging angiosperms rapidly diversified during the angiosperm radiation, later establishing a plateau of 110 families during a 20 million year interval after the initial angiosperm radiation. Third, these two diversity maxima were separated during the angiosperm radiation by a diversity minimum, the Aptian–Albian gap, indicating major turnover and time-lag effects associated with the extirpation and

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acquisition of plant associations. Last, insect lineages most affected during this interval were herbivores and pollinators, exophagous feeders, and those hosting gymnosperms, angiosperms and gymnosperm → angiosperm transitions. These data largely explain the flat or even decreased level of insect diversity immediately before, during, and after the initial angiosperm radiation.

13.1 Introduction

In 1993, Labandeira and Sepkoski published a report in *Science* documenting the fossil diversity of insects from an assessment of their family-level lineage diversity through time. One of the results of this study was the clear presence of stasis in the rate of origination of insect diversity immediately before, during, and after the initial radiation of angiosperms in the mid-Cretaceous (Fig. 13.1). Some of the reaction to this discovery was negative, particularly from some paleoentomologists and paleobotanists. The discontent was attributable to the view that a slackening of insect diversity contravened a well-received view that the diversity of associated herbivores and pollinators should have significantly increased in concert with sharply increased diversification of angiosperm lineages. This "coevolutionary" view presumed that an expected, coordinated evolution would occur between angiosperms and their various insect associates in a multiplicative and opportunistic manner during an interval of resource expansion that would include food, shelter, mating sites, and other features essential for survival of insects and their host–plants. An unexpressed corollary to this view was that earlier gymnosperms were largely unavailable to insect lineages that potentially could interact with plants.

During the early 1990s to mid-2000s not much was known about the Mesozoic fossil record of insects and land plants. This ignorance affected understanding of gymnosperm relationships with insects prior to the major emergence of angiosperms during the Aptian to Turonian stages from 125 to 90 million years ago. There was limited evidence for the consumption of live plant tissues (Labandeira 2013), although a few studies documented several Eurasian, mid-Mesozoic insect lineages with pollen as gut contents (Krassilov et al. 2007). There was isolated documentation, overwhelmingly from paleobotanists, that evidence for insect herbivory was present on gymnospermous plants typical of mid-Mesozoic floras, such as puncture wounds on cheirolepidiaceous conifers (Watson 1977), borings in conifer woods (Zhou and Zhang 1989), and galls on bennettitalean foliage (Harris 1942), but these reports were too few to provide any convincing conclusion that preangiospermous floras had insects that used gymnosperms appreciably for food. Only recently have gymnosperm-dominated floras been systematically studied to document broad patterns of herbivory within specific habitat settings (Ding et al. 2014).

During this time, there were additional examinations of insect family-level diversity in the fossil record (Jarzembowski and Ross 1993, 1996; Alekseev et al. 2001).

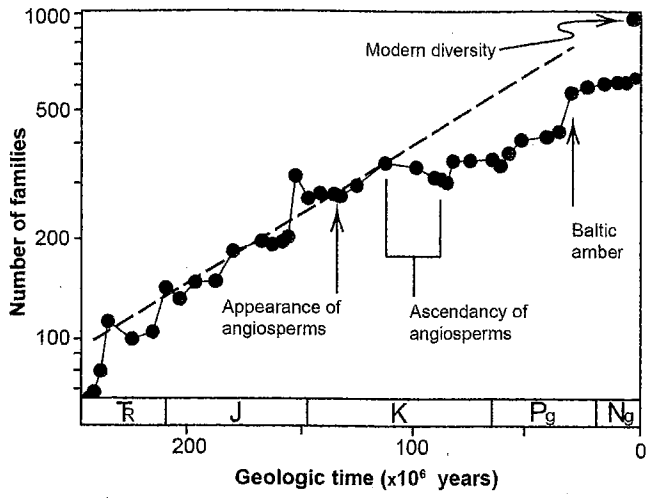

Fig. 13.1 A reproduction of Fig. 4 from Labandeira and Sepkoski (1993), showing insect family-level diversity increasing monotonically from the Middle Triassic to the Late Jurassic, stabilizing throughout the Cretaceous during the ascendancy of the angiosperms, and rising again during the Paleogene, indicated by the Baltic amber spike. The vertical axis is semilogarithmic and the dashed line is interpretive, indicating a divergence from exponential diversification during the Cretaceous. The only change to this figure has been relabeling of the abandoned "Tertiary Period" to reflect its modern division into an earlier Paleogene Period (Pg) and later Neogene Period (Ng). Reproduced with permission from American Association for the Advancement of Science

These reports confirmed that relative stasis existed for insect family-level diversity throughout the same interval of the angiosperm radiation, even though the data came from largely separately assembled datasets (Dmitriev and Zherikhin 1988; Rasnitsyn 1988; Labandeira 1994; Jarzembowski and Ross 1996). After publication of these studies and during the 2000s, a different approach was pursued—examination of the evidence for preangiospermous plant–insect interactions, focusing on herbivory, pollination, and eventually mimicry. Long-term projects with multiple colleagues were initiated to examine diverse preangiospermous, gymnosperm-dominated floras (Labandeira 2006; Ding et al. 2014). Current preliminary studies of Mesozoic herbivory use a similar methodology as those for the early Permian (Labandeira and Allen 2007; Schachat et al. 2014), the Cretaceous–Paleogene (K-Pg) boundary (Labandeira et al. 2002; Wilf et al. 2006), and the mid-Paleogene climate events (Wilf et al. 2005; Wappler et al. 2012; Currano et al. 2009). In addition, studies of mid-Mesozoic pollination have centered principally on the preangiospermous mid-Mesozoic (Ren et al. 2009; Labandeira 2010; Peñalver et al. 2012). Recently, there has been detection of mid-Mesozoic mimicry (Wang et al. 2012b). The purpose of these efforts in examining different aspects of plant–insect interactions and associations with gymnosperms in floras prior to the angiosperm radiation was to establish independent lines of evidence for

understanding why there was no increase in diversity commensurate with the angiosperm radiation.

In this contribution, a comprehensive summary of family-level, plant-associated lineages with dominantly cryptogam/fern, gymnosperm, and angiosperm host relationships is provided for an interval of time encompassing the Jurassic, Cretaceous, and Paleogene periods from 201 to 23 million years ago. The major focus of this report is to assess the diversity pattern and effects that the initial rise of angiosperms had on insect families that previously hosted cryptogams, ferns, and gymnosperms, and whether the subsequent shift of insect lineages toward angiosperm hosts is associated with a marked increase in their diversity. It is hoped that this exercise would spur other examinations of insect diversity patterns, such as assessments at the genus rank, through this formative time interval that resulted in much of the modern terrestrial world.

13.2 Methods and Definitions

13.2.1 Herbivory: Dominant Feeding Guilds, Functional Feeding Groups, and Plant Hosts

The first of these dietary habits of insects is the feeding guild (Table 13.1, Fig. 13.2). Five major feeding guilds are considered to encompass the variety of insect relationships with plants that are specified in the primary documentation (Table 13.1, Fig. 13.2). These dominant feeding guilds are *herbivory, pollination, herbivory–pollination, pollination–mimicry*, and *xylophagy*. The feeding guilds characterize family-level lineages of the eleven major orders of plant-associated insects during the Jurassic to Paleogene periods: Orthoptera, Phasmatodea, Thysanoptera, Hemiptera, Neuroptera, Coleoptera, Trichoptera, Lepidoptera, Mecoptera, Diptera, and Hymenoptera. These principal insect lineages constitute a broad variety of habitus types affiliated with orthopteroid, hemipteroid, and holometabolous developmental modes.

Herbivory is an antagonistic interaction defined as the consumption of live, photosynthetic plant tissues such as foliage, stems, and other organs. Although pollination is an interaction that may include the consumption of photosynthetic or non-photosynthetic tissues such as seeds, it is primarily characterized as the transfer of pollen from the pollinate to the ovulate reproductive organ of a conspecific plant host. When an insect taxon harbors two dominant plant-interactional strategies, such as an immature insect instar (nymph, larva) feeding on foliar tissues and an adult actively pollinating a different suite of host plants, such an interaction is herbivory–pollination. Similarly, a few pollinators possess the nonfeeding interaction of mimicry to deter or otherwise avoid insect predation but frequently are pollinators as well, in which case they are pollinator–mimics. Last, xylophagy is the consumption of wood, but for this study the feeding guild obligately includes the consumption of associated live tissue, such as subcortical

Table 13.1 Ranges and major habits of seed plant-associated family-level insect taxa during the Jurassic, Triassic and Cretaceous periods[a]

Order, family[b]	Geochronologic range[c]	Dominant feeding guild[d]	Major FFG[e]	Dominant hosts and host transitions[f]	Fig. 13.2 entry
Orthoptera (N = 16)					
Acrididae	J (Tith)–Recent	Herbivore	EF	Gymno → Angio	1
Elcanidae	P (Arti)–K (Apti)	Herbivore	EF	Gymno	2
Eumastacidae	J (Oxfo)–Recent	Herbivore	EF	Gymno → Angio	3
Haglidae	Tr (Anis)–Recent	Herb/Poll	EF	Gymno → Angio	4
Haglotettigoniidae	K (Albi)–K (Albi)	Herbivore	EF	Angio	5
Locustopseidae	Tr (Olen)–Pg (Chat)	Herbivore	EF	Gymno → Angio	6
Myrmecophilidae	K (Apti)–Recent	Herbivore	EF	Angio	7
Phasmomimidae	J (Toar)–Pg (Than)	Herbivore	EF	Gymno → Angio	8
Pneumoridae	K (Albi)–Recent	Herbivore	EF	Angio	9
Promastacidae	Pg (Than)–Pg (Than)	Herbivore	EF	Gymno	10
Prophalangopsidae	J (Hett)–Recent	Herb/Poll	EF	Gymno → Angio	11
Raphidiophoridae	K (Apti)–Recent	Herbivore	EF	Angio	12
Tetrigidae	K (Albi)–Recent	Herbivore	EF	Angio	13
Tettigoniidae	J (Sine)–Recent	Herbivore	EF	Gymno → Angio	14
Tuphellidae	Tr (Ladi)–J (Oxfo)	Herbivore	EF	Gymno	15
Vitimiidae	Tr (Ladi)–K (Albi)	Herbivore	EF	Gymno	16
Phasmatodea (N = 3)					
Phasmatidae	Pg (Pria)–Recent	Herbivore	EF	Angio	17
Phyllidae	Pg (Lute)–Recent	Herbivore	EF	Angio	18
Susmaniidae	J (Call)–Pg (Dani)	Herbivore	EF	Gymno → Angio	19
Thysanoptera (N = 11)					
Aeolopthripidae	K (Berr)–Recent	Herb/Poll	P&S	Gymno → Angio	20
Heterothripidae	K (Camp)–Recent	Herb/Poll	P&S	Angio	21
Karataothripidae	J (Oxfo)–J (Oxfo)	Herb/Poll	P&S	Gymno	22
Liassothripidae	J (Oxfo)–J (Oxfo)	Herb/Poll	P&S	Gymno	23
Lophioneuridae	P (Arti)–K (Albi)	Herb/Poll	P&S	Gymno	24
Melanthripidae	K (Albi)–Recent	Herb/Poll	P&S	Gymno → Angio	25
Merothripidae	K (Apti)–Recent	Herb/Poll	P&S	Angio	26
Moundthripidae	K (Apti)–K (Apti)	Herb/Poll	P&S	Gymno	27
Phlaeothripidae	K (Sant)–Recent	Herb/Poll	Gall	Angio	28
Stenurothripidae	K (Apti)–Recent	Herb/Poll	P&S	Angio	29
Thripidae	K (Apti)–Recent	Herb/Poll	P&S	Angio	30
Hemiptera (N = 103)					
Acanthosomatidae	Pg (Lute)–Recent	Herbivore	P&S	Angio	31
Adelgidae	K (Turo)–Recent	Herbivore	Gall	Gymno	32
Aleyrodidae	J (Oxfo)–Recent	Herbivore	P&S	Gymno → Angio	33
Alydidae	K (Haut)–Recent	Herbivore	P&S	Gymno → Angio	34
Anoecidae	Pg (Pria)–Recent	Herbivore	P&S	Angio	35
Anthocoridae	K (Berr)–Recent	Herbivore	SP	Gymno → Angio	36
Aphididae	J (Kimm)–Recent	Herbivore	P&S	Gymno → Angio	37
Aphrophoridae	Pg (Than)–Recent	Herbivore	P&S	Angio	38
Archescytinidae	C (Gzhe)–J (Toar)	Herbivore	P&S	Gymno	39
Archijassidae	Tr (Carn)–K (Apti)	Herbivore	P&S	Gymno	40
Berytidae	Pg (Pria)–Recent	Herbivore	P&S	Angio	41
Boreoscytidae	P (Kung)–K (Apti)	Herbivore	P&S	Gymno	42
Canadaphididae	K (Sant)–K (Camp)	Herbivore	P&S	Gymno	43

(continued)

Table 13.1 (continued)

