Chapter 14
Expansion of Arthropod Herbivory in Late Triassic South Africa: The Molteno Biota, Aasvoëlberg 411 Site and Developmental Biology of a Gall

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Abstract The Carnian Aasvoëlberg 411 (Aas411) site of the Molteno Formation in South Africa provides exceptional data for understanding how plants, their arthropod herbivores and interactions responded to the P-Tr ecological crisis approximately 18 million years earlier. Our study lists six consequences stemming from the P-Tr event. First, Aas411 was one of the most herbivorized of Molteno's 106 sites, consisting of 20,358 plant specimens represented by 111 plant form-taxa that includes 14 whole-plant taxa (WPT); the insect damage consists of 11 functional feeding groups (FFGs), 44 damage types (DTs) and 1127 herbivorized specimens for an herbivory value of 5.54%. Second, the seven most herbivorized hosts, in decreasing importance, were the conifer *Heidiphyllum elongatum*; corystosperm *Dicroidium crassinervis*; ginkgophyte *Sphenobaiera schenckii*, peltasperms *Lepidopteris stormbergensis* and *L. africana* and horsetail *Zonulamites viridensis*. Third, generalized feeding damage and 11 host-specialized associations were present that targeted 39 of 111 plant taxa. Fourth, the *Heidiphyllum elongatum* WPT was most herbivorized, harboring an extensive herbivore component community containing 81.8% of FFGs, 63.6% of DT categories, 40.9% of DT occurrences, and 36.4% of specialized interactions at the site. Fifth, eriophyioid gall DT70 was

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host-specialized on *Dicroidium crassinervis*, where it constitutes 70.1% of all Molteno DT70 occurrences and revealing a distinctive developmental ontogeny. Sixth, herbivory levels significantly surpassed those of the Late Permian.

Keywords Carnian • Component community • Damage Type • *Dicroidium crassinervis* • End-Permian extinction • Gondwana • *Heidiphyllum elongatum* • Karoo Basin • Mite gall • Plant–insect interactions

14.1 Introduction

The most consequential event for the Phanerozoic history of life was the end-Permian ecological crisis (P-Tr event) that extinguished numerous, indeed an overwhelming majority, of lineages in the marine and terrestrial realms (Erwin 2006). For the terrestrial realm, most subordinate lineages and many major lineages of plant and arthropod clades experienced a major extinction (Labandeira 2005; Hochuli et al. 2010), although some fungal clades may have had an opposite response (Visscher et al. 1996). This event undoubtedly resulted in permanent removal or degradation of many antagonistic interactions, mutualistic associations and other varied and diffuse relationships (Krassilov and Karasev 2008; Labandeira et al. 2016; Feng et al. 2017). As important as the ravages of the taxonomic extinctions were, the devastation of more ecologically specialist interactions likely was greater (Shcherbakov 2000; Wang et al. 2009; Feng et al. 2017). The demise of particular specialized interactions resulted in a shift from an intricate, developing nexus of inter-organismic relationships present in the Late Permian to the virtual absence of such interactions during the Early Triassic. Terrestrial lineages that survived into the Early Triassic represented a small subset of the previously existing diversity of life and their relationships occurring in the Late Permian (Lopingian) (Labandeira 2006a). Nevertheless, it was these surviving, taxonomically depauperate lineages and their few trophic inter-relationships that sowed the seeds of a recovery. After the 10 million-year-long recovery interval of the Early Triassic (Induan and Olenekian stages) and first part of the Middle Triassic (Anisian Stage), there was by contrast a spectacular flourishing of plant, insect and even fungal lineages and their ecological networks (Labandeira et al. 2016). Many interactions that appeared during the later Triassic were the same types of associations that were extinguished during the Late Permian (Roopnarine and Angielczyk 2015; Labandeira et al. 2016; Feng et al. 2017). The difference was that the Triassic plant, insect and fungal participants originated from different, unrelated clades than those of the Permian (Béthoux et al. 2005; Labandeira 2005; Hochuli et al. 2010; Ponomarenko 2016; Yang et al. 2012), attributable to an ecological sorting process during the P-Tr event (Sidor et al. 2013; Prinzing et al. 2017).

One approach toward understanding this major transformation in the relationships between plants and insects before and after the P-Tr crisis is documentation of insect-induced damage diversity and intensity on Late Permian floras and post-event successor floras throughout the Triassic (e.g., Prevec et al. 2009; Labandeira et al. 2016). Such an encompassing study would document (i), the Late Permian baseline of ecological interactions; (ii), an ecological decline resulting in depauperate interactions immediately following the P-Tr crisis and into the earlier Triassic; and (iii), the subsequent, post-crisis pattern of ecological recovery and clade diversification during the later Triassic (Roopnarine and Angielczyk 2015; Labandeira et al. 2016). Comparisons between these three intervals—Late Permian, earlier Triassic, and later Triassic—could yield considerably more finer-grained insights than previous, coarser-grained approaches (Labandeira 2006b, 2013a), especially regarding how insect herbivores were finely partitioning host-plant tissues and to what extent insect herbivore guild structure was changed before, soon after, and later in the Triassic after the P-Tr event. There are several levels at which such a comparative analysis can be investigated. At the histological level, one productive method is detailed, qualitative recording of plant tissue types that were being consumed by insects, as revealed by damage on organs such as foliage, stems, seeds and fructifications before and after the event (Labandeira 2013a; Schachat et al. 2014). A second avenue is to assess functional feeding group (FFG) or damage-type (DT) diversity and frequency as well as herbivory level on bulk floras before and after the event, such as the analogous Paleocene–Eocene Thermal Maximum event (Wilf and Labandeira 1999; Wilf et al. 2001, 2006). A third type of examination is to determine the extent of damage diversity of the insect herbivore component community on the most intensely herbivorized host-plant species in a flora before and after the event (Labandeira et al. 2016). An herbivore component community consists of all of the insect herbivore species consuming tissues of a single source plant (Root 1973). Such component communities can reveal varying and differential patterns of herbivory in space and time that accrue from both historical incumbency (Prinzing et al. 2017), as well as the ecological processes favoring partitioning of host-plant tissue types by particular feeding guilds of insect herbivores (Lawton 1982; Futuyma and Mitter 1996).

The current project is part of ongoing documentation of a 35 million-year-long interval from the middle Permian (Guadalupian) to Late Triassic (Carnian) interval designed to evaluate the effect of the P-Tr event for plant–insect interactions in the Karoo Basin of South Africa. To date, one late Permian (Lopingian) site, Clouston Farm, has been assessed (Prevec et al. 2009), although two other Permian localities (Gastaldo et al. 2005) currently are being evaluated. In this contribution, we examine plant–insect interactions for the most specimen-abundant site of all Karoo Basin localities, the Late Triassic Aasvoëlberg 411 (Aas411) site, which is one of a series of Carnian-age localities from the Molteno Formation, in the Karoo Basin of South Africa. The consequences of the P-Tr event will be evident from a comparison of plant–insect interactions of the Aas411 site to equivalent, earlier interactions from Middle Triassic and Late Permian localities (Prevec et al. 2009; Wappler et al. 2015; Labandeira et al. 2016). (Early Triassic localities with sufficient, well preserved plant fossils to study are virtually absent.) Empirical analyses of richly preserved plant–insect interactions across this time interval can provide ecologically robust data for interpreting the response of the P-Tr event for variously herbivorized plant-host lineages and for diverse feeding guilds of arthropod herbivores in a variety of habitats.

14.2 Early to Late Triassic Plant–Insect Interactions

14.2.1 Overview

During the Permian, the diversity and frequency of plant–insect interactions apparently reached a plateau, based on data from about a dozen time slices during the Cisuralian and Lopingian that represent a variety of habitats in Gondwana and Euramerica (Adami-Rodrigues et al. 2004; Prevec et al. 2009; Schachat et al. 2014; Schachat and Labandeira 2015; Labandeira et al. 2016). This trend was disrupted by the end-Permian (P-Tr) ecological crisis (Ponomarenko 2016), resulting in a reset of the associational clock at the beginning of the Triassic. Previous studies (Shcherbakov 2008b) providing documentation of plant–insect associational diversity indicates that the recovery period was prolonged.

14.2.2 Olenekian and Induan Interactions

After the P-Tr crisis, the Early Triassic was a time of exceedingly diminished diversity on land, as determined by the empirical record (Labandeira 2006a; Chen and Benton 2012) and by ecological model results (Roopnarine and Angielczyk 2007, 2015). Unfortunately, very few deposits provide fossil data that are appropriate for evaluating insect diversity during the Induan and Olenekian stages of the Early Triassic. Exceptions probably include the Solling Formation of the Lower Buntsandstein sequence that contains the Bremke and Fürstenberg floodplain floras in Germany (Kustatscher et al. 2014), and the Newport Formation at Turrimetta Head, in the Sydney Basin of New South Wales in Australia (McLoughlin 2011). The Solling Formation material provides the more insightful glimpse regarding rare herbivory of the two deposits; this deposit records eight, distinctive, DT occurrences from an Early Triassic flora that included some apparently specialized associations. One notable plant host was the fern *Tongchuanophyllum* that exhibits multiple DTs of external foliage feeding, a midveinal gall, and lenticular to ovoidal oviposition scars (Wappler et al. 2015).

Other sporadic examples of insect herbivory have been documented for the Early Triassic. A probable Olenekian-age gall occurs on the pinnae and rachis of the corystosperm *Dicroidium odontopteroides* (McLoughlin 2011), a species that also occurs in the Molteno Formation, is notable for its distinctive physiognomy. This plant host represents one of the few host-specialized associations known from the

Early Triassic. In earlier Induan-age deposits immediately above the P-Tr boundary, the earliest known Triassic herbivory has been described (Lozovsky et al. 2016), which notably includes the earliest known leaf mine (Krassilov and Karasev 2008).

14.2.3 Anisian Interactions

Several lower Middle Triassic localities of Anisian age have been explored worldwide for plant–arthropod interactions. These studies indicate the gradual accumulation of plant–insect interactional diversity within the first 5–10 million years after the P-Tr ecological crisis. One of the most prominent of these associations is the Upper Buntsandstein sequence from the Grès à Voltzia deposits in the northern Voltzia Mountains of northeastern France. Grès à Voltzia associations include exophytic and endophytic oviposition on horsetails, external foliage feeding on the seed plant *Neuropteridium*, and a distinctive host-specialized gall present on the herbaceous conifer *Aethophyllum stipulare* (Grauvogel-Stamm and Kelber 1996). Also found in this deposit were the wings of a tettigoniid orthopteran that mimicked the venation and other surface foliar features of a seed plant (Papier et al. 1997).

Several other examples of insect herbivore associations are known from Anisian deposits. One site is the Dhauari Hill bed of the Parsora Formation, in the South Rewa area of the Gondwana Basin in central India (Ghosh et al. 2015). At this deposit, the Triassic corystosperm *Dicroidium hughesii*—a taxon also recorded in the Anisian Burgersdorp Formation hosted a distinctively spheroidal and heavily walled gall on the host's pinnules. Another significant occurrence is the early Anisian Fremouw Formation of the central Transantarctic Mountains along the Palmer Peninsula in Antarctica (Hermsen et al. 2006). Although this material exhibits rare root detritivory by oribatid mites (Kellogg and Taylor 2004), a cycad specimen of *Antarcticyas schopfi* shows tunneling in thickened cataphyll tissue that may indicate pollination by an unknown beetle (Hermsen et al. 2006; also see Klavins et al. 2005). In the penecontemporaneous Burgersdorp Formation of South Africa, Labandeira (2006a) mentioned a sparse record of herbivory, although these plant–insect interactions await formal description.

14.2.4 Ladinian Interactions

During the Ladinian there was a significant qualitative and quantitative increase in insect herbivory from the earlier level documented in Anisian floras. This expansion of herbivory is best demonstrated by four major occurrences, particularly from Western Europe. The Lower Keuper and Lettenkohle formations of Franconia, Germany, and adjacent Alsace in France and in Switzerland were first mentioned by Heer (1877), who noted likely oviposition scars on the horsetail *Equisetites*.

Oviposition lesions later were documented on the horsetail *Neocalamites* (Roselt 1954). Subsequent studies indicated borings in *Agathoxylon*-type wood (Linck 1949), and particularly several types of margin and hole feeding on *Taeniopteris angustifolia* and *Schizoneura paradoxa* (Geyer and Kelber 1987; Kelber and Geyer 1989). Grauvogel-Stamm and Kelber (1996) documented examples of clustered, endophytic, ellipsoidal to ovoidal oviposition marks on *Equisetites arenaceus* and linear, end-to-end arrays of oviposition on *T. angustifolia*.

A quantitative and intensive study documented a wealth of interactions for the Monte Agnello Site from the Dolomites Region of the Southern Alps in Northern Italy (Wappler et al. 2015; Labandeira et al. 2016). A wide variety of herbivore damage was represented by 20, distinctive DTs that were scored for host plants such as horsetails, ferns including *Neuropteridium*, *Phlebopteris*, *Cladophlebis* and *Thaumatopteris*, the seed-fern *Scytophyllum*, the cycadophytes *Bjuvia* and *Nilssonia*, and the voltzialean conifer *Voltzia*. The repertoire of damage included external foliage feeding, piercing and sucking, leaf mining, and galling, all of which display partitioning of a variety tissue types (see Labandeira 2013a). Of particular note was the component community structure of the seed-fern *Scytophyllum bergeri*, which harbored 11 distinctive DTs within the functional feeding groups (FFGs) of external foliage feeding, piercing and sucking, oviposition, galling and leaf mining, mostly indicating host specialization, and contributing to the most diverse component community known from any Ladinian deposit. The component community of *Scytophyllum bergeri* was compared to that of the Late Permian (Wuchiapingian) conifer *Pseudovoltzia liebeana* from a nearby site, the latter of which harbored a mere four DTs, only one of which, a foliar gall, was a host specialist (Labandeira et al. 2016). This Lopingian to Ladinian contrast in component-community structure provides additional evidence for the demise of the ecological web of herbivore interactions based on single host-plant species resulting from the P-Tr ecological crisis.

Another site with Ladinian plant–insect interactions is the Xinigua Flora of the Santa Maria Formation, from Rio Grande do Sul in southeastern Brazil, which displays borings in *Agathoxylon*-type wood (Minello 1994). Other Ladinian localities represent single occurrences of particular plant–insect associations, but nevertheless provide supplemental evidence documenting the subtle but sustained increase in herbivory throughout this interval. However, it was during the Carnian that a dramatic increase in herbivory has been recorded, particularly in the Karoo Basin of South Africa.

14.2.5 Carnian Interactions

There are five major deposits with diverse floras that have recorded the considerable expansion of plant–insect associations during the Carnian. In addition to the Molteno Formation discussed later in this report, the Lunz Formation of Lunz-am-See in the Northern Calcareous Alps of eastern Austria is characterized by frequently exquisitely preserved material that is recorded mostly on cycads and bennettitaleans. One notable feature of insect damage at Lunz-am-See are oviposition lesions that retain altered histological features of foliar epidermis and cuticle of the bennettitalean host *Nilssoniopteris haidingeri*, as well as damage that reveals details of egg chlorion and other microstructural features of eggs oviposited endophytically, probably by a dragonfly of the Odonatoptera (Pott et al. 2008). A variety of marginal and nonmarginal feeding also has been recorded on other bennettitalean foliage, but principally on *Nilssoniopteris* (Wappler et al. 2015). Other interaction features of the Lunz-am-See deposit are a probable leaf mine on a frond pinnule of the cycad *Nilssonia* (Meller et al. 2011), and presence of structural defenses in the foliage of the possible ginkgophyte *Glossophyllum florini* (Pott et al. 2007).

From the Blackstone Formation of the Sydney Basin of New South Wales, in Australia, several distinct types of herbivory reveal that stereotyped and host-specific plant–insect associations were present across a broader swath of Gondwanan floras other than just the Molteno Biome. These include distinctive leaf mines (DT71) on the voltzialean broadleaved conifer *Heidiphyllum elongatum* (Tillyard 1922; Rozefelds and Sobbe 1987) and on the ginkgophyte *Ginkgoites* (Wappler et al. 2015). Other interactions likely are endophytic oviposition scars and epiphytic deposition of eggs on the fern *Dictyophyllum* (Webb 1982), interaction types that also occur in the Molteno Biome. In a different environment, Strullu-Derrien et al. (2012) reported interactions that are very rarely described from plants, specifically a community of arthropod detritivores, including oribatid mites that consumed cortical tissues of probable bennettitalean roots. Notably, the permineralized peat of this site—Hopen Island from Svalbard Archipelago of Norway—also preserves root galls, some of which may have been interacting with live tissues of larger root branches. These below-ground interactions compliment the above-ground associations described in other Carnian floras, indicating that the component community of arthropods on bennettitaleans included detritivores and herbivores consuming almost all organs and tissues of their plant hosts.

14.2.6 Norian Interactions

The primary site for Norian plant–insect interactions is the Chinle Formation of Petrified Forest National Park, in northeastern Arizona, USA. The Chinle floras containing these interactions have been radiometrically dated to 220.6–209.9 million years (Ramezani et al. 2014; Sadler et al. 2015), and thus are early Norian in age (Walker et al. 2013) and perhaps the only Late Triassic flora that has been radiometrically dated (Ash, pers. comm.). Multiple stratigraphic members of the Chinle Formation have been examined for virtually all major types of insect herbivory. With the exception of leaf mining and seed predation, all of the major modes of insect herbivore feeding have been found on Chinle plant hosts. These include a variety of external foliage feeding on ferns and seed plants, principally *Cynepteris*, *Sphenopteris*, *Zamites*, *Nilssoniopteris*, *Macrotaeniopteris*, *Marcouia* and

Dechellyia, the latter of which also features a distinctive, polymorphic, foliar gall (Ash 1997, 1999, 2000, 2009, 2014). Oviposition has been recorded for the seed plant *Dechellyia* and the horsetail *Equisetites*. Wood borings, attributed to beetles, have been described for multiple woods such as *Itopsidema* and *Schilderia* but especially *Agathoxylon* (Walker 1938; Ash and Savidge 2004; Creber and Ash 2004; Tapanila and Roberts 2012). Although foliar herbivory from Chinle strata have not been systematically sampled qualitatively and quantitatively, these preliminary inventories of plant hosts and their herbivore damage strongly indicate a continuation of interaction diversity largely established earlier during the Carnian.

Two other Norian localities house significant plant–insect interactional data. Evidence was established for one of the earliest examples of skeletonization from the fossil record, on the fern *Dictyophyllum nathorstii*, in a second site from the Yipinglang flora of Yunnan, in southern China (Feng et al. 2014). Earlier, lunate-shaped bite marks were documented from a species of *Mixopteris* from the same flora (Hsü et al. 1974). From the Laguna Colorada Formation of Santa Cruz, Argentina, a spectrum of herbivory representing many DTs and several major FFGs were documented from this diverse flora (Adami-Rodrigues et al. 2004).

14.2.7 Rhaetian Interactions

Compared to previous plant–insect interaction data, few Rhaetian data are available. One of the best known studies is the likely oviposition scars on the voltzialean conifer *Podozamites* from the Pälsjo site in Scania, Sweden (Nathorst 1876, 1878). The paucity of investigations of Rhaetian plant–insect interactions may be attributable to an absence of studies or could represent the prelude of depressed diversity prior to the terrestrial Triassic–Jurassic extinction event (McElwain et al. 2009). However, additional Gondwanan interactions have been described from younger deposits from the La Ternera Formation of Quebrada la Cachivarita and from the Las Breas Formation near Vicuña, both in Chile. The age of these deposits range from Upper Triassic to Lower Jurassic (Moreno and Gibbons 2007). These deposits reveal, respectively, distinctive oviposition damage on the cycad *Pseudoctenis harringtoniana* and on the probable bennettitalean *Taeniopteris* sp. B (Gnaedinger et al. 2014), both of which resemble damage on their congeneric Molteno hosts.

14.2.8 General Patterns

Although additional global analyses of Triassic plant–insect interactions are sorely needed, there are a few tentative inferences about insect herbivory that can be established. First, virtually nothing is known about plant–insect interactions of the

Early Triassic. This absence may represent either considerable taphonomic loss or the intrinsic lack of insect interactions with plants. Second, interactions for the Anisian, recorded in Western Europe and informally observed in the Karoo Basin, likely represent a very modest increase of generalized associations but minimal specialized associations, except for rare galls and possibly some patterned oviposition marks. Third, there is a significant increase in the diversity and frequency of plant–insect interactions during Ladinian times, including a demonstrable uptick in specialized damage patterns. This is particularly true for sites in Western Europe and eastern Australia. Fourth, there appears to be an overwhelming increase in associational diversity and herbivory levels during the Carnian that is evident in several regions worldwide. And last, based principally on data from the Chinle Formation, it appears that the diversity of interactions equilibrates or perhaps decreases somewhat during the Norian and Rhaetian. However, these conclusions should be tempered by problems in correlation of Triassic strata.

14.3 Methods

14.3.1 Obtaining Associational Data from Aasvoëlberg 411 Specimens

All adequately preserved plant specimens greater than 0.25 cm^2, including foliage, stems, roots and reproductive structures such as cones and seeds were exhaustively examined at the Aasvoëlberg 411 (Aas411) site. When present, fungal damage on plants and the presence of insect body fossils was recorded. Fossil intactness from the Aas411 site ranged from robust to delicate, and specimens often were preserved as single occurrences with considerable intervening matrix, to more dense accumulations with minimal matrix evident, to rare leaf mats of superimposed foliage. Whereas preservation of plant and insect material typically was good, occasionally specimens were exceptionally well preserved and revealed considerable plant anatomical detail as well as specific features of plant response to insect damage. Specimens very infrequently were abraded along their margins, and they almost always significantly exceeded the threshold for detection of arthropod-mediated damage.

The process for the examination of specimens is summarized as follows. An initial, overall evaluation was made of whether plant specimens from the fossil assemblage were sufficiently well preserved for analyses. Because of exceptionally good preservation, virtually all plant material from Aas411, including practically every recognizable leaf, stem, reproductive organ, and rare root mass was selected for data-set inclusion. Pollen organs were not included in the analyses because as a class of organs, they uniformly lacked evidence for herbivory throughout the

Molteno Biome. The principle plant material examined was foliage. The term, foliage, was operationally defined as any photosynthetic organ, including true leaves, scale leaves, pinnules, cataphylls, short shoots, horsetail stems or analogous structures (Schachat et al. 2014). After initial assessment, the specimen number of each fossiliferous slab, beginning with the prefix PRE/F/ was recorded. For each slab, specific plant specimens were assigned a specimen number, separated by a hyphen from the slab number, beginning with a "1" for the first specimen, and continuing until all plant specimens for that slab were numbered. (For example, one particular Aas411 slab that had three plant specimens was designated PRE/F/22051. The third arbitrarily numbered specimen on this slab is PRE/F/22051-3, which is part of a *Dicroidium odontopteroides* leaf that is designated on the ExCel database but not marked on the slab. Importantly, care was taken to recognize parts and counterparts so as to not count plant specimens twice.

Each plant specimen was taxonomically identified to the lowest rank possible. In most cases identification was to the level of species, such as the Linnaean binomial of *Heidiphyllum elongatum* or *Pseudoctenis sanipassiensis*. In other cases, a genus-level designation was used, such as *Sphenobaiera* scale leaf or *Yabeiella* sp. Less commonly, unidentifiable or isolated plant organs were designated as "seed indet. C", "unidentifiable woody axis", "unidentifiable foliage" or an analogous name. Seeds were an important contribution to the plant inventory and most were preserved as dispersed specimens. However, if seeds were encountered dispersed singly, the species name was placed in parentheses, as in *Peltaspermum* (*turbinatum*); however, if the seed was attached to a reproductive structure, its name was left outside of parentheses, as in *Avatia bifurcata*. Major Molteno plant groups were identified by the use of several monographic sources. For formal descriptions and classifications of horsetails, Anderson and Anderson (2017) was used; for ferns, the source was Anderson and Anderson (2008); for *Dicroidium* seed plants, it was Anderson and Anderson (1983, 2003); for seed plants excluding *Dicroidium*, Anderson and Anderson (1989, 2003) was employed; and for seed-plant female and male reproductive material, Anderson and Anderson (2003) and unpublished recent updates were consulted.

Linnaean binomials were used for those Molteno taxa that have been formally monographed taxonomically. However, some groups have not been taxonomically monographed, principally mosses, liverworts, lycopods, specimens of uncertain taxonomic position, several provisional species of seed-plant foliage whose encompassing genera already have been formally established, and approximately 75 additional seed, scale and ovulate morphotypes, the vast majority of which originate from the Aas411 site. As for use of DTs connected with Aas411 described plant taxa and undescribed plant morphotypes, the identification of insect damage was based on the FFG and DT system, informally referred to *Damage Guide* (Labandeira et al. 2007), used in previous studies (Wilf and Labandeira 1999; Wilf et al. 2006; Schachat et al. 2014; Ding et al. 2015). Although most of the DTs at Aas411 were described previously (Labandeira et al. 2007), newly encountered DTs were added to the data base and will be updated in forthcoming version 4 of the *Damage Guide*.

Procedurally, each Aas411 plant specimen was entered as a row into an ExCel database and associated data were expressed in six column fields. The columns were: (i), fossil site designation; (ii), specimen number; (iii), plant-host morphotype; (iv), DT assignments, if any; (v), macrophotography–microphotography log; and (vi), comments. The raw data are presented in Figs. 14.1, 14.2, 14.3, 14.4, 14.5, 14.6, 14.7, 14.8, 14.9, 14.10, 14.11, 14.12, 14.13 and Tables 14.1, 14.2, 14.3. Further analyses of the Aas411 site will await a more integrative meta-analysis of the plant–insect interactions across all 106 localities within the Molteno Biome.