Order, family[b]	Geochronologic range[c]	Dominant feeding guild[d]	Major FFG[e]	Dominant hosts and host transitions[f]	Fig. 13.2 entry
Carsidaridae	Pg (Pria)–Recent	Herbivore	P&S	Angio	44
Cercopidae	J (Call)–Recent	Herbivore	P&S	Gymno → Angio	45
Cercopionidae	Tr (Carn)–K (Apti)	Herbivore	P&S	Gymno	46
Cicadellidae	J (Kimm)–Recent	Herbivore	P&S	Gymno → Angio	47
Cicadidae	K (Ceno)–Recent	Herbivore	P&S	Angio	48
Cixiidae	Tr (Rhae)–Recent	Herbivore	P&S	Gymno → Angio	49
Clastopteridae	Pg (Pria)–Recent	Herbivore	P&S	Angio	50
Coccidae	Pg (Lute)–Recent	Herbivore	P&S	Angio	51
Coreidae	J (Call)–Recent	Herbivore	P&S	Gymno → Angio	52
Cretamyzidae	K (Camp)–K (Camp)	Herbivore	P&S	Gymno	53
Cuneocoridae	J (Plie)–J (Toar)	Herbivore	P&S	Gymno	54
Cydnidae	K (Berr)–Recent	Herbivore	P&S	Gymno → Angio	55
Dactylopiidae	Pg (Chat)–Recent	Herbivore	P&S	Angio	56
Delphacidae	Pg (Ypre)–Recent	Herbivore	P&S	Angio	57
Derbidae	Pg (Lute)–Recent	Herbivore	P&S	Angio	58
Diaspididae	K (Albi)–Recent	Herbivore	Gall	Angio	59
Dictyopharidae	K (Sant)–Recent	Herbivore	P&S	Angio	60
Drepanosiphidae	K (Turo)–Recent	Herbivore	P&S	Angio	61
Dunstaniidae	P (Road)–J (Sine)	Herbivore	P&S	Gymno	62
Dysmorphoptilidae	P (Arti)–J (Oxfo)	Herbivore	P&S	Gymno	63
Elektraphididae	K (Sant)–Ng (Piac)	Herbivore	P&S	Angio	64
Eoscarterellidae	P (Chan)–K (Berr)	Herbivore	P&S	Gymno	65
Eriococcidae	K (Turo)–Recent	Herbivore	Gall	Angio	66
Flatidae	Pg (Sela)–Recent	Herbivore	P&S	Angio	67
Fulgoridae	J (Toar)–Recent	Herbivore	P&S	Gymno → Angio	68
Fulgoridiidae	J (Hett)–L (Vala)	Herbivore	P&S	Gymno	69
Genaphididae	J (Call)–K (Tith)	Herbivore	P&S	Gymno	70
Granulidae	J (Call)–K (Apti)	Herbivore	P&S	Gymno	71
Hormaphididae	J (Kimm)–Recent	Herbivore	Gall	Gymno → Angio	72
Hylicellidae	P (Wuch)–J (Oxfo)	Herbivore	P&S	Gymno	73
Inkaidae	K (Sant)–K (Sant)	Herbivore	P&S	Angio	74
Ipsviciidae	P (Road)–J (Sine)	Herbivore	P&S	Gymno	75
Issidae	Pg (Lute)–Recent	Herbivore	P&S	Angio	76
Karabasiidae	J (Bath)–K (Haut)	Herbivore	P&S	Crypt/Fern	77
Karajassidae	J (Bath)–K (Apti)	Herbivore	P&S	Gymno	78
Kermesidae	Pg (Lute)–Recent	Herbivore	Gall	Angio	79
Kobdocoridae	K (Berr)–K (Apti)	Herbivore	P&S	Gymno	80
Lachnidae	Pg (Chat)–Recent	Herbivore	P&S	Gymno	81
Lalacidae	J (Call)–K (Apti)	Herbivore	P&S	Gymno	82
Largidae	Pg (Pria)–Recent	Herbivore	P&S	Angio	83
Latiscutellidae	K (Barr)–K (Apti)	Herbivore	P&S	Gymno	84
Liadopsyllidae	J (Toar)–K (Turo)	Herbivore	P&S	Gymno	85
Ligavenidae	K (Apti)–K (Apti)	Herbivore	P&S	Gymno	86
Lophophidae	J (Toar)–Recent	Herbivore	SP	Gymno → Angio	87
Lygaeidae	J (Bajo)–Recent	Herbivore	P&S	Gymno → Angio	88
Margarodidae	K (Haut)–Recent	Herbivore	Gall	Angio	89
Matsucoccidae	Pg (Lute)–Recent	Herbivore	P&S	Gymno	90

(continued)

Table 13.1 (continued)

Order, family[b]	Geochronologic range[c]	Dominant feeding guild[d]	Major FFG[e]	Dominant hosts and host transitions[f]	Fig. 13.2 entry
Membracidae	Pg (Lute)–Recent	Herbivore	P&S	Angio	91
Mesozoicoaphididae	K (Camp)–K (Camp)	Herbivore	P&S	Gymno	92
Mindaridae	K (Albi)–Recent	Herbivore	Gall	Gymno	93
Miridae	J (Oxfo)–Recent	Herbivore	P&S	Gymno → Angio	94
Neopsylloididae	J (Oxfo)–J (Oxfo)	Herbivore	P&S	Gymno	95
Nogodinidae	K (Berr)–Recent	Herbivore	P&S	Gymno → Angio	96
Ortheziidae	K (Apti)–Recent	Herbivore	P&S	Cryp/Fern → Angio	97
Oviparosiphidae	J (Toar)–K (Apti)	Herbivore	P&S	Gymno	98
Pachymeridiidae	Tr (Rhae)–K (Apti)	Herbivore	SP	Gymno	99
Palaeoaphididae	K (Berr)–K (Camp)	Herbivore	P&S	Gymno	100
Palaeontinidae	Tr (Ladi)–K (Apti)	Herbivore	P&S	Gymno	101
Pemphigidae	K (Sant)–Recent	Herbivore	Gall	Angio	102
Pentatomidae	K (Albi)–Recent	Herbivore	P&S	Angio	103
Pereboridae	P (Arti)–K (Barr)	Herbivore	P&S	Gymno	104
Phylloxeridae	K (Camp)–Recent	Herbivore	Gall	Angio	105
Piesmatidae	K (Albi)–Recent	Herbivore	P&S	Angio	106
Pityococcidae	Pg (Lute)–Recent	Herbivore	P&S	Angio	107
Pricecoridae	K (Barr)–Pg (Lang)	Herbivore	P&S	Angio	108
Procercopidae	J (Hett)–K (Barr)	Herbivore	P&S	Gymno	109
Progonocimicidae	P (Chan)–K (Apti)	Herbivore	P&S	Cryp/Fern	110
Protocoridae	J (Hett)–J (Hett)	Herbivore	P&S	Gymno	111
Protopsyllidiidae	P (Kung)–K (Apti)	Herbivore	P&S	Gymno	112
Pseudococcidae	Pg (Rupe)–Recent	Herbivore	Gall	Angio	113
Psyllidae	J (Oxfo)–Recent	Herbivore	Gall	Gymno → Angio	114
Pyrrhocoridae	Pg (Pria)–Recent	Herbivore	P&S	Angio	115
Rhopalidae	J (Call)–Recent	Herbivore	P&S	Gymno → Angio	116
Ricaniidae	Pg (Than)–Recent	Herbivore	P&S	Angio	117
Scutelleridae	Pg (Than)–Recent	Herbivore	P&S	Angio	118
Scytinopteridae	P (Kung)–K (Barr)	Herbivore	P&S	Gymno	119
Serpentivenidae	P (Word)–Pg (Sela)	Herbivore	P&S	Gymno → Angio	120
Shaposhnikoviidae	J (Bajo)–K (Sant)	Herbivore	P&S	Gymno	121
Sinojuraphidae	J (Call)–J (Call)	Herbivore	P&S	Gymno	122
Steingeliidae	K (Apti)–Recent	Herbivore	P&S	Angio	123
Stenoviciidae	P (Capi)–K (Berr)	Herbivore	P&S	Gymno	124
Tajmyraphididae	K (Apti)–K (Sant)	Herbivore	P&S	Gymno	125
Tettigarctidae	Tr (Carn)–Recent	Herbivore	P&S	Gymno → Angio	126
Tettigoniidae	Pg (Dani)–Recent	Herbivore	P&S	Angio	127
Thaumastocoridae	Pg (Ypre)–Recent	Herbivore	SP	Angio	128
Thelaxidae	K (Apti)–Recent	Herbivore	SP	Gymno	129
Tingidae	K (Berr)–Recent	Herbivore	Gall	Gymno → Angio	130
Velanthocoridae	J (Call)–K (Camp)	Pollinator	P&S	Gymno	131
Venicoridae	J (Call)–K (Barr)	Herbivore	P&S	Gymno	132
Weiwoboidae	Pg (Ypre)–Pg (Ypre)	Herbivore	P&S	Angio	133
Neuroptera (N = 4)					
Kalligrammatidae	J (Call)–K (Barr)	Poll/Mimic	SFF	Gymno	134
Nemopteridae	K (Apti)–Recent	Poll/Mimic	SFF	Angio	135
Staurosmylidae	J (Call)–J (Oxfo)	Poll/Mimic	SFF	Cryp/Fern	136
Panfiloviidae	J (Oxfo)–K (Apti)	Herbivore	SFF	Gymno	137

(continued)

Table 13.1 (continued)

Order, family[b]	Geochronologic range[c]	Dominant feeding guild[d]	Major FFG[e]	Dominant hosts and host transitions[f]	Fig. 13.2 entry
Coleoptera (N = 42)					
Aderidae	Pg (Lute)–Recent	Herbivore	EF	Angio	138
Anobiidae	K (Haut)–Recent	Xylophage	WB	Gymno → Angio	139
Attelabidae	K (Albi)–Recent	Herbivore	EF	Angio	140
Belidae	K (Barr)–Recent	Herb/Poll	Paly	Gymno	141
Boganiidae	J (Oxfo)–Recent	Pollinator	Paly	Gymno	142
Bostrichidae	J (Oxfo)–Recent	Xylophage	WB	Gymno → Angio	143
Brentidae	K (Barr)–Recent	Xylophage	WB	Angio	144
Bruchidae	K (Barr)–Recent	Herbivore	SP	Angio	145
Buprestidae	J (Call)–Recent	Xylophage	WB	Gymno → Angio	146
Byrrhidae	J (Oxfo)–Recent	Herbivore	EF	Cryp/Fern	147
Byturidae	Pg (Lute)–Recent	Pollinator	EF	Angio	148
Caridae	J (Oxfo)–Recent	Herb/Poll	EF	Gymno	149
Cerambycidae	K (Barr)–Recent	Xylophage	WB	Angio	150
Chrysomelidae	J (Call)–Recent	Herbivore	EF	Gymno → Angio	151
Curculionidae	J (Call)–Recent	Herb/Poll	EF	Gymno → Angio	152
Dascillidae	K (Apti)–Recent	Herbivore	EF	Angio	153
Erotylidae[g]	Pg (Ypre)–Recent	Herbivore	EF	Angio	154
Glaresidae	K (Barr)–Recent	Pollinator	EF	Angio	155
Ithyceridae	J (Call)–Recent	Herb/Poll	EF	Gymno → Angio	156
Lasiosynidae	J (Toar)–K (Apti)	Herb/Poll	EF	Gymno	157
Lymexylidae	K (Apti)–Recent	Xylophage	WB	Angio	158
Meloidae[h]	Pg (Lute)–Recent	Pollinator	SFF	Angio	159
Melyridae	K (Turo)–Recent	Pollinator	EF	Angio	160
Mordellidae	J (Call)–Recent	Pollinator	SFF	Gymno → Angio	161
Mycteridae	Pg (Ypre)–Recent	Pollinator	EF	Angio	162
Nemonychidae	J (Call)–Recent	Herb/Poll	Paly	Gymno	163
Nitidulidae	J (Call)–Recent	Herbivore	SFF	Gymno → Angio	164
Obrieniidae	Tr (Carn)–J (Oxfo)	Herbivore	EF	Gymno	165
Oedemeridae	Pg (Pria)–Recent	Herbivore	EF	Angio	166
Oxycorynidae	J (Oxfo)–Recent	Pollinator	SP	Gymno	167
Pandrexidae	J (Bajo)–K (Apti)	Herbivore	EF	Gymno	168
"Praemordellidae"[i]	J (Call)–J (Oxfo)	Pollinator	EF	Gymno	169
Protocucujidae	K (Apti)–Recent	Herbivore	EF	Angio	170
Protoscelidae	J (Call)–J (Oxfo)	Herbivore	EF	Gymno	171
Pythidae	Pg (Pria)–Recent	Xylophage	WB	Gymno	172
Ripiphoridae[j]	K (Albi)–Recent	Pollinator	SFF	Angio	173
Salpingidae	Pg (Ypre)–Recent	Herbivore	EF	Gymno	174
Scarabaeidae	J (Oxfo)–Recent	Pollinator	EF	Gymno → Angio	175
Scraptiidae	K (Berr)–Recent	Pollinator	EF	Gymno → Angio	176
Silvanidae	K (Albi)–Recent	Herbivore	SP	Angio	177
Ulyanidae	K (Apti)–K (Albi)	Herbivore	EF	Angio	178
Unnamed family	J (Call)–J (Call)	Pollinator	EF	Gymno	179
Trichoptera (N = 3)					
Dipseudopsidae	K (Turo)–Recent	Polllinator	SFF	Angio	180
Necrotauliidae[k]	Tr (Ladi)–K (Albi)	Pollinator	SFF	Gymno	181
Plectrotarsidae	J (Tith)–Recent	Pollinator	SFF	Gymno → Angio	182

(continued)

Table 13.1 (continued)