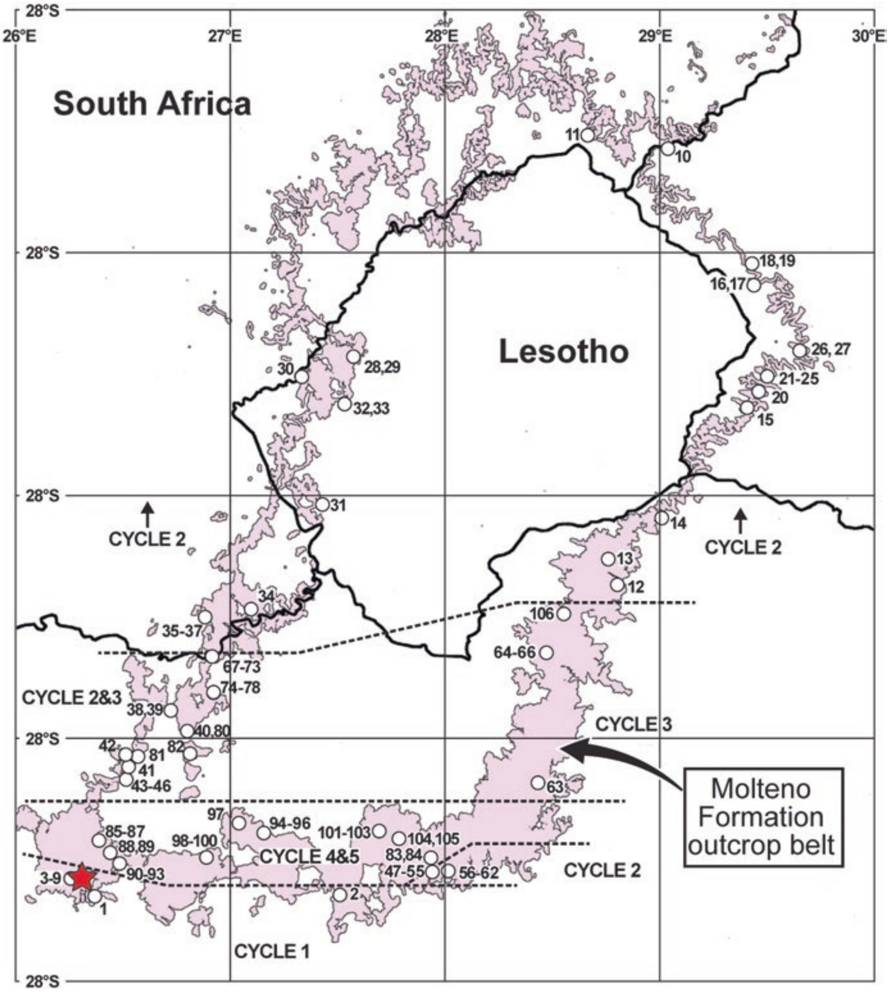

Fig. 14.1 The outcrop belt of the Molteno Formation in the Karoo Basin of South Africa, showing localities numbered in Table 14.1. The Aasvoëlberg 411 (Aas411) site is indicated at the *red star* in the *lower-left* corner, adjacent the Cycle 1 to Cycle 2 boundary

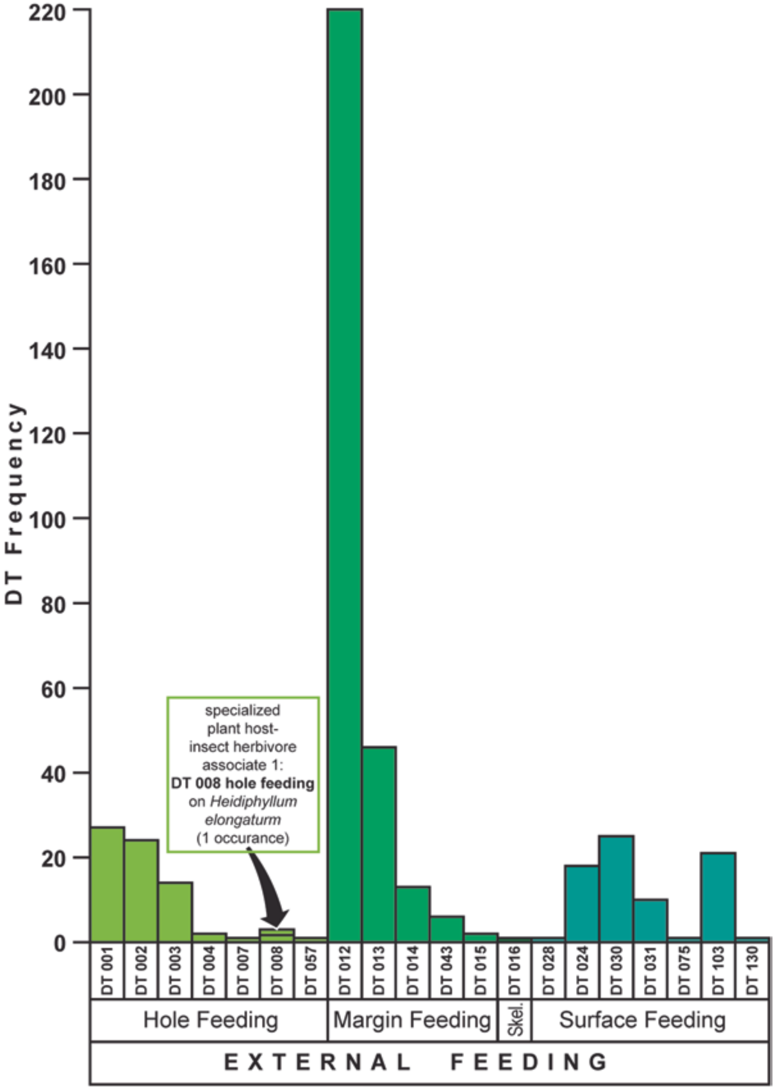

Fig. 14.2 Frequency distribution of external feeding damage types (DTs) by functional feeding group (FFG) and damage type (DT) at the Aasvoëlberg 411 (Aas111) site in the Karoo Basin of South Africa. Note that the only host-specialized association is DT8 slot feeding, a type of hole feeding. The hachured pattern in DT8 indicates the proportion of occurrences present on the host *Heidiphyllum elongatum*. (Also see Table 14.3)

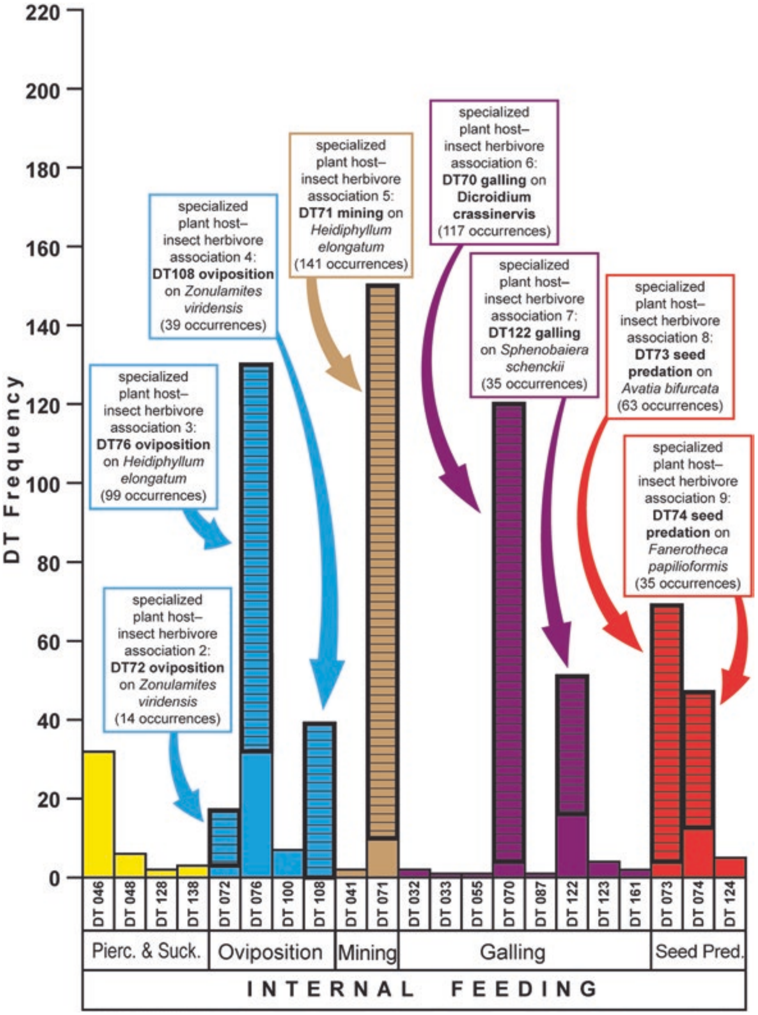

Fig. 14.3 Frequency distribution of internal feeding damage types (DTs) by functional feeding group (FFG) and damage type (DT) at the Aasvoëlberg 411 (Aas411) site in the Karoo Basin of South Africa. Note the abundance of nine host-specialized associations. Such host specializations include three types of oviposition (DT72 on *Zonulamites viridensis*, DT76 on Heidiphyllum *elongatum*, DT108 on *Z. viridensis*), one leaf mining (DT71 on *H. elongatum*), two types of galling (DT70 on *Dicroidium crassinervis*, DT122 on *Sphenobaiera schenckii*) and two types of seed predation (DT73 on *Avatia bifurcata* and DT74 on *Fanerotheca papilioformis*). One additional host-specialized association, DT124 seed predation on *Dordrechtites elongatus*, is not shown for spatial considerations. *Vertical columns with hachured pattern* indicates the proportion of occurrences for the specialized association indicated for a given DT present on a particular plant host. (Also see Table 14.3.)

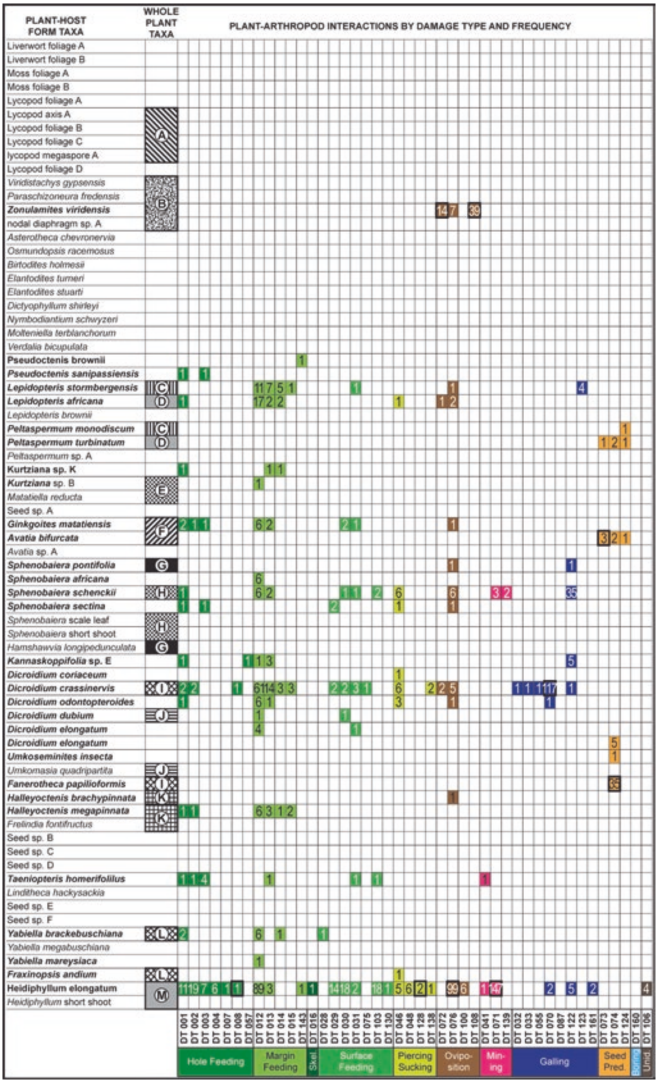

Fig. 14.4 Raw plant–insect interaction data for the Aasvoëlberg 411 site, ordinated by functional feeding group (*colors*) and constituent DTs at *bottom* and plant taxa at *left* with herbivorized hosts in *bold font*. Fifteen whole-plant taxa are indicated at *left* but exclude relevant pollen-organ form taxa. Presence/absence data in *grid* indicate the number of plant specimens with one or more occurrences of the specified DT on a particular plant host. *Cells with thick black* outlines indicate the 11 host-specialist associations indicated in Table 14.3 and in text. Fungal damage DT58 is not shown. Associational data of seven of the most intensely herbivorized of the 14 whole plant taxa (WPT) are provided in Tables 14.2 and 14.3. These data are continued on the folowing page

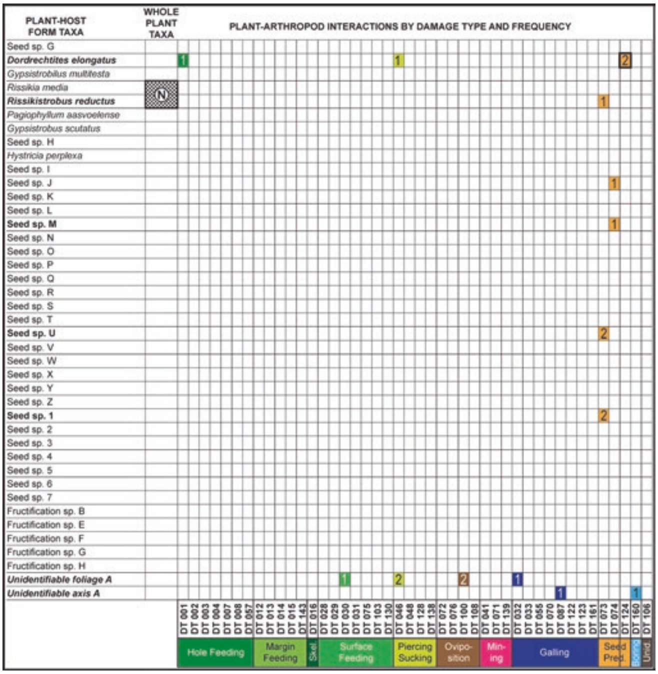

Fig. 14.4 (continued)

14.3.2 Herbivory and its Differentiation from Detritivory

The distinctive types of insect-mediated DTs serves as the basis for categorizing and analyzing herbivory in compressed fossil floras. However, damage on fossil plant specimens initially must be categorized as to whether it is due to detritivory (feeding on dead plant tissues) or attributable to herbivory (feeding on live plant tissues). This separation is accomplished by using five features that occur on live plant tissues and define a particular mode of diagnostic damage (Labandeira 2006a). First, herbivory is indicated for those DTs that have certain distinctive features of size, shape, pervasiveness, and position on the host plant. Second, herbivore damage typically consists of an iterative pattern of stereotyped insect damage that is repeated on a particular host-plant tissue, organ or species. Third are the structural features induced by the plant response to herbivory that typically involve production of teratological tissue, such as callus that involves hypertrophy (increase in cell size) and hyperplasia (increase in cell number). A fourth indicator is the presence of dead tissue occurring along the affected area, including necroses that often are a response of secondary infection by pathogens (Labandeira and Prevec 2014). Last, the occurrence of small, specific, insect-produced features such as small cuspate chew marks along leaf edges or stylet crater marks on surfaces, also are distinctive indicators of herbivory (Johnson and Lyon 1991; Labandeira et al. 2007).

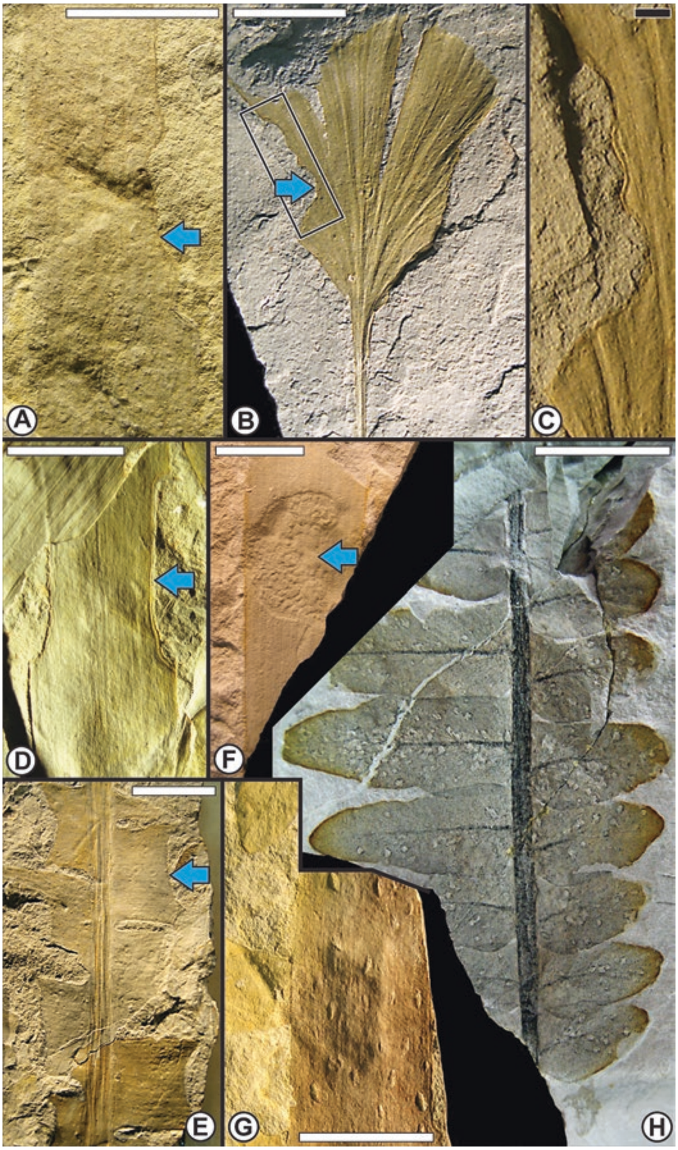

Fig. 14.5 Margin feeding, hole feeding, surface feeding, piercing and sucking and oviposition at the Aasvoëlberg 411 site, from the Late Triassic Molteno Formation of South Africa. (**a**) Cuspate DT12 margin feeding (*blue arrow*) on the conifer *Heidiphyllum elongatum*; PRE/F/12863-6. (**b**) Continuous DT143 margin feeding (*blue arrow*) on the ginkgophyte *Ginkgoites matatiensis*; PRE/F/21065-1. (**c**) Enlargement of DT143 outlined in (**b**). (**d**) Cuspate DT12 margin feeding (*blue arrow*) on *H. elongatum*; PRE/F/21443a-16. (**e**) Pinnule-tip DT13 margin feeding (*blue arrow*) on the cycad *Pseudoctenis* sp.; PRE/F/20636-1. (**f**) Ovoidal DT128 scale impression mark (*blue arrow*) on *H. elongatum*; PRE/F/21912-1. (**g**) Extensive DT76 oviposition on *H. elongatum*; PRE/F/12905-2. (**h**) Extensive DT1 hole feeding on the corystosperm *Dicroidium odontopteroides*; PRE/F/12229-4. *Blue arrows* indicate insect damage; scale bars for all figures: white, 1 cm; black, 1 mm

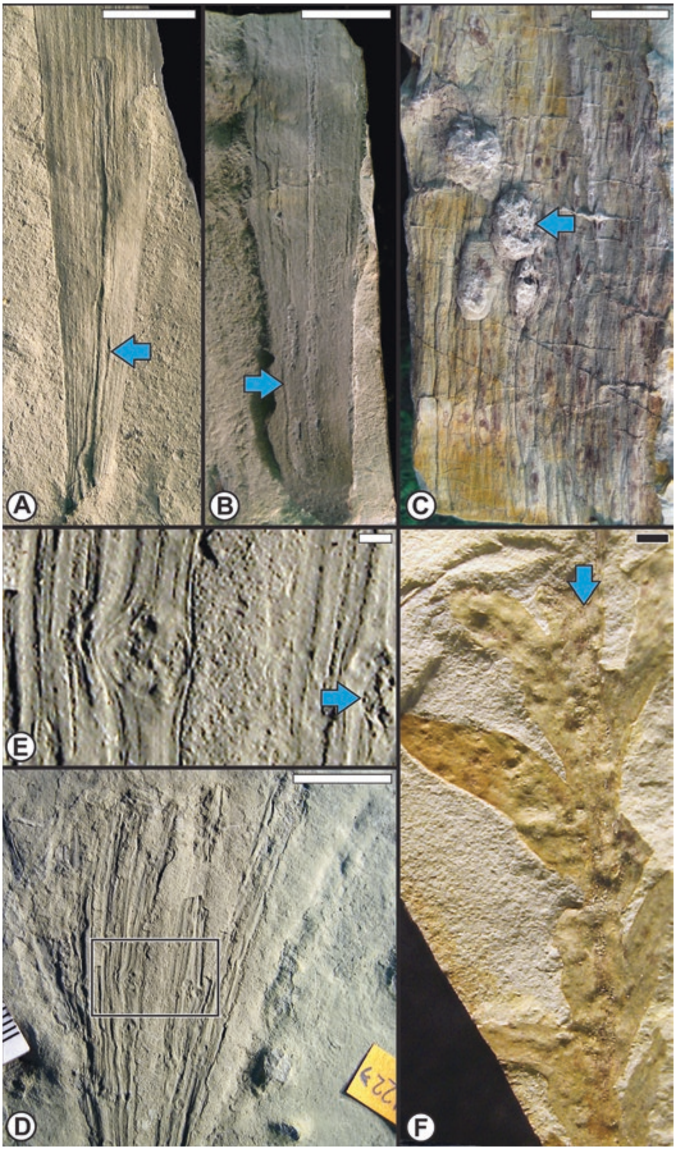

Fig. 14.6 Mining, oviposition and galling at the Aasvoëlberg 411 site, from the Late Triassic Molteno Formation of South Africa. (**a**) A linear leaf mine with the serpentine frass trail of DT71 (*blue arrow*), on *Heidiphyllum elongatum*; PRE/F/21921-2. (**b**) Another distinctive DT71 leaf mine (*blue arrow*) on *H. elongatum*; PRE/F/20710a-1. (**c**) A cluster of deep-seated DT72 oviposition marks on the stem of the horsetail *Zonulamites viridensis*; PRE/F/12047-6. (**d**) The gall DT122 showing distortions in the foliage of the ginkgophyte *Sphenobaiera schenckii*; PRE/F/12857a-23. (**e**) An enlargement of a galled area outlined in (**d**); microscope image. (**f**) Foliage of *Dicroidium crassinervis* with extensive DT122 gall damage; PRE/F/12238b. *Blue arrows* indicate insect damage; scale bars: white, 1 cm; black, 1 mm

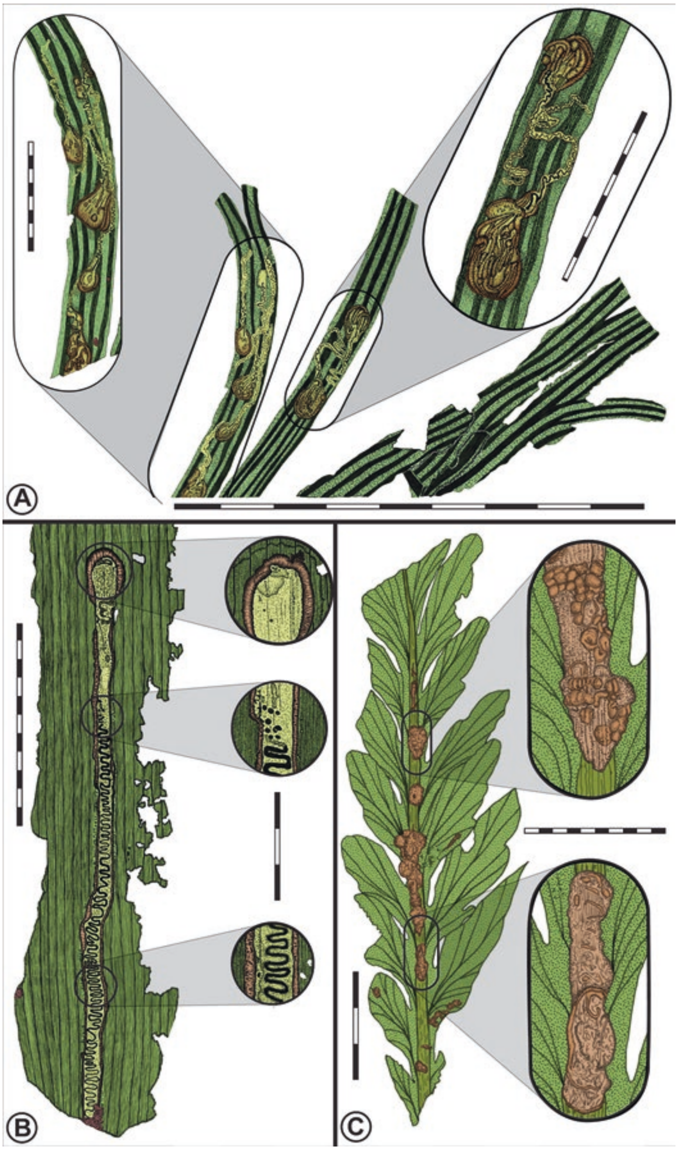

Fig. 14.7 Two mines and a gall on foliage of the dominant plant hosts of the Aasvoëlberg 411 site, as they may have appeared in life during the Carnian. Colorized versions of inked camera-lucida drawings. (**a**) Mine DT139 on *Sphenobaiera schenckii*; PRE/F/12472-1; all scale bars, mm. (**b**) Mine DT71 on *Heidiphyllum elongatum*; PRE/F/1902a, but from sister site of Aas311 (Aasvoëlberg 311); left and right scale bars, mm. (**c**) Gall DT122 on *Dicroidium crassinervis*; PRE/F/21912-2; scale bars: lower left, cm; center-right, mm

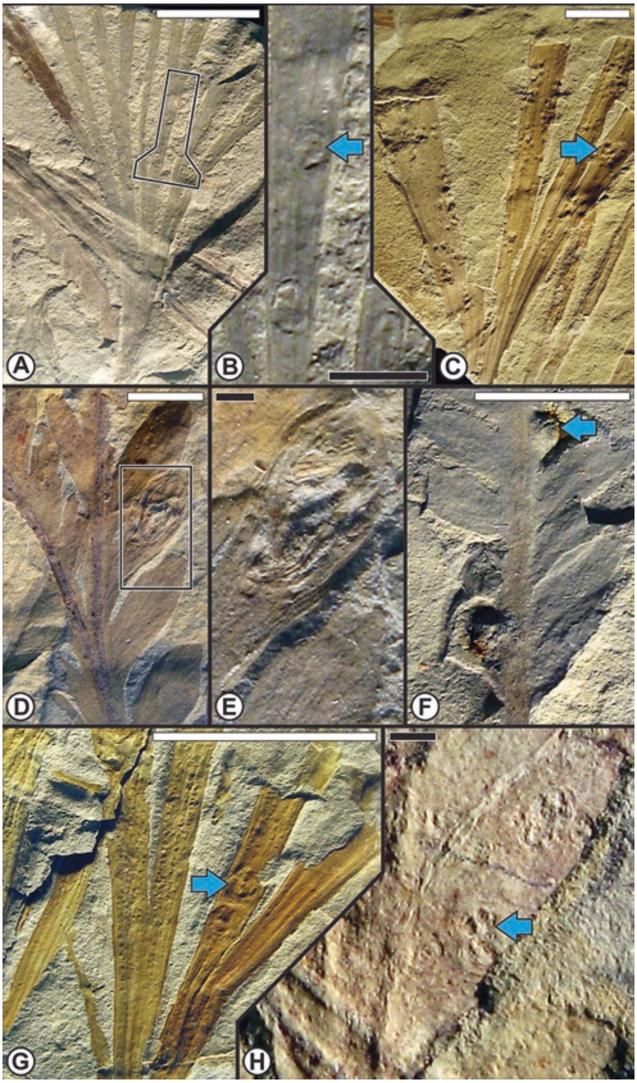

Fig. 14.8 Galling at the Aasvoëlberg 411 site, from the Late Triassic Molteno Formation of South Africa. (**a**) Bulbous DT122 galls on the foliage of the ginkgophyte *Sphenobaiera schenckii*; PRE/F/12103a-1. (**b**) Enlargement of galls (*blue arrow*) from template in (**a**). (**c**) Incipient DT122 galls (*blue arrow*) on the foliage of *S. schenckii*; PRE/F/12254-7. (**d**) An early-stage (immature) expression of the DT70 mite gall on the corystosperm *Dicroidium crassinervis*; PRE/F/12351-1. (**e**) Enlargement of galled pinnule at (**d**), showing surface structure of the galled pinnule. (**f**) An immature, early phase of the DT70 gall on *D. crassinervis*; PRE/F/21923-1. (**g**) An early phase of DT122 galls on its *S. schenckii* host; PRE/F/12396a-2. (**h**) Multiple, DT122 galls on pinnules of *D. crassinervis*; PRE/F/12242-1. *Blue arrows* indicate insect damage; scale bars: white, 1 cm; black, 1 mm

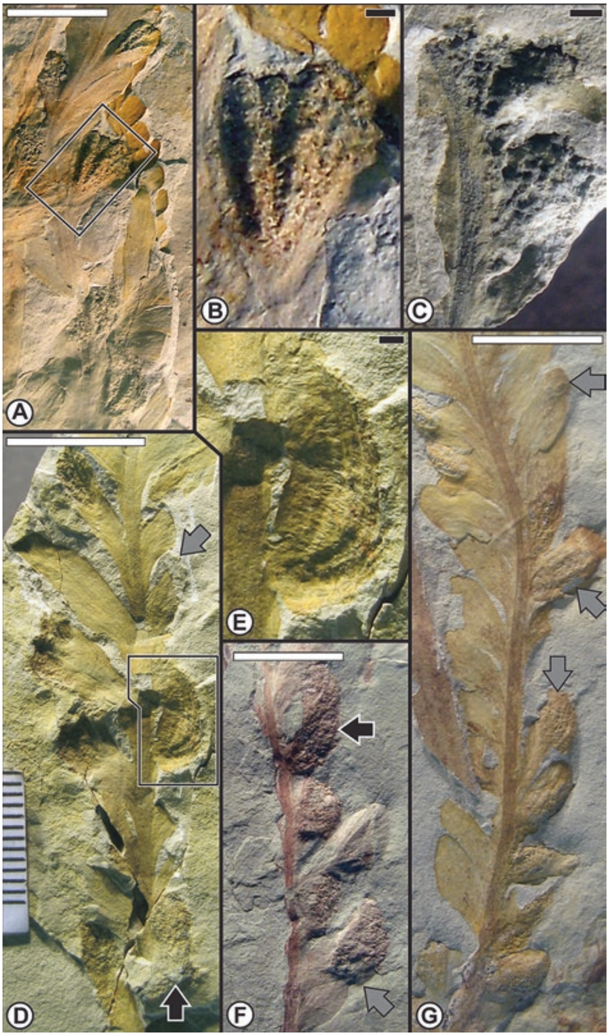

Fig. 14.9 DT70 galls on *Dicroidium crassinervis* at the Aasvoëlberg 411 site, from the Late Triassic Molteno Formation of South Africa. (**a**) Holotype of a mature, pustulose, DT70 gall, showing engulfment of the entire deltoid-shaped leaf and preservation of relict fasciculate venation of pinnule; PRE/F/12392-1. (**b**) Enlargement holotype DT70 gall at template at (**a**); microscope image. (**c**) Mature DT70 gall showing later stage, coarser pustulation on pinnular surface, and galled tissue connecting adjacent pinnules along the rachis; PRE/F/21416-1. (**d**) Approximately nine separate galls on a rachis showing various stages of maturity, ranging from establishment at pinnular tips (*grey arrow*) to an entire pinnule enveloped by gall tissue at the polygonal template (*black arrow*); PRE/F/12389b-1. (**e**) Enlargement of gall outlined in (**d**), showing relict pinnular venation and extensive pustulose surface. (**f**) Four mature (*black arrow*) or mostly mature galls occurring on one side of a rachis; PRE/F/12387a-1. (**g**) A long frond displaying approximately 11 galls ranging from small patches of galled tissue at pinnular tips (*top grey arrow*), to pinnules having a greater extent of galled tissue (*bottom grey arrow*) to near engulfment by galled tissue (*center grey arrow*); PRE/F/20880b. *Black arrows*, mature galls; *grey arrows*, immature damage; scale bars: white, 1 cm; black, 1 mm

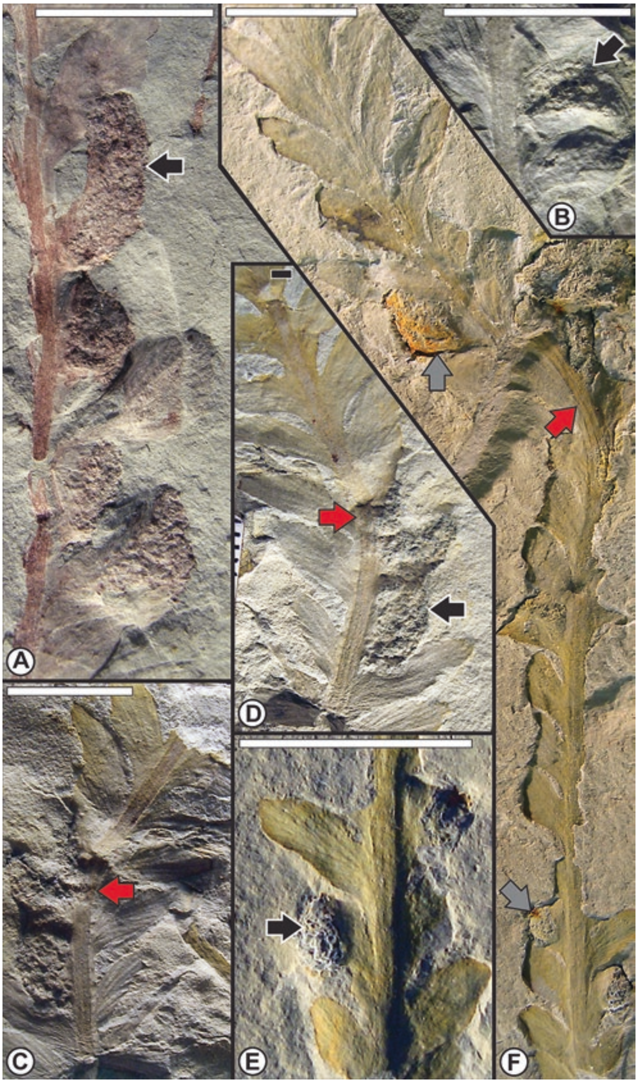

Fig. 14.10 DT70 galls on *Dicroidium crassinervis* at the Aasvoëlberg 411 site, from the Late Triassic Molteno Formation of South Africa. (**a**) Frond consisting of very mature galls, displaying breached pustules that expose inner cavities (*black arrow*); PRE/F/12387b-1, the enlarged counterpart of Fig. 14.8f. (**b**) Gall showing relict pinnular vein structure at *black arrow*; PRE/F/12394-1. (**c**) Portion of frond with five galled pinnules and distinctive teratological bend of the rachis at *red arrow*; PRE/F/12396a-1. (**d**) Another rachis segment with two pinnules, one indicated by a *black arrow* and revealing mature galls, and rachis bend at *red arrow*, representing the counterpart to (**c**); PRE/F/12396b-1. (**e**) Frond segment showing three, half mature galls, the left one (*black arrow*), showing upraised galled tissue; PRE/F/21908a-1. (**f**) Long frond branch with distinctive gall-induced crook at *red arrow* and immature galls (*lower grey arrow*) and more mature galls (*upper grey arrow*); PRE/F/21908-1. *Black arrows*, mature galls; *grey arrows*, immature galls; *red arrows*, rachis bends; scale bars: white, 1 cm; black, 1 mm

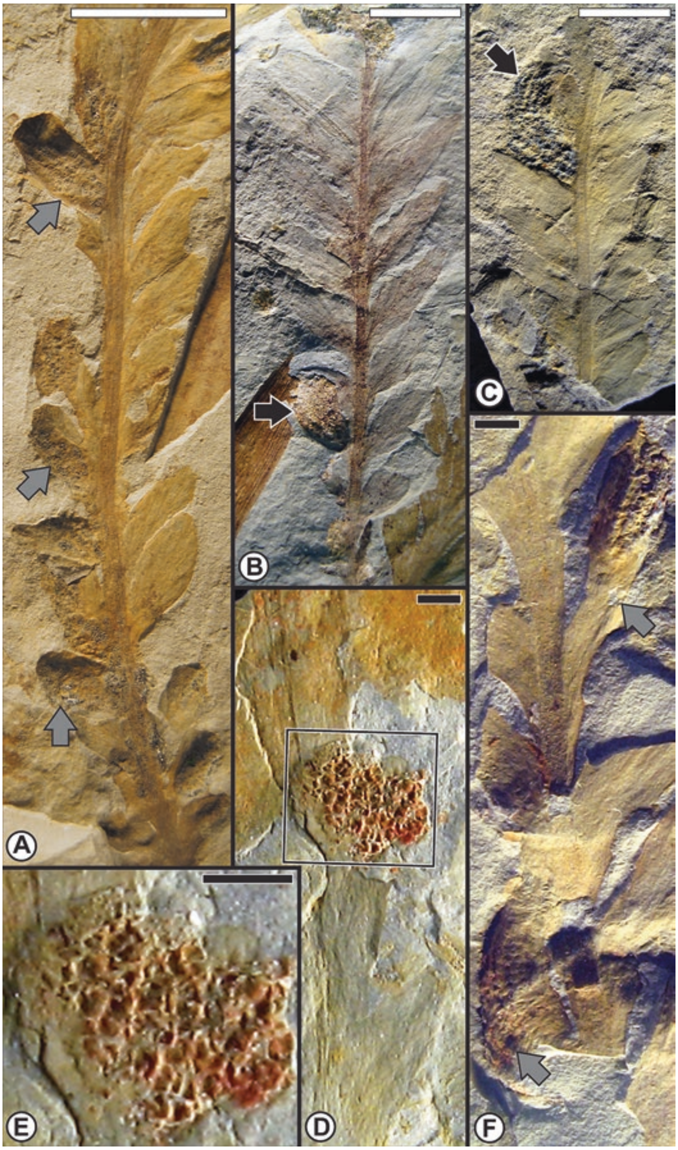

Fig. 14.11 DT70 mite galls on *Dicroidium crassinervis* at the Aasvoëlberg 411 site, from the Late Triassic Molteno Formation of South Africa. (**a**) A long frond segment with 12 galls that vary in the amount of pinnular coverage with galled tissue (*grey arrows*); PRE/F/20880a-1. (**b**) A frond with several incipiently galled pinnules and a highly galled pinnule (*black arrow*) that may have supplied colonizing mites for adjacent pinnules; PRE/F/2144a-1. (**c**) A gall (*black arrow*) with pustules occurring along the primary fasciculate venation of the pinnule; PRE/F/21920b-1. (**d**) A massive spheroidal gall that has obliterated pinnular structures such as veins and margin; PRE/F/21909-1. (**e**) Enlargement of gall surface detail in (d). (**f**) Frond segment bearing several galls, one of which is a mature gall (*bottom grey arrow*), and another immature gall showing the initial colonization of gall mites along pinnular primary veins (*top grey arrow*); PRE/F/21920b-1. *Black arrows*, mature galls; *grey arrows*, immature galls; scale bars: white, 1 cm; black, 1 mm

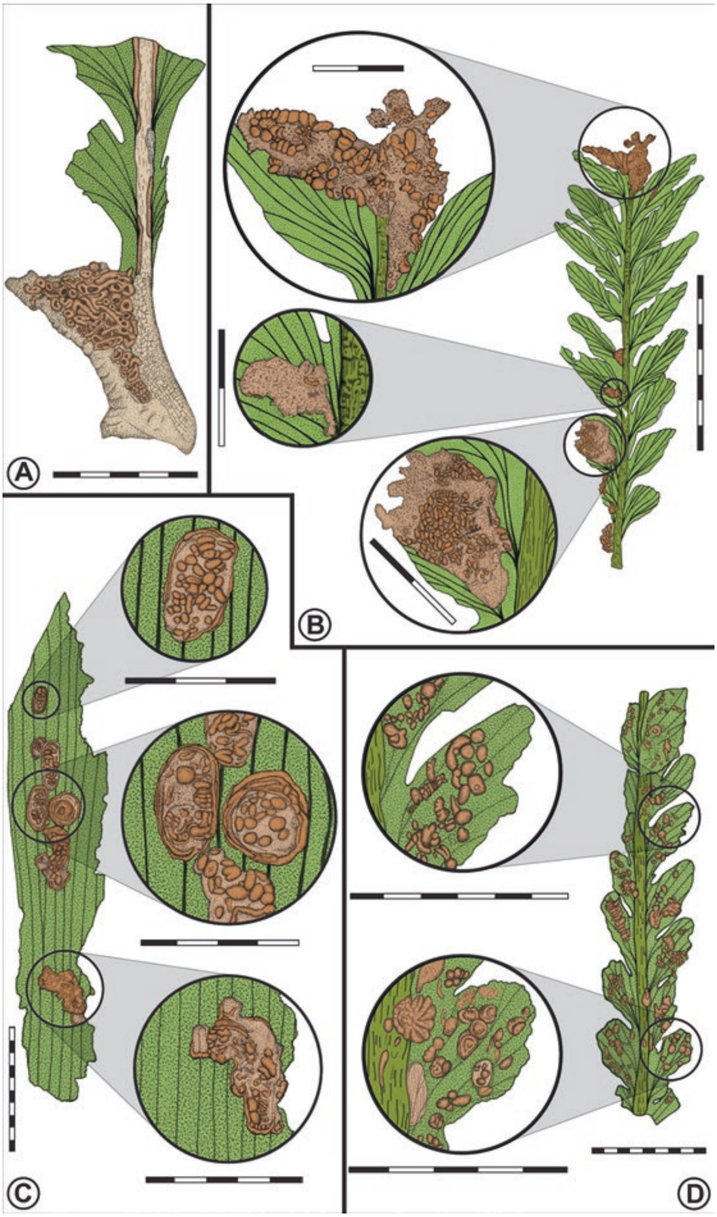

Fig. 14.12 Two galls on foliage of the two dominant plant hosts of the Aasvoëlberg 411 site, as they may have appeared in life during the Carnian. Colorized versions of inked camera-lucida drawings. (**a**) Gall DT70 on *Dicroidium crassinervis*; PRE/F/20883-3; scale bar, mm. (**b**) Gall DT70 on *D. crassinervis*; PRE/F/21144a-7; all scale bars, mm. (**c**) Gall DT122 on *Heidiphyllum elongatum*; PRE/F/12684a-10; all scale bars, mm. (**d**), Gall DT70 on *D. crassinervis*; PRE/F/21050-2; scale bars, mm

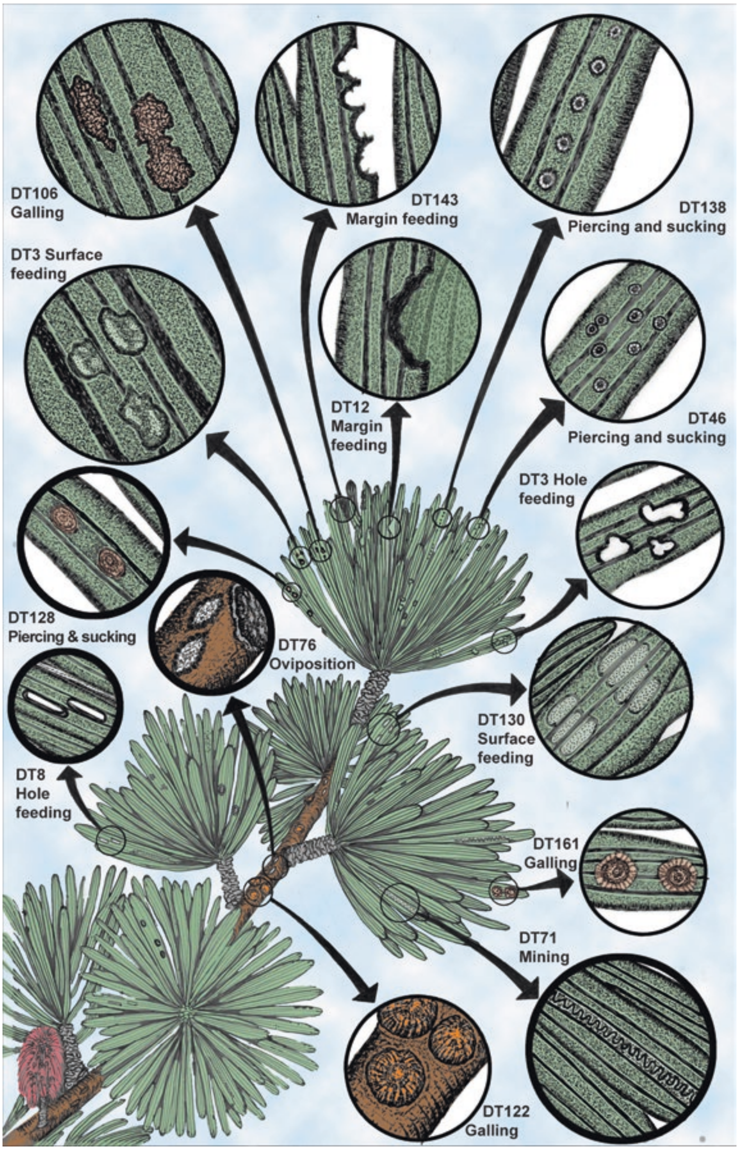

Fig. 14.13 The component herbivore community of the *Heidiphyllum elongatum–Heidiphyllum* short shoot–*Telemachus elongatus–Odyssianthus crenulatus* whole-plant taxon, from the Aasvoëlberg 411 (Aas411) site. DT numbers refer to damage types occurring on *H*. *elongatum* in Fig. 14.4. Only 14 of the 28 documented interactions (50%) of the *H*. *elongatum* herbivore component community are shown. Circular insets with thin ring enclosures are generalized interactions while those of thick ring enclosures are host-specialized associations, and match the same convention in Fig. 14.4. The basis of reconstruction is taken from Anderson and Anderson (2003) and Bomfleur et al. (2013)

Table 14.1 Patterns of herbivory throughout the Molteno Formation localities in the Karoo Basin of South Africa

Site name (abbreviation)	Stratigraphic position[a]	Habitat[a]	Whole plant taxa[b]	Dominant functional feeding group[c]	Total DT occurrences	Total plant specimens	Inter action index[d]	Total kinds of DTs	Plant morphotypes
Kenegapoort 111 (Ken111)	106	*Dicroidium* Open Woodland	0	Margin feeding	6	162	0.037	6	6
Navar 111A (Nav111B)	105	Horsetail Marsh	0	[none]	0	31	0	0	1
Navar 111B (Nav111B)	104	Horsetail Marsh	0	Margin feeding	5	212	0.0235	2	7
Cala Road 211 (Cal211)	103	Horsetail Marsh	0	Margin feeding, piercing & sucking	6	178	0.0215	5	3
Cala Road 111A (Cal111A)	102	Horsetail Marsh	1	Margin feeding	18	517	0.1451	6	9
Cala Road 111B (Cal111B)	101	*Dicroidium* Open Woodland	1	Galling	39	990	0.0283	6	12
Birds River 211 (Bir211)	100	*Sphenobaiera* Closed Woodland	1	Margin feeding	13	358	0.0363	7	15
Birds River 311 (Bir311)	99	*Sphenobaiera* Closed Woodland	4	Piercing & sucking	7	245	0.0288	5	20
Birds River 111 (Bir111)	98	*Sphenobaiera* Closed Woodland	9	Seed predation	2501	15,503	0.1598	41	72
Dordrecht 111 (Dor111)	97	*Heidiphyllum* Thicket	0	Margin feeding	5	144	0.0347	4	6
Greenvale 121 (Gre121)	96	*Heidiphyllum* Thicket	2	Hole feeding	104	2966	0.035	12	12
Greenvale 111A (Gre111A)	95	*Sphenobaiera* Closed Woodland	1	Surface feeding	5	281	0.0177	3	15
Greenvale 111B (Gre111B)	94	Horsetail Marsh	4	Oviposition	14	634	0.0220	3	22

(continued)

Table 14.1 (continued)

Site name (abbreviation)	Stratigraphic position[a]	Habitat[a]	Whole plant taxa[b]	Dominant functional feeding group[c]	Total DT occurrences	Total plant specimens	Inter action index[d]	Total kinds of DTs	Plant morphotypes
Boesmanshkoek 111A (Boe111A)	93	[indeterminate]	2	Margin feeding	11	369	0.0298	3	13
Boesmanshkoek 111B (Boe111B)	92	Horsetail Marsh	2	Oviposition	1	148	0.0068	1	9
Boesmanshkoek 111C (Boe111C)	91	*Dicroidium* Open Woodland	1	Margin feeding	22	700	0.0314	6	13
Boesmanshkoek 112 (Boe112)	90	*Dicroidium* Open Woodland	3	Margin feeding	6	1197	0.005	2	18
Cyphergat 111A (Cyp111C)	89	*Dicroidium* Open Woodland	3	Seed predation	168	6377	0.0263	27	32
Cyphergat 111B (Cyp111B)	88	*Heidiphyllum* Thicket	0	Surface feeding	1	180	0.0055	1	2
Molteno 211 (Mol211)	87	*Sphenobaiera* Closed Woodland	1	Oviposition	6	57	0.1052	4	10
Molteno 311 (Mol311)	86	*Sphenobaiera* Closed Woodland	0	Margin feeding	7	112	0.0625	6	5
Molteno 111 (Mol111)	85	*Sphenobaiera* Closed Woodland	0	[no damage]	0	27	0	0	6
Kannaskop 112 (Kan112)	84	*Heidiphyllum* Thicket	3	Piercing & sucking	44	1538	0.0286	9	29
Kannaskop 111 (Kan111)	83	Fern-*Kannaskoppifolia* Meadow	4	Margin feeding	42	2387	0.0176	11	15
Telemachus Spruit 111 (Tel111)	82	*Heidiphyllum* Thicket	3	Margin feeding	99	6681	0.015	14	38
Kommandantskop 111(Kom111)	81	Fern-*Kannaskoppifolia* Meadow	3	Hole feeding	23	1213	0.019	10	20

Vineyard 111 (Vin111)	80	*Dicroidium* Open Woodland	1	Margin feeding	63	2217	0.028	10	14
Elandspruit 111 (Ela111)	79	*Dicroidium* Open Woodland	3	Margin feeding	55	1154	0.0477	10	22
Kraai River 311 (Kra311)	78	*Dicroidium* Open Woodland	0	Galling	43	1387	0.031	6	8
Kraai River 211 (Kra211)	77	*Heidiphyllum* Marsh	1	Oviposition	2	401	0.005	1	2
Kraai River 222 (Kra222)	76	*Heidiphyllum* Marsh	0	[no damage]	0	50	0	0	1
Kraai River 221 (Kra221)	75	[indeterminate]	1	[no damage]	0	38	0	0	5
Kraai River 111 (Kra111)	74	*Dicroidium* Open Woodland	2	Margin feeding	22	2006	0.011	9	21
Lutherskop 111 (Lut111)	73	*Heidiphyllum* Thicket	1	Margin feeding	9	472	0.0191	4	5
Lutherskop 511 (Lut511)	72	*Heidiphyllum* Thicket	1	Surface feeding	28	634	0.0442	11	6
Lutherskop 4112 (Lut4112)	71	*Heidiphyllum* Thicket	1	Oviposition, mining, galling	13	744	0.0164	6	12
Lutherskop 4111 (Lut4111)	70	Horsetail Marsh	0	Surface feeding, oviposition	2	184	0.0109	2	2
Lutherskop 311 (Lut311)	69	*Heidiphyllum* Thicket	6	Mining	206	5784	0.034	23	39
Lutherskop 231 (Lut221)	68	Horsetail Marsh	0	[no damage]	0	46	0	0	3
Lutherskop 211 (Lut211)	67	Horsetail Marsh	1	Margin feeding	7	63	0.1111	4	10
Tina Bridge 121 (Tin121)	66	*Sphenobaiera* Closed Woodland	2	[no damage]	0	80	0	0	13
Tina Bridge 111 (Tin111)	65	Horsetail Marsh	2	Piercing & sucking	3	497	0.0024	1	9
Tina Bridge 111 (Tin131)	64	*Heidiphyllum* Thicket	0	Margin feeding, mining	7	148	0.0405	4	8
Waldeck 111 (Wal111)	63	*Sphenobaiera* Closed Woodland	1	Margin feeding	97	1695	0.0572	12	22

(continued)

Table 14.1 (continued)

Site name (abbreviation)	Stratigraphic position[a]	Habitat[a]	Whole plant taxa[b]	Dominant functional feeding group[c]	Total DT occurrences	Total plant specimens	Inter action index[d]	Total kinds of DTs	Plant morphotypes
Konings Kroon 223 (Kon223)	62	*Dicroidium* Open Woodland	4	Margin feeding	5	517	0.001	4	26
Konings Kroon 222 (Kon222)	61	*Dicroidium* Open Woodland	6	Margin feeding	31	2973	0.0105	13	35
Konings Kroon 211A & 221 (Kon211A & Kon221)	60	Fern-*Kannaskoppifolia* Meadow	2	Margin feeding	36	774	0.0466	10	33
Konings Kroon 211B (Kon211B)	59	*Heidiphyllum* Thicket	0	Hole feeding	1	168	0.006	1	5
Konings Kroon 111A (Kon111A)	58	*Dicroidium* Open Woodland	3	Margin feeding	19	1190	0.016	5	29
Konings Kroon 111B (Kon111B)	57	Horsetail Marsh	0	[no damage]	0	35	0	0	4
Konings Kroon 111C (Kon111C)	56	*Heidiphyllum* Thicket	2	Margin feeding	30	573	0.0526	11	14
Peninsula 111 (Pen111)	55	*Dicroidium* Open Woodland	0	Margin feeding	4	73	0.0548	2	6
Peninsula 321 (Pen321)	54	*Dicroidium* Open Woodland	4	Margin feeding	37	2315	0.0135	9	28
Peninsula 211 (Pen211)	53	*Dicroidium* Open Woodland	1	Margin feeding	3	307	0.0098	2	13
Peninsula 222, 221 (Pen221 & Pen221)	52	*Dicroidium* Open Woodland	0	Margin feeding	7	342	0.0205	3	13
Peninsula 511 (Pen511)	51	Horsetail Marsh	1	Oviposition	10	286	0.0347	7	5
Peninsula 421 (Pen421)	50	*Dicroidium* Open Woodland	2	Margin feeding	22	870	0.0256	13	18

Peninsula 431 (Pen431)	49	*Dicroidium* Open Woodland	0	Margin feeding	7	241	0.0292	3	11
Peninsula 311 (Pen311)	48	*Heidiphyllum* Thicket	1	Margin feeding	36	1785	0.0178	11	20
Peninsula 411 (Pen411)	47	*Heidiphyllum* Thicket	2	Oviposition	234	6807	0.0335	18	18
Klein Hoek 111A (Kle111A)	46	Horsetail Marsh	1	Piercing & sucking, oviposition	1	115	0.0087	1	7
Klein Hoek 111B (Kle111B)	45	[indeterminate]	3	Margin feeding, surface feeding	39	1267	0.0308	9	21
Klein Hoek 111C (Kle111C)	44	*Heidiphyllum* Thicket	3	Oviposition	141	2930	0.0478	17	15
Klein Hoek 211 (Kle211)	43	*Sphenobaiera* Open Woodland	0	[no damage]	0	34	0	0	1
Kullfontein 111 (Kul111)	42	*Sphenobaiera* Closed Woodland	0	[no damage]	0	5	0	0	4
Kappokraal 111 (Kap111)	41	*Dicroidium* Riparian Forest (Immature)	7	Margin feeding	554	1965	0.2819	27	39
Vineyard 211 (Vin211)	40	Horsetail Marsh	0	Oviposition	4	287	0.0134	2	1
Elandspruit 112A (Ela112A)	39	Horsetail Marsh	3	Seed predation	78	1295	0.0593	7	19
Elandspruit 112B (Ela112B)	38	*Heidiphyllum* Thicket	0	Margin feeding	12	546	0.0220	5	5
Nuwejaarspruit 111A (Nuw111A)	37	Horsetail Marsh	2	Oviposition	45	709	0.0634	6	11
Nuwejaarspruit 111B	36	*Dicroidium* Open Woodland	3	Margin feeding	76	2188	0.0347	20	24
Nuwejaarspruit 211 (Nuw211)	35	*Dicroidium* Open Woodland	1	Piercing & sucking	89	763	0.1153	13	13

(continued)

Table 14.1 (continued)

Site name (abbreviation)	Stratigraphic position[a]	Habitat[a]	Whole plant taxa[b]	Dominant functional feeding group[c]	Total DT occurrences	Total plant specimens	Inter action index[d]	Total kinds of DTs	Plant morphotypes
Winnaarspruit 111 (Win111)	34	*Heidiphyllum* Thicket	0	Margin feeding	80	1679	0.0478	17	16
Morija 111-A (Mor111A)	33	*Dicroidium* Open Woodland	2	Margin feeding	39	539	0.0724	3	3
Morija 111-B (Mor111B)	32	*Dicroidium* Open Woodland	2	Margin feeding	59	1628	0.0362	7	14
Qualasi Hill 111 (Qua111)	31	*Dicroidium* Open Woodland	2	Margin feeding	1	235	0.0043	1	11
Makoaneng 111 (Mak111)	30	*Dicroidium* Open Woodland	2	Margin feeding	22	1308	0.0168	7	14
Mazenod 111 (Maz111)	29	*Dicroidium* Riparian Forest (Immature)	2	Margin feeding	73	1041	0.0701	11	22
Mazenod 211 (Maz211)	28	*Dicroidium* Riparian Forest (Immature)	7	Margin feeding	254	2279	0.11	32	34
Mooi River 111 (Moo111)	27	*Dicroidium* Open Woodland	1	Margin feeding, oviposition	2	186	0.0108	2	9
Mooi River 121 (Moo121)	26	*Sphenobaiera* Closed Woodland	0	[no damage]	0	44	0	0	5
Hlatimbe Valley 111 (Hla111)	25	Horsetail Marsh	0	[no damage]	0	287	0	0	2
Hlatimbe Valley 111 (Hla111)	24	*Dicroidium* Riparian Forest (Immature)	3	Margin feeding	11	515	0.037	8	25
Hlatimbe Valley 212 (Hla212)	23	*Dicroidium* Riparian Forest (Immature)	4	Margin feeding	21	723	0.034	10	29
Hlatimbe Valley 213 (Hla213)	22	*Dicroidium* Riparian Forest (Immature)	7	Margin feeding	95	1943	0.0474	19	59