Order, family[b]	Geochronologic range[c]	Dominant feeding guild[d]	Major FFG[e]	Dominant hosts and host transitions[f]	Fig. 13.2 entry
Lepidoptera (N = 39)					
Adelidae	Pg (Lute)–Recent	Herb/Poll	EF	Angio	183
Agathiphagidae	K (Haut)[l]–Recent	Herb/Poll	SP	Gymno	184
Archaeolepidae	J (Sine)–J (Sine)	Herb/Poll	EF	Gymno	185
Ascololepid-opterigidae	J (Call)–J (Call)	Herb/Poll	EF	Gymno	186
Bucculatricidae	K (Turo)–Recent	Herb/Poll	LM	Angio	187
Coleophoridae	K (Ceno)–Recent	Herb/Poll	LM	Angio	188
Copromorphidae	Pg (Pria)–Recent	Herb/Poll	EF	Angio	189
Cosmopterigidae	Pg (Chat)–Recent	Herb/Poll	LM	Angio	190
Cossidae	Pg (Chat)–Recent	Xylophage	WB	Angio	191
Elachistidae	Pg (Lute)–Recent	Herb/Poll	LM	Angio	192
Eolepidopterigidae	J (Call)–J (Oxfo)	Herb/Poll	EF	Gymno	193
Gelechiidae	Pg (Lute)–Recent	Herb/Poll	EF	Angio	194
Geometridae	Pg (Pria)–Recent	Herb/Poll	EF	Angio	195
Gracillariidae	K (Albi)–Recent	Herb/Poll	LM	Angio	196
Heliodinidae	Pg (Lute)–Recent	Herb/Poll	EF	Angio	197
Heliozelidae	Pg (Lute)–Recent	Herb/Poll	LM	Angio	198
Hesperiidae	Pg (Chat)–Recent	Herb/Poll	EF	Angio	199
Incurvariidae	Pg (Ypre)–Recent	Herb/Poll	LM	Angio	200
Lasiocampidae	Pg (Lute)–Recent	Herb/Poll	EF	Angio	201
Libytheidae	Pg (Pria)–Recent	Herb/Poll	EF	Angio	202
Lycaenidae	Pg (Chat)–Recent	Herb/Poll	EF	Angio	203
Lyonetiidae	Pg (Ypre)–Recent	Herb/Poll	LM	Angio	204
Micropterygidae	K (Apti)–Recent	Herb/Poll	Paly	Cryp/Fern → Angio	205
Mesokristenseniidae	J (Call)–J (Call)	Herb/Poll	EF	Gymno	206
Nepticulidae	K (Albi)–Recent	Herb/Poll	LM	Angio	207
Noctuidae	Pg (Lute)–Recent	Herb/Poll	EF	Angio	208
Nymphalidae	Pg (Ypr)–Recent	Herb/Poll	EF	Angio	209
Oecophoridae	Pg (Lute)–Recent	Xylophage	WB	Angio	210
Papilionidae	Pg (Ypre)–Recent	Herb/Poll	EF	Angio	211
Pieridae	Pg (Pria)–Recent	Herb/Poll	EF	Angio	212
Plutellidae	Pg (Lute)–Recent	Herb/Poll	EF	Angio	213
Psychidae	Pg (Lute)–Recent	Herb/Poll	EF	Angio	214
Pterophoridae	Pg (Chat)–Recent	Herb/Poll	EF	Angio	215
Pyralidae	Pg (Lute)–Recent	Herb/Poll	EF	Angio	216
Saturniidae	Pg (Lute)–Recent	Herb/Poll	EF	Angio	217
Thyrididae	Pg (Lute)–Recent	Xylophage	WB	Angio	218
Tortricidae	Pg (Lute)–Recent	Herb/Poll	EF	Angio	219
Undopterigidae[m]	J (Oxfo)–K (Apti)	Herb/Poll	LM[n]	Gymno	220
Zygaenidae	Pg (Chat)–Recent	Herb/Poll	EF	Angio	221
Mecoptera (N = 4)					
Aneuretopsychidae	J (Oxfo)–K (Apti)	Pollinator	SFF	Gymno	222
Cimbrophlebiidae	J (Toar)–Pg (Lute)	Poll/Mimic	EF	Gymno → Angio	223
Mesopsychidae	P (Wuch)–K (Barr)	Pollinator	SFF	Gymno	224
Pseudopolycen-tropodidae	Tr (Ladi)–K (Albi)	Pollinator	SFF	Gymno	225
Diptera (N = 27)					
Acroceridae	J (Oxfo)–Recent	Pollinator	SFF	Gymno → Angio	226
Agromyzidae	Pg (Dani)–Recent	Herbivore	LM	Angio	227
Anthomyiidae	Pg (Pria)–Recent	Pollinator	SFF	Angio	228

(continued)

Table 13.1 (continued)

Order, family[b]	Geochronologic range[c]	Dominant feeding guild[d]	Major FFG[e]	Dominant hosts and host transitions[f]	Fig. 13.2 entry
Anthomyzidae	Pg (Lute)–Recent	Herbivore	SFF	Angio	229
Apsilocephalidae	K (Albi)–Recent	Herbivore	SFF	Angio	230
Atelestidae	K (Berr)–Recent	Pollinator	Paly	Gymno → Angio	231
Athericidae	K (Berr)–Recent	Pollinator	SFF	Gymno → Angio	232
Bombyliidae	K (Berr)–Recent	Pollinator	Paly	Gymno → Angio	233
Cecidomyiidae	K (Haut)–Recent	Herbivore	Gall	Angio[o]	234
Chloropidae	Pg (Lute)–Recent	Herbivore	Gall	Angio	235
Cratomyiidae	K (Apti)–K (Apti)	Pollinator	Paly	Gymno	236
Hilarimorphidae	K (Haut)–Recent	Pollinator	SFF	Gymno → Angio	237
Lonchopteridae	K (Apti)–Recent	Pollinator	SFF	Gymno → Angio	238
Mydidae	K (Apti)–Recent	Pollinator	SFF	Gymno → Angio	239
Nemestrinidae	J (Call)–Recent	Pollinator	SFF	Gymno → Angio	240
Opomyzidae	Pg (Chat)–Recent	Herbivore	SFF	Angio	241
Platypezidae	K (Sant)–Recent	Herbivore	SFF	Angio	242
Protapioceridae[p]	J (Barr)–Recent	Pollinator	SFF	Angio	243
Scenopinidae	J (Oxfo)–Recent	Pollinator	SFF	Gymno → Angio	244
Stratiomyidae	K (Barr)–Recent	Pollinator	SFF	Angio	245
Syrphidae	K (Sant)–Recent	Pollinator	Paly	Angio	246
Tabanidae[q]	K (Berr)–Recent	Pollinator	SFF	Gymno → Angio	247
Therevidae	J (Oxfo)–Recent	Pollinator	SFF	Gymno → Angio	248
Tipulidae	Tr (Carn)–Recent	Pollinator	SFF	Gymno → Angio	249
Vermileonidae	J (Oxfo)–Recent	Pollinator	SFF	Gymno → Angio	250
Xylomyiidae	K (Albi)–Recent	Herbivore	SFF	Angio	251
Xylophagidae	K (Ceno)–Recent	Pollinator	WB	Angio	252
Hymenoptera (N = 28)					
Agaonidae	Pg (Rupe)–Recent	Pollinator	Gall	Angio	253
Anaxyelidae	J (Call)–Recent	Xylophage	WB	Gymno → Angio	254
Andrenidae	Pg (Lute)–Recent	Pollinator	SFF	Angio	255
Apidae	K (Maas)–Recent	Pollinator	SFF	Angio	256
Argidae	Pg (Than)–Recent	Herbivore	EF	Angio	257
Blasticotomidae	Pg (Lute)–Recent	Herbivore	WB	Cryp/Fern	258
Cephidae	J (Bajo)–Recent	Herbivore	EF	Gymno → Angio	259
Chalcididae	Pg (Ypre)–Recent	Herbivore	Gall	Angio	260
Cimbicidae	Pg (Than)–Recent	Herbivore	EF	Angio	261
Cynipidae	K (Camp)–Recent	Pollinator	Gall	Angio	262
Diprionidae	Pg (Rupe)–Recent	Herbivore	EF	Gymno	263
Electrotomidae	Pg (Lute)–Pg (Lute)	Herbivore	EF	Angio	264
"Gigasiricidae"[i]	K (Plie)–K (Apti)	Xylophage	WB	Gymno	265
Halictidae	Pg (Ypre)–Recent	Pollinator	SFF	Angio	266
Masaridae	K (Albi)–Recent	Pollinator	Paly	Angio	267
Megachilidae	Pg (Than)–Recent	Pollinator	SFF	Angio	268
Melittidae	Pg (Ypre)–Recent	Pollinator	SFF	Angio	269
Melittosphecidae	K (Albi)–K (Albi)	Pollinator	SFF	Angio	270
Pamphiliidae	J (Oxfo)–Recent	Herbivore	EF	Gymno → Angio	271
"Praesiricidae"[i]	J (Call)–K (Apti)	Herbivore	EF	Gymno	272
Scoliidae	J (Kimm)–Recent	Pollinator	SFF	Gymno → Angio	273
Sepulcidae	J (Plie)–K (Ceno)	Herbivore	EF	Gymno	274
Siricidae	J (Plie)–Recent	Xylophage	WB	Gymno → Angio	275
Tenthredinidae	J (Kimm)–Recent	Herbivore	LM	Cryp/Fern → Angio	276

(continued)

Table 13.1 (continued)

Order, family[b]	Geochronologic range[c]	Dominant feeding guild[d]	Major FFG[e]	Dominant hosts and host transitions[f]	Fig. 13.2 entry
Xiphydriidae	K (Albi)[12]–Recent	Xylophage	WB	Angio	277
Xyelidae	Tr (Ladi)–Recent	Pollinator	Paly	Gymno	278
"Xyelotomidae"[i]	J (Oxfo)–K (Barr)	Herbivore	EF	Cryp/Fern	279
"Xyelydidae"[i]	J (Toar)–K (Barr)	Herbivore	EF	Gymno	280

Notes

[a] Major data sources for this table are: Miller (1956), Lewis (1973), McAlpine et al. (1981, 1987, 1989), Gauld and Bolton (1988), Dmitriev and Zherikhin (1988), Naumann et al. (1991), Dolling (1991), Carpenter (1992), Ross and Jarzembowski (1993), Goulet and Huber (1993), Labandeira (1994), Evenhuis (1994); Schuh and Slater (1995), Rasnitsyn and Quicke (2002), Grimaldi and Engel, 2005), Yeates and Wiegmann (2005), Ren (2010), Sohn et al. (2012), Marshall (2012), Lawrence and Ślipiński (2013) and the Paleobiology Database (PBDB, 2014). Entries for ecological data categories indicate major attributes for the indicated taxon

[b] Depending on the authority, several of these family-level taxa (N = 280) have been reassigned to subfamily rank. Other family-level designations are currently in flux and require revision

[c] Abbreviations: The geologic periods, from oldest youngest, are: *C*, Carboniferous; *P*, Permian; *Tr*, Triassic; *J*, Jurassic; *K*, Cretaceous; *Pg*, Paleogene; and *Ng*, Neogene. The geologic stages, from oldest to youngest are the following. For the Carboniferous: *Gzhe*, Gzhelian. For the Permian: *Arti*, Artinskian; *Kung*, Kungurian; *Road*, Roadian; *Word*, Wordian; *Capi*, Capitanian; *Wuch*, Wuchiapingian; *Chan*, Changhsingian. For the Triassic: *Olen*, Olenekian; *Anis*, Anisian; *Ladi*, Ladinian; *Carn*, Carnian; *Rhae*, Rhaetian. For the Jurassic: *Hett*, Hettangian; *Sine*, Sinemurian; *Plie*, Pliensbachian; *Toar*, Toarcian; *Bajo*, Bajocian; *Bath*, Bathonian; *Call*, Callovian; *Oxfo*, Oxfordian; *Kimm*, Kimmeridgian; *Tith*, Tithonian. For the Cretaceous: *Berr*, Berriasian; *Vala*, Valanginian; *Haut*, Hauterivian; *Barr*, Barremian; *Apti*, Aptian; *Albi*, Albian; *Ceno*, Cenomanian; *Turo*, Turonian; *Sant*, Santonian; *Camp*, Campanian; *Maas*, Maastrichtian. For the Paleogene: *Dani*, Danian; *Sela*, Selandrian; *Than*, Thanetian; *Ypre*, Ypresian; *Lute*, Lutetian; *Pria*, Priabonian; *Rupe*, Rupelian; *Chat*, Chattian. For the Neogene: *Piac*, Piacenzian

[d] Abbreviations for the dominant feeding guilds of herbivory, pollination, xylophagy and mimicry are: *Herbivore*, *Pollinator*, *Herb/Poll*, *Poll/Mimic*, and *Xylophage* indicates the most dominant or otherwise most important feeding guild within the group under consideration

[e] Abbreviations for major functional feeding groups (*FFGs*) are: *EF*, external feeding; *Gall*, Galling; *LM*, leaf mining; *Paly*, pollen or spore consumption; *P&S*, piercing and sucking; *SFF*, surface fluid feeding; *SP*, seed predation; *WB*, wood boring

[f] Abbreviations for dominant hosts and transitions: *Cryp/Fern*, Cryptogams and/or ferns; *Gymno*, Gymnosperms; *Angio*, Angiosperms; *Cryp/Fern* → *Angio*, cryptogam or fern to angiosperm transition; *Gymno* → *Angio*, gymnosperm-to-angiosperm transition

[g] These pleasing fungus beetles include the Languriidae, the taxon of interest

[h] The relevant taxon is the Nemognathinae, with specialized, anthophilous mouthpart features

[i] These are stem groups possessing features of several derived taxa, and are considered here as distinctive lineages

[j] The relevant taxon is *Macrosiagon* and related genera, which possess specialized, anthophilous mouthpart features

[k] Probably more appropriately assigned to the Aphiesmenoptera, as a stem lineage to the Trichoptera + Lepidoptera

[l] Probable occurrence

[m] This family is not recognized by Sohn et al. (2012)

[n] Inferred larval feeding pattern

[o] Evidence suggests that the basal clades of Cecidomyiidae were not gall-forming, and that the gall-forming life habit evolved after angiosperms were established

[p] The Protapioceridae may be confamilial with the modern Apioceridae; alternatively, this lineage also may be ancestral to the Mydidae and Apioceridae. It is considered a distinct lineage herein