Hlatimbe Valley 311 (Hla311)	21	*Dicroidium* Riparian Forest (Immature)	0	[no damage]	0	10	0	0	5
Umkomaas 111 (Umk111)	20	*Dicroidium* Riparian Forest (Mature)	12	Margin feeding	639	12,788	0.0481	38	109
Champagne Castle 111 (Cha111)	19	*Dicroidium* Open Woodland	0	[no damage]	0	17	0	0	1
Champagne Castle 211 (Cha211)	18	*Dicroidium* Open Woodland	0	[no damage]	0	10	0	0	2
Injasuti Valley 111 (Inj111)	17	*Dicroidium* Open Woodland	1	Margin feeding	2	22	0.091	1	4
Injasuti Valley 211 (Inj211)	16	*Dicroidium* Open Woodland	0	[no damage]	0	55	0	0	5
Sani Pass 111 (San111)	15	*Dicroidium* Riparian Forest (Immature)	4	Margin feeding	34	1340	0.0254	10	33
Mngeni Valley 111 (Mng111)	14	*Dicroidium* Open Woodland	2	Margin feeding	6	398	0.051	1	14
Qachasnek 111 (Qac111)	13	*Heidiphyllum* Thicket	2	Hole feeding	15	2130	0.007	7	11
Matatiele 111 (Mat111)	12	*Dicroidium* Riparian Forest (Immature)	6	Margin feeding	237	6343	0.0365	22	55
Golden Gate 111 (Gol111)	11	*Dicroidium* Riparian Forest (Immature)	2	Margin feeding	119	1326	0.09	17	13
Little Switzerland 111 (Lit111)	10	*Dicroidium* Riparian Forest (Mature)	6	Margin feeding	663	9912	0.0669	31	64
Aasvoëlberg 611 (Aas611)	9	*Heidiphyllum* Thicket	1	Hole feeding, margin feeding, galling	6	229	0.0278	4	7
Aasvoëlberg 111 (Aas111)	8	*Heidiphyllum* Thicket	1	Margin feeding	35	3308	0.0103	12	24
Aasvoëlberg 211 (Aas211)	7	*Heidiphyllum* Thicket	1	Margin feeding	103	2061	0.05	12	16

(continued)

Table 14.1 (continued)

Site name (abbreviation)	Stratigraphic position[a]	Habitat[a]	Whole plant taxa[b]	Dominant functional feeding group[c]	Total DT occurrences	Total plant specimens	Inter action index[d]	Total kinds of DTs	Plant morphotypes
Aasvoëlberg 311 (Aas311)	6	*Heidiphyllum* Thicket	1	Mining	1209	11,677	0.1313	18	18
Aasvoëlberg 411 (Aas411)	5	*Sphenobaiera* Closed Woodland	15	Margin feeding	1127	20,358	0.0554	44	112
Aasvoëlberg 511 (Aas511)	4	*Dicroidium* Open Woodland	0	Surface feeding	5	85	0.0588	3	11
Aasvoëlberg 711 (Aas711)	3	*Sphenobaiera* Closed Woodland	1	Galling	3	47	0.0638	2	5
Askeaton 111 (Ask111)	2	Horsetail Marsh	2	Margin feeding	45	1061	0.0424	8	21
Bamboesberg 111 (Bam111)	1	*Dicroidium* Open Woodland	0	Margin feeding	6	284	0.0211	4	7

[a] In stratigraphic order: the youngest site is Kenegapoort 111 at *top* (site 106) and the oldest site is Bamboesberg (site 1) at *bottom*

[b] The seven primary habitats of the Molteno Biome are illustrated and defined by Anderson and Anderson (2003) and MacRae (1999)

[c] Based on the greatest number of damage-type (DT) occurrences of a functional feeding group (FF) for each site

[d] The interaction index is calculated as the total number of DT occurrences divided by the number of plant specimens examined, providing a number expressing the density of interactions for each site

Table 14.2 Herbivory metrics of the seven most herbivorized whole-plant-taxa of the Late Triassic Aasvoëlberg 411 site, Karoo Basin of South Africa

Whole-plant taxon (WPT)[1] and host affiliation	Functional feeding groups	Number of DTs	DT occurrences	Specialized associations	Importance rank
Heidiphyllum elongatum——*Telemachus acutisquamus*——*Odyssanthus crenulata* (conifer) [WPT: **M**]	9	28	472	4	**1**
Dicroidium crassinervis——*Fanerotheca papilioformis*——*?Petruchus matatimajor* (corystosperm) [WPT: **I**]	7	20	265	2	**2**
Sphenobaiera schenckii——*Sphenobaiera*-short shoot——*Hamshawvia longipeduncu-lata*——*Stachyopitys gypsianthus* (ginkgophyte) [WPT: **H**]	7	11	65	1	**3**
Ginkgoites matatiensis——*Avatia bifurcata*——*Eosteria eosteranthus* (ginkgophyte) [WPT: **F**]	5	11	88	1	**4**
Lepidopteris africana——*Peltaspermum turbinatum*——*Antevsia* sp. (peltasperm) [WPT: **D**]	5	10	30	0	**5**
Lepidopteris stormbergensis——*Peltaspermum monodiscum*——*Antevsia* sp. (peltasperm) [WPG: **C**]	5	8	31	0	**6**
Zonulamites viridensis——nodal diaphragm A–*Viridistachys gypsensis*——*Paraschizo-neura fredensis* (horsetail) [WPT: **B**]	1	3	60	2	**7**

[1] Plant organs forming each whole plant taxon, lettered in Fig. 14.4, are indicated by the WPT designation

Table 14.3 Specialized associations of the five most herbivorized whole-plant-taxa of the Late Triassic Aasvoëlberg 411 site, compared to other relevant Molteno localities, Karoo Basin of South Africa

	Specialized Associations						
Whole-plant taxon (WPT)[a] and host affiliation	Functional Feeding group	Host specialized DT	Aas411 DT occurrences	Total Molteno localities with the DT	Total Molteno DT occurrences	Proportion of FFG DTs at Aas411	Dominant Molteno habitat[b]
Heidiphyllum elongatum——*Telemachus acutisquamus*——*Odyssanthus crenulata* (conifer) [WPT: **M**]	**Hole Feeding**	DT8	1	21	78	1.3%	HT
	Piercing and Sucking	DT128	2	4	40	5.05	HT
	Oviposition	DT76	99	30	472	21.0%	HT
	Mining	DT71	147	23	1271	11.8%	HT
Dicroidium crassinervis——*Fanerotheca papilioformis*——*Petruchus matatimajor* (corystosperm) [WPT: **I**]	**Galling**	DT70	117	12	167	70.1%	DOW
	Seed Predation	DT74	35	10	700	5.0%	DOW
Sphenobaiera schenckii——*Sphenobaiera*-short shoot——*Hamshawvia longipeduncu-lata*——*Stachyopitys gypsianthus* (ginkgophyte) [WPT: **H**]	**Galling**	DT122	35	5	49	71.4%	SCW
Ginkgoites matatiensis——*Avatia bifurcata*——*Eosteria eosteranthus* (ginkgophyte) [WPT: **F**]	**Seed Predation**	DT73	63	7	1130	5.6%	SCW
Zonulamites viridensis—nodal diaphragm A–*Viridistachys gypsensis*—*Paraschizoneura fredensis* (horsetail) [WPT: **B**]	**Oviposition**	DT72	14	9	38	36.8%	HM
	Oviposition	DT108	39	2	40	97.5%	HM,SCW
Dordrechtites elongatus/*D. mazocirrus* (conifer)	**Seed Predation**	DT124	2	2	13	15.4%	SCW,DRF-I

[a] Whole plant taxa (WPT) are indicated in Fig. 14.4, with their herbivore damage types (DTs) and functional feeding groups (FFGs)

[b] Habitat abbreviations: *DOW* Dicroidium Open Woodland, *HM* Horsetail Marsh, *HT* Heidiphyllum Ticket, *SCW* Sphenobaiera Closed Woodland, *DRF-I* Dicroidium Riparian Forest, immature phase (Anderson and Anderson 2003)

Although the consumption of live plant tissue is quite different from the consumption of dead plant tissue (Brues 1924; Mitter et al. 1988), both types of biological interactions are quite different from physical destruction of plants by the environment, such as leaf damage attributable to wind, water or the impact of gravity (Wilson 1980; Vincent 1990; Vogel 2012). For detritivory, the five classes of evidence listed immediately above typically are absent. For example, detritivory does not produce callus and other teratological plant-response tissues that typically result when insect-induced herbivory targets live plant tissues. Importantly, detritivory almost always lacks the delicate microstructural features of damage, such as veinal stringers and necrotic tissue flaps that occur along the margins or surfaces of herbivorized plant organs.

14.3.3 Functional Feeding Groups, Damage Types and Component Communities

The arthropod damage present at Aas411 was categorized based on the FFG–DT system of Labandeira et al. (2007), consisting of data (Tables 14.2, 14.3; Figs. 14.2, 14.3, 14.4) and illustrations of damage (Figs. 14.5, 14.6, 14.7, 14.8, 14.9, 14.10, 14.11, 14.12, 14.13). A functional feeding group (FFG) is a major mode of insect feeding defined by the way an insect consumes its food and is associated with particular insect mouthpart structure, feeding mode and plant damage pattern (Labandeira 1997, 2002b). A FFG is subdivided into multiple damage types (DTs), each of which is a distinctive, defined pattern of damage that represents the most restrictive level of diagnosis and constitutes the fundamental unit of analysis in this and other such studies (Wilf and Labandeira 1999; Schachat et al. 2014; Ding et al. 2015).

There are, however, a few complexities to this system of insect-damage analysis. Oviposition also is considered a FFG, even though it represents the insertion of eggs into plant tissues by a sword-like abdominal feature, the ovipositor, and technically is not a type of plant consumption. However, oviposition has an abundant and rich fossil record of insect-mediated plant damage and is represented by a wide variety of DTs (Sarzetti et al. 2009; McLoughlin 2011; Gnaedinger et al. 2014), and has been treated as a FFG in this and previous studies. In addition, some DTs are combined into a damage-type suite that has two or more associated DTs that are linked organically to the same insect maker. For example, the base of deciduous gall DT186 has attachments to leaves that exactly match the holes of DT148 that occur on the same host plant of the same deposit, indicating a match that represents a deciduous gall and the dehisced leaf scar from which it originated (Labandeira et al. 2007). Another example of a damage-type suite is the leaf mine DT280 that likely originated from oviposition lesion DT101 on the same leaf taxon, and whose adult feeding damage likely is DT103, also occurring the same host-plant organ (Ding et al. 2014).

Herbivore component communities were established for the major plant hosts at Aas411. A component community consists of all species that trophically are dependent on a single, live, host-plant species (Root 1973). Some Molteno vascular-plant species are a host to herbivores that consist of a single organ, whereas others are designated as a host consisting of a whole plant taxon (WPT) that consists of multiple affiliated plant organs. The component community of each plant host includes all dependent herbivores and their derivative consumers, including predators and parasitoids, as well as saprobes that are trophically linked to that source-plant species through the same food web. Many arthropod herbivores and predators are known for the Molteno Biome in general and Aas411 in particular, as discussed below. In modern component communities, the source plant constitutes approximately 90% of the total component community biomass; insect herbivores account for about 10%; and generally 1% is attributable to consumers of the herbivores (Schmitz 2008). A relevant consideration here is that insect parasites and parasitoids are a feeding guild that did not appear until the Early Jurassic (Labandeira 2002a), and thus are excluded from the component community structure of Molteno plant species, which was characterized by top-to-down regulation by insect and ultimately vertebrate predators.

14.4 The Molteno Formation

14.4.1 Geological Backdrop

The Late Triassic (Carnian) Molteno Formation is a thick, wedge-shaped sequence of conglomerate, sandstone, shale and coal that occupies the eastern limb of the Karoo Basin in South Africa. (Hancox 2000). The Molteno sedimentary package consists of a well exposed, approximately quadrangular outcrop pattern that extends approximately 200 km in an east–west and 450 km in south–north directions (Fig. 14.1). This sedimentary package thickens to 650–600 m from the south (Hancox 2000), adjacent the Triassic sediment source of the then substantial mountains of the Cape Fold Belt, and thins to the north where it is unconformably underlain by the older Middle Triassic (Anisian) Burgersdorp Formation, the uppermost unit of the Beaufort Group. The Molteno Formation conformably intergrades laterally and distally into a red-bed facies of the Lower Elliot Formation (Anderson et al. 1998). The portion of the Karoo Basin housing the Molteno Formation consists of a foreland basin established by tensional tectonism from the break-up of Gondwana. This tectonic separation of landmasses formed a rift between northern Antarctica and South American toward the south from southern Africa, while Gondwana drifted northward during the Triassic.

14.4.2 Lithostratigraphy

Although the lower contact of the Molteno Formation with the Burgersdorp Formation is unconformable, generally the lowermost strata of the Molteno Formation is considered as the first appearance of conglomeratic and coarse-grained sandstone strata, typical of the transition from an earlier phase of suspension-load flow to a later phase of bed-load flow. This switch parallels a distinct change in outcrop color from red and purple to grey and buff hues (Cairncross et al. 1995; Anderson et al. 1998). This marked sedimentologic and color break coincides with a change in the depositional environment from a floodplain of ephemeral streams to a braided-stream system, and is marked by an unconformity that probably is regional in scope. It is likely that this changeover was caused by initiation of an offshore, tensional tectonic regime, occasioned by the rifting of Antarctica and South America from southern Africa. Deposits of the Molteno Formation consist of buff-colored to grey, often yellowish brown and pale bluish to light grey sandstones that interdigitate with grey to olive-grey and reddish brown siltstones and mudstones (Cairncross et al. 1995; Anderson et al. 1998). These strata occasionally contain sedimentary ichnofossils (Turner 1978). Carbonaceous mudstones often are present, but coals are rare, with thermal rank intensity decreasing in a westerly direction (Hancox 2000). After deposition of the Molteno sediments, there was another colorimetric shift in the Lower Elliot Formation, from buff-colored hues and grays to reds and purples, as well as a distinctive change to finer-grained strata that represent a stepwise increase in flooding events (Cairncross et al. 1995; Anderson et al. 1998).

14.4.3 Depositional Environment and Cycles

During the interval of Molteno sedimentation, as the Cape Fold Belt Mountains to the south were eroded to a remnant of their former size, there was a sedimentary wedge of strata that fanned out toward the north and formed a variety of depositional environments (Hancox 2000). These environments consisted of braided and subordinate meandering fluvial systems that consisted of three primary facies. These facies were: (i), channel-fill deposits of coarse grained and upward-fining sequences; (ii), upward-coarsening crevasse splays and sheet-flood strata; and (iii), interspersed laminated lake and waterlogged shales indicating lacustrine or palustrine conditions. The beginning of Molteno sedimentation was characterized by a braided-stream style of fluvial deposition, and small inter-channel bodies of water. By contrast, toward the end of Molteno deposition there was a shift toward meandering-river systems and the establishment of more extensive lakes (Anderson et al. 1998).

The Molteno Formation is subdivided into six, distinctive, sedimentary cycles (Fig. 14.1). Each cycle repeats a fining-upward sequence of sedimentation that resulted from a pulse of mostly fault-controlled uplift (Turner 1975). The uplifts that produced the sedimentary cycles originated from the south in cycles 1 and 2, and from the southeast for cycles 3 through 6 (Anderson et al. 1998). Each of the six sedimentary cycles in the Molteno Formation typically produced a coarse-grained sandstone to fine-grained sandstone to a siltstone–shale–coal succession that displayed more resistant strata at the base and less resistant strata at the top of each sequence. The sedimentary cycles begin with the Bamboesberg Member representing cycle 1, and end with the Loskop Member of cycle 6. The physical environment and habitat type of a Molteno site are contingent on where in the sedimentary cycle landscape that it occurs. More stable, proximal localities closer to the source area tend to favor mature forests bordering lakes, whereas more distal localities occur along distributary channels that prefer ephemeral vegetation in disturbed environments.

14.4.4 Molteno Localities and the Broader Context

For this and following studies of Molteno plant–insect interactions, the total data-set consists of 106 localities containing 177,297 separately examined plant specimens from which 10,165 interactions have been recorded (Table 14.1). The number of localities for each habitat type, detailed below, are: two localities of Mature Dicroidium Riparian Forest, nine localities of Immature Dicroidium Riparian Forest, 33 of Dicroidium Open Woodland, 15 of Sphenobaiera Closed Woodland, 23 of Heidiphyllum Thicket, 18 of Horsetail Marsh, three of Fern–Kannaskoppia Meadow, and three of indeterminate habitat. These Molteno data represent the most extensive database of plant–insect interactions in the fossil record and will be included with eight Anisian localities and approximately ten Guadalupian and Lopingian Permian localities, all from the Karoo Basin, in future analyses. This broader study will examine the effects on Molteno plant–insect interactions that were inflicted by the P-Tr ecological crisis approximately 35 million-years earlier.

14.4.5 The Aasvoëlberg 411 Site

Of the 106 plant assemblages collected from the Molteno Formation, the Aas411 site is the second most intensively sampled in terms of human labor. Specimens were excavated from Aas411 on 11 separate field trips, covering 40 days and include a total of 512 person-hours splitting slabs on site or back in the lab by John and Heidi Anderson and colleagues. A total of 2535 catalogued slabs originate from Aas411, of which 242 were part/counterpart slabs, that consist of 20,358 examined individual plant specimens averaging to about eight plant specimens per slab. The Aas411 site has the most numerically abundant specimens from the Molteno Formation; the Bir111 (Birds River 111) site is second at 15,503 specimens. All fossil plants from the Molteno Formation currently is housed at the Evolutionary

Studies Institute (ESI) at the University of the Witwatersrand, in Johannesburg, South Africa, under the curation of Dr. Marion Bamford.

Geographically the Aas411 site occurs in the far southwestern corner of the Molteno Formation outcrop belt, in the north-central part of the Eastern Cape Province, approximately 50 km southwest of the town of Molteno, after which the formation is named. Strata of the Aas411 site crop out within the Bamboesberg Member, the stratigraphically lowest of six defined members (cycles) in the formation. Of the 106 sampled plant assemblages, Aas411 is the fourth lowest in the Molteno sequence. Of the seven primary habitats recognized as characterizing the Molteno Biome, Aas411 represents Sphenobaiera Closed Woodland, a habitat which typically occurs along floodplains surrounding lakes.

The fossiliferous stratum yielding the Aas411 material consists of about a two m-thick bed of rhythmically alternating, thinly laminated, yellowish-grey shale to slate with very good cleavage. The strata are significantly altered thermally, resulting from the heating effect of nearby dolerite sills and dikes. Preservation is exclusively in the form of impressions, though with excellent clarity of detail. The local bed from which the specimens originate is exposed intermittently along a grassy hillslope for some 140 m, but its full extent is uncertain, as is its uniformity of thickness and lithology.

The preserved Aas411 flora consists of 30 vegetative species, of which 22 are gymnosperms and eight are non-gymnosperms. The Aas411 flora is dominated by several species each of the corystosperm *Dicroidium* (60%) and the ginkgophyte *Sphenobaiera* (30%), which, together with non-dominant plants, probably represent distinct woodland communities within the Sphenobaiera Closed Woodland habitat that bordered floodplain lakes. Generally, the constituents and preservation of the flora, considering the foliage, cones, scales and seeds, suggest quiescent conditions occurring adjacent to a sizable water body. The insect fauna is composed of a high-diversity cockroaches, beetles and dragonflies which form an association represented by 129 individuals. These informal insect taxa provisionally have been assigned to 30 genera and 43 species across a wide spectrum of 13 orders. The numerical dominance of cockroaches, consisting of 54 individuals, hints at the surrounding woodland having a dense cover with mostly a closed canopy and well-developed leaf litter layer.

14.4.6 Habitats

There are seven distinctive, primary habitats that characterize the floodplain environments of the Molteno Biome (Cairncross et al. 1995; Anderson et al. 1998). These habitats were determined by physiognomic features of the plants, such as abundance patterns, plant growth form, leaf architecture, and recurring plant associations. In addition, features of the environment are relevant for determination of the habitat, such as sedimentologic features of the deposit, indications of climate-based aridity, and inferred water saturation levels in soils (Anderson and Anderson

2003). These seven habitats occupy particular, confined settings on the regional landscape that consist of particular plant associations or monodominant communities that have been determined for 103 of the 106 floras of the Molteno Formation. Floras from three of the Molteno localities have not been assigned to any of the seven habitats.

The climax, or mature, phase of Dicroidium Riparian Forest consists of a multistory, close-canopied, high diversity forest of plant taxa and morphotypes occurring adjacent to active and abandoned and meandering water channels that are superimposed on an earlier Triassic erosional surface. By contrast, the pre-climax, or immature, phase of Dicroidium Riparian Forest is characterized by single story, mostly closed canopy, medium diversity forest adjacent various floodplains. These channels are mostly braided and occur on alluvial flood plains. Dicroidium Open Woodland consists of a low to medium diverse woodland with a considerable intervening open spaces occurring along floodplains bordering water courses that are subject to intermittent sheet flooding. Sphenobaiera Closed Woodland, such as the Aas411 site, is comprised of a moderately diverse woodland with a minimally interrupted canopy that borders lakes and is present on floodplains. Heidiphyllum Thicket represents almost monodominant, dense stands of shrubby coniferous plants and associated lianas rooted in soils with an elevated water table along floodplains or on mid-stream sandbars. Horsetail Marsh consists of highly monodominant stands of horsetails along sandbars in channels, floodplain marshes, and poorly drained wetland soils that surround lakes. Fern–Kannaskoppifolia Meadow is a rare habitat of a low-diversity, mostly herbaceous in form that occupies median channel bars or braided-river sandbars, often in ruderal environments.

Each habitat type has a characteristic spectrum of plant species whose rank-order of abundance is distinctive at the genus level (see Sect. 14.5.14). Preliminary observations indicate that 43 localities and most habitats have produced insect fossils that express different combinations of and dominance of particular insect taxa. Insects of the Molteno Biome are Ephemeroptera (mayflies), Odonatoptera (dragonflies and related forms), Plecoptera (stoneflies), Blattodea (cockroaches), Orthoptera (forms related to grasshoppers and crickets), Hemiptera (cicada-like forms and bugs), Coleoptera (beetles), Neuroptera (lacewings), Hymenoptera (sawflies) and Mecoptera (scorpionflies) (MacRae 1999; Anderson and Anderson 2003). About half of these groups are overwhelmingly are herbivorous or have significant herbivore lineages, and undoubtedly assumed a major role in the plant–insect interactions in the Molteno Biome (Scott et al. 2004; Labandeira 2006a, 2012, 2016).

14.5 Molteno Plant Hosts

14.5.1 Overview

A broad variety of plants characterize the Molteno Flora, collectively representing the most diverse assemblage worldwide of plants from the Late Triassic. The Molteno Flora from the Karoo Basin of South Africa and Lesotho is a Late Triassic

Gondwanan assemblage that is floristically consistent with all of the major groups of cryptogams, ferns, and seed plants that typically occur in other floras of the supercontinent at the genus and frequently the species level. The Molteno Flora represents a rich assemblage of bryophytes (mosses, unpublished data), hepatophytes (liverworts, unpublished data) and lycopods (clubmosses, unpublished data), horsetails (Anderson and Anderson 2017), ferns (Anderson and Anderson 2008) and seed plants (Anderson and Anderson 1983, 1989, 2003). The seed plants represent the majority of the plant lineages present, and include virtually all major Late Triassic taxa of cycads, conifers, peltasperms, diverse ginkgophytes, corystosperms, bennettitaleans and probably gnetaleans. Additional unaffiliated taxa also occur. Based on an assessment of success following five criteria established by Anderson and Anderson (2003), the five most prominent foliage genera, in order of prominence, are the corystosperm *Dicroidium*, the conifer *Heidiphyllum*, the ginkgophyte *Sphenobaiera*, the bennettitopsid *Taeniopteris*, and the ginkgophyte *Kannaskoppifolia*.

14.5.2 Bryophytes

Most Molteno bryophytes currently are undescribed, although a preliminary tally of these rare to uncommon herbaceous taxa indicates that they bore a thallus representing a broad variety of morphologies among mosses, liverworts and an indeterminate taxon. Bryophytes collectively occur in about a fourth of the 106 Molteno localities. Mosses are represented by a single species of undescribed *Muscites* and 12 undescribed species of *Thallites* that are present in 18 localities and predominantly inhabited the immature and mature phases of Dicroidium Open Woodland. Liverworts are equally speciose, comprised of 13 undescribed species of *Marchantites* foliage from 19 localities that occurred on soils principally in Heidiphyllum Thicket and subordinately in the immature and mature phases of Dicroidium Riparian Forest, Dicroidium Open Woodland and Sphenobaiera Closed Woodland. The species of moss foliage primarily inhabited five localities, dominantly in Heidiphyllum Thicket and both developmental phases of Dicroidium Riparian Forest. One undescribed, monospecific genus was present in two localities of Sphenobaiera Closed Woodland, including Aas411. Although modestly diverse, the above four bryophyte genera were present at low frequencies and were an insignificant part of the flora, occurring on or within a few centimeters of the soil surface.

14.5.3 Lycopods

Largely undescribed, herbaceous or small single-stemmed, arborescent lycopods consisted of five undescribed genera and 13 species of stems, foliage and cones informally assigned to a new, undescribed lycopodialean family and the extinct isoëtalean Pleuromeiaceae. Lycopods occurred in about a tenth of the Molteno localities, are present at significantly lower frequencies than bryophytes, and are represented by six genera and 13 species that formally have not been described. A single undescribed genus of lycopod cone was present at one site of Sphenobaiera Closed Woodland. By contrast, another undescribed genus of lycopod cone is represented by five species that occurred in five localities across a landscape of varied habitats. Lycopod megaspores have been found in two localities, including Aas411. Three genera of lycopod foliage are present at three localities, principally in Sphenobaiera Closed Woodland, all three of which occur at Aas411. A genus of lycopod stems is represented at one site whereas another morphotype of lycopod stems occurs in five localities, including a species at Aas411, amid a broad spectrum of habitats. Like bryophytes, lycopods were present in those localities with the most diverse biotas, especially at Aas411, Umk111 and Bir111. Molteno lycopods represent several new, higher-level taxa not known elsewhere from the Late Triassic and many had distinctive stem morphologies.

14.5.4 Horsetails

Horsetails, or sphenopsids, are one of the plant groups that persistently are present throughout the Molteno Biome, whose stems, foliage and cones were present in 77 of the 106 localities (73%) and occasionally occur in some localities as monodominant or nearly monodominant stands in a variety of habitats (Anderson and Anderson 2017). Molteno horsetails consist of two orders, three families, 13 genera and 37 species representing fertile and sterile taxa. These taxa were present predominantly in the three habitat types of Horsetail Marsh, Heidiphyllum Thicket and Dicroidium Open Woodland. In addition, horsetails form a significant floral component in Fern-Kannaskoppia Meadow, present in all three localities of this distinctive community type, and also are documented in all 11 localities of the immature and mature phases of Dicroidium Riparian Forest. Horsetails are considerably less abundant in the six localities of Sphenobaiera Closed Woodland but are present in all three localities of indeterminate habitat type. Within the mostly wetlands-inhabiting horsetails, there was a considerable diversity of stem architecture, foliage types, reproductive structures and apparently a division between smaller, shorter statured herbaceous forms versus considerably taller, reed-like to arborescent forms.

Horsetails consist of two ordinal-level ranks, Echinostachyales, represented by fertile and sterile material, and Equisetales, affiliated with vegetative material. The Echinostachyales is comprised of the Echinostachyaceae and a second family of uncertain taxonomic status. The Echinostachyaceae consists of the cone genus of *Echinostachys*, represented by one species, and the foliage genera of *Schizoneura* (two species) and *Paraschizoneura* (four species), all of which occur in seven localities. The second family, an extinct, family-level lineage of uncertain position, consists of *Cetistachys*, *Moltenomites* and *Balenosetum*, that uniquely is present only at the Umk111 site. The Equisetales are represented by vegetative and sterile material and consist of the single extant family, Equisetaceae, but represent extinct taxa housing the six genera of *Kraaiostachys* with one species, *Anisetum* (one species), *Viridistachys* (two species), *Zonulamites* (four species), *Townroviamites* (three species), *Equisetostachys* (nine species), and *Equisetites* (six species), collectively present in 12 localities that include all seven localities containing members of the Echinostachyaceae. For the horsetails of the Molteno Biome, the most speciose horsetail taxa are the vegetative organs of *Zonulamites* and *Equisetostachys* (Anderson and Anderson 2017).

14.5.5 Ferns

The moderately diverse ferns are represented in 50 of the 106 localities (47%) and are the third most abundant vascular plant group, after horsetails and seed plants. Molteno ferns are divided into four major lineages (Anderson and Anderson 2008), the first three of which are extant, although the evolutionary relationship of the fourth, unaffiliated group remains unknown. The first group consists of the eusporangiate Marattiaceae, represented by two species of *Drepanozamites*, and Asterothecaceae consisting of three species of *Asterotheca*. These eusporangiate ferns collectively inhabit six localities, and occur predominantly amid the arborescent vegetation of Dicroidium Riparian Forest and to a lesser extent in Sphenobaiera Closed Forest and Dicroidium Open Woodland. The second major group is affiliated with leptosporangiate Osmundaceae, also representing fertile material, and consists of 12 species of *Osmundopsis*, *Rooitodites*, *Birtodites* and *Elantodites*. The osmundaceous taxa are found in 22 localities, predominantly in Heidiphyllum Thicket and Dicroidium Open Woodland, and subordinately in the remaining five habitats.

A third group of ferns is assigned to the Dipteridaceae and an unaffiliated family. The Dipteridaceae is represented by the three species of *Dictyophyllum* that occur in eight localities, preferring Heidiphyllum Thicket and subordinately the immature and mature phases of Dicroidium Riparian Forest, Sphenobaiera Closed Woodland and Dicroidium Open Woodland. The unassigned family is represented by three species across a broad swath of localities and habitats. The fourth group consists of vegetative material of uncertain taxonomic position that lack spore or sporangial features that would provide an affiliation to a known lineage. The unaffiliated ferns of sterile foliage from the fourth group are *Cladophlebis*, *Sphenophyllum*, *Birmoltia*, *Nymbopteron*, *Parsorophyllum*, *Stormbergia*, *Nymboidiantum*, *Displinites* and *Molteniella* that occur in 47 localities. Habitats colonized by Dipteridaceae ferns are dominantly Dicroidium Open Woodland and Heidiphyllum Thicket, somewhat less so for Dicroidium Riparian Forest, and minor elements in the remaining habitats.

Molteno ferns constitute three or four families, 16 genera and 49 species, inclusive of fertile and vegetative taxa. This spectrum of fern lineages is the product of three ancient fern radiations, consisting of older, late Paleozoic eusporangiate lineages of the Marattiaceae and Asterothecaceae; the basal leptosporangiate lineages of the Osmundaceae originating during osmundalean radiation of the late Paleozoic to earliest Mesozoic; and an early lineage of the younger still Dipteridaceae that likely originated during the earliest Mesozoic polypodialean radiation (Anderson and Anderson 2008; also see Pryer et al. 2004). Ecologically, all fern groups were distributed in the seven habitats described for the Molteno (MacRae 1999), although they did not prefer overwhelmingly any particular habitat, except perhaps Heidiphyllum Thicket, which appears particularly well populated by fern taxa.

14.5.6 Cycads

Cycad foliage is well represented in the Molteno flora (Anderson and Anderson 1989), although the only known fructification, *Androstrobus*, is indeed rare and represented by two specimens that occur at the Kra311 (Kraai River 311) and Pen321 (Peninsula 321) localities (Anderson and Anderson 2003). Molteno cycad foliage is probably affiliated with Cycadaceae, an extant major lineage of cycads that are basal within the modern clade (Condamine et al. 2015), but extend to the early Mesozoic and possibly late Paleozoic (Anderson et al. 2007). The most diverse Molteno genus is *Pseudoctenis*, a pinnate frond of medium to large size represented by 10 species that occur in 23 of the 106 localities (22%). The habitats in which *Pseudoctenis* resided are Dicroidium Open Woodland and the immature and mature phases of Dicroidium Riparian Forest; although it also is found subordinately in Sphenobaiera Closed Woodland and Fern–Kannaskoppia Meadow. Three, other, less commonly occurring foliage genera are *Jeanjacquesia*, with four species inhabiting four localities; *Ctenis*, consisting of two species found in two localities; and *Moltenia* that consists of four species confined to five localities of Dicroidium Riparian Forest. Localities with the greatest number of cycad species are Hla212 (Hlatimbe 212), Kon211A + Kon221 (Konigs Kroon 211A and 221 combined), and Kon221 (Konigs Kroon 221). Molteno cycads were generally small and had a pachycaul plant form similar to modern cycads, and occurred in all habitats except Horsetail Marsh and Heidiphyllum Thicket.

14.5.7 Conifers

Conifers are richly represented in the Molteno flora and consist of three, perhaps four, family-level groupings (Anderson and Anderson 1989, 2003). Most commonly present is Voltziaceae, a lineage that consists of ubiquitous *Heidiphyllum elongatum* foliage, the affiliated ovulate organ *Telemachus*, and affiliated pollen organ *Odyssianthus*. Vegetative and reproductive material of Voltziaceae occur in 76 of the 106 floras (72%), attributable to the overwhelmingly dominance of *H. elongatum* and associated conspecific reproductive taxa. *Heidiphyllum elongatum* occurs in every Molteno habitat, but especially is prominent in Heidiphyllum Thicket and

Dicroidium Open Woodland; much less so in Sphenobaiera Closed Woodland, the immature and mature phases of *Dicroidium* Riparian Forest and Horsetail Marsh; and rarely in Fern–Kannaskoppifolia Meadow. *Telemachus* consists of ten distinctive species occurring in 28 localities and occurs in approximately in the same proportions and habitats as *H. elongatum*. By contrast, one specimen of *Odyssianthus* was found at Telemachus Spruit (Tel111), a site rich in associated *Telemachus* ovulate material and *H. elongatum* foliage. A probably related, unnamed ovulate fructification has been found only at the Aas411 site. The possibly related, monospecific foliage of *Clariphyllum clarifolium* was found at three localities of the immature and mature phases of Dicroidium Riparian Forest. *Heidiphyllum* and *Clariphyllum* are considered as woody, small to medium-size shrubs with a bamboo like habit (Anderson and Anderson 2003; Barboni and Dutra 2015).

A second group of vegetative and reproductive conifer material, tentatively assigned to Podocarpaceae, consists of the leaf genus *Rissikia*, with two species that occur in 25 localities. Associated with *Rissikia* is the ovulate cone, *Rissikistrobus*, comprised of four species occurring in eight localities, and the pollen cone, *Rissikianthus*, with four species that are found in five localities. The *Rissikia–Rissikistrobus–Rissikianthus* affiliation forms a whole-plant taxon that was a minor member at Aas411, and was present sporadically throughout the Molteno Biome, preferentially inhabiting Dicroidium Riparian Forest. A third conifer group, the Dordrechtitaceae, consists of the ovulate cone *Dordrechtites* with four species and the monospecific male cone *Gypsistrobus* that collectively occur in 28 localities—a lineage exhibiting a habitat preference for Heidiphyllum Ticket, Dicroidium Open Woodland and Dicroidium Riparian Forest, and to a lesser extent Sphenobaiera Closed Woodland, occurring rarely in other habitats. The last group, monospecific *Pagiophyllum*, is another conifer foliage genus also occurring at Aas411; however, this enigmatic taxon has an uncertain taxonomic position. The reconstruction of the *Rissikia–Rissikistrobus–Rissikianthus* source plant is that of a large tree that occurred in wetlands and riparian border habitats (Anderson and Anderson 2003). The parent plant of the Dordrechtitaceae remains unknown, whereas *Pagiophyllum* is reconstructed as a small tree.

14.5.8 Peltasperms

Peltasperms are a major seed-plant group of the Permian to mid Mesozoic whose Mesozoic representatives are characterized by *Lepidopteris* foliage and associated, distinctive *Peltaspermum* ovulate organs and *Antevsia* pollen organs (Anderson and Anderson 1989, 2003). Molteno peltasperms are typified by the common Gondwanan foliage genus *Lepidopteris*, consisting of two species, both of which occur at Aas411. The two species of *Lepidopteris* are found in 37 of the 106 Molteno localities (35%), and are dominant in Dicroidium Open Woodland, less so in the immature and mature phases of Dicroidium Riparian Forest and Sphenobaiera Closed Woodland, and becoming uncommon to insignificant in Heidiphyllum Thicket, Horsetail Marsh and Fern–Kannaskoppia Meadow. The affiliate ovulate organ, *Peltaspermum*, has been assigned to five species that occur in 30 localities, and is dominant in Dicroidium Open Woodland, less so in the immature and mature phases of Dicroidium Riparian Forest and Heidiphyllum Thicket, and is rare in the remaining localities. All but 8 of the 30 localities that have *Peltaspermum* fructifications also have *Lepidopteris* foliage, thereby indicating conspecificity in association (Anderson and Anderson 2003). The monospecific pollen organ, *Antevsia*, is represented in five localities that are dominated by the immature and mature phases of the Dicroidium Riparian Forest habitat, frequently in association with *Lepidopteris* and *Peltaspermum*. For the Molteno Biome, the *Lepidopteris–Peltaspermum–Antevsia* whole-plant taxon is reconstructed as a medium sized shrub occupying riverine forest (Retallack and Dilcher 1988; Anderson and Anderson 2003).

14.5.9 Corystosperms

Of any Late Triassic plant lineage, it is the Umkomasiales, commonly called corystosperms, which have been the most iconic representative of Late Triassic vegetation throughout Gondwana. The family Umkomasiaceae was the most ubiquitous plant group present in the Molteno Biome (Anderson and Anderson 1983), whose foliage of *Dicroidium* is conspicuously represented in 92 of the 106 localities (87%), the most for any Molteno plant group (Anderson and Anderson 2003). *Dicroidium* consists of species that occur mostly in Dicroidium Open Woodland habitat (36%), less so in Heidiphyllum Thicket, and subordinately in Sphenobaiera Closed Woodland, Horsetail Marsh and the immature and mature phases of Dicroidium Riparian Forest. *Dicroidium* also occurs in all three localities of Fern–Kannaskoppia Meadow. The rarity or absence of *Dicroidium* is most pronounced in Horsetail Marsh and Heidiphyllum Thicket habitats.

Of the nine species of *Dicroidium* foliage in the Molteno Biome, five occur at Aas411. The affiliations between species of *Dicroidium* foliage and seeds that are either dispersed or part of ovulate fructifications are complex, although certain species-level whole-plant taxa can be established in particular localities. Major corystosperm ovulate organs or seeds potentially affiliated with *Dicroidium* foliage are common. They are (i) *Umkomasia* seeds; (ii), the very common *Fanerotheca* (attached ovules)—*Feruglioa* (dispersed seed) complex; (iii), three species of a rare, undescribed seed genus; and (iv), a very rare, additional undescribed seed genus. These four, major seed morphologies probably are affiliated with particular species of *Dicroidium* and the pollen organ *Petruchus* in the same site, but species affiliations remain unknown. *Umkomasia* and *Fanerotheca–Feruglioa* seeds are represented in 53 and 58 of the Molteno localities, respectively, and preferentially occur in Dicroidium Open Woodland, subordinately in the immature and mature phases of Dicroidium Riparian Forest, Sphenobaiera Closed Woodland and Heidiphyllum Thicket; they are much less present in Fern–Kannaskoppia Meadow and Horsetail Marsh. The three species of the less common, undescribed seed is found at 12 localities, and preferentially occurs in both the immature and mature phases of Dicroidium Riparian Forest. Other corystosperm material consists of single site occurrences of foliage and seeds that remain undescribed. The pollen organ affiliated with *Dicroidium* foliage, *Petruchus*, consists of four species that occur in eight localities and preferentially is represented in Dicroidium Riparian Forest and Dicroidium Open Woodland habitats. The whole plant taxon with *Dicroidium* foliage generally is reconstructed as a shrub to large tree; depending on the species, that occupied forest to woodland landscapes (Retallack and Dilcher 1988; Anderson and Anderson 2003).

14.5.10 Ginkgophytes

Ginkgophytes were the most diverse group of plants in the Molteno Biome. The group consists of four or five major lineages or groupings of plants for which foliage and reproductive material are affiliated to various degrees (Anderson and Anderson 1989, 2003). In addition, there are certain genera that likely are ginkgophytes but remain unplaced within the broader ginkgophyte alliance.

The Hamshawviaceae consists of *Sphenobaiera* foliage, *Hamshawvia* ovulate fructifications and *Stachyopitys* pollen organs. *Sphenobaiera* is considered as one of the several most prominent foliage types throughout Gondwana in general and the Molteno Biome in particular, consisting of nine species, excluding short shoot and scale leaf morphotypes, and has been recorded in 56 of 106 localities (53%). This distinctive, mostly lobate leaf with deep incisions ecologically predominates in Dicroidium Open Woodland habitat, but occurs at lesser frequencies in other habitats with mostly woody plant taxa such as Sphenobaiera Closed Woodland, the immature and mature phases of Dicroidium Riparian Forest and in Heidiphyllum Thicket. It is represented sparingly in Horsetail Marsh and Fern–Kannaskoppia Meadow. The ovulate organ, *Hamshawvia*, is considerably rarer and consists of five species from six localities. *Stachyopitys*, the pollen organ, consists of six species occurring in eight localities that has a predilection for woodland and forested habitats. *Sphenobaiera* is reconstructed as a shrub or a tree of medium size that inhabited lake margins, as attested to its presence in Sphenobaiera Closed Woodland along the lakeshore plant communities of Aas411 and Bir111.

The second, major ginkgophyte group is Matatiellaceae, which consists of *Kurtziana* foliage and affiliated *Matatiella* ovulate fructifications. The pollen organ remains unknown. The uncommon to rare leaf genus *Kurtziana* consists of 14 undescribed species occurring in 17 of 106 Molteno localities (16%), and exhibits a preference for occupying the immature and mature phases of Dicroidium Riparian Forest and Heidiphyllum Thicket habitats. *Matatiella* which comprises seven species and is present in 10 localities, exhibits a similar broad range of habitat occupation as the foliage. The *Kurtziana* plant has been reconstructed as a small tree that occupied principally floodplain woodland (Anderson and Anderson 2003).

A third major ginkgophyte group, Avatiaceae, is represented by *Ginkgoites* foliage, *Avatia* ovulate fructifications and seeds, and *Eosteria* pollen organs (Anderson and Anderson 2003). *Ginkgoites* foliage consists of seven Molteno species present in 21 of the 106 localities (20%), and displays a habitat preference for the shrubby to arborescent habitats of Dicroidium Open Woodland, Sphenobaiera Closed Woodland and the immature and mature phases of Dicroidium Riparian Forest, but is rare to absent in other habitats. The affiliated and occasionally very common *Avatia* is monospecific, occurs in 20 localities, and has a preference for Heidiphyllum Thicket, with a much lesser presence in other habitats. The pollen organ, *Eosteria*, consists of two species that occupy only Sphenobaiera Closed Woodland and Heidiphyllum Thicket. The *Ginkgoites–Avatia–Eosteria* whole-plant taxon is reconstructed as a shrub to a tall tree inhabiting floodplain woodland habitats. The very rare foliage of *Paraginkgo*, a second related lineage, occurs only in the two localities of San111 (Sani Pass 111) and Lit111 of Dicroidium Riparian Forest. *Paraginkgo* lacks known, affiliated reproductive organs.

The fourth, major ginkgophyte group, Kannaskoppiaceae, combines *Kannaskoppifolia* foliage with *Kannaskoppia* ovulate fructifications and *Kannaskoppianthus*, pollen organs (Anderson and Anderson 2003). *Kannaskoppifolia* foliage consists of 12 undescribed species occupying 34 of the 106 Molteno localities (32%), and ecologically is best represented in Heidiphyllum Thicket, somewhat less so in Dicroidium Riparian Forest and Dicroidium Open Woodland, and is least present in other habitats. *Kannaskoppia* ovulate fructifications consist of three species occurring in six localities and inhabit a broad swath of habitat types. *Kannaskoppianthus* pollen organs are divided into four species, are present in eight localities, and occur in almost all habitats, but with a strong preference for Heidiphyllum Thicket. The growth form of the *Kannaskoppifolia–Kannaskoppia–Kannaskoppianthus* plant is said to be an herbaceous, ruderal pioneer in a variety of habitats (Anderson and Anderson 2003). An herbaceous habit is a very rare occurrence among gymnosperms.

Within ginkgophytes, the highly polymorphic foliage of *Dejerseya* remains taxonomically unplaced. *Dejerseya lunensis*, the only recognized Molteno species, bears polymorphic foliage that range from very long, linear leaves with entire margins to much shorter, lobate forms to deeply sinuate, lobed foliage. The female reproductive organ affiliated with *Dejerseya* is unclear, and could be a *Matatiella*-like structure or an extremely rare undescribed taxon, Seed sp. A, which occurs in at the Aas411 site. Such an attribution, however, is inconclusive. A more likely affiliation is a species of the rare pollen organ, *Switzianthus* that is found in four localities amid a variety of habitats. Considerably more abundant is monospecific *Dejerseya* foliage, which is found in ten localities and is best represented in habitats of Heidiphyllum Thicket and the immature and mature phases of Dicroidium Riparian Forest. The *Dejerseya* plant is considered a shrub to small tree occupying woodland to forest habitats (Anderson and Anderson 2003).

14.5.11 Bennettitopsids

Although bennettitopsids became one of the most prominent seed-plant groups during the Jurassic and Early Cretaceous, their earliest occurrences were during the Middle and Late Triassic (Pedersen et al. 1989; Anderson et al. 2007). By Late Triassic time, there are early lineages present in a several geographically disparate deposits. For the Molteno Biome, the elongate, entire-margined foliage genus *Taeniopteris*, assigned to the Lindthecaceae (Anderson and Anderson 1989, 2003), was present with nine species. *Taeniopteris* has been found in 45 of the 106 Molteno localities (42.5%), and ecologically was best represented in Dicroidium Open Woodland, much less so in Dicroidium Riparian Forest, Heidiphyllum Thicket and Sphenobaiera Closed Woodland, and is sparse in the remaining habitats. The affiliate ovulate organ of *Taeniopteris* foliage is the monospecific *Lindtheca*, found only at the Aas411 site in Sphenobaiera Closed Woodland. A second, undescribed, ovulate fructification was found only at the Kra111 (Kraai River 111) site, and perhaps is affiliated with *T. anavolans* at this site. The pollen organ affiliated with *Taeniopteris* is unknown. The *Taeniopteris–Lindtheca* plant is reconstructed as a shrub to small tree that commonly occurred in forested and woodland habitats (Anderson and Anderson 2003).

A second lineage of bennettitopsids, attributed to the Fredlindiaceae, is represented by *Halleyoctenis* foliage, affiliated with a *Fredlindia* ovulate fructification and a *Weltrichia* pollen organ, whose dispersed, deciduous, bracts are known separately as *Cycadolepis*. *Halleyoctenis*, a long pinnate frond with oppositely inserted pinnules, is represented by three species that occur in 11 of the 106 Molteno localities (10%) but preferentially are present in Dicroidium Open Woodland, and to a lesser extent in Sphenobaiera Closed Woodland. The affiliated female organ, monospecific *Fredlindia*, is a rather massive, strobilus-like structure that occurs at six localities, principally in Sphenobaiera Closed Woodland and Dicroidium Open Woodland. The male organ, *Weltrichia*, presumably associated with detached *Cycadolepis* bracts found at other localities, consists of two very rare species that occur individually only at the Kon222 (Konigs Kroon 222) and Lit111 localities. The *Cycadolepis*-like bract that bears a pollen sac, Seed sp. B, occurs at Aas411 and also may have originated from a *Weltrichia* pollen organ. Other probable bennettitalean affiliate pollen organs, Seed sp. E and Seed sp. F, also occur at the Aas411 site. The *Halleyoctenis–Fredlindia–Weltrichia* plant is considered a cycad-like, pachycaulous shrub to small tree occupying forest and woodland habitats (Anderson and Anderson 2003).

14.5.12 Gnetophytes

There are three major lineages of the Molteno Biome that are assigned to gnetophytes. These gnetophyte taxa are sparse to very rare and are among the earliest occurrences of this major lineage in the fossil record (Cornet 1996; Anderson et al. 2007). Gnetophytes became prominent during the Late Jurassic to Early Cretaceous, but subsequently declined to their current relictual status. Molteno gnetophyte lineages consist of five foliage genera, two of which have affiliated ovulate fructifications, although pollen organs have not been identified that are attributable to this group.

The Fraxinopsiaceae is the most prominent of the Molteno gnetophyte lineages, and is comprised of two foliage genera. The foliage is comprised of *Taeniopteris*, resembling *Yabeiella* but bearing the affiliated seed *Fraxinopsis*; and the cycad-like *Jungites*, which lacks affiliated reproductive material. *Yabeiella* is the most prominent gnetophyte foliage in the Molteno Biome, occurring in 35 of the106 localities (33%), and has an ecological preference for Dicroidium Open Woodland. *Yabeiella* also occurs in significant numbers in Dicroidium Riparian Forest, Heidiphyllum Thicket and Sphenobaiera Closed Woodland, and is present, albeit rarely, in Horsetail Marsh and Fern–Kannaskoppia Meadow. *Fraxinopsis* consists of three species occurring in 20 localities, three-fourths of which also are *Yabeiella* containing localities. The ecological distribution of this *Fraxinopsis* favored Sphenobaiera Closed Woodland and Dicroidium Riparian Forest habitats. The *Yabeiella–Fraxinopsis* whole-plant reconstruction is a large tree that occurs sparsely in riverine forest (Anderson and Anderson 2003). By contrast, the very rare *Jungites* is an obscure foliage type consisting of one species occurring only at the Umk111 site within mature Dicroidium Riparian Forest.

The Nataligmaceae consists of *Gontriglossa* foliage and *Nataligma* ovulate organs. *Gontriglossa* is a medium-size, *Glossopteris*-resembling leaf consisting of a single species, occurring in eight localities, and displaying an ecological preference for the immature and mature phases of Dicroidium Riparian Forest. The affiliated ovulate fructification, the monospecific *Nataligma*, is found only at the Umk111 site. The *Gontriglossa–Nataligma* whole-plant reconstruction is a sparsely occurring, ruderal plant, presumably herbaceous in growth form, and inhabiting water-margin habitats.

A third gnetophyte lineage, of indeterminate familial affiliation, consists of the foliage genera *Cetiglossa* and *Graciliglossa*, both of which lack affiliated reproductive organs. *Cetiglossa* and *Graciliglossa* each consist of one species that have been found only in the Umk111 site, where they inhabited mature Dicroidium Riparian Forest. The extremely rare *Cetiglossa* is inferred to have been herbaceous undergrowth in riverine forest, whereas the very rare *Graciliglossa* presumably was a slender liana and also was established in riverine forest (Anderson and Anderson 2003).

14.5.13 Taxa of Uncertain Relationships

The Molteno Biome houses numerous taxa of uncertain relationships, principally seed- taxa, but also several other foliage types. The approximately 38 genera of known unaffiliated seeds likely is an under-representation of the true seed diversity, and these will be described and discussed in a subsequent contribution. Other, mostly foliage-based taxa of uncertain relationships, are the possible ginkgophyte *Dejeryseya*–Seed sp. A and *Cetifructus*–Seed sp. H whole-plant taxa; seed taxa belonging to a third, undescribed, possible bennettitalean lineage; and families of uncertain class affiliation: Hlatimbiaceae, Alexaceae and a third, undescribed family. These taxa, representing foliage and female and male reproductive material that currently are difficult to place taxonomically, await additional collected specimens before progress can be made on their taxonomic placement.

14.5.14 General Patterns

Although there are many ways of evaluating the prominence of Molteno plants (Anderson and Anderson 2003), there are three approaches employed below for assessing the omnipresence of Molteno plant taxa at the genus level. The first method simply provides a measure of abundance. In the first method, the abundance of the most commonly occurring genera at the 106 localities is a most commonly used metric. A second method is an overall assessment of success, as used by the FUDAL rating system, as outlined by Anderson and Anderson (2003). A third method is to provide a sense of habitat dominance. For the Molteno flora, the five most abundant taxa, followed by their percentage representation in the 106 floras, are: (i), the most abundant is the voltzialean conifer *Heidiphyllum* (95%); then (ii), the umkomasialean corystosperm *Dicroidium* (90%); (iii), the hamshawvialean ginkgophyte *Sphenobaiera* (30%); (v), the matatiellalean ginkgophyte *Dejerseya* (11%); and (vi) the cycad of indeterminate affinities *Pseudoctenis* (3%). All other Molteno taxa are at abundance levels of 2% or less.

The second mode of evaluation is the FUDAL system was established by Anderson and Anderson in 1989 to provide a measure of success for specified Molteno plant genera. The FUDAL concept was revised by Anderson and Anderson (2003) to provide a more accurate rating system for the prominence of Molteno plant genera. The acronym is an abbreviation for the first letters of frequency, ubiquity, diversity, abundance and longevity for Molteno plant genera. Frequency is the repetitiveness of occurrences of a Molteno genus, as measured directly from the specific distribution of a particular genus in the 85 localities across five Gondwanan continents. Ubiquity is a measure of the general range of specimen occurrence, expressed as the number of the five continental regions across Gondwana in which the genus in question has been recorded. Diversity is a measure of speciation, radiation and variability, as expressed by the number of species of the genus established for the Gondwanan Triassic. Abundance is a measure of quantity, as determined by the abundance of a particular plant genus in Molteno floras. Longevity is a measure of the duration of the lineage in the 35 internationally recognized biozones in which the genus occurs. Based on these FUDAL criteria, the scores and ranks of the five most prominent Molteno genera are: the corystosperm *Dicroidium* (score of 188, rank of 5), the conifer *Heidiphyllum* (147, 4), the ginkgophyte *Sphenobaiera* (99, 4), the bennettitalean *Taeniopteris* (69, 3), and the ginkgophyte *Kannaskoppia* (62, 3). The first five plant genera in the Molteno ranking approximately parallel the ranking of major plant genera in floras across the Gondwanan Triassic (Anderson and Anderson 2003). This suggests there are supercontinent-wide floristic similarities in the dominance of the same genera.

A habitat-based measure of importance expresses the rank order of the three most abundant Molteno genera in each of the seven habitats (Anderson and Anderson 2003). For the (i), mature phase of Dicroidium Riparian Forest the dominant genera are, in decreasing order of abundance, *Dicroidium*, *Heidiphyllum* and *Sphenobaiera*. For the (ii), immature, or pre-climax, phase of Dicroidium Riparian Forest the analogous ranked taxa are *Dicroidium*, *Heidiphyllum* and horsetails. For (iii), Dicroidium Open Woodland, the respectively ranked taxa are *Dicroidium*, *Heidiphyllum* and *Sphenobaiera*, although the species of *Dicroidium* and *Sphenobaiera* are different than those of the mature phase of Dicroidium Riparian Forest. For (iv), Sphenobaiera Closed Woodland the respective ranked taxa are *Sphenobaiera*, *Dicroidium* and *Heidiphyllum*. For (v), Heidiphyllum Thicket the respective ranked taxa are *Heidiphyllum*, *Dicroidium* and horsetails. For (vi), Fern–Kannaskoppia Meadow the respective ranked taxa are ferns, *Sphenobaiera* and *Dicroidium*. And last, for (vii), Horsetail Marsh the respective ranked taxa are horsetails, *Dicroidium* and ferns. All three evaluative methods indicate that it is the same limited number of plant groups that exhibit prominence in the Molteno Biome, albeit under various combinations and based on different methods of measurement.

14.6 Molteno and Gondwanan Late Triassic Insect Herbivores

14.6.1 Overview

In this section an overview is provided for the major herbivorous mite and insect groups that had interactions with plants or are inferred to have been present during the Carnian Stage in the Karoo Region of South Africa. Because of the regional uniqueness of the Gondwanan biota, the body-fossil record of insects are reviewed for the Karoo Basin of South Africa in particular as well as penecontemporaneous insect faunas from other Gondwanan localities in general (Schlüter 1990; Anderson et al. 1998), principally those of Australia and South America. While the discussion below is not exhaustive, the known, major suspected herbivore mite and insect groups are covered, many of which had major lineages that experienced ancient evolutionary radiations (Krantz and Lindquist 1979; Whitfield and Kjer 2008). Simultaneously, these taxa provide inferences regarding the ecological structure to Late Triassic plant–insect interactions that now are documented in the Molteno Biota (Scott et al. 2004; Labandeira 2006a). Approximately 3000 insect specimens are known from 43 localities of the Molteno Formation (Schlüter 2003). This material currently is being examined and documented by Torsten Wappler of the Senckenberg Institute in Frankfurt, Germany, and by Olivier Béthoux of the National Museum of Natural History in Paris, France.

14.6.2 Mites

The broader group, Arachnida, to which plant-interacting mites are a member, is virtually absent in Gondwanan deposits. The only formally described occurrence is the predatory araneomorph spider *Triassaraneus andersonorum*, which was described from the Umk111 and Tel111 (Telemachus Spruit 111) localities of the Molteno Formation (Selden et al. 1999, 2009). *Triassaraneus* is a member of the Arachnopulmonata, but no members of another arachnid group, Acariformes, have been found at any Molteno site, an absence attributable to the diminutive size and inconspicuousness of mites, the overwhelmingly dominant phytophagous members of this group. However, oribatid mites are known from their distinctive wood borings, found in the Middle Triassic Fremouw Formation of the Palmer Peninsula of Antarctica (Kellogg and Taylor 2004). More exceptional is the presence of three distinctive genera of plant-feeding mites anatomically preserved in Triassic amber from the late Carnian Heiligkreuz Formation in the Dolomite Alps of northeastern Italy (Sidorchuk et al. 2015). These mites belong to a new superfamilial lineage, Triasacaroidea, associated with amber of the extinct conifer lineage, Cheirolepidiaceae (Sidorchuk et al. 2015). Their occurrence is consistent with earlier estimates of the Eriophyoidea appearing phylogenetically during the late Paleozoic (Krantz and Lindquist 1979).