[q] The plant-associated subfamily, Pangioninae, is the relevant subgroup of Tabanidae that is considered herein

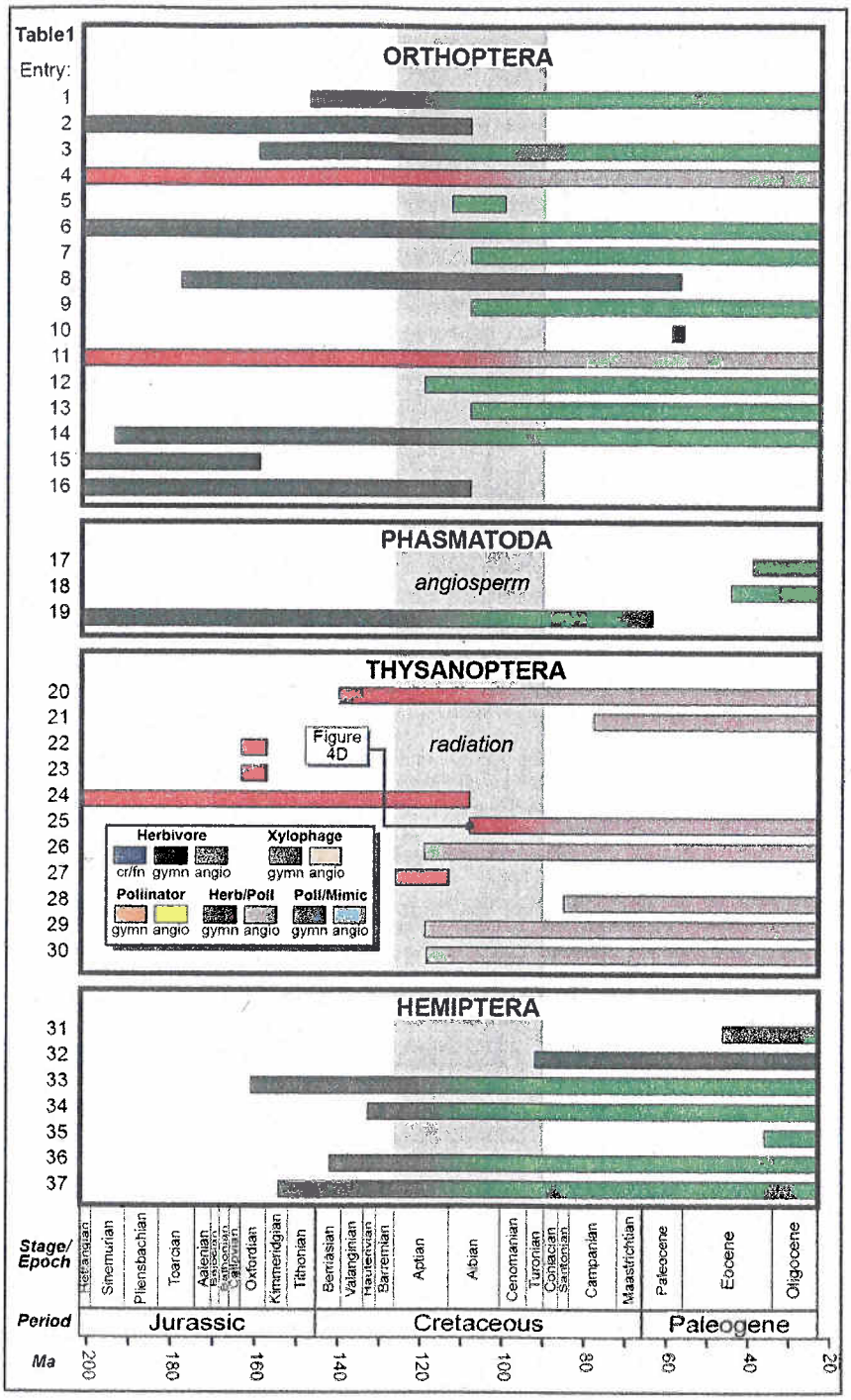

Fig. 13.2 (continued)

◀ **Fig. 13.2** Distribution of the eleven major, plant-associated insect lineages and their host–plant assignments during the Jurassic to Paleogene interval. The 35 million year-long angiosperm radiation encompasses the Aptian through Turonian stages of the mid Cretaceous as a vertical gray column at center. Major plant–host associations of herbivory, pollination, xylophagy, herbivory–pollination, and herbivory–mimicry, and their dominance in cryptogam/fern (*cr/fn*), cryptogam/fern → angiosperm, gymnosperm (*gymno*), gymnosperm → angiosperm and angiosperm (*angio*) hosts are indicated in the inset. Darker hues indicate gymnosperm hosts; lighter hues indicate angiosperm hosts. Data are from Table 13.1

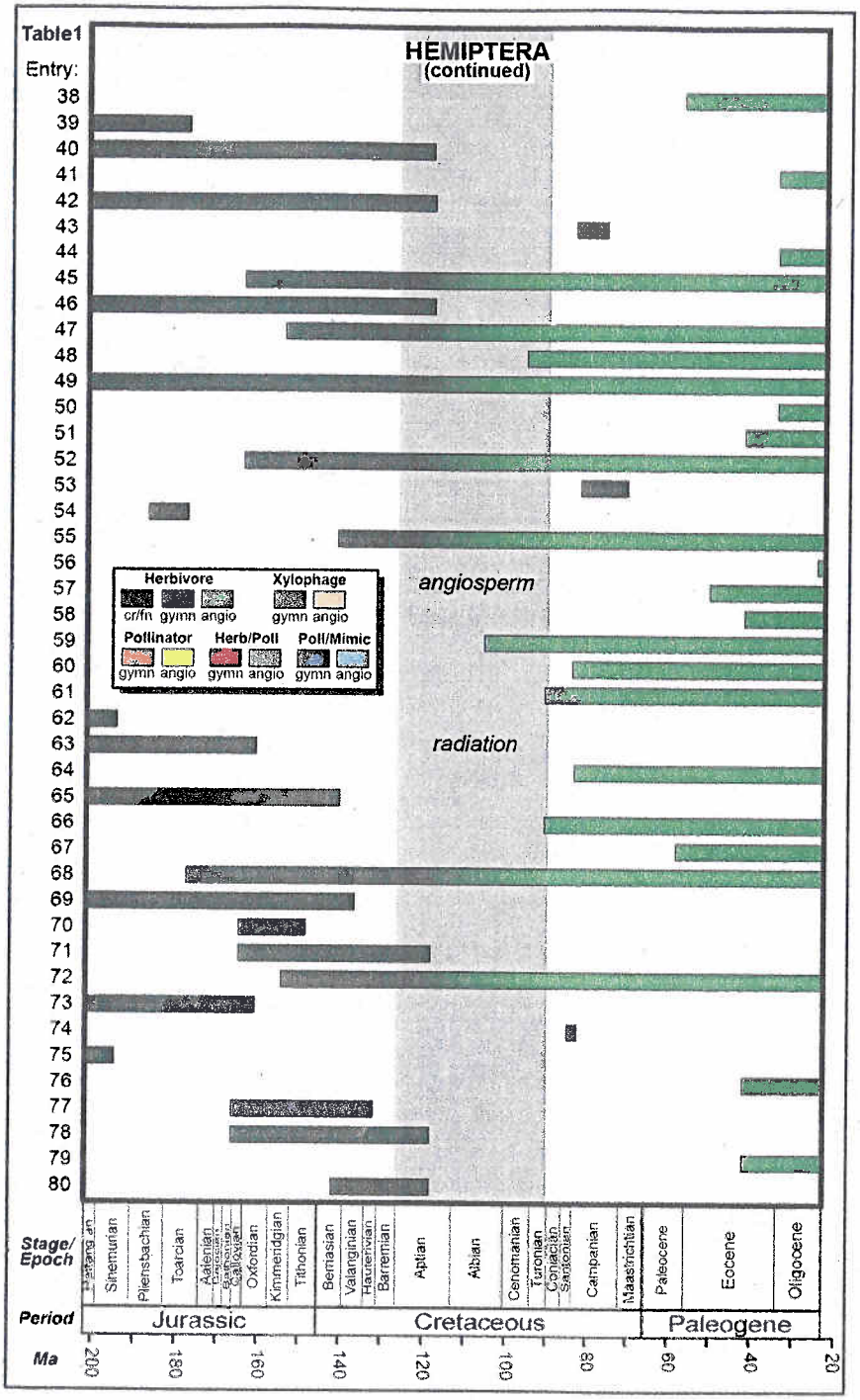

Fig. 13.2 (continued)

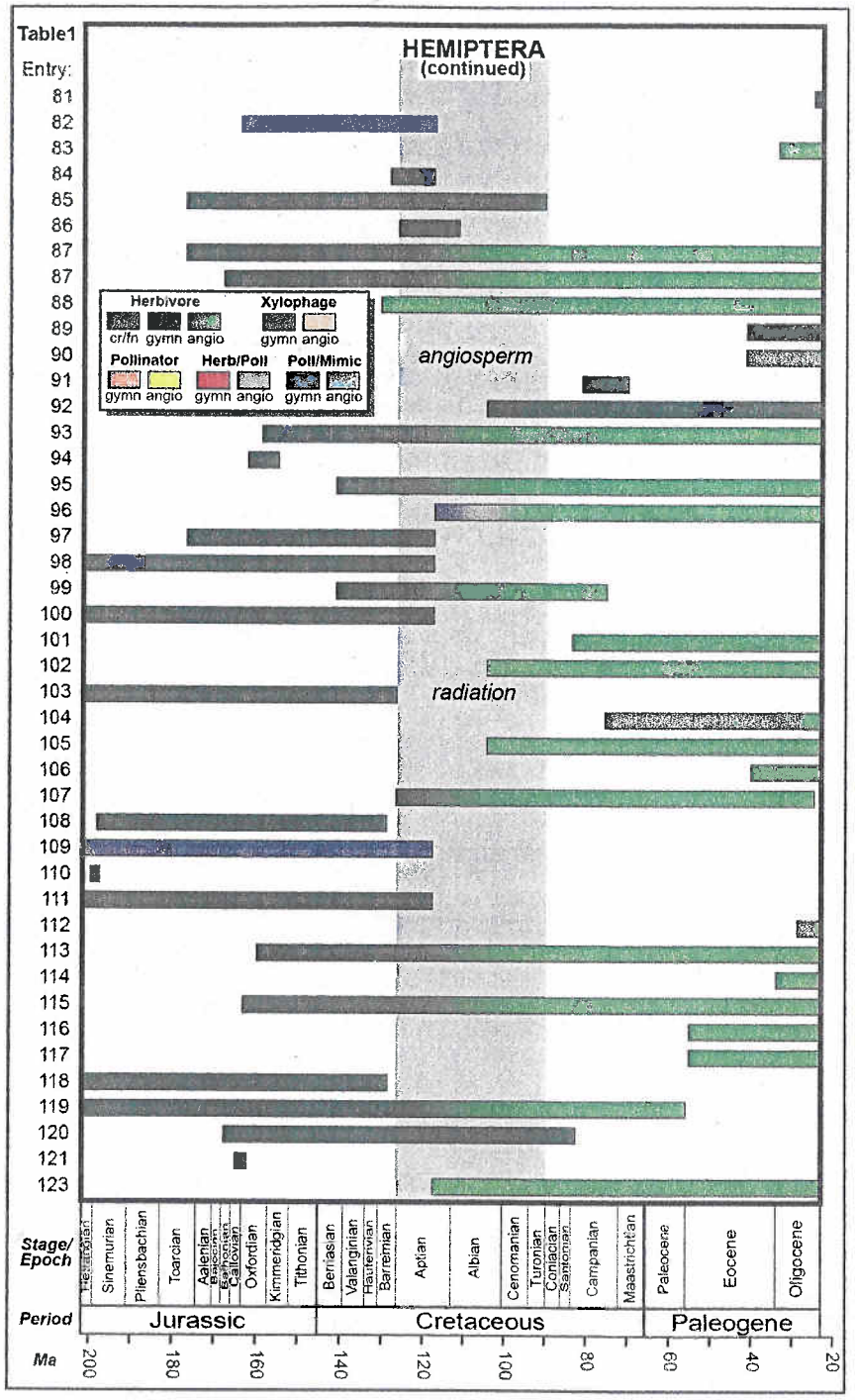

Fig. 13.2 (continued)