14.6.3 Odonatopterans

Odonatopterans are dragonflies, damselflies and related archaic Paleozoic and early Mesozoic lineages that are obligately predatory in the adult and subadult stages. However, most odonatopteran females insert eggs by a piercing structure, the ovipositor, which is used to slice into stems and other plant tissues of live vascular plants that typically occur as emergent or slightly submergent positions along bodies of water in terrestrial environments (Wesenberg-Lund 1913; Moisan et al. 2012). The resulting lenticular to ellipsoidal lesions were likely produced by a variety of Molteno odonatopterans, including *Triassoneura andersoni* and two other congeneric species, of uncertain family assignment (Riek 1976a; Labandeira 2005), as well as the meganisopterid *Triassologus biseriatus* (Riek 1976a), representing a Paleozoic lineage that survived the P-Tr ecological crisis.

Triassic Odonatoptera occur in other Gondwanan continents. A damselfly nymph of Zygoptera, attributable to the form genus, *Samarura*, was recovered from the Late Triassic Aberdare Conglomerate of Queensland, Australia (Rozefelds 1985). From the Late Triassic Ipswich beds, of similar age, the taxon *Triassolestes epiophlebioides* was described by Tillyard and Dunstan (1916); additional conspecific material was illustrated by Rozefelds (1985). Later, Tillyard (1918a, b, 1922, 1923) described three additional genera of Odonatoptera from The Ipswich Beds in Queensland. From South America, Carpenter (1960) erected *Triassothemis mendozensis*, a taxonomically unaffiliated wing, from Cerro Cachueta of Mendoza, Argentina, of Late Triassic age (Gallego and Martins-Neto 1999).

14.6.4 Cockroaches

The presence of various cockroach specimens have been mentioned in several Late Triassic deposits. Besides the Molteno Formation (Riek 1974, 1976a), Late Triassic deposits that bore cockroaches include Australia (Tillyard 1919b, 1937) and South America (Pinto and de Ornellas 1974; Gallego 1997; Gallego and Martins-Neto 1999). Several early to mid-Mesozoic cockroach lineages that possessed long external ovipositors, such as the Mesoblattinidae (Vishniakova 1968; Grimaldi and Engel 2005), likely were responsible for some of the ovipositional damage in Late Triassic plants, particularly those with smaller, circular cross-sectional areas (Meng et al. 2017). These cockroaches were replaced by oothecate forms originating during the Late Jurassic to Early Cretaceous from very modified and reduced ovipositor morphologies (Gao et al. 2017).

14.6.5 Orthopteroids

The most speciose, documented group of herbivorous insects in Late Triassic Gondwana probably were Orthopteroidea (Zherikhin 2002). For the Molteno Formation, approximately 23 species of Orthoptera have been described by Riek (1974, 1976a) and Wappler (1999, 2000a, b). Six species of Haglidae, the relict hump-winged crickets, are known, including: *Hagla contorta*, two undescribed species of *Hagla*, *Zeunerophlebia margueritae*, and two undescribed species of another genus of Haglidae (Wappler 2001). Eight species of the second family of Orthoptera, the extinct Proparagryllacrididae described by Riek (1976a) and Wappler (1999), likely were herbivorous as were *Dordrechtia robusta*, *D. aasvoelbergensis*, *Dordrechtia* sp., *Gryllacrimima johnski*, *Gryllacrimima* sp., and Proparagryllacrididae gen. et sp. indet 1, gen. et sp. indet 2 and gen et sp. 3 (Wappler 1999). The extinct

Xenopteridae is a third family of probable herbivorous Orthoptera that included only *Lutheria dewetii* (Wappler 1999).

The Grylloblattida were another group of orthopteroids that encompassed the extant, relict ice crawlers, that presently have detritivorous feeding habits in cool, north temperate habitats, but during the earlier Mesozoic, this group was considerably more diverse and possibly included herbivorous forms. Molteno Grylloblattida consisted of seven or eight species that were represented primarily by Geinitziidae, consisting of four species of *Fletchitzia*, two undescribed species an undescribed genus of Geinitziidae, and two undescribed species from an indeterminate family of Grylloblattida (Riek 1976a; Wappler 1999). Haughton (1924) earlier described *Protogryllus stormbergensis* as a member of the Gryllidae, which most likely was detritivorous in habits. All Molteno orthopteroid taxa that are suspected herbivores currently are either extinct or relict, and likely were replaced later in the Mesozoic by herbivorous forms that persist to the present day or are ancestors of currently relict lineages.

In other parts of Gondwana, such as Australia and South America, the documented diversity of orthopteroids was considerably less than that of the Karoo Basin. The Late Triassic Blackstone Formation of the Ipswich Basin in southeastern Queensland contains the grasshopper-like Locustopseidae indicated by *Triassolocusta leptoptera* (Tillyard 1922, 1923). The spectacularly large *Mesotitan scullyi*, a member of the Mesotitanidae and assigned to the orthopteroid order Titanoptera occurs in earlier, Middle Triassic deposits at Deewhy in New South Wales, Australia (Tillyard 1925). Recent interpretation of this distinctive group of huge, geochronologically short-lived insects, however, indicate that they likely were insectivorous rather than herbivorous (Zherikhin 2002). In South America, two deposits of late Middle Triassic to Late Triassic age, the Potrellos Formation of Mendoza Province and the Los Rastros Formation of La Rioja Province, preserves several taxa of Orthoptera, including *Hagla* sp. (Haglidae), *Elcana* sp. (Elcanidae), *Nothopamphagopsis* (no family affiliation), and perhaps *Eolocustopsis* sp. (Locustopseidae) (Gallego 1997; Gallego and Martins-Neto 1999). Assuming that the herbivore assignments of these taxa are correct, the varied geographic distribution of orthopteroid taxa across Gondwana, such as those from the Santa Juana Formation in Chile (Gallego et al. 2005), indicates a well-established orthopteroid herbivore insect fauna by Late Triassic times.

14.6.6 Hemipteroids

Piercing-and-sucking hemipteroids currently are a major group of insect herbivores on plants (Pollard 1973). Given their elevated diversity relative to other Late Triassic herbivores, such as mandibulate feeding orthopteroids, hemipteroids likely were a major force in Molteno herbivory. Late Triassic hemipteroids consisted of two major groups: Thysanoptera (thrips) (Childers 1997; Retana-Salazar and Nishida 2007), for which Molteno fossils are lacking, and Hemiptera (other piercing-and-sucking groups) (Weber 1930; Cobben 1978), which have been rather abundant from the Permian to the present day (Zherikhin 2002). Hemiptera principally consists of six major lineages. They are: (i) Psylloidea, or plant lice; (ii) Aleyrodoidea, or white flies; (iii) Aphidoidea, or aphids; and (iv) Coccoidea, or scale insects and mealy bugs, these four of which collectively constitute the Sternorrhyncha; (v) Auchenorrhyncha, comprising cicadas, plant hoppers and tree hoppers; and (vi) Heteroptera, or true bugs. The Molteno Biome hosted some of these groups, including the sternorrhynchan lineage Protopsyllidiidae, known from a protopsyllidid nymph (Riek 1974, 1976a). The most abundant group within the Molteno Biome were Auchenorrhyncha, represented by Cicadoprosbolidae, consisting of *Prosobolomorpha clara* and *Leptoprosbole lepida*; Scytinopteridae, represented by *Scytinoptera distorta*; Mesogereonidae, with *Triassogereon distinctum*; Dysmorphoptilidae, exemplified by the cicada-like *Tennentsia protuberans*; and Dunstaniidae, an early group of large, hirsute, cicada-like forms exemplified by *Dunstania petrophila* and *Fletcheriana magna* (Riek 1974, 1976a; Labandeira 2005). To date, no Heteroptera have been described from the Molteno Biome. Nevertheless, these eight species of Hemiptera define a broad variety of sizes, shapes, body plans and mouthpart stylet and ovipositor types that likely resulted in partitioning host-plant tissues in intricate ways and employing the same ways as modern hemipterans (Funkhouser 1917; Hori 1971).

For Gondwanan Late Triassic herbivores, the Hemiptera of Australia exhibits the greatest known diversity of any Late Triassic herbivore group, consisting minimally of 33 species that are recorded principally from the Ipswich Basin of southwestern Queensland. The suborder Auchenorrhyncha consisted of the five families of Mesogereonidae that was comprised of five species of *Mesogereon*; the leafhopper-like Cicadellidae with *Mesojassus ipsviciensis*, *Eurymelidium australe* and *Triassojassus proavitus*; Scytinopteridae, occurring as two species of *Mesoscytina*, *Triassoscarta subcostalis*, *Apheloscyta mesocampta*, *Chiliocycla scolopoides*, *Polycytella triassica* and three species of *Mesodiphthera*; the distinctive, fulgoromorph Cixiidae, exemplified by *Mesocixius triassicus*, *Triassocixius australicus* and three species of *Mesocixiodes*; Dunstaniidae, represented by *Dunstania pulcra*, *Dunstaniopsis triassica* and *Paradunstania affinis*; and Ipsviciidae, with *Ipsvicia jonesi*, *I. maculata* and *I. acutipennis* (Tillyard 1918c, 1920, 1921, 1922, 1923; Evans 1971). Late Triassic Auchenorrhyncha were a distinctive group perhaps related to modern Cercopidae, commonly known as froghoppers and spittlebugs. The Heteroptera, or true bugs, have been described as three or four species of *Triassocoris*, members of the Triassocoridae (Tillyard 1923). Collectively, this Australian, Late Triassic assemblage of Hemiptera included xylem, phloem and mesophyll feeders, and probably were engaged in the same or very similar type of feeding as their relatives do today (Hori 1971; Günthart and Günthart 1983; Golden et al. 2006).

There have been considerably fewer occurrences of Hemiptera from strata of similar age in South America. From the Santa Maria Formation at Passo das Tropas in Rio Grande do Sul, Brazil, a wing, *Sanctipaulus mendesi*, was assigned to the fulgoromorph Auchenorrhyncha, and affiliated with the Derbidae (Pinto 1956). In a somewhat older deposit of the Potreillos Formation of Mendoza Province in Argentina, Gallego (1997) assigned *Mesocixiella* sp. to the Cixiidae, representing another member of the Auchenorrhyncha. At the nearby site of Cerro Cachueta, of younger Triassic age, Tillyard (1926) described *Wielandia rhaetica* and assigned it to the Scytinopteridae. In a review of the Mesozoic insect fauna of Argentina, Gallego and Martins-Neto (1999) mentioned the auchenorrhynchans *Dysmorphoptiloides acostai* of the Dysmorphoptilidae, and *Argentinocicada magna*, *A. minima* and *Potrerillia nervosa* of the Scytinopteridae from Late Triassic sites of west-central Argentina. While these taxa are assigned to lineages that also are found in South Africa, Australia, and South America, they apparently also indicate regional taxonomic differentiation across Gondwana, at least for some insects at the genus level.

14.6.7 Beetles

Permian beetles have been described from the Karoo Basin (Geertsema and Van den Heever 1996; Geertsema et al. 2002), but their affinities lie either with a primitive, paraphyletic lineage to Coleoptera (McKenna et al. 2015), or alternatively as an archaic member of Archostemata, the most basal extant major lineage (Grimaldi and Engel 2005). However, virtually nothing can be said of the finer-grained taxonomic affinities of these or any other Permian beetle lineages, with one exception from north-central China occurring lodged in a complex gallery–tunnel network in a Lopingian conifer host (Feng et al. 2017). Similarly, Early and Middle Triassic beetles, with few exceptions (Grimaldi and Engel 2005; Ponomarenko 2016), also are taxonomically enigmatic, although there are exceptions (Fraser et al. 1996). These Late Triassic exceptions include several identifiable lineages of beetles that are known with some confidence, including Cupedidae (reticulated beetles) of the suborder Archostemata, extinct Trachypachidae of the suborder Adephaga, and Hydrophilidae (water scavenger beetles), Staphylinidae (rove beetles), Artematopodidae (soft-bodied plant beetles), Scirtidae (marsh beetles) and Elateridae (click beetles) of the suborder Polyphaga. Polyphaga are the most diverse, extant major clade, currently representing 85% of all beetle species, and likely were the beetles contributing at least some of the co-associations and herbivory found in the Molteno Biome (Anderson et al. 1999). Independent evidence from plant–insect interaction data suggest, from a process of elimination of potential culprit taxa, that some Late Triassic beetle lineages contributed to a variety of plant damage, including leaf mining (Rozefelds and Sobbe 1987; Labandeira 2006a), wood boring (Walker 1938; Linck 1949; Tapanila and Roberts 2012), and possibly margin and surface feeding (Ponomarenko 2016). Phylogenetic evidence indicates, curiously, that many of the beetle lineages, which would have been responsible for Late Triassic endophytic damage such as leaf mining and wood boring, had not evolved (McKenna et al. 2015). By contrast, several basal polyphagan lineages already were present, such as the Artematopodidae and Scirtidae that are good herbivore candidates for a variety of external foliage feeding.

For the Late Triassic Molteno Biome, nine beetle taxa have been described, some of which are based on anatomy other than elytra. Molteno beetles include three species of *Ademosyne* in the Permosynidae; *Moltenocupes townrowi* in the Cupedidae; undetermined Ommatinae of the Ommatidae; *Umkomaasia depressa*, possible Carabidae; two species of *Pseudosilphites* that are possible Silphidae (carrion beetles); and an undetermined family (Zeuner 1961; Riek 1974, 1976a; Anderson et al. 1998). Considerably more beetle taxa, approximately 62 species, have been described from the Late Triassic of Australia (Tillyard 1918b, 1923; Tillyard and Dunstan 1923), although these taxonomic assignments remain uncertain and need to be confirmed. From the Middle Triassic Los Rastros Formation of La Rioja Province in Argentina, several taxa have been established, including *Argentinocupes* sp. in Permocupedidae; two species of *Ademosyne* in Ademosynidae; *Tillyardiopsis* sp., possible Curculionidae (weevils); and *Mesostigmodera frenguelli*, possible Buprestidae (metallic wood-boring beetles) from the Middle Triassic Los Rastros Formation of La Rioja Province (Gallego 1997; Gallego and Martins-Neto 1999). As with the Australian beetle material, the South American occurrences need confirmation.

14.6.8 Sawflies

The fossil record of the Symphyta, a group of approximately 14, overwhelmingly plant-associated, basalmost lineages within Hymenoptera are characterized by a diverse repertoire of exophytic and endophytic herbivory, including xylophagy. (The most derived lineage, the parasitoid Orussidae, is the sole nonherbivorous group.) This group collectively is termed sawflies, and their consumption of live plant tissues takes a variety of forms that notably includes external foliage feeding, leaf mining, galling, pith tunneling, seed predation, pollen feeding and wood boring (Blank et al. 2006). The adults are adept in ovipositing eggs in plant tissues and some are implicated in pollination (Burdick 1961). Almost all of the earliest known fossils of Symphyta originate from the Middle Triassic of Central Asia (Rasnitsyn 1969), although two taxa of wings are known from the Late Triassic of Gondwana: one from the Mt. Crosby Formation of southern Queensland, in Australia (Riek 1955), and the other from the Molteno Formation in South Africa (Schlüter 2000). The Molteno specimen is *Moltenia rieki*, found at the Bir111 site, and is identified as a probable member of the Xyelidae (Schlüter 2000). The larval stages provide the overwhelming bulk of plant consumption in sawflies, and their diet probably has the broadest range of functional feeding groups of any larval clade.

14.6.9 Scorpionflies

One of the most taxonomically enigmatic insects of the fossil record is *Mesoses optata*, a broad, incomplete forewing from the Molteno Formation (Riek 1976a). It once was assigned to the "Paratrichoptera" (Shields 1988), a polyphyletic assemblage of antliophoran and amphiesmenopteran stem-group lineages that recently have been reassigned to other insect orders (Schlüter 1997), including Mecoptera (scorpionflies), Diptera (flies), Trichoptera (caddisflies) and Lepidoptera (moths and butterflies). *Mesoses* now is considered an early member of Mesopsychidae, a basal lineage of the Mecoptera that is confined to the early Mesozoic. Notably, *Mesoses* precedes evolutionarily the origin of the long-proboscid condition in successor mesopsychid taxa, such as *Mesopsyche*, *Lichnomesopsyche* and *Vitimopsyche* from the Eurasian Middle Jurassic to Early Cretaceous (Lin et al. 2016). Given the relationship between these long-proboscid scorpionfly taxa and deep-throated gymnosperm fructifications such as the bennettitalean *Weltrichia*, it is highly likely that *Mesoses*, though lacking a long proboscis, was a pollinator feeding on the pollination drops of contemporaneous Molteno fructifications (Anderson and Anderson 1993; Labandeira 2010).

14.6.10 General Patterns

In this survey of described arthropod fossils from the Molteno Biome, eight major mite and insect groups of herbivores have been identified. These herbivore groups were available potentially to produce the 10 major types of arthropod damage on Molteno plants of margin feeding, hole feeding, skeletonization and surface feeding, collectively known as external foliage feeding, as well as internal feeding damage resulting from piercing and sucking, oviposition, mining, galling, seed predation and wood boring. Based on the diversity of body-fossil taxa in each group discussed above, three general patterns emerge. First, the most diverse group, beetles, have an uncertain role in Molteno herbivory due to poor taxonomic assignments and the absence of any dietary and feeding data to make reasoned inferences about what subgroups inflicted particular types of damage. Second, the next, two, equally represented groups, orthopteroids and hemipteroids, would have produced the known damage spectra of external foliage feeding and piercing and sucking, respectively. Third, the remaining groups are either very nondiverse, consisting of very few known taxa, particularly odonatopterans, sawflies, and scorpionflies, or there is the absence of relevant taxa in the Molteno Biome, such as mites, to indicate a reliance of relevant fossils elsewhere in Triassic Gondwanan that would be responsible for a particular type of Molteno herbivory. Certain Late Triassic taxa such as mayflies (Riek 1976b) and lacewings and relatives (Tillyard 1917, 1919a, b) likely lacked interactions with plants. Nevertheless, for the eight plant-interacting groups, such as hemipteroids, there is considerable more diversity of documented insect body-fossil taxa elsewhere in Gondwana, particularly Australia, than there is in the Karoo Basin. This imbalance suggests the absence of adequate preservation, under-collection of fossils, or more likely a delays in the formal descriptions of fossils in South Africa.

14.7 Plant–Insect Interactions of the Molteno Biota

14.7.1 Overview

Examination of the plant–insect interactions of the 106 localities from the Molteno Biota is part of a broader assessment of the effects of the P-Tr ecological crisis on plants and their insect herbivores. The results of the current study of herbivory at the Aas411 site is part of an ongoing, more detailed, quantitative analyses of existing data which will ferret out generalized and specialized patterns of plant–insect interactions based on host plants, functional feeding groups, damage types, habitats, regional geography, stratigraphic position and other environmental and biotal features of all relevant localities. The broader analysis of the Molteno Biota will be integrated along a 35 million-year-long interval that includes additional earlier Triassic and later Permian deposits. The current, detailed analysis of the most plant-specimen-rich site, the Aas411 site, focuses principally on patterns of host use, host specialization, component community formation, the role of habitat on associational richness, and in particular the biology of gall DT70. Detailed study on the development and other aspects of the biology of gall DT70 will be followed in other contributions from examinations of prominent interactions throughout the Molteno Formation and other Karoo Basin deposits from the Permian to Triassic studied interval.

14.7.2 Molteno Plant–Insect Interactions

The total Molteno data set of 106 stratigraphically ordinated localities that consists of 383 total plant form-species (Table 14.1). Of the total species in the Molteno flora there are 27 bryophytes, 17 lycophytes, 37 sphenophytes, 37 ferns, 22 cycads, 10 peltasperms, 35 corystosperms, 69 ginkgoopsids, 20 bennettitaleans, 13 gnetophytes, 33 coniferophytes and 63 plants of uncertain position that includes foliage and mostly seeds based on published sources (Anderson and Anderson, 1983, 1989, 2003, 2008, 2017) and unpublished updates (J.M. Anderson, H.M. Anderson and C.C. Labandeira, pers. observ.). For all major plant groups except bryophytes, affiliated form-taxa occurring in the same site were associated with 52 separate, whole plant species for the Molteno Biome. These whole-plant taxa consist of multiple, affiliated plant parts such as foliage, female and male reproductive material, and other plant parts, and were evaluated using a confidence scale of 1–5, with 5 being a direct association such as an attachment or the housing of a seed in an encompassing female fructification. For example, whole-plant taxon suite 13, the *Sphenobaiera schenckii* whole plant taxon, consisted of the *S. schenckii* leaf, *Sphenobaiera* sp. scale leaf, *Sphenobaiera* sp. short shoot, *Hamshawvia longipedunculata* ovulate organ and *Stachyopitys* sp. pollinate organ with a confidence value of 4.5 (Anderson and Anderson 2003; also see Barboni and Dutra 2015). The *Sphenobaiera schenckii* whole-plant taxon occurs at the Kan111 (Kannaskop 111), Nuw111B (Nuwejaarspruit 111B), Gol111 (Golden Gate 111) and Aas411 localities. These unaffiliated plant taxa occur in various and distinct proportions among the seven habitats within the Molteno Biome. The most well represented habitat is Dicroidium Open Woodland, consisting of 33 localities; by contrast, Heidiphyllum Thicket has 23 localities; Horsetail Marsh consists of 18 localities, Sphenobaiera Closed Woodland includes 15 localities, Immature Dicroidium Riparian Forest is attributed to nine localities, Fern-Kannaskoppia Meadow has three localities, Mature Dicroidium Riparian Forest, only has two localities. Three localities that could not be assigned to a particular habitat.

The Molteno database consists 177,297 examined specimens that contain 10,165 separate DT occurrences of herbivory. This ratio corresponds to 5.73% of the specimens that have one or more DTs, a significant level of plant–insect interaction diversity for the early Mesozoic (Labandeira 2006b, 2013b, 2016). Molteno plant–insect interactions consist of two basic groups of FFGs. Some are exophytic in nature, typified by external feeding or consumption from without, represented by hole feeding (13 DTs), margin feeding (6 DTs), skeletonization (2 DTs) and surface feeding (9 DTs). The other major assemblage of functional feeding groups are endophytic in nature, and are characterized by internal feeding or consumption from within, consisting of piercing and sucking (8 DTs), oviposition (10 DTs), mining (7 DTs), galling (15 DTs), seed predation (4 DTs) and borings (2 DTs). Generalized fungal damage was scored as DT58, but was not subdivided into more discrete DTs. This spectrum of 10 functional feeding groups that encompass 76 DTs, of which external feeding is represented by 30 DTs and internal feeding is represented by 46 DTs, is the single highest number of DTs detected in any pre-angiosperm fossil biome examined to date. One site, Aasvoëlberg 311 (Aas311), is the only early Mesozoic site of a possible insect outbreak, specifically insect leaf mining (DT71) on the broadleaved conifer host *Heidiphyllum elongatum* (Labandeira 2012). A comprehensive analysis is being prepared that will assess the effects of the P-Tr ecological crisis on insect herbivory from late Guadalupian and Lopingian floras of, respectively the Middleton Formation and Balfour Formation, to the post-event Anisian Burgersdorp Formation and Carnian Molteno Formation.

A preliminary survey of the plant–insect interactions of the Molteno Biome (Table 14.1) provides basic data regarding the basic ecological context relevant for the plant–insect interactions at each site. Table 14.1 provides a record of site stratigraphic position; habitat; number of whole-plant taxa, if any; dominant functional feeding group; and other data involving the types of and numbers of plant morphotypes/species, DTs and the interaction index. The interaction index is the total number of DT occurrences divided by the number of plant specimens for each examined site, and serves as a comparative measure of herbivory intensity across all Molteno localities. For these five latter types of data, the localities display a wide range of values that can approach or exceed four orders of magnitude. This wide range of values are: total DT occurrences, ranging from 0 for several localities to 2501 for Bir111; total plant specimens, ranging from 5 for Kullfontein 111 (Kul111) to 20,358 for Aas411; interaction index, ranging from 0 for several localities to 0.2819 for Kappokraal 111(Kap111); total kinds of DTs, ranging from 0 for several localities to 44 for Aas411; and total number of plant species and morphotypes, with as few as 1 for Navar 111 (Nav111), Kraai River 222 (Kra222), Klein Hoek 111A (Kle111A), Vineyard 111 (Vin111) and Champagne Castle (Cha111) to 111 for Aas411. The interaction index is an important measure, and expresses, through the use of presence–absence data, the considerable difference in the incidence of attack on plant specimens from zero to the exceptionally high 28.19% in the case of Kap111. Most Molteno values were in the range of 2.0–6.0%, in accord with typical levels of herbivory in the fossil record of plant–insect interactions (Q. Xu, C. Labandeira and H. Jin, unpublished data).

14.8 Plant–Insect Interactions of the Molteno Aasvoëlberg 411 Site

14.8.1 Overview

The preserved biological diversity of the Molteno Biome has been statistically extrapolated from extant biodiversity from similar environments, indicating a significantly elevated level compared to other, equivalent, Triassic biotas (Anderson et al. 1996). Although not specifically addressed in the Anderson et al. study (1996), plant–insect interactions are an excellent indicator of ecological diversity in terrestrial habitats, and can serve as a measure of biodiversity when expressed as FFGs and DTs (Labandeira 2002b; Carvalho et al. 2014). Each FFG results from insects that bear distinctive mouthpart morphologies engaged in particular modes of feeding (Labandeira 1997). Exophytic interactions representing external feeding are defined by the consumption of plant tissues wherein the insect is positioned outside of the tissue being consumed. Such interactions are synonymous with external foliage feeding that is subdivided into hole feeding, margin feeding, skeletonization and surface feeding FFGs. The frequency distribution of these four external feeding FFGs and their 20 constituent DTs, including the presence of one specialized association, are given in Fig. 14.2 for the Aas411 site.

By contrast, endophytic interactions are defined by the consumption of internal tissues in which feeding occurs, with the entire body or at least the mouthparts embedded within the plant-host tissue. There are two categories of endophytic interactions. One category consists of those interactions in which the body of the consumer lies mostly outside of the tissue, on the plant surface, such as the piercing and sucking and oviposition FFGs. The second type of endophytic interaction is when the consumer is embedded with the plant tissue, which is comprised of the galling, leaf mining, seed predation and borer FFGs. Modern examples of these FFGs, discussed below, are taken from the plant–insect interactional literature, and emphasize vascular plant hosts other than angiosperms that are more anatomically and phylogenetically related to those present during the Carnian. Lastly, host specialized interactions are defined by the presence of a particular damage type that occurs on the same host-plant species or closely-related group of species throughout multiple habitats across the Molteno Biome. The frequency distribution of the five internal feeding FFGs and their 21 constituent DTs, including the distribution of eight specialized associations, are given in Fig. 14.3 for the Aas411 site. The complete host-plant–DT matrix showing the distribution of all FFGs, including the three interactions of a wood boring, an undefined association and fungal damage, is provided in Fig. 14.4.

14.8.2 *Exophytic Interactions*

Four, major, exophytic FFGs characterize the Molteno Biome. These are the four standard categories of plant–insect interactions that occur in virtually all modern and fossil floras, given sufficient sampling intensity. They are hole feeding (Alford 1991)), margin feeding (Gangwere 1966), skeletonization (Carvalho et al. 2014) and surface feeding (Johnson and Lyon 1991). Typically margin feeding is the most abundant and skeletonization is the least frequent of exophytic FFGs in modern and fossil floras. This pattern of exophytic interactions is repeated for most Molteno localities, and in particular applies for external feeding documented from the Aas411 site (Fig. 14.2).

Hole Feeding: For modern insect herbivores, hole feeding is one of the most ubiquitous and most conspicuous types of feeding (Alford 1991; Johnson and Lyon 1991). At Aas411 there were eight hole-feeding DTs, responsible for 71 occurrences on plant specimens. The most frequently occurring hole feeding is DT1, characterized by small perforations less than 1 mm in maximum diameter, consisting of DT occurrences on 27 plant specimens, and representing 32.4% of all hole-feeding damage. A typical example is DT1 on *Dicroidium odontopteroides* (Fig. 14.5h). Given the variety of hole-feeding that emphasizes the smaller sized holes of DT1, DT2 and DT3 (Labandeira et al. 2007), it is likely that the responsible insect herbivores were small orthopteroids and beetles. These generalized interactions contrast with the presence of stereotypical slot feeding, DT8, on *H. elongatum*, which more likely is attributable to beetle feeding, akin to leaf beetles on the modern fern *Pteris* (Patra and Bera 2007). Distinctive slot feeding occurs in other Molteno localities with abundant *H. elongatum*, and indicates a specialized association. This association occurs in 21 other Molteno localities, predominantly in Heidiphyllum Thicket habitats, and rarely is present at high frequencies, although the 16 occurrences in Gre-121 is an exception. Consistent with the observation that *H. elongatum* is overwhelmingly the most intensely herbivorized host at Aas411, 57.7% of all damage by hole feeders targeted this host.