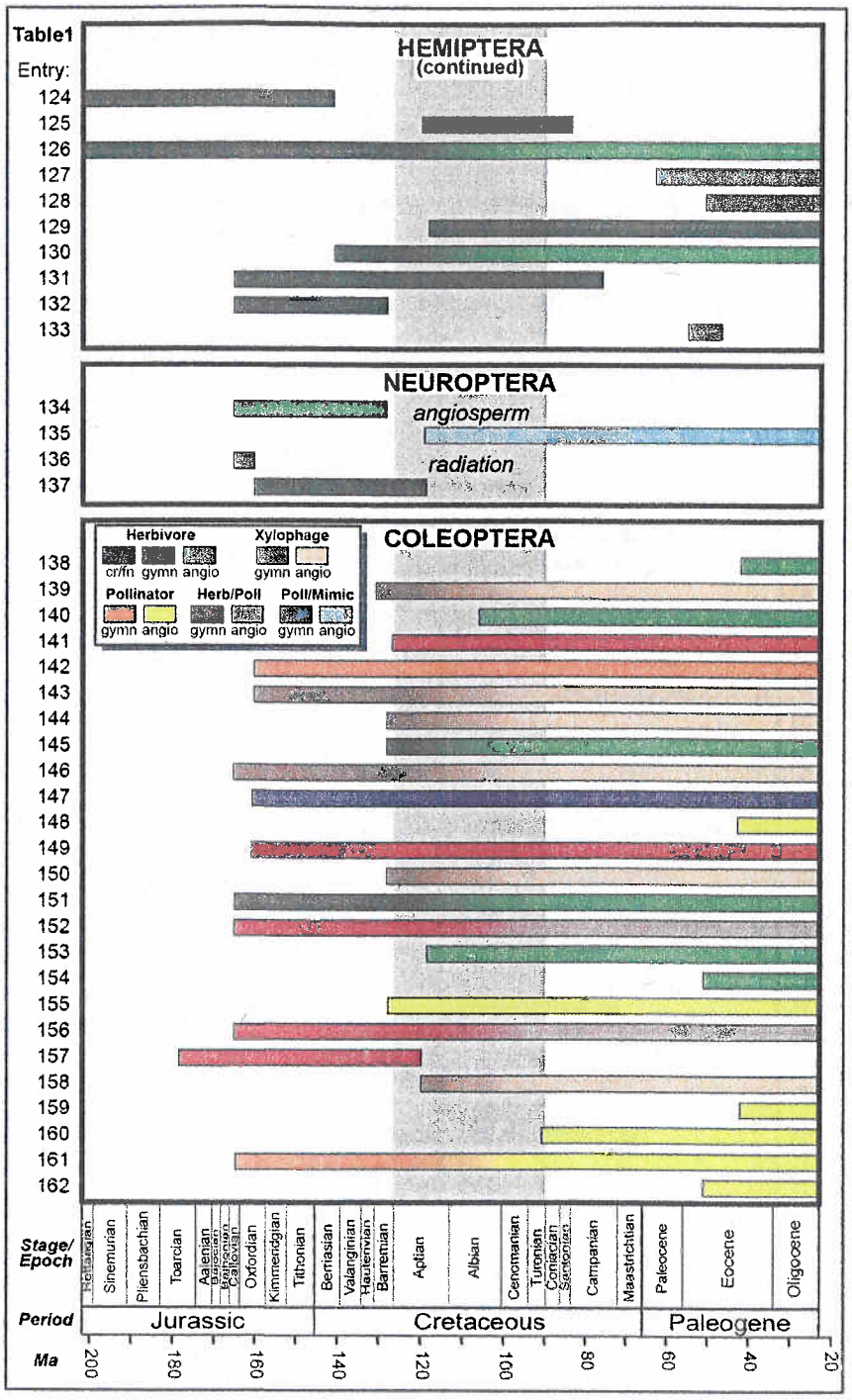

Fig. 13.2 (continued)

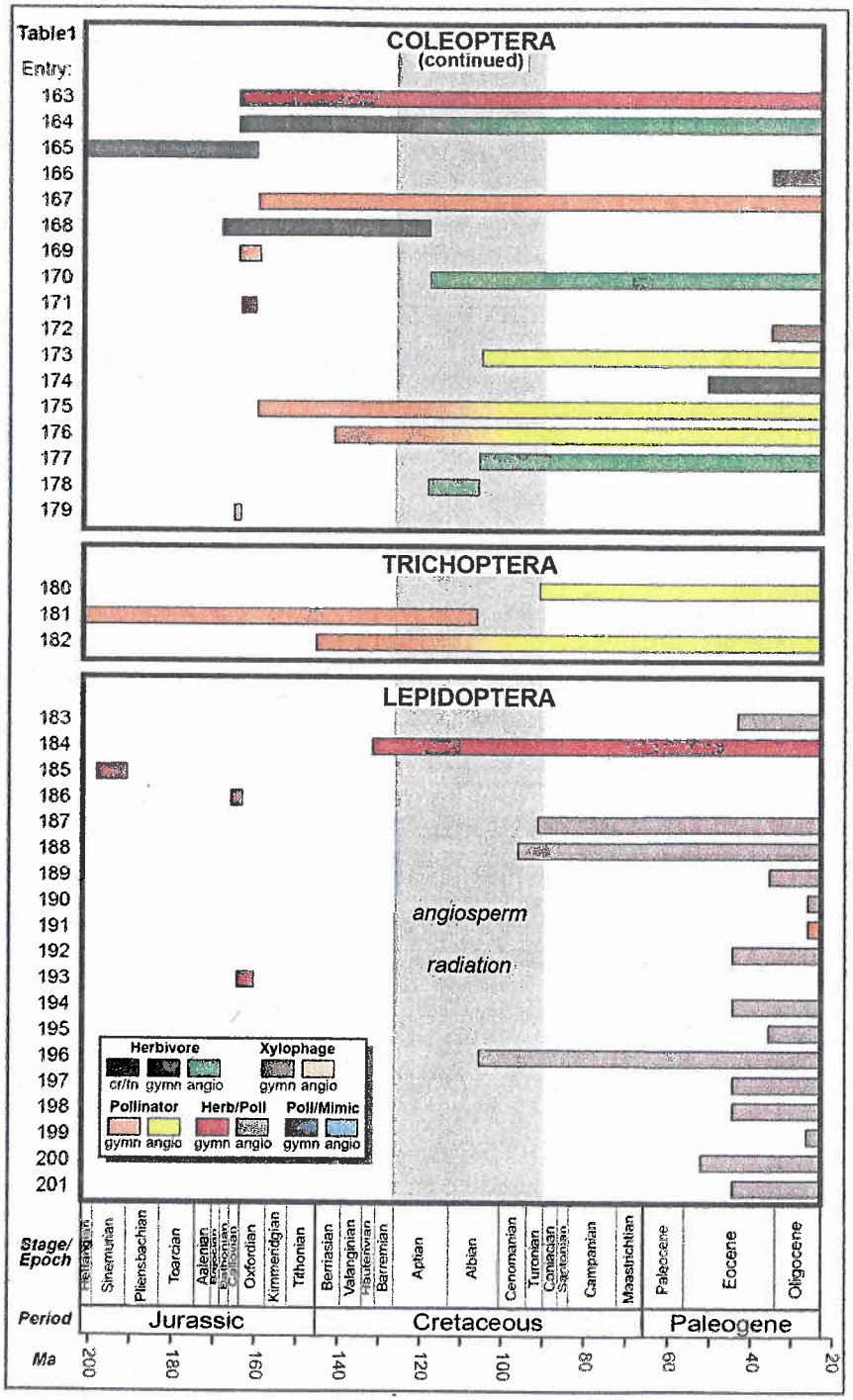

Fig. 13.2 (continued)

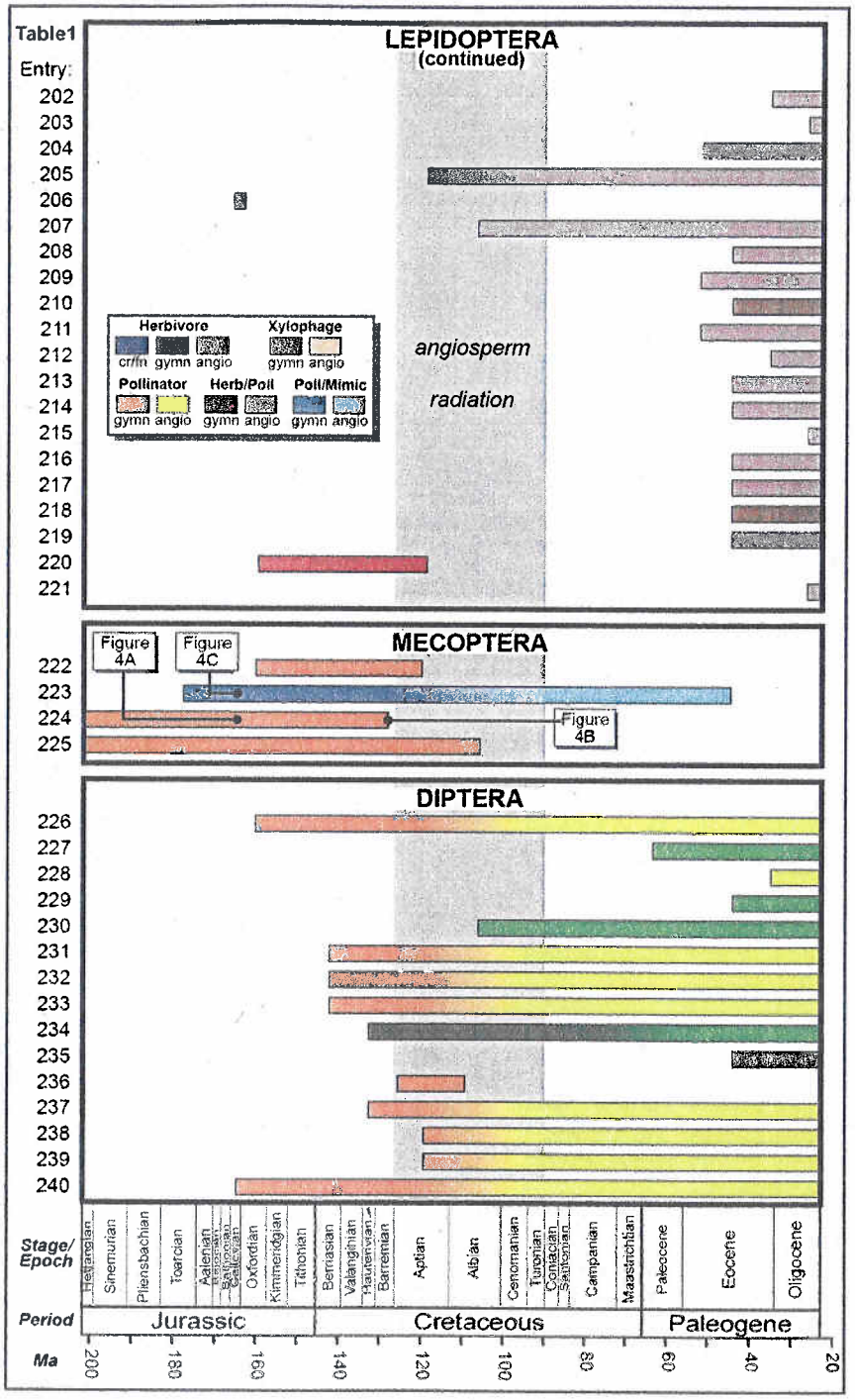

Fig. 13.2 (continued)

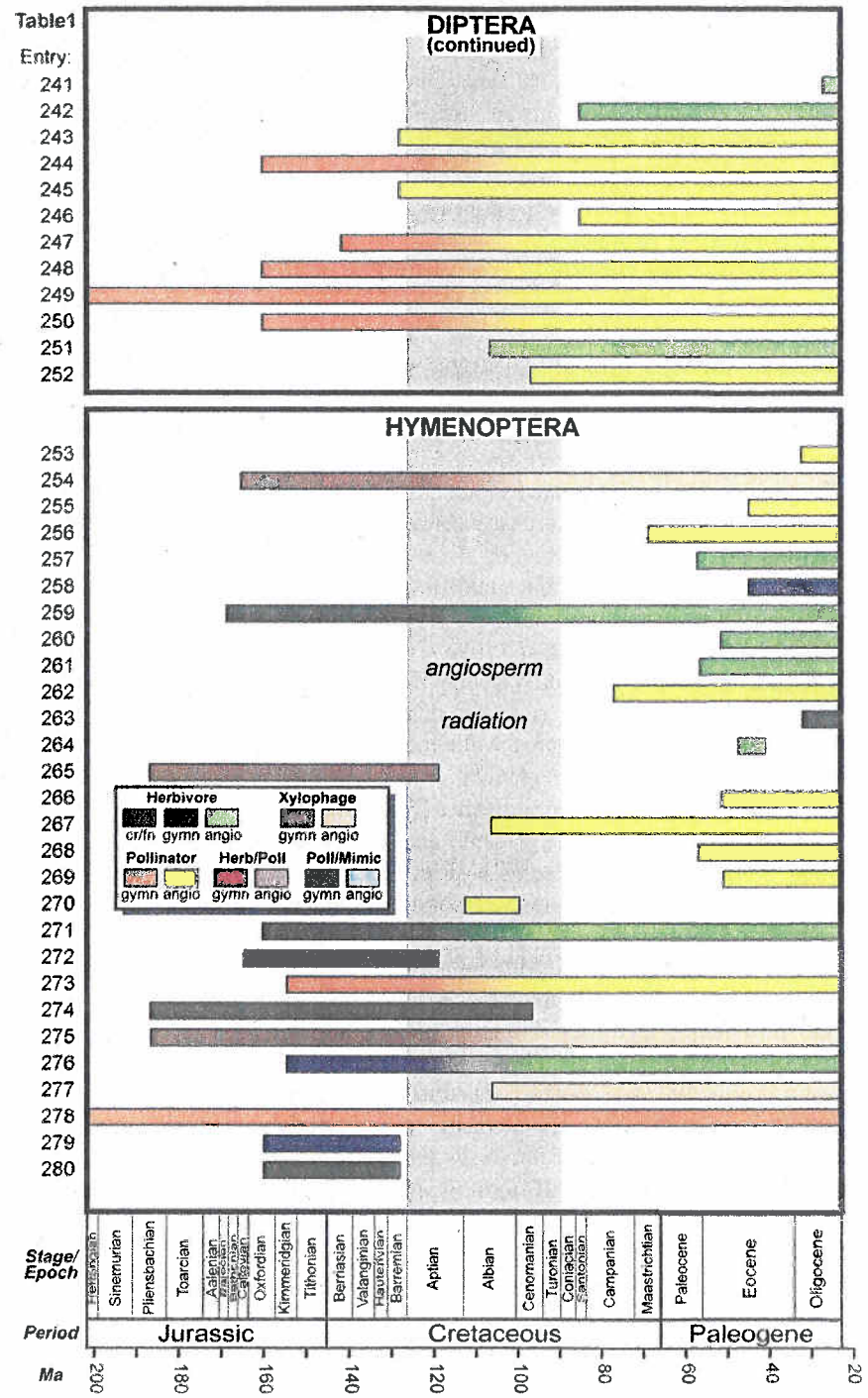

Fig. 13.2 (continued)

cambia, pith parenchyma, or other meristematic tissues that include live, actively dividing cells.

The second dietary habit is the functional feeding group. The data are divided into eight functional feeding groups for a more discrete, ecologically different characterization (Tables 13.1 and 13.2). The functional feeding groups are the modes of access to food that are effected principally through the action of mouthparts. *External feeding* is the consumption of foliage such as skeletonization and margin feeding in which the insect is outside of the tissue being consumed. *Piercing and sucking* consists of puncturing host tissues by specialized, stylate mouthparts and the subsequent sucking of fluid food. *Surface fluid feeding* is where surface fluids, such as pollination drops, floral or extrafloral nectar, or other plant exudates, are imbibed without inflicting a wound. *Palynivory*, or consumption of pollen, can be achieved by a variety of insect mouthpart types, in which ingestion may represent punctured pollen grains or entire to highly fragmented pollen clusters. Most pollinating insects are surface fluid feeders or palynivores.

The four previous functional feeding groups are ectophagous, occurring with the insect to the outside of the tissue consumed; by contrast, the following four interactions are endophytic, whereby the insect, typically an immature such as a larva or nymph, is lodged within plant tissues. *Galling* is a complex interaction whereby an insect immature inhabits a chamber surrounded by tumor-like plant tissues of newly created, inner, nutritive tissue for larval sustenance, outer hardened tissues for protection, and vascular tissue for food and water supply. Gall interactions are essentially parasitic and the galler arthropod hormonally controls the plant–host tissue and organ development adjacent the gall. *Leaf mining* is another endophytic interaction wherein an egg hatches into a larva that begins to consume foliage tissue, leaving a distinct frass trail and a leaf-mine with features such as successive width enlargements and a terminal chamber often used for pupation. *Seed predation* represents a variety of herbivore feeding types that have the common effect of consuming the embryonic and sustaining tissues of an ovule or seed. *Wood boring* consists of consumption of live meristematic tissues and parenchyma, often associated with tunneling through wood, the fabrication of borings, galleries and pupal chambers, and the consumption of associated fungi.

The third major characterization of dietary attributes of insect lineages in Table 13.1 is the dominant plant hosts and host transitions, linked to Fig. 13.2. We present five principle hosts and host transitions during the 174 million year interval from the Triassic–Jurassic to the Paleogene–Neogene boundaries. First, some insect lineages targeted cryptogam or fern hosts (*cryp/fern*) only. Second, other cryp/fern insect lineages have transitioned from cryp/fern to angiosperm hosts (*cryp/fern* → *angio*). Third, many insect lineages have always had dominantly gymnosperm hosts in their history. Fourth, some insect lineages on gymnosperms have switched their dominant hosts to angiosperms (*gymno* → *angio*). Fifth, more recent insect lineages have always had angiosperms (*angio*) as their dominant hosts.

Cryptogams included the familiar groups of liverworts, mosses, and lycopods; ferns consist of horsetails and marattialean and filicalean ferns. By contrast, gymnosperms include a diverse spectrum of extinct lineages (Taylor et al. 2009),

Table 13.2 Ecological attributes of the eleven insect lineages associated with the Mid-Mesozoic gymnosperm-to-angiosperm transition

Lineage examined	Dominant feeding guild					Major functional feeding group[a]								Dominant hosts and transitions[b]				
	Herbivore	Herb/ Poll	Pollinator	Poll/ Mimic	Xylophage	EF	P&S	Gall	SP	SFF	WB	Paly	LM	A Cryp/ Fern	B Cryp/ Fern → Angio	C Gymno only	D Gymno → Angio	E Angio only
Orthoptera	14	2	–	–	–	16	–	–	–	–	–	–	–	–	–	4	7	5
Phasmatodea	3	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	1	2
Thysanoptera	–	11	–	–	–	–	10	1	–	–	–	–	–	–	–	4	2	5
Hemiptera	103	–	–	–		–	87	12	4	–	–	–	–	2	1	43	22	35
Neuroptera	1	–	–	3	–	–	–	–	–	4	–	–	–	1	–	1	–	1
Coleoptera	16	6	13	–	7	25	–	–	3	4	7	3	–	1	–	13	14	14
Trichoptera	–	–	3	–	–	–	–	–	–	3	–	–	–	–	–	1	1	1
Lepidoptera	–	36	–	–	3	24	–	–	1	–	3	1	10	–	1	6	–	32
Mecoptera	–	–	3	1	–	1	–	–	–	3	–	–	–	–	–	3	1	–
Diptera	8	–	19	–	–	–	–	2	–	19	1	4	1	–	–	1	15	11
Hymenoptera	13	–	11	–	4	10	–	3	–	7	5	2	1	2	1	6	5	14
Totals	158	55	49	4	14	79	97	18	8	40	16	10	12	4	3	82	68	120

[a] Abbreviations for major functional feeding groups (*FFGs*) are: *EF*, external feeding; *Gall*, galling; *LM*, leaf mining; *Paly*, pollen or spore consumption; *P&S*, piercing and sucking; *SFF*, surface fluid feeding; *SP*, seed predation; *WB*, wood boring

[b] Abbreviations for dominant hosts and transitions: *Cryp/Fern*, cryptogams and/or ferns; *Gymno*, gymnosperms; *Angio*, angiosperms; *Cryp/Fern → Angio*, cryptogam or fern to angiosperm transition; *Gymno → Angio*, gymnosperm-to-angiosperm transition

such conifers, caytonialean and corystospermalean seed ferns, diverse ginkgophytes, bennettitaleans, and pentoxylaleans. Most gymnosperm sublineages became extinct during the angiosperm radiation, although several lineages now are known to have survived into the Gondwanan Paleogene, such as cheirolepidiaceous conifers (Barreda et al. 2012), corystosperm seed ferns (McLoughlin et al. 2008), Mesozoic-style ginkgoaleans (Hill and Carpenter 1999), and bennettitaleans (McLoughlin et al. 2011). By the close of the angiosperm radiation, all major groups of angiosperm lineages were established, including basal "paleoherb" lineages, monocots, Chloranthaceae, eumagnoliids, and core eudicots (Friis et al. 2010), and achieved ecological prominence in local habitats (Crane 1987).

13.2.2 Data Collection

Several initial conventions were used to provide a chronology of the summarized data (Table 13.1, Fig. 13.2). The 174 million year interval from the Triassic–Jurassic boundary at 201 Ma to the Paleogene–Neogene boundary at 23 Ma was used to document time durations of all identified plant-associated lineages. This time interval, consisting of the Jurassic, Cretaceous, and Paleogene periods, is divided into ca. 75 million years before the beginning of the angiosperm radiation at 125 Ma, and ca. 75 million years after its end at 90 Ma, providing a sufficiently long interval to record lineage turnover, long-term host–plant associations and major host transitions. These host associations occurred during the 35 million year-long angiosperm radiation from 125 Ma (ca. Barremian–Aptian boundary) to 90 Ma (ca. Turonian–Coniacian boundary). Insect lineage occurrence data were plotted at the midpoint for each geologic stage in which the insect lineage occurred. The range-through method was used (Labandeira and Sepkoski 1993), in which the first occurrence datum and last occurrence datum defined the continuous presence of the lineage, whether or not it has been recorded in intervening stages. Occurrence data for the Jurassic and Cretaceous periods were plotted at the level of the geologic stage, whereas Paleogene stage-level data were amalgamated at the more inclusive level of the geologic epoch. The most recent, internationally approved, standardized geochronology was used (Gradstein et al. 2012).

A second set of guidelines circumscribed the early angiosperm fossil record. Background information for the Jurassic through Paleogene record of land plants originated from several sources, including the mutually consistent and occasionally rich palynological, mesofossil, and macrofossil records (Friis et al. 2011). Of relevance to data collection is the origin of angiosperms during the early Cretaceous Period, consistent with a wide variety of paleobotanical and plant-morphological evidence (Crane et al. 1995), and increasingly with molecular evidence (Bell et al. 2010; Magallón 2010). The origin of angiosperms is taken as no earlier than the mid-Hauterivian stage at ca. 135 Ma (Friis et al. 2011). The subsequent, primary diversification interval of angiosperms occurred during the 35 million year interval

from the Barremian–Aptian stage boundary to the Turonian–Coniacian stage boundaries (Hughes 1994).

A third group of procedures were employed to establish the presence of fossil insect lineages. Several compendia were consulted to determine occurrence data for fossil insect lineages (Dmitriev and Zherikhin 1988; Rasnitsyn 1988; Carpenter 1992; Ross and Jarzembowski 1993; Labandeira 1994; Evenhuis 1994; Rasnitsyn and Quicke 2002; Grimaldi and Engel 2005; Sohn et al. 2012), buttressed by updates from recent taxonomic insect literature and the online Paleobiology Database (PBDB, 2014), accessed through the Fossil Works portal. As many of the earlier compendia had spurious occurrences, it was essential to consult considerably more modern sources to rectify synonymies, delete unvetted data, add new occurrences, and provide more current time-range extensions or contractions. After these filters were used, the culled dataset consisted of 280 family-level fossil insect lineages. The family was the focal taxonomic rank of interest. Alternative, more modern, classifications occasionally demote families to subfamily rank, a consequence that was taken into account in constructing Fig. 13.2. The insect lineage dataset consisted of 36.8 % Hemiptera, by far the most represented group; ca. 14 % each of Coleoptera and Lepidoptera; ca. 10 % each for Diptera and Hymenoptera; ca. 4–6 % each for Orthoptera and Thysanoptera, and 1–1.5 % each for the least abundant lineages of the Phasmatodea, Neuroptera, Trichoptera, and Mecoptera (Table 13.1, Fig. 13.1).

13.2.3 Establishing Feeding Guild, Functional Feeding Group and Plant–Host Assignments

Eight criteria were used to establish plant–host assignments of herbivory, pollination, xylophagy, and mimicry. These criteria can be divided into habitat-related ecological features and insect-specific morphological attributes. For broad-scale ecological features, the first consideration consists of broad, host–plant affiliations and related ecological attributes of modern descendant taxa, particularly if significant agricultural, entomological, or botanical information is available (Labandeira 1998). This process is taxonomic uniformitarianism (Dodd and Stanton 1990), and assumes that no or minimal host–plant shifts have occurred since the earliest fossil occurrence of the insect lineage in question. A second criterion involves the taxonomic spectrum of herbivorized plants of the flora in which an insect taxon co-occurs. Obviously, the host preferences of an insect in a preangiospermous flora can be safely attributed to a cryptogam, fern or gymnosperm. Conversely, an insect occurring in a diverse flora and consisting only of angiosperms can reasonably be associated with an angiosperm host. A third criterion involves specification of a particular damage type (Labandeira et al. 2007b) that could be attributed to a certain, family-level taxon. An example is the assignment of distinctive leaf mines occurring on angiosperm leaves of a sycamore host species (Platanaceae) from the early Paleocene of Montana, United States, to the dipteran family Agromyzidae (Winkler et al. 2010).

Four additional criteria indicate that host affiliations may be based on morphological features. The fourth criterion is the mouthpart structure of a representative insect taxon from the group in question (Labandeira 1997), which in some instances can be linked to particular types of herbivore damage, pollinator access, or wood boring in the same flora. An example would be the distinctive and specialized phytophagous mouthparts of weevils from the Yixian Formation in northeastern China (Davis et al. 2013), that also would imply gymnospermous plant hosts. Fifth, is presence of gut contents consisting of plant material (Rasnitsyn and Krassilov 2000) or pollen (Krassilov et al. 2007), which provides direct evidence of host affiliations of the insect consumer. Sixth, for pollinator assignment to plant hosts, certain features can be important, such as pollen plastered or attached to the mouthparts, or ventral aspect of the head capsule the associated insect with specialized, pollen-gathering structures such as bee corbiculae (Engel 2000) or thrips ring setae (Peñalver et al. 2012). The seventh criterion, also applicable to pollinators, is the presence of particular plant features that would indicate pollination (Labandeira et al. 2007a). For gymnosperm pollinators of the mid-Mesozoic, probed structures such as integumental tubes, deep funnels, and channels in ovulate organs were used by long-proboscid insects to access nectar-like pollination drops (Ren et al. 2009).

Last, in the case of mimicry, occasionally plant foliage shares an uncanny, detailed resemblance (the models) to particular co-occurring insect species (the mimics). Examples include strong resemblance of wings from one neuropteran species to a particular fern pinnule (Wang et al. 2010); or the entire body of another neuropteran species to a particular ginkgophyte leaf (Wang et al. 2012b).