Margin Feeding: Margin feeding is the most abundant functional feeding group at Aas411. Margin feeding consists of five DTs that are responsible for 273 occurrences on particular plant specimens, and amounts to 24.6% of all Aas411 associations. The most frequently occurring margin-feeding is DT12, accounting for DTs on 221 plant specimens and representing 81% of all margin feeding. DT12 is characterized by cuspate excisions on foliar margins that do not extend to primary veins or leaf tips. The dominance of margin feeding in general and DT12 in particular is a common pattern seen in many late Paleozoic and early Mesozoic floras, including those of the Molteno Biome. The likely insect culprits of DT12 and other types of margin feeding are medium to large sized orthopteroids, and possibly equally large beetles. Molteno external foliage feeding damage is analogous to damage caused by the nymphs and adults of stick insects and grasshoppers (Floyd 1993; Gangwere 1966), and larvae of owlet and looper moths and common sawflies (Comstock 1939; Welke 1959; Weintraub et al. 1994) on ferns. None of the margin feeding at Aas411 represents a specialized association. The most intensively attacked hosts by margin feeders are *H. elongatum* (Fig. 14.5a,d) and *D. crassinervis* for DT12, representing 34.1% and 29.7% of occurrences, respectively, and subordinately *Lepidopteris stormbergensis* and *L. africana*, representing 16.5% of total margin-feeding DTs. Continuous margin feeding of DT143 is present on *Ginkgoites matatiensis* (Fig. 14.5b,c), and DT13 occurs as the snipped pinnule margins of *Pseudoctenis* sp. (Fig. 14.5e).

Skeletonization: Skeletonization is represented by one occurrence of DT16 on *H. elongatum*. Skeletonization is absent to very rare in Middle Pennsylvanian to Late Triassic floras of Gondwana and Laurasia (Beck and Labandeira 1998; Prevec et al. 2009; Feng et al. 2014) and does not become particularly abundant until the Cenozoic (Wilf and Labandeira 1999).

Surface Feeding: Of the seven surface-feeding DTs at Aas411, the most frequently occurring is DT30, consisting of 25 occurrences on foliage, and representing 32.9% of all surface feeding. The dominance of surface-feeding herbivory, particularly DT29, DT30 and DT103, occurs principally on *H. elongatum* and corresponds to 70% of the total surface-feeding occurrences. DT103, the consumption of surface tissues in the interveinal area between two adjacent, mostly parallel veins, is similar to that of the modern leaf beetle *Aulacoscelis* on the cycad host *Zamia* (Windsor et al. 1999), and other leaf-beetle species on the fern *Pteris* (Patra and Bera 2007). The concentration of these three damage types on *H. elongatum* contrasts with more scattered and fewer occurrences of other surface feeding DTs on other seed-plant taxa at Aas411. The likely culprits for surface feeding on *H. elongatum* are beetles, and perhaps certain orthopteroid clades. However, such surface-feeding lineages would require modified chewing mouthparts for accessing and delaminating surface tissue layers.

14.8.3 Endophytic Interactions

There are six major endophytic interactions that characterize the Molteno Biome in general and Aas411 in particular. These interactions are given in Fig. 14.3, and includes eight specialized associations mapped on some of these endophytic DTs, with the exclusion of borings. The Aas411 site has all six FFGs of piercing and sucking (Weber 1930; Cobben 1978), oviposition (Wesenberg-Lund 1943; Childers 1997), mining (Needham et al. 1928; Hering 1951), galling (Felt 1917; Meyer 1987; Rohfritsch 1992), seed predation (Shepard 1947; Janzen 1971), and borings (Solomon 1995). Collectively, these interactions exhibit a robust partitioning of internal tissues.

Piercing and Sucking: The piercing-and-sucking FFG consists of four DTs that have resulted in damage to 38 plant specimens at Aas411. The most abundant is DT46, consisting of 27 instances on plant specimens and representing 71.1% of all piercing-and-sucking occurrences. DT46 is a generalized interaction consisting of small, isolated puncture marks typically with a surrounding, crater-like rim, analogous to modern punctures produced by thysanopterans (Childers 1997) and hemipterans (Günthart and Günthart 1983). Although stereotypical Molteno piercing-and-sucking damage of scale impression marks by sternorrhynchan hemipterans, such as DT77 or DT158, are absent at Aas411, there are two occurrences of DT128 on *H. elongatum* present at the site. DT128, is a specialized interaction always on *H. elongatum* hosts that also is present at Maz211 (Mazenod 211) with 36 examples, and at the Lut311 (Lutherskop 311) and Win111 (Winnarspruit 111) localities. DT128 is a very distinctive, broadly elliptical scale impression mark characterized by a roughened inner surface, a distinctive bordering rim and an anterior notch (Fig. 14.5f), and closely resembles modern black pineleaf scale, a diaspidid scale insect, on red pine (Johnson and Lyon 1991; also see Maskell 1887). An intermediate specialized association is DT138, which targets particular vascular tissues, whose linear rows of punctures occur along major veins of *H. elongatum* and *D. crassinervis* indicative of feeding on xylem or phloem tissue. The linear tracking of vascular tissue by piercing-and-sucking hemipterans is common in modern plants, and the same DT138 feeding pattern has been recorded on modern pine needles by a typhlocybine leaf hopper (Günthart and Günthart 1983).

Oviposition: Ovipositional damage at Aas411 typically consists of lenticular and less commonly ellipsoidal to circular lesions on the foliage and stems of plants. Endophytic oviposition is characterized by inner disturbed tissue, rarely with evidence for a lodged egg (Labandeira and Currano 2013), and a prominent, surrounding border of callus or other scar tissue. There are four DTs of oviposition, which have left damage on 188 plant specimens. The most frequently occurring is DT76, consisting of 125 DT occurrences on specimens and representing 66.5% of the all oviposition occurrences. The DT76 specialized association accounts for 99 DT examples (52.7%) of damage occurrences that frequently occur on *H. elongatum* (Fig. 14.5g). DT76 lesions are very similar to the modern odonatan *Calopteryx* ovipositing in the stems of emergent semiaquatic plants (Corbet 1999). Analogous examples of modern DT76 damage include *Ceresa* tree hoppers, terrestrial hemipterans that insert eggs into twigs that result in lenticular oviposition lesions surrounded by scar tissue (Funkhouser 1917), and also by the aquatic water scorpion, *Ranatra*, a hemipteran that oviposits on submerged hydrophyte stems (Wesenberg-Lund 1943).

The specialized interaction, DT72, consists of 14 examples (7.4%) of lenticular lesions whose long axis is oriented parallel to the vasculature of *Zonulamites viridensis* horsetail stems (Fig. 14.6c). The third association is DT108 which occurs again on the horsetail *Zonulamites viridensis*, and is responsible for 39 examples (20.7%) of the damage and closely resembles modern *Stictocephala* tree hopper damage to the tissues of small twigs (Funkhouser 1917; Yothers 1934). A considerable amount of the oviposition damage, particularly DT72 and DT108, overwhelmingly targeted horsetails, particularly *Zonulamites viridensis* (Anderson and Anderson 2017). Although the likely culprit for most ovipositional damage are early lineages of odonatopteran dragonflies, other groups, principally orthopteroids and sawflies, may have been responsible for damage as well. These non-odonatan examples could have inflicted DT100 (e.g. Wesenberg-Lund 1913) and DT101 (e.g. Jurzitza 1974).

Mining: There are 154 mining occurrences at Aas411 that are allocated to three DTs: They are: DT41 (not illustrated), the very rare threadlike and delicate leaf mine with two occurrences (1.3%); the vastly more abundant and robust DT71 (Fig. 14.6a,b), represented by150 occurrences (97.4%); and the very rare DT139 with two occurrences (1.3%). DT41 is a common leaf mine type that is quite abundant in Late Cretaceous and Paleogene biotas where it is generally affiliated with a lepidopteran culprit (Doorenweerd et al. 2015). However, the presence of DT41 in the Late Triassic could be attributed to another major lineage of insects, such as a nematoceran fly (Swezey 1915). By contrast, DT71 is one of the most conspicuous, persistent and abundant of the host-specialized associations throughout the Molteno Biome, of which 1247 DT occurrences are recorded on its host plant, *H. elongatum*. The DT71 interaction is present at 23 Molteno localities, half of which are Heidiphyllum Thicket habitats.

At Aasvoëlberg 311 (Aas311), a sister-site of Aas411, there are 740 occurrences of DT71 on host *H. elongatum*, representing 59.3% of all DT71 Molteno leaf mining occurrences (Fig. 14.7b), and providing some of the best evidence for a pest outbreak in the fossil record (Labandeira 2012). DT71 mines are distinctive, full-depth mines that have a loosely sinusoidal frass trail in early instars that becomes more tightly sinusoidal later instars, but always are characterized by particulate fecal pellets whose size changes with instar molt shifts (Fig. 14.6a,b). The leaf mines occupy the intercostal areas between the major veins of the monocot-like, parallel-veined *Heidiphyllum* leaf; apparently, the smaller veinules embedded in mesophyll were consumed by the mine occupant. Miner emergence frequently occurred at the leaf edge, where an enlargement of the mine may represent a pupation chamber. The DT71 mine closely resembles the mine of extant *Charixena iridoxa*, a plutellid moth from New Zealand that mines the structurally very similar, parallel-veined foliage of the liliaceous monocot *Astelia montana*.

DT139 is a short, serpentine, full depth mine with a large, expansive and rounded terminal chamber that typically has an irregular course between major veins of host *Sphenobaiera schenckii* (Fig. 14.7a). This mine also occurs on other unrelated hosts such as *Paraginkgo antarctica* at Lit111, *H. elongatum* at Win111, *Pseudoctenis fissa* at Kap111 (Kappokraal 111), and *Kannaskoppifolia lacerata* at Kan112 (Kannaskop 112), indicating that occurrences on *S. schenckii* at Aas411 are not host specific. The DT139 mine is similar to a metallic wood-boring beetle mine of modern *Pachyschelus coeruleipennis* (Buprestidae) on the euphorbiaceous angiosperm, *Croton floribundus* (Queiroz 2002; Ding et al. 2014), as well as the leafminer moth mine of modern *Parectopa zorionella* (Gracillariidae) on the rubiaceous angiosperm *Coprosma grandifolia* (Watt 1920). Most likely, however, the DT71 and DT139 leaf-mining associations are likely attributable to an early-derived polyphagan beetle, possibly a buprestoid (metallic wood-boring beetles and relatives) or an elateroid (click beetles and relatives) that resemble other leaf mines in broadleaved conifers from the more recent fossil record (Ding et al. 2014; Donovan et al. 2016).

Galling: Unlike mining, which presents the three types of damage of DT41, DT71 and DT139, the 182 galls at Aas411 are distributed across eight DTs and represent a wide variety of galling strategies. Insect galls are present on the intercostal areas between leaf veins (DT32), on primary leaf veins (DT33), on leaf petioles (DT55), and on small, woody twigs (DT87). Modern DT32 is a common type of gall, made by a variety of modern insect gallers, including the mite "*Eriophyes*" *nalepai* on the polypodialean fern *Nephrolepis biserrata* (Gieshagen 1919). DT33 also is a common gall, made by a cecidomyiid midge on the foliar midrib of the gnetalean, *Gnetum neglectum* (Docters van Leeuwen-Reijnvaan and Docters van Leeuwen 1926). The petiole gall DT55 ranges in shape from a modest petiolar expansion to a considerably more bulbous, broadly ellipsoidal to spheroidal structure (Labandeira et al. 2007), for which the gall of the gall midge *Lasioptera ephedrae* on the gnetalean *Ephedra trifurca* is a structural analog (Felt 1917). Another modern twig gall, very similar to DT55, is produced by a gelechiid moth on the polypodialean fern *Microgramma squamulosa* (Kraus et al. 1993), which is prominently and centrally positioned on the twig axis and has a symmetrical bulbous expansion. As for DT87, a modern example is a gall by a gall midge, also on the epiphytic polypodialean fern *M. squamulosa*, but one that rather results in a projecting bulbous prominence broadly attached along one surface of a twig (Maia and Santos 2011). Each of these gall types are characterized by different micromorphologies of hardened wall tissues, an inner nutritive tissue layer surrounding the larval chamber, and co-optation of host-plant vascular tissue to supply nutrients to gall tissues.

Different, more specialized strategies are represented by galls such as DT123, DT161 and DT122. DT123 is a distinctive gall caused by small insects such as mites, aphids and thrips that display collapse of individual plant cells and unusual foliar thickenings, causing abnormal cupping and enrollment of foliage. Such foliar distortions are analogous to the gall of the phlaeothripid thrips *Jersonithrips galligenus* on the polypodialean fern *Elaphoglossum morani* (Retana-Salazar and Nishida 2007), or to various eriophyid mites in which pinnular cupping is established by early stages of mite feeding (Boughton and Pemberton 2011), resulting from styletal modification of epidermal cells into nutritive tissue for nymphal gall-mite feeding (Freeman et al. 2005). DT161, by contrast, is a roughened, circular blister gall with pustulose centers and lineations that radiate to the outer periphery of the gall wall, similar to an eriophyid blister gall on the foliage of a *Carya* (hickory) species (Johnson and Lyon 1991). The two host-specialized galls are DT70 and DT122. The specialized mite gall, DT70 (Figs. 14.8d–f, h, 14.9, 14.10, 14.11, 14.12a,b,d), occurs almost exclusively on *D. crassinervis* and is represented by 167 occurrences in 12 localities throughout the Molteno Biome that represent a broad variety of habitats. At Aas411, DT70, discussed in detail below, consists of 120 occurrences.

The host-specialized gall other than DT70 is DT122. DT122 is a medium sized, bulbous, ellipsoidal gall that is oriented parallel to the venation of the ginkgophyte, *Sphenobaiera schenckii* (Figs. 14.6d,e, 14.7c, 14.8a–c,g). This gall represents a recurring association found in several other localities in the Molteno Biome and occasionally on other hosts, such as *D. crassinervis* (Fig. 14.6f) and *H. elongatum* (Fig. 14.12c), where there evidently is not a host-specialist association. The culprit for this gall remains unknown, but it shares a superficial resemblance to certain galls of the same size, shape and outer surface texture as the pteromalid wasp *Aditrochus* sp. on coigüe, *Nothofagus nitida* (Nothofagaceae), in the southern Andes of South America (Quintero et al. 2014).

Seed Predation: For a function feeding group with few DTs, seed predation has a considerable number of specialized associations. From 121 seed-predation DTs at Aas411, 100, or 82.6%, are associated with the three specialized DTs of DT73, DT74 and DT124. The first damage type, DT73, consists of 63 occurrences (52.1%) of all seed predation at Aas411, and is a lenticular to narrowly ellipsoidal perforation into the central body of *Avatia bifurcata* dispersed seeds. Each DT73 occurrence on a predated seed can have from one to several perforations through the seed central body (Anderson and Anderson 2003; Labandeira 2006a, 2016). *Avatia bifurcata* is affiliated with *Ginkgoites matatiensis* foliage and *Eosteria eosteranthus* pollen organs, the three of which constitute a ginkgoopsid whole-plant taxon. The likely culprit was a heteropteran hemipteroid with a laterally compressed stylet bundle and sheath found in some extant seed-feeding heteropterans (Weber 1930; Cobben 1978) such as Lygaeidae (seed bugs) or Miridae (capsid bugs) that match the cross-sectional aspect ratios of damage to modern flowering plants (Hori 1971; Burdfield-Steel and Shuker 2014).

The second damage type, DT74, is represented by 35 occurrences (28.9%) of the seed predation damage at Aas411. DT74 consists of circular to occasionally slightly and laterally compressed subcircular perforations into the central body of *Fanerotheca papilioformis* dispersed seeds, equivalent to *Feruglioa samaroides* seeds when attached to an ovulate organ. The corystosperm whole-plant taxon consists of *Dicroidium crassinervis* foliage, *Fanerotheca papilioformis* (*Feruglioa samaroides*) seeds and possibly *Pteruchus* sp. pollen organs. The likely culprit of DT74 damage was a hemipteroid different than the fabricator of DT73, also a heteropteran, but with a smaller, circular cross-sectional styletal apparatus common in some modern taxa (Handley and Pollard 1993) and with a distinctive mode of inflicting damage (Golden et al. 2006).

The third damage type, very rare DT124, is a minor element of seed predation at Aas411. DT124 consists of the major removal of nutritive and embryonic tissues from a *Dordrechtites* cone scale. The affiliation of *Dordrechtites* cone scales, however, remains enigmatic. The seed likely originates from the cone of a coniferalean plant that is known but lacks attribution to foliage; such a source plant has not been identified in the Molteno Biome (Anderson and Anderson 2003). Nevertheless, the culprit of DT124 is very different than those of DT73 and DT74, and shows damage evidence indicating a mandibulate larval insect similar to modern larval sawfly (Bird 1926) or bruchid or other beetle damage on gymnosperm (Bedard 1968) or angiosperm (Shepard 1947) seeds.

Borings: Borings are an extremely rare plant–insect interaction in the Molteno Biome and are represented at Aas411 by one occurrence of DT160. By comparison there are only three other occurrences of borings at Molteno—two instances of DT160 at Bir111 and a single example of DT174 at Lit111. The Aas411 boring consists of a tunnel circular to ellipsoidal in cross section, approximately 5.0 mm in maximum diameter, and oriented parallel to the xylary grain in petioles or twigs.

Other Interactions: There are four instances of damage at Aas411 that are not assigned to any functional feeding group. DT106 probably represents thermal stress or nutrient deficiencies to the leaf margin of *H. elongatum* (Labandeira and Prevec 2014). Also occurring on *H. elongatum* is fungal damage, all of which is allocated to DT58, likely representing primary fungal colonization of the leaf surface. Fungal damage at Aas411 resembles much of the damage found on plants such as the ascomycete *Cephalosporium* that forms necrotic blotches on the polypodialean fern *Pteris* (Schneider 1966).

14.8.4 Herbivory Patterns

From the distribution of the above interaction data on the plant hosts at Aas411 (Fig. 14.4), there are six major patterns that are present. These patterns involve comparisons of plant host, DT, host specialization, component community and other categories within the Aas411 site, and also observations comparing the Aas411 site to other such Molteno localities.

Number of DT Occurrences: There are 1127 DT occurrences on specific plant specimens, based on presence–absence data at Aas411. This value is the sum of all recorded occurrences for each DT that is present on a single, inventoried plant specimen. As these occurrences represent presence–absence data, for a DT occurrence to be recorded on a plant specimen, it must occur at least once, although (unrecorded) multiple occurrences may be present. The FFG abundance data, in decreasing rank, for the number of DTs per FFG is: margin feeding, 286 occurrences; oviposition, 188; galling, 182; leaf mining, 154; seed predation, 121; surface feeding, 76; hole feeding, 66; unidentified DTs, 4; fungi, 3; and skeletonization, 1. The abundance of margin feeding and virtual absence of skeletonization is expected, as margin feeding typically has the most elevated occurrences of any FFG and skeletonization is very rarely represented in the Paleozoic and Mesozoic. However, it is notable that there is a greater abundance of the endophytic FFGs of piercing and sucking, oviposition, leaf mining, galling, and seed predation, representing 681 DT presence–absence occurrences, over the exophytic FFGs of hole feeding, margin feeding, skeletonization and surface feeding that represent 429 DT presence–absence occurrences. This latter comparison, where endophytic DTs exceed exophytic DTs by a factor of almost 1.6, represents a condition rarely seen in other Molteno localities.

Number of DT Categories: The pattern of DT diversity per FFG is different than that of individual DT occurrences on plant specimens per FFG measured above. For exophytic FFGs, hole feeding is represented by seven DTs, margin feeding by five DTs, skeletonization by one DT and surface feeding by seven DTs for a total of 20 DTs. For endophytic FFGs, piercing and sucking is represented by four DTs, oviposition by four DTs, mining by three DTs, galling by eight DTs, seed predation by three DTs and borings by one DT for a total of 23 DTs. The exophytic to endophytic DT ratio is 1.15 or approaching equivalence and is significantly different than that of the individual DT occurrences. This indicates that modes of feeding on tissues is approximately equivalent under exophytic or endophytic feeding regimes, but the intensity, as measured by individual feeding events that target plant specimens, is substantially greater under endophytic feeding. This also is indicated by the galling FFG having the greatest number of eight DTs at Aas411.

Plant Hosts: Of the 111 plant form-taxa, 35 are combined into 14 separate whole-plant taxa. Of these 14 whole-plant taxa, seven are the principal plant species that are the most herbivorized at Aas411 (Table 14.2). Often multiple organs are herbivorized within a whole-plant taxon, such as foliage, stems and seeds. The ranking of herbivory intensity is provided from evidence of four attributes for each whole-plant taxon. The attributes are: (i), the numbers of functional feeding groups; (ii), the number of DT categories; (iii), the number of individual DT occurrences; and (iv), the number of specialized associations for each whole-plant taxon. The most herbivorized plant host by far (Fig. 14.4; Table 14.3), is the *Heidiphyllum elongatum–Telemachus acutisquamus–Odyssanthus crenulata* whole-plant taxon (Anderson and Anderson 2003; Bomfleur et al. 2013), representing the affiliated foliage, ovulate organ and pollen organ of a prominent voltzialean conifer. (This convention of sequential characterization of whole-plant taxa by their foliage, female organ and male organ taxa will be used for all seed-plant taxa.) The second ranked, most herbivorized taxon is the *Dicroidium crassinervis–Fanerotheca papilioformis–?Pteruchus matatimajor* whole plant taxon (Retallack and Dilcher 1988; Anderson and Anderson 2003), an umkomasialean corystosperm. The third most herbivorized whole-plant taxon is the *Sphenobaiera schenckii–Sphenobaiera* short shoot–*Hamshawvia longipeduncula–Stachyopitys gypsianthus* whole-plant taxon, a ginkgophyte (Anderson and Anderson 2003; Barboni and Dutra 2015). These three plant-host taxa at Aas411 also are the three most prominent taxa that parallel in the same rank order the Molteno Biome as a whole (Anderson and Anderson 2003).

Other than the three major herbivorized plant hosts, those whole-plant taxa with significant but less herbivory are three seed plants and a horsetail. The fourth most herbivorized taxon is another ginkgophyte, the *Ginkgoites matatiensis–Avatia bifurcata–Eosteria eosteranthus* whole-plant-taxon (Anderson and Anderson 2003). The fifth most herbivorized taxon, the peltasperm *Lepidopteris africana–Peltaspermum turbinatum–Antevsia mazenodensis* whole-plant-taxon and the sixth most herbivorized taxon, the congeneric peltasperm *Lepidopteris stormbergensis–Peltaspermum monodiscum–Antevsia* sp. whole-plant-taxon, which likely occupied similar habitats (Anderson and Anderson 2003). The seventh most herbivorized taxon is the only plant host with elevated damage that is not a seed plant, and unlike the other six whole-plant taxa, the *Zonulamites viridensis*–nodal diaphragm A–*Viridistachys gypsensis–Paraschizoneura fredensis* whole-plant taxon is a horsetail that has insect damage only as oviposition. These four, less dominant, whole-plant taxa do not follow the same rank order of prominence throughout the entire Molteno Biome, as do the *Heidiphyllum*, *Dicroidium* and *Sphenobaiera* host sequence. Rather, fourth ranked Aas411 *Ginkgoites* occurs as seventh position in the Molteno Biome as a whole, fifth and sixth ranked Aas411 *Lepidopteris* occurs collectively as the eighth Molteno position, and seventh-ranked Aas411 *Zonulamites* is unranked within Molteno Biome (Anderson and Anderson 2003).

Persistent Specialized Associations: One of the features determining the most herbivorized whole-plant taxa at the Aas411 site is the number of specialized associations. Host-specialized interactions are defined by the presence of the same recurring, stereotypical damage type that is present on the same host-plant species or closely-related group of species throughout multiple localities across the Molteno Biome. In addition, host specificity can be assessed by the extent to which the herbivore modifies the tissues of its plant host, which in the case of gallers implies an intimate association that results from the gall extending the limits of its phenotype to include galled host tissues (Stone and Schönrogge 2003). The *Heidiphyllum elongatum* whole-plant-taxon houses the greatest number and most diverse repertoire of host-specialized associations of any Aas411 host plant, or for that matter, of any plant host from a Molteno site (Tables 14.2, 14.3; Figs. 14.2, 14.3, 14.13). These recurring host-specialized associations include DT8 of hole feeding (not figured), DT128 of piercing and sucking (Fig. 14.5f), DT76 of oviposition (Fig. 14.5g), and DT71 of mining (Fig. 14.6a,b). These four, pervasive associations of the *H. elongatum* whole-plant taxon are present at other Molteno localities; in the case of distinctive DT76 oviposition, 30 other Molteno localities have this interaction. For the distinctive, highly host specific leaf mine of DT71, 98.4% occur on the *H. elongatum* whole-plant taxon across Molteno localities. This association has 147 occurrences at Aas411, but is matched by 1124 other occurrences in 22 other localities within the Molteno Biome (Table 14.3).

Four, other, highly stereotyped associations on hosts other than *H. elongatum* are noteworthy (Tables 14.2, 14.3; Figs. 14.2, 14.3, 14.13). One notable, persistent association of specialized damage is the highly stereotyped mite gall DT70, found almost exclusively on the foliage of *D. crassinervis* (Tables 14.2, 14.3; Figs. 14.8d–f, h, 14.9, 14.10, 14.11, 14.12a,b,d). At Aas411 there are 117 occurrences of DT70 on *D. crassinervis*, but 50 other occurrences are found on the same host at 11 other Molteno localities. A second example are distinctive DT73 seed-predation lesions on *Avatia bifurcata*, the affiliated platysperm seed of *Ginkgoites matatiensis* foliage (Labandeira 2016). Seed damage of DT73 is found on 63 specimens at Aas411, but this DT has 1067 occurrences at six other Molteno localities, of which 1045 *A. bifurcata* seeds show this damage at the Bir111 site. A third example is the characteristic DT72 oviposition lesions in the stems of the horsetail *Zonulamites viridensis* whole-plant taxon (Fig. 14.6c), of which 14 occurrences are present at Aas411, and 30 other occurrences are found in nine other localities across the Molteno Biome on *Z. viridensis* at Gre111B (Greenville 111B), Bir111 and two, other, closely related species of *D. annumensis* from Lit111, Nuwejaarspruit 111A (Nuw111A) and Peninsula 511 (Pen511); and *D. elandensis* at Elandspruit 111 (Ela111), Lutherskop 4111 (Lut4111), Boesmanshkoek 111B, (Boe111B) and Cala Road 111A (Cal111A). Last is the excavation of megagametophytic tissues of DT124 seed predation on *Dordrechtites elongatus*, an unaffiliated pinopsid cone (Anderson and Anderson 2003). This distinctive ovulate reproductive structure has both of its two occurrences at Aas411 that exhibit damage, but also has 11 occurrences with damage in the closely related *D. mazocirrus* at the Maz211 site.

Component Community Structure: The *Heidiphyllum elongatum* whole-plant taxon has the most diverse and balanced component community at Aas411 of any plant host (Tables 14.2, 14.3; Figs. 14.3, 14.13). However, pending additional analyses, the *H. elongatum* whole-plant taxon likely is the most diverse and thoroughly herbivorized plant throughout the Molteno Biome, as it occurs in 78 of the 106 Molteno localities. This whole-plant taxon is represented by nine of the ten FFGs at Aas411, including the unknown FFG of DT106, and displays 28 DTs (Tables 14.2 and 14.3; Fig. 14.13). The only missing FFGs for *H. elongatum* are wood boring and seed predation. As for seed predation, no affiliate seed or female ovulate organ has been assigned to *H. elongatum* at Aas411, assuming that the present *Dordrechtites elongatus* is not the affiliate ovulate organ and neither is the possible affiliate ovulate organ *Telemachus*, which interestingly is absent at Aas411. (See the discussion on page 62 of Anderson and Anderson [2003] for a full discussion of this enigma.) If *Dordrechtites elongatus* is the ovulate organ of *H. elongatum*, as may be suspected, then the highly stereotyped seed-predation association of DT124 would almost complete the tally of ten functional feeding groups contained in the *H. elongatum* whole-plant taxon, five of which would include the host-specialized associations of DT8 hole feeding, DT128 piercing and sucking, DT76 oviposition, DT71 leaf mining and DT124 seed predation. Much of the component community structure of the *Heidiphyllum elongatum* whole-plant taxon is illustrated in Fig. 14.13.