13.2.4 Rationale for Understanding Gymnosperm-to-Angiosperm Host Transitions

The initial phase of angiosperm diversification established all major angiosperm lineages during a 35 million-year-long interval that encompassed the four mid-Cretaceous stages of the Aptian, Albian, Cenomanian, and Turonian. It would have been during this time interval that many insect lineages associated with gymnosperm hosts but known to have angiosperm-dominant associations in the more recent part of the geologic record would have shifted to angiosperm hosts (Tables 13.1, 13.2, and 13.3). Given that the angiosperm radiation is represented by four geologic stages during which the shift occurred, transfer ratios were allocated to each of the four constituent stages to represent a linear, monotonic shift from gymnosperm to angiosperm hosts. For the Aptian stage, 25 % of 60 insect lineages were transferred from gymnosperm → angiosperm hosts (column D of Tables 13.2 and 13.3, in bold lettering) to angiosperm-only hosts (column E of Tables 13.2 and 13.3); analogous values for the Albian stage were 50 % of 56 families; for the Cenomanian, 75 % of 63 families; and for the Turonian, 100 % of 64 families, after

Table 13.3 The Mid-Mesozoic transition from gymnosperm- to angiosperm-dominated host plants[a]

Period and time interval[c]	Geologic stage or epoch[d]	Dominant host-plant preferences of phytophagous lineages[b]					Number of families and their transfer ratio from column *D* to column *E* during the four stages of the angiosperm radiation[e]
		A Cryptogam and fern hosts only	B Cryptogam → angiosperm transitions	C Gymnosperm hosts only	D Gymnosperm → angiosperm host transitions	E Angiosperm hosts only	
Paleogene (23–66 Ma)	Oligocene	2	0	12	0	179	
	Eocene	2	0	13	0	171	
	Paleocene	1	0	11	0	121	
Cretaceous (66–145 Ma)	Maastrichtian	1	0	10	0	111	
	Campanian	1	0	13	0	111	
	Santonian	1	0	16	0	110	
	Coniacian	1	0	14	0	104	
	Turonian	**1**	**0**	**14**	**0**	**104**	**100 % of 64 families**
	Cenomanian	**1**	**1**	**14**	**16**	**87**	**75 % of 63 families**
	Albian	**1**	**3**	**17**	**27**	**58**	**50 % of 56 families**
	Aptian	**2**	**3**	**20**	**45**	**33**	**25 % of 60 families**
	Barremian	3	1	37	58	8	
	Hauterivian	4	1	39	57	2	
	Valanginian	4	1	38	55	0	
	Berriasian	4	1	40	55	0	

(continued)

Table 13.3 (continued)

Period and time interval[c]	Geologic stage or epoch[d]	Dominant host-plant preferences of phytophagous lineages[b]					Number of families and their transfer ratio from column *D* to column *E* during the four stages of the angiosperm radiation[e]
		A Cryptogam and fern hosts only	B Cryptogam → angiosperm transitions	C Gymnosperm hosts only	D Gymnosperm → angiosperm host transitions	E Angiosperm hosts only	
Jurassic (145–201 Ma)	Tithonian	3	1	41	44	0	
	Kimmeridgian	2	1	43	42	0	
	Oxfordian	4	0	44	39	0	
	Callovian	2	0	49	26	0	
	Bathonian	1	0	38	14	0	
	Bajocian	1	0	32	14	0	
	Aalenian	1	0	29	14	0	
	Toarcian	1	0	28	14	0	
	Pliensbachian	1	0	27	10	0	
	Sinemurian	1	0	27	9	0	
	Hettangian	1	0	26	7	0	

[a] Data are taken from Fig. 13.1
[b] There are 280 phytophagous insect families used in this table (Fig. 13.1)
[c] Geologic time periods are in bold; age dates and all geochronologic time intervals are from Gradstein et al. (2012)
[d] The Paleogene period is divided into epochs whereas the Cretaceous and Jurassic periods are divided into stages. The four stages of the angiosperm radiation, the Aptian through Turonian stages inclusive, are highlighted in bold
[e] These ratios represent the percentage of major gymnosperm-to-angiosperm host–plant transitions occurring during the angiosperm radiation. See text for details

which all families with gymnosperm-to-angiosperm host transitions were tabulated in the angiosperm-only host column. These transfers are independent of the gymnosperm-only host column which retained dominantly gymnosperm hosts but never acquired dominantly angiosperm hosts.

In a manner parallel to that of the gymnosperms detailed above, insect lineages associated with cryptogams and ferns were evaluated during the angiosperm radiation (column A of Tables 13.2 and 13.3). Similarly, lineages were assessed that possessed dominant cryptogam or fern associations which shifted to angiosperm-dominant associations during the angiosperm radiation (column B of Tables 13.2 and 13.3).

13.3 Results

Figure 13.2 depicts range-through occurrences of 280 vertically arrayed, family-level lineages that represent eleven plant-associated insect orders along a Jurassic through Paleogene time series. The insect lineages are characterized by the dominant feeding modes of herbivore, pollinator, herbivore–pollinator, pollinator–mimic, and xylophage, and whether their dominant hosts are cryptogams/ferns (purple), gymnosperms (darker hue), or angiosperms (lighter hue), as indicated in the legend insets. Major gymnosperm-to-angiosperm host–plant transitions during the angiosperm radiation (gray vertical column) are indicated. The data in Fig. 13.2 are restated in Table 13.3, which is a geochronologic stage-by-stage summary of the raw data in Table 13.1. Summary Fig. 13.3 details the trivariate relationship between (i) the diversity of fossil insect families in the vertical axis), (ii) their major plant–host associations of cryptogams/ferns (purple), gymnosperms (dark green), and angiosperms (light green) in the field of the figure, and (iii) stage-level geologic time in the horizontal axis. While not expressed graphically, the functional-feeding-group data in Table 13.1 is presented in summary form in the middle columns of Table 13.2. These data provide a qualitative description of functional feeding strategies for each insect lineage that are not apparent from their role in a dominant feeding guild or from their host–plant associations.

13.3.1 Plant-Feeding Features of Jurassic to Paleogene Insect Lineages

The dataset of 280 plant-associated insect families are categorized by order and partitioned into three feeding-related ecological attributes (Table 13.2). The first feeding attribute is the dominant feeding guild, the second is the major functional feeding group, and the third is the dominant plant hosts and their transitions. For the dominant feeding guild, the most frequently encountered category are herbivores (56.4 % of all occurrences), then herbivore–pollinators (19.6 %), pollinators

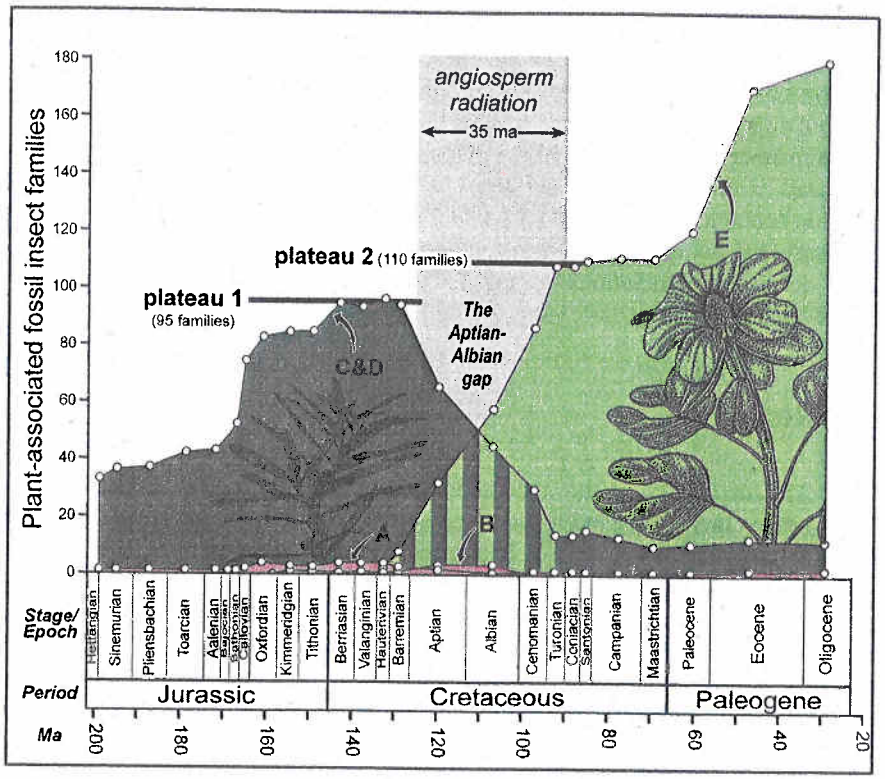

Fig. 13.3 Plot of the major plant hosts (*field of view*) associated with plant-associated fossil insect families (*vertical axis*) versus geologic time (*horizontal axis*). Data are derived from Table 13.1, summarized in Table 13.3. The *purple* color indicates cryptogam and fern hosts; *dark green* indicates gymnosperm hosts; *light green* indicates angiosperm hosts. The *vertical column* indicates the interval of time represented by the initial angiosperm radiation

(17.5 %), xylophages (5.0 %), and pollinator–mimics (1.4 %). Of these five categories, herbivory dominates all other interactions in the dataset.

For the functional feeding group (Table 13.2), the most frequently encountered mode is piercing and sucking (34.6 % of all occurrences), then external feeding (28.2 %), surface fluid feeding (14.3 %), galling (6.4 %), wood boring (5.7 %), leaf mining (4.3 %), palynivory (3.6 %) and seed predation (2.9 %). These proportions indicate that external (ectophagous) feeding predominates for ca. four-fifths of the occurrences whereas internal (endophagous) feeding contributes to only one-fifth of the data.

The third attribute is the identity of the dominant plant hosts and the amount of host switching among the dominant insect families. Those lineages with angiosperms as the dominant host represent 42.9 % of all families, whereas those with gymnosperms as the dominant hosts consisted of 29.3 %. Lineages hosting gymnosperm hosts and existing prior to the advent of angiosperms but later shifting to angiosperm-dominant

hosts provided 24.3 % of families. Cryptogams and ferns played a minor role as major hosts of insect lineages, consisting of 1.4 % of all cryptogam/fern-only occurrences and similarly 1.1 % of all cryptogam/fern lineages transitioning onto angiosperms.

13.3.2 Gymnosperm Versus Angiosperm Host Use Before, During, and After the Angiosperm Radiation

Data from Table 13.3 are plotted in Fig. 13.3. Shown in purple for Fig. 13.3 are insect families that retained their dominant cryptogam/fern hosts to the end of the Paleogene Period (trajectory A), recorded from column A of Table 13.3; and those that shifted dominantly to angiosperms during the angiosperm radiation (trajectory B), recorded from column B of Table 13.3. Likewise, shown in dark green are insect families that have kept their dominantly gymnosperm hosts, recorded from column C of Table 13.3, to which are added those insect lineages that transitioned from earlier gymnosperm-dominant hosts to angiosperm-dominant hosts after the angiosperm radiation, recorded from column D of Table 13.3 in bold lettering (See Sect. 13.2.4 for details). Insect family-level diversity with gymnosperm hosts thus represent the summation of columns C and D in Table 13.3, plotted as trajectory C + D in Fig. 13.3. Insect families with dominantly angiosperm hosts and originating during or after the angiosperm radiation are shown in light green and provide the most sustained increase of a host-affiliated insect group (trajectory E).

Two derivative features involving insect families with particular plant–host affiliations are depicted in Fig. 13.3. First, insect families with gymnosperm-dominant plant hosts, shown in trajectory C + D, form a distinct diversity plateau of ca. 95 families during the 20 million year-long Berriasian to Barremian interval, perhaps extending back in time to a decreased level of ca. 85 families to the Oxfordian stage another 20 million years earlier. After the Barremian stage, and the angiosperm radiation, insect lineages with gymnosperm hosts decrease linearly and monotonically to a flat diversity level of 10–14 insect families. By contrast, insect families with angiosperm-dominant hosts of trajectory E increase linearly and monotonically commencing at the angiosperm radiation, and reaching a sustained plateau of 110 families for the ca. 20 million years of the Turonian through Maastrichtian stages. Thereafter, insect families with angiosperm-dominant hosts increase dramatically into the late Paleogene.

Other than these two diversity plateaus, Fig. 13.3 illustrates a distinctive gap between the trajectories of C + D and E. Before and after the crossover between the gymnosperm-dominant and angiosperm-dominant family diversity curves of insects, there is a collective diversity minimum, the Aptian–Albian gap. The Aptian–Albian gap spans the angiosperm radiation and represents a significant decrease of 45 % from the earlier gymnosperm plateau of 95 families and 53 % of the later angiosperm plateau of 110 families.

13.4 Discussion

Three broader aspects of these findings deserve an extended mention. An obvious issue is to what extent does the data presented here explain the presumed "counterintuitive" result reported in Labandeira and Sepkoski (1993) that there was no increase in insect diversity during the formative interval of initial angiosperm diversification (Fig. 13.1)? Secondly, what is the meaning of the earlier gymnosperm and later angiosperm plateaus that bracket the angiosperm radiation, and do they have any relationship to the intervening Aptian–Albian gap (Fig. 13.3)? Last, is there a broader message about attempting to understand the role of fossil insect diversity vis-à-vis the angiosperm radiation, and vice versa, by using multiple approaches of investigation (Fig. 13.4).

13.4.1 Reasons for the Mid-Mesozoic Constancy of Insect Family-Level Diversity

There are several, independent explanations that could explain the relative stasis of family-level insect diversity during the angiosperm radiation. One reason, based on evidence from this report, is that an expectation of elevated insect diversification during the angiosperm radiation that would range from diffuse to intimate coevolution (Friis et al. 2011), needs to be balanced by evidence indicating equally high associational diversity between insects and gymnosperms prior to the angiosperm radiation. Given recent developments in understanding the associational diversity between gymnosperms and insects prior to and during the angiosperm radiation (e.g., Ratzel et al. 2001; Ren 1998; Ren et al. 2009; Labandeira 2010; Wang et al. 2012b; Peñalver et al. 2012; Ding et al. 2014), it is highly likely that gymnosperm–insect interactions preceding the angiosperm radiation were almost or just as diverse as angiosperm interactions that followed the event.

A second reason involves the Mesozoic Lacustrine Revolution, which evidently changed food-web structure of lotic and lentic ecosystems during the late Jurassic to early Cretaceous (Buatois et al. 2015). The environmental context of this transformation involves the change from detritivore based, typically hypotrophically stratified water bodies (Zherikhin et al. 1999), to herbivore dominated, typically pseudoligotrophically stratified water bodies (Sinitshenkova 2002). This physiochemical and biological turnover in aquatic ecologic structure occurred during the mid-Cretaceous and is synchronous with an aquatic insect extinction event (Sukatsheva 1991; Buatois et al. 2014). Approximately 20 family-level insect lineages became extinct at the Mesozoic Lacustrine Revolution (Buatois et al. 2014), supplemented by an additional 30 % of the plant-associated insect families during the same time interval.