There is considerable structure in the component communities of the remaining whole-plant taxa as well. The *Dicroidium crassinervis* whole-plant taxon is the second most diverse component community at Aas411, housing seven FFGs and 20 DTs that includes hole feeding, margin feeding, piercing and sucking, oviposition, galling and seed predation. The *Sphenobaiera schenckii* whole-plant taxon houses the third most complete component community, containing all the FFGs occurring in *Dicroidium crassinervis*, except for the presence of leaf mining, the absence of seed predation, and about half of the number of DTs. The *Ginkgoites matatiensis*, *Lepidopteris africana* and *L. stormbergensis* whole-plant taxa have two less, or five FFGs, and 8–11 DTs each. By contrast, the horsetail *Zonulamites viridensis* component community has a very limited component herbivore community, consisting only of one FFG and three DTs of oviposition. This paucity of diverse damage in horsetails is attributable to herbivory that largely is limited to stem tissues embedded with silica deposits and also to the presence of foliage resistant to arthropod consumption (Law and Exley 2011).

Role of Habitat: The dominant habitat for the specialized associations of five of the most herbivorized associations at Aas411 also match the stated site habitat of their plant hosts at other localities across the Molteno Biome. Perhaps not surprisingly, the habitat of the four host-specialized associations representing the distinct FFGs of DT8 hole feeding, DT128 piercing and sucking, DT76 oviposition and DT71 mining of the *H. elongatum* whole-plant-taxon is Heidiphyllum Thicket. Similarly, for the two host-specialized associations of DT70 and DT74, representing two FFGs of the *D. crassinervis* whole-plant taxon, is Dicroidium Open Woodland. The single host-specialized associations of DT122 galling for the *S. schenckii* and DT73 seed predation for the *G. matatiensis* whole-plant-taxa is Sphenobaiera Closed Woodland. Last, the two host-specialized associations of DT72 and DT108 oviposition for *Z. viridensis* is Horsetail Marsh. It appears that because of the host-plant ecological preferences for certain habitats, that their more intimate interactions with insect herbivores also are closely tied to a specific habitat within the Molteno Biome.

14.9 Early Gall History and Gall DT70 on *Dicroidium crassinervis*

14.9.1 Early Arthropod Gall History

Terrestrial fossil galls have their earliest occurrence in a liverwort host from the Middle Devonian of New York state, attributed to an unknown small arthropod (Labandeira et al. 2014). The gall record increases substantially during the Pennsylvanian Period, particularly in Euramerica, in which galls overwhelmingly are hosted on plant axial tissues of the rachises of *Psaronius* tree ferns (Labandeira and Phillips 1996) and the terminal strobili of calamitalean horsetails (van Amerom 1973; Kelber 1988). During the early Permian (Cisuralian), a variety of gall morphologies, representing approximately ten DTs, colonized the foliage of seed plants, particularly in southwestern (Schachat et al. 2014; Schachat and Labandeira 2015) and central-south (Labandeira et al. 2016) Euramerica. This shift toward and expansion of galling on foliage rather than axes such as stems continued in Gondwana until the Lopingian, where almost all occurrences are on glossopterid hosts (Adami-Rodrigues et al. 2004; Prevec et al. 2009; McLoughlin 2011). These plant–gall interactions largely were eliminated globally at the P-Tr ecological crisis (Labandeira 2006a), as there is minimal evidence from depauperate Early Triassic deposits to suggest the survival of recognizable Permian gall interactions on particular hosts later into the Triassic. An exception includes a midveinal gall on the probable seed fern *Tongchuanophyllum* of the Olenekian Solling Formation in southern Germany (Kustatscher and van Konijnenburg-Van Cittert 2013; Kustatscher et al. 2014). Additionally, a distinctive, circular to broadly ovoidal gall with thick enveloping walls on *Dicroidium odontopteroides*, probably of Olenekian age, have been described from the Newport Formation of the Sydney Basin in Australia (McLoughlin 2011).

Well documented insect damage on Anisian, Ladinian and Carnian Triassic floras throughout Pangaea indicate the re-evolution of the galling habit by several insect lineages on multiple plant hosts. In stark contrast to the Permian, Middle Triassic galling interactions occur on very different plant hosts in Euramerica and Gondwana (Anderson and Anderson 1985, 1989, 2003, 2008, 2017; Visscher et al. 1996; Anderson et al. 2007; Krassilov and Karasev 2009). Similarly, the evolution of new insect groups with potentially newly evolved galler lineages during the Middle Triassic to early Late Triassic is indicated by their body-fossil record (Tillyard 1923; Riek 1974; Gallego 1997; Béthoux et al. 2005; Labandeira 2005). The insect body-fossil record was supplemented by newly appearing lineages of mites (Sidorchuk et al. 2015), sternorrhynchans (Evans 1971; Shcherbakov 2000), thrips (Fraser et al. 1996), beetles (Ponomarenko 2016; also see McKenna et al. 2015), sawflies (Rasnitsyn 1969; Schlüter 2000), and flies (Krzeminski 1992; Shcherbakov et al. 1995). Consequently, the insect body-fossil record indicates that many major insect lineages were present during the Anisian, Ladinian and early Carnian that would have supplied taxa engaged in the galling habit on a broad repertoire of available, newly emerging plant hosts (Larew 1992). The fossil mite record, particularly for those taxa engaged in gall associations with fern and especially conifer hosts, is ancient, based examinations of the fossil record (Sidorchuk et al. 2015), phylogenetic studies (Boczek and Shevchenko 1996; Fenton et al. 2000) and biogeographical inference (Gerson 1996; Oldfield 1996; Lewandowski and Kozak 2008).

During this time interval, evidence for Anisian galling associations comes from the Dont Formation of the Dolomites Region in northeastern Italy, especially DT32 and DT80 galls on cycadophytes, such as *Bjuvia dolomitica*. In the penecontemporaneous Valle San Lucano Flora of the Agordo Formation, also in the Dolomites Region, DT11 galls (erroneously reported as surface feeding) occur on the cycadophyte *Taeniopteris* sp. and DT32 galls have been found on a second cycadophyte, *Nilssonia neuberi* (Labandeira et al. 2016). From the upper Grès à Voltzia, or upper Buntsandstein, beds of the Röt Formation in Alsatian France, there is a distinctive gall on the voltzialean conifer *Aethophyllum stipulare* (Larew 1992; Grauvogel-Stamm and Kelber 1996), presumably of herbaceous habit. This gall is notable for its considerable expansion of anomalous tissue in the peduncular base of the male conifer cone. A second gall affects another conifer at the same site, an undetermined species of *Voltzia*, which resembles a witch's broom deformity, characterized by the bending of shoot axes and extensive proliferation of derivative foliage, similar to a

DT121 aldelgid gall (Grauvogel-Stamm and Kelber 1996; also see Labandeira and Allen 2007, for a Permian example). Notably, no galls have been observed on any plant host among the 1386 plant specimens from the Anisian Burgersdorp Formation of South Africa (Labandeira et al., unpubl. observ.).

Plant material displaying Ladinian galls overwhelmingly originated from the same regions in Western Europe as Anisian galls. Some Ladinian gall associations may have been described as oviposition scars by Grauvogel-Stamm and Kelber (1996). However, the best evidence for Ladinian galls comes from several sites of the Dolomites Region of northeastern Italy (Wappler et al. 2015; Labandeira et al. 2016). One such site contains the Monte Agnello Flora, from the Vulcanites Formation, revealed a DT121 bud gall on the conifer *Voltzia* sp. 1 (Wappler et al. 2015), very similar to the gall on an undetermined species of *Voltzia* from the penecontemporaneous Grès à Voltzia material in Alsatian France mentioned above (Grauvogel-Stamm and Kelber 1996). The diverse gall component of plant–insect interactions from the Monte Agnello Flora also includes the small, nondescript, hemispheroidal, DT80 galls on the fern *Phlebopteris fiemmensis*, cycadophyte *Bjuvia* cf. *dolomitica*, and seed fern *Scytophyllum bergeri* (Wappler et al. 2015; Labandeira et al. 2016). A different species of *Phlebopteris* at Monte Agnello exhibits a DT106 gall likely caused by a mite (Labandeira et al. 2007, 2016). Two other Ladinian floras from the Dolomites Region, the St. Veit–Innerkohlbach and Forcela da Cians floras, contain the seed fern *Ptilozamites sandbergeri* that display generalized, indistinct galls of DT32 and DT80 (Labandeira et al. 2016). Anisian and Ladinian data indicate that gall morphologies, with the exception of the conifer-borne galls, were generalized, hemispherical, well protected and probably single chambered.

During the Carnian, particularly in the early part of the stage, galling insects increased their geographic range and entered into new associations with plant hosts that produced novel gall morphologies. These new gall types were present at different regions, occupied different habitats, and colonized new plant hosts when compared to those of the Middle Triassic. One such gall is a pustulose, compound gall on the net-veined fern *Dictyophyllum bremerense* from the Blackstone Formation of the Sydney Basin in Australia (Webb 1982). A second occurrence comes from the De Geerdalen Formation of Svalbard, Norway, which is a permineralized peat deposit bearing anatomically preserved bennettitalean roots that contain cortex-embedded, single chambered, spheroidal galls with walls having an inner ragged surface and a smooth outer surface (Strullu-Derrien et al. 2012). The broad affinities of the arthropod galler forming this distinctive gall remains unknown. From deposits of about the same age, there are 15 distinctive gall DTs described from the Molteno Formation, about half of which are present at the Aas411 site. These and other Molteno galls indicate a variety of galling strategies, in particular the blister gall DT11; the generalized gall DT34 occurring on secondary veins; small, undistinguished hemispherical galls of DT80; elliptical midveinal expansions of DT85; pustulose, surficial galls of DT107; and the large, bulbous and ellipsoidal galls of DT127. Later during the Triassic, a distinctive, irregularly bulbous gall deformed the pinnules of the probable gnetalean host, *Delchellyia gormani*, from the early

Norian Chinle Formation of the Petrified Forest National Park, in northeastern Arizona (Ash 1972, 1997). The culprit of this gall most likely is a tenthredinoid sawfly, based on details of modern sawfly galls (Bird 1926; Meyer 1987; Zinovjev 2006). These Carnian occurrences of new, distinctive, gall morphotypes collectively suggest a major diversification of the galler FFG that expanded the plant hosts and life habits of mites and insects.

14.9.2 Systematics and Biology of Gall DT70

Ichnogenus ***Pustuleon*** Krassilov, 2008

Etymology: From the Latin, *pustula -ae*, meaning a blister or pimple (feminine).

Type species: *Pustuleon gregarium* Krassilov 2008 (in Krassilov et al. 2008).

Diagnosis: "Dense aggregates of minute distinct ostiolate pustules on or near the stronger veins" (Krassilov et al. 2008, p. 81).

Remarks: Krassilov (2008, p. 81) also states: "Aggregates of minute pustules are induced and then used for egg emplacement by eriophyid mites." (Krassilov et al. 2008, p. 84). Additional comments are: "In extant eriophyid mites, a sting by fundatrix may induce a similar cluster of numerous pustules. Vein twisting by the gall is also typical of cecidogenous eriophyid effects. Occasional black fusiform bodies among the pustules … may represent an adult mite (compare fig. 2c in Westphal 1977). However, it must be admitted that interpretation of the interior structures remains ambiguous because of insufficient preservation of the scanned material."

Ichnospecies ***Pustuleon parvicubiculites*** C.C. Labandeira, J.M. Anderson and H.M. Anderson

Etymology: From the Latin, *parvus -a -um*, meaning little or small (neuter); and from *cubiculum –i*, diminutive form meaning a (small) bedchamber or bedroom, often taken to mean any small chamber The gender is masculine.

Holotype: PRE/F/12392-1; this report: Fig. 14.8a,b; Labandeira 2006a, figs. 36, 38.

Description: A variously shaped foliar epidermal gall distributed in small patches, enlarging to a more robust structure that is well developed along pinnular veins and consisting of a pustulose to ragged surface texture; gall edge irregularly confluent with pinnule margin and often with expanded pinnular base; surface pockmarked with miniscule spheroidal chambers typically 0.1–0.3 mm diameter, occasionally breached, exposing inner cavities and significant, embedded hypertrophic and hyperplasic epidermal tissue appearing as a roughened and abraded surface. Gall ontogeny starts as small patches of small pustules often on tips of pinnules that represent immature galls, later growing to larger areas extending to major portions of pinnules, eventually engulfing an entire pinnule, at which time pustules are visibly larger and occasionally marked by extension of galled tissue along the adjacent rachis and colonization of nearby pinnules.

Measurements: Holotype gall 6.7 mm long measured medially from near the base of the pinnule to pinnule tip, and 5.5 mm across the widest portion of the gall near the pinnule tip; pustules ca 0.1–0.2 mm in longest dimension (Fig. 14.8a,b).

Occurrence: Bamboesberg Member (Cycle 1) of the Molteno Formation, assigned to a Late Triassic age (Anderson and Anderson 2003). Although a search for volcanic strata with zircons is ongoing, short of any absolute dates, the precise age of the Molteno Formation and its duration, remains uncertain. Based on global biostratigraphic correlations (Anderson et al. 2007), a generic age of Late Carnian has been established for the Molteno Formation.

There are 167 occurrences of the DT70 gall on *Dicroidium crassinervis* in 12 Molteno localities. The overwhelmingly majority of specimens with DT70 galls exhibit multiple galls per frond or frond fragment. Frequently, galled fronds exhibit multiple galled pinnules that occasionally are connected along an intervening galled rachis. DT70 galls are found in the following Molteno localities, from oldest to youngest: Aas411, with 117 occurrences discussed in this report; Umk111, with four occurrences; Mazenod 211 (Maz211), with one occurrence; Elandspruit 112B (Ela112B), with one occurrence; Kap111, with two occurrences; Klein Hoek 111C (Kle111C), with six occurrences; Klein Hoek 111B (Kle111B), with five occurrences; Peninsula 421 (Pen421), with three occurrences; Cyphergat 111A (Cyp111A), with three occurrences; and Cala Road 111B (Cal111B), with 23 occurrences (see Table 14.1 for site data). DT70 galls have not been documented at fossil localities other than those of the Molteno Formation, although other, structurally different mite galls co-occurring in the Molteno Formation resemble modern eriophyioid galls. There is no preference of the DT70 gall by habitat, as this gall occurs in five of the seven habitats in the Molteno Biome—Sphenobaiera Closed Woodland, Mature Dicroidium Riparian Forest, Immature Dicroidium Riparian Forest, Heidiphyllum Thicket, and Dicroidium Open Woodland—as well as present in one site whose habitat was indeterminate. These habitats are characterized by the presence of *Dicroidium*, especially *D. crassinervis* and *D. odontopteroides*, as the dominant or subdominant taxon.

Assigned Functional Feeding Group and Damage Type: Galling; DT70 (Labandeira 2006b; Labandeira et al. 2007).

Host Plant: *Dicroidium crassinervis* (Geinitz 1876) Anderson and Anderson 1982, comb. nov. (Umkomasiales: Umkomasiaceae), a corystosperm seed fern. The distribution of DT70 is greatest at Aas411, with 117 occurrences, 70.1% of the total for the entire Molteno Biota. DT70 is present at nine other localities representing 48 additional occurrences. The presence of DT70 at sites other than Aas411 range from one to six occurrences per site, with the exception of Cal111B, where it is represented by 23 occurrences, or about half of the total for the non Aas411 associations in the Molteno Biota.

Host-Plant Specificity: Throughout the Molteno Flora DT70 is found almost always on the single host-plant, *Dicroidium crassinervis*, and is given a value of 3, indicating monospecificity, following the host-specialization categories in Labandeira et al. (2007). The monospecific relationship of the DT70 gall on *D. crassinervis* involves an attack rate of 3.82% (3064/117) for the DT70 gall on *D.*

crassinervis at the Aas411 site. Typically, eriophyoid mites are "highly host specific" according to Oldfield (2005, p. 35).

Inferred Culprit: The damage is most consistent with an eriophyoid mite (Acari: Eriophyoidea). Eriophyoid mites have been documented from penecontemporaneous Triassic amber of northeastern Italy (Sidorchuk et al. 2015). Also see remarks below.

Figured Material: DT70 is figured in this report as follows: Fig. 14.8d,e: PRE/F/12351-1; Fig. 14.8f: PRE/F/21923-1; Fig. 14.9a,b: PRE/F/12392-1; Fig. 14.9c: PRE/F/21416-1; Fig. 14.9d,e: PRE/F/12389b; Fig. 14.9f: PRE/12387a-1; Fig. 14.9g: PRE/F/20880a-1; Fig. 14.10a: PRE/F/12387a-1 (different illumination than Fig. 14.9f); Fig. 14.10b: PRE/F/12394-1; Fig. 14.10c: PRE/F/12396a-1; Fig. 14.10d: PRE/F/12396b (counterpart to Fig. 14.10c); Fig. 14.10e: PRE/F/21908a-4; Fig. 14.10f: PRE/F/21908-1; Fig. 14.11a: PRE/F/20880a-1; Fig. 14.11b: PRE/F/21144a-7 (gall detail figured in Fig. 14.12b); Fig. 14.11c: PRE/F/21920b-1; Fig. 14.11d,e: PRE/F/21909-1; Fig. 14.11f: PRE/F/12389a-1; Fig. 14.12a: PRE/F/20883-2; Fig. 14.12b: PRE/F/21144a-7 (photo in Fig. 14.11b); and Fig. 14.12d: PRE/F/21050-2. Previous illustrations: Scott et al. 2004, fig. 2h, erroneously referred to as an "irregular blotch mine"; and Labandeira 2006a, figs. 36 and 38.

Other Material: The DT70 gall occurs in 12 localities within the Molteno Biome, represented by a total of 167 specimens, all of which are found on its host, *D. crassinervis*. The Aas411 site accounts of 117, or 70.1%, of all Molteno DT70 occurrences. With the exception of the Cal111B site which has 23 specimens of DT70, the remaining 10 localities have on average three specimens each. The most commonly occurring habitat supporting DT70 on *D. crassinervis* is Dicroidium Open Woodland. To our knowledge DT70 has not been described from any other Gondwanan site of similar age nor from any other site in the fossil record.

Repository: Palaeobotanical Collections ("Molteno Room"); Evolutionary Studies Institute of the University of the Witwatersrand; Johannesburg, South Africa.

Remarks: The DT70 gall is a histioid gall that results in cellular modification such that an existing, affected organ is histologically changed to produce a new structure of abnormal tissue, typically a gall (Meyer 1987). Histioid galls are classified into cataplasmas or prosoplasmas. Cataplasmic galls have a relatively organized appearance through growth and shape changes, but do not form specific, differentiated tissues (Dreger-Jauffret and Shorthouse 1992). By contrast, cataplasmic galls are less organized than prososplasmic galls, and form anomalous structures from existing tissues by an increase in the number (hyperplasia) and size (hypertrophy) of cells, and often forming one or more layers of parenchymatous cells (Dreger-Jauffret and Shorthouse 1992; Rohfritsch 1992). Accordingly, DT70 is a histioid, cataplasmic gall that did not form an organized, three-dimensional, symmetrical structure, but rather had a disorganized, more two-dimensional configuration of embedded nutritive cells exhibiting a pustulose surface that resulted from mouthpart puncturing of individual cells by arthropods. The arthropod culprits undoubtedly had specialized, piercing and sucking mouthparts consisting of an armature of protractible stylets (Vacante 2016). These punctured cells evidently were transformed into enlarged, bulbous, nutritive cells by salivary secretions of eriophyoid mites that transformed normal tissues of epidermal and parenchymatous cells into abnormal, galled tissues (De Lillo and Monfreda 2004).

With the exception of galls produced by certain gall midge larvae with specialized mouthparts that puncture individual cells (Rohfritsch 1992), there only are three other piercing-and-sucking arthropod groups capable of producing similar cataplasmic, histioid galls: thrips, sternorrhynchan hemipterans, and mites (Rohfritsch 1992). Galls of thrips are open and not sealed structures, but more typically result in leaf folding or curling along the leaf margin, or otherwise have irregular leaf folding with unsightly teratologic forms, including the production of massive peapod-like structures up to 20 cm long (Meyer 1987; Ananthakrishnan and Raman 1989). Sternorrhynchan hemipterans, such as aphids, scale insects, whiteflies and psyllids, also produce cataplasmic histioid galls, but because their stylate mouthparts differ from thrips and mites, they do not pierce shallowly positioned individual cells of the epidermis that result in eventual tissue necrosis. Rather, sternorrhynchan hemipterans have an intercellular stylet trajectory and target deeper seated vascular tissue, principally phloem, for nutrition rather than consuming large nutritive cells at the surface. Sternorrhynchan hemipterans deposit distinctive, mucilaginous salivary sheaths surrounding the puncture marks. Enlarged, bulbous nutritive cells, whose protoplasts are rich in nutrients, form around the punctures on the epidermal surface, but are not teratologically transformed as are thrips-punctured epidermal cells (Westphal 1992). Eriophyoid mites, in contrast to thrips and sternorrhynchan hemipterans, are ca. 10 times smaller and thus target individual epidermal cells during feeding. The piercing-and-sucking feeding style of mites result in abundant nutritive tissue, occurring as excrescences on surface tissue that consist of individual, bloated nutritive cells or enlarged trichomes. Hyperplasia is common and cellular necroses typically ensue after feeding has terminated (Westphal 1977; Larew 1981). Of these three groups of potential culprits—thrips, sternorrhynchans, and eriophyoid mites—the DT70 gall is consistent with a mite galler. Gall midges of the Cecidomyiidae are a remote possibility, but do not extend to the Late Triassic (Nel and Prokop 2006). As well, thrips and sternorrhynchan hemipterans produce considerably larger and differently structured galls that are reflected in the very different feeding habits than those of eriophyoid mites.

In addition to classification as a histioid cataplasmic gall, DT70 also is considered a cover gall. Cover galls form by an inducer, in this case a mite with piercing mouthparts, which provokes a response from its host *D. crassinervis* by producing of hyperplasic and hypertrophic tissue. This tissue proliferation gradually surrounds and covers the gall mites. This is done by the formation of minute chambers, often with limited access to the outside such as through an ostiole (Meyer 1987). It is strongly suspected that the particular type of cover gall DT70 represents is an erineum gall. Erineum galls are provided with enlarged but small nutritive cells, sometimes in the form of expanded trichomes, but whose contents are activated from stylet punctures of individual cells by mites (Larew 1981). Typical live erineum galls appear reddish to pinkish from mites that attack foliage and are characterized by unsightly bulging of tissues and distortions that can spread to other contiguous plant organs (Westphal and Manson 1996). A variety of erineum galls occur on ferns, gymnosperms and angiosperms (Castagnoli 1996), some of which are economically important. Common examples include the fern mite *Hemitarsonemus tepidariorum* on the fern, *Pteris* sp., in California (Pritchard 1951); the pear leaf-blister mite *Eriophyes pyri* on pear, *Pyrus communis*, in Lebanon (Talhouk 1969); and *Aceria dactylonyx*, on hīnau, *Elaeocarpus dentatus*, in New Zealand (Lamb 1953). In particular, foliose mite galls, including erinea, that are morphologically very similar to DT70, prominently include *Eriophyes tetratrichus* on basswood, *Tilia platyphyllos* (Tiliaceae). This mite gall has macroscopic similarities to DT70, exhibiting foliar thickening and puffiness along the leaf margin that apparently migrates inwardly to the leaf median axis as the gall matures (von Schlechtendal 1916; Jeppson et al. 1975).

There are several additional defining features of DT70 on *D. crassinervis*, beyond the description above, and including additional figures (Figs. 14.8d–f, 14.9, 14.10, 14.11, 14.12a,b,d), and unfigured material from Aas411. The DT70 gall occasionally is interrupted by larger, bulbous and spheroidal to ellipsoidal features that often are breached to reveal an inner cavity similar to those mentioned by Larew (1981) and illustrated in his plate 4, figure 6. These structures also are similar to the eriophyoid gall on the dryopteridaceous fern *Nephrolepis* sp. (Nalepa 1909). The larger bulbous structures are interpreted as chambers inhabited by mites, whereas the smaller-sized pustules considerably less than 0.1 mm in longest dimension are interpreted as engorged nutritive cells. These features resemble the meristematic surfaces of some eriophyid pouch galls (Arnold 1965). Another major condition of the gall are upraised surfaces aligned between major pinnular veins. In some instances it appears that the incompletely galled pinnular margins exhibit curling. There is no evidence for enlarged pinnular trichomes containing nutritive protoplasts that many modern mite galls have, possibly attributable to the failure of trichome preservation in all examples of galled *D. crassinervis*. A major defining aspect of the gall is the ontogeny of DT70 that involves gall development progressing through four phases. Early galls are (i), small patches on pinnules (Fig. 14.8g, *grey arrows*); that later enlarge to (ii), broader pinnular patches (Fig. 14.9f, *grey arrows*); to (iii), a condition where the entire pinnule is engulfed by a gall (Figs. 14.8a–f, 14.9a, 14.10c, *black arrows*); and finally (iv), adjacent rachis tissue and nearby pinnules are invaded by the gall (Fig. 14.10a, *black arrow*; Fig. 14.12a), that occasionally undergo rachial bending (Figs. 14.9c,d,f, *red arrows*).

14.10 Discussion

During the late Permian (Lopingian), plant–insect interactions of the earlier Wuchiapingian Stage in Gondwana and Euramerica were moderately diverse, indicated by the Clouston Farm flora in KwaZulu-Natal in South Africa (Prevec et al. 2009) and by the Bletterbach flora in northeastern Italy (Labandeira et al. 2016). For the Clouston Farm site, 9772 plant specimens were assessed, consisting of 23 plant morphotypes, 22 DTs and resulting in a 1.40% level of herbivory, of which 62.5% was generalized and 37.5% specialized (Prevec et al. 2009). The most common insect herbivorized plant was glossopterid morphotype C2a and most pervasive type of insect damage was DT12. For the Bletterbach site, 1531 plant specimens were examined, consisting of 23 plant morphotypes, 16 DTs and resulting in a 1.95% level of herbivory, of which 68.7% was generalized and 31.3% specialized (Labandeira et al. 2016). At Bletterbach, the most common insect herbivorized plant was *Taeniopteris* sp. A, and DT12 was the most prevalent insect damage. The South African and Italian Wuchiapingian floras harbored interactions dominated by the exophytic interactions of hole feeding, margin feeding and surface feeding and much lesser occurrences of the endophytic interactions of piercing and sucking, oviposition and galling. A broad summary for both floras can be expressed as: (i), levels of herbivory were approximately 1.7%; (ii), two-thirds of the interactions were generalized and one-third were specialized; and (iii), the dominant herbivorized plant was a seed plant that had a plurality of DT12 damage (Prevec et al. 2009; Labandeira et al. 2016). The Clouston Farm site, in addition, is notable for a significant amount of oviposition (Prevec et al. 2009), which may express a broader pattern across Gondwanan floras (McLoughlin 2011; Cariglino and Gutiérrez 2011; Labandeira and Currano 2013), that is not present in Euramerican floras.

The Wuchiapingian floras collectively established a baseline level of herbivory that apparently did not change during the Changhsingian Stage of the later Lopingian (Labandeira et al., unpubl. observ.). A sparse, depauperate flora of uppermost Lopingian age, described from the Sokovka site in the Volga Basin of European Russia (Lozovsky et al. 2016), has yielded specimens of the peltasperm *Vjaznikopteris rigida* (Krassilov and Karasev 2008, 2009). At this site specimens of *V. rigida* house a histioid mite gall and a robust, serpentine leaf mine (Krassilov and Karasev 2008), attributable to a beetle and indicating significant endophytic penetration of plant internal tissues immediately prior to the P-Tr ecological crisis. After this Changhsingian prelude was upstaged by the P-Tr event, all available evidence indicates that terrestrial ecosystems were devastated during the ecological crisis (Erwin 2006). This event particularly wreaked havoc on plants (Visscher et al. 1996; Gastaldo et al. 2005), devastated insect lineages (Labandeira 2005; Ponomarenko 2016), and significantly diminished the manifold interactions between these most diverse elements of terrestrial ecosystems (Labandeira and Currano 2013).

In the aftermath of the P-Tr global crisis, former Changhsingian terrestrial ecosystems that were drastically degraded show little evidence of recovery or regeneration during the Induan and Olenekian stages of the Early Triassic. Most plant–insect interactions succumbed to substantial ecological deterioration or otherwise were eliminated