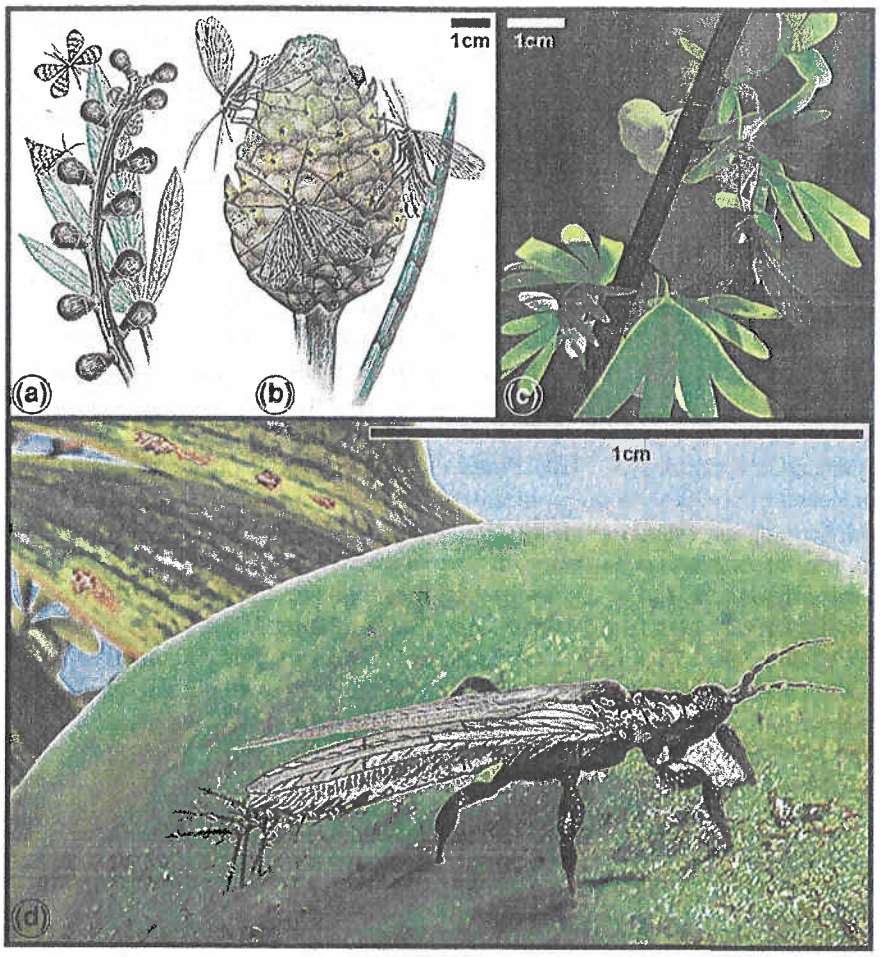

Fig. 13.4 Three mecopteran and a thysanopteran insect association with mid-Mesozoic gymnosperms. **a** The mecopteran long-proboscid pollinator, *Lichnomesopsyche gloriae* (Mesopsychidae, entry 224 of Table 13.1 and Fig. 13.2), with proboscis entering an integumental channel in the ovulate organ of *Caytonia sewardi* (Caytoniaceae) from the Callovian of Inner Mongolia, China. **b** Another mecopteran long-proboscid pollinator, *Vitimopsyche kozlovi* (Mesopsychidae, also entry 224 of Table 13.1 and Fig. 13.2), bearing *Classopollis* pollen and probing the ovulate organ catchment funnel of *Alvinia bohemica* (Cheirolepidiaceae) from the Barremian of Liaoning, China. **c** The mecopteran leaf mimic, *Juracimbrophlebia ginkgofolia* (Cimbrophlebiidae, entry 223 of Table 13.1 and Fig. 13.2), resembling a multilobed *Ginkgoites* leaf of *Yimaia capituliformis* (Ginkgoaceae) from the Callovian of Inner Mongolia, China. **d** The thysanopteran punch-and-suck pollinator, *Gymnopollisthrips minor* (Melanothripidae, entry 25 of Table 13.1 and Fig. 13.2), with *Cycadopites* sp. pollen grains on the ovulate organ of *Nehvezdyella bipartita* (Nehvezdyellaceae) from the Aptian of Spain. Drawings reprinted with permission: (**a**) and (**b**) courtesy of Mary Parrish, N.M.N.H. Department of Paleobiology in Washington, DC, USA; (**c**) courtesy of Wang Chen, C.N.U. College of Life Sciences in Beijing, China; and (**d**) courtesy of Enrique Peñalver, Instituto Geológico y Minero de España in Madrid, Spain)

A third cause for the constancy of diversity involves the parasitoid diversification of especially Hymenoptera, and to a lesser extent Diptera, during the Jurassic and Early Cretaceous (Rasnitsyn 1980). This major radiation of major, high-ranked lineages (Labandeira 2002) had a major effect not only on top to down regulation of herbivores in terrestrial webs, but significantly increased Jurassic and Early Cretaceous insect diversity that are captured in global compendia (Table 13.1, footnote 2) and in derivative plant–insect studies (Labandeira and Sepkoski 1993; Jarzembowski and Ross 1996; Alekseev et al. 2001). The inclusion of parasitoid insect families prior to the angiosperm radiation would have the effect of increasing insect diversity and balancing diversity levels after the angiosperm radiation.

Last, there is considerable evidence from modern molecularly based phylogenetic analyses that some plant-associated insect lineages diversified preceding the angiosperm radiation. Evidence for this comes from the major hyperdiverse clades such as the Hemiptera (Moran et al. 2005; Cocroft et al. 2008; Wang et al. 2012a), Hymenoptera (Rasnitsyn 1980; Davis et al. 2010), Coleoptera (Farrell 1998; McKenna et al. 2009; Wang et al. 2013), Diptera (Ren 1998; Labandeira 2005), and Lepidoptera (Imada et al. 2011; Zhang et al. 2013). The deeper extensions suggest that these lineages were diverse and actively consuming live tissues of cryptogams, ferns, and gymnosperms from millions to a few tens of millions of years before the initial angiosperm diversification interval.

Contributions of family-level insect taxa from these four data sources would provide relative stasis in family-level insect diversity throughout the late Jurassic and into the early Paleogene (Fig. 13.1). However, of these data sources, plant–host-associated families of insects likely were most important.

13.4.2 Host Switching, Diversity Plateaus and the Aptian–Albian Diversity Low

The pattern of gymnosperm-to-angiosperm host–plant dominance throughout the 100 million year interval from the Callovian (166 Ma) to the K-Pg extinction event at the end of the Cretaceous (66 Ma) potentially reveals the family-level insect dynamics associated with this shift (Fig. 13.3). An upper limit of 95 families was reached for insect lineages whose hosts were dominantly to exclusively gymnosperms, supplemented by a minor level of cryptogam and fern associations. This plateau disappeared at the beginning of the angiosperm radiation, as major older insect lineages with gymnosperm (and cryptogam and fern) hosts shifted onto new angiosperm hosts (Peñalver et al. 2012; Ding et al. 2014), or became extinct, and as new major insect lineages initially hosting angiosperms increased dramatically in diversity (Labandeira et al. 1994; Hartkopf-Fröder et al. 2011). By the Santonian stage (85 Ma) of the Late Cretaceous, an upper limit of 110 families was established, which remained until a dramatic diversity increase following the K-Pg event.

Separating the earlier plateau of gymnosperm-dominated families from subsequent and somewhat more elevated plateau of angiosperm-dominated families is

the Aptian–Albian gap, which represents an interval of time characterized by transition from gymnosperm to angiosperm hosts. The probable cause of this gap is time lags that occur between when a food resource is available and when it becomes herbivorized. Geochronologic lags have been demonstrated at time intervals such as the appearance of vascular plant tissues in the earlier Devonian, and when they are later herbivorized during the mid-Paleozoic (Labandeira 2007); additionally, time delays occur in the colonization of eudicot plant hosts by lepidopteran leaf-mining genera during the late Cretaceous and Cenozoic (Lopez-Vaamonde et al. 2006). This downturn in plant-associated insect diversity is evident in the coarse-grained epoch-level analysis of Jarzembowski and Ross (1993) and the fine-grained stage-level analyses of Alekseev et al. (2001), although the gap appears phase-shifted toward the late Cretaceous by a stage or two. An Aptian–Albian minimum also may be present in aquatic insect lineages (Buatois et al. 2014), but no relevant analysis of family-level aquatic insect diversity has been made for this interval.

The presence of two, successive upper bounds for insect lineages with gymnosperm- and angiosperm-dominant hosts separated by a diversity minimum (Fig. 13.3), suggests a global event and major plant–host replacement during this 35 million-year interval. Such an event would represent a significant scaling up from considerably more spatiotemporally and taxonomically confined host shifts illustrated between plants and insects from a variety of modern habitats (Pellmyr and Seagraves 2003; Cocroft et al. 2008). One particular system is nymphaline butterflies (fritillaries) and their angiosperm lamialean (mints and relatives) and asteraceous (daisies and relatives) hosts. One study (Nylin and Wahlberg 2008) indicates that host shifts of angiosperm food plants by fritillary butterflies likely were associated with a previous extensive period of polyphagy, wherein multiple, unrelated, colonized plant lineages were replaced by a major shift to a novel host unrelated to the previous spectrum of consumed plants. This host shift was accelerated by a major plant extinction event at the K-Pg boundary, which restricted the range of new potential hosts available to certain fritillaries (Nylin and Wahlberg 2008). Significant range expansions of post-event surviving fritillary taxa may have enhanced the probability of new host shifts (Weingartner et al. 2006). Such an event, between fritillaries and their dicot hosts, when multiplied and writ large geographically, could provide a model for understanding the extensive, global gymnosperm-to-angiosperm shift of many insect lineages during the mid-Cretaceous.

13.4.3 Questions of the Fossil Record That Only Can Be Answered by Multidisciplinary Data

Back in 1993, the study by Labandeira and Sepkoski was purely an exploratory venture toward understanding the insect fossil record. One of the patterns noted by some and engendering significant negative animus was the pattern of long-term stasis of insect families that encompassed the considerable stretch of time from the Late Jurassic to the early Paleogene, notably including the angiosperm radiation.

This result provided an opportunity to subsequently pursue alternative research to test the conclusion of Labandeira and Sepkoski (1993) that the angiosperm radiation had no effect on family-level insect diversity. One approach assessed features of suspect insect pollinators in preangiospermous floras to determine whether gymnosperms were being actively pollinated (Fig. 13.4a, b, d) (Labandeira et al. 2007a; Ren et al. 2009; Labandeira 2010; Peñalver et al. 2012). A second tack involved the presence, extent, and type of mimicry in preangiospermous biotas (Fig. 13.4c) (Wang et al. 2010, 2012b). A third opportunity allowed investigation of early angiospermous and older gymnospermous Mesozoic floras to establish quantitative levels of herbivory diversity and intensity before and after the angiosperm radiation (Ding et al. 2014). A fourth procedure is the examination of ecosystem food-web structure before (currently no data) and after (Dunne et al. 2014) the angiosperm radiation. And last, modern molecularly based evolutionary biology studies indicate that significant radiations of plant-associated insect lineages occurred earlier than the angiosperm radiation (Farrell 1998; Davis et al. 2010). These approaches suggest that the ecological and evolutionary biological infrastructure of insect lineages associated with gymnosperm hosts was a 40 million-year-long feature of Late Jurassic to mid-early Cretaceous terrestrial habitats. This process was rivaled by insect lineages occurring on diverse angiosperm hosts that persisted for a 20 million-year interval during the Late Cretaceous.

13.5 Conclusions

This report should be seen as a first attempt in addressing the reciprocal roles of insects and angiosperms during the initial radiation of angiosperms. Although there are three major conclusions derived from the data presented in this report, additional analyses with more improved, taxonomically resolved and geochronologically constrained data would go far to ferret out further these patterns.

1. *The angiosperm radiation.* Herbivory is one of the fundamental attributes of insects, and the host plants consumed by insects are resources that have an important fossil record. One of the major episodes in the evolution of insect herbivory is the transition from gymnosperm- to angiosperm-dominant hosts during the initial diversification of angiosperms 125 to 90 million years ago. Exploring the patterns and evolutionary and ecological mechanisms responsible for this global taxonomic shift in consumer resources is a goal of this report.
2. *The pattern.* Evidence indicates that plant-associated insect families that hosted gymnosperms prior to the angiosperm radiation consisted of a sustained peak of ca. 95 families for 40 million years. This was followed by a switchover by insect lineages that acquired angiosperm hosts, eventually reaching a level of ca. 110 lineages for a 20 million-year interval during the Late Cretaceous. After this stasis in diversity, there was a rapid increase in angiosperm-hosted insect lineages well into the Paleogene Period. Thus, a major gap occurred

during these two diversity maxima levels present on both sides of the angiosperm radiation, attributable to turnover in the plant–host preferences of insect lineages and time-lag effects resulting in the shift from gymnosperm to angiosperm hosts. Notably, the plateau established by earlier insect lineages with gymnosperm hosts was 86.4 % that of the later insect lineages with angiosperm hosts.

3. *Implications.* The pattern and inferred processes outlined here indicates that modern insect lineages retain only a very minor legacy of their former Middle Jurassic to mid-Cretaceous gymnosperm hosts. By contrast, insect lineages with dominantly gymnosperm hosts during the preangiospermous Late Jurassic to Early Cretaceous rivaled in diversity insect lineages with dominantly angiosperm hosts after the mid-Cretaceous angiosperm radiation and throughout the Late Cretaceous. The ecology of interactions between these older insect lineages and their dominantly gymnosperm hosts needs to be explored further to establish an entrée into this earlier world devoid of angiosperms.

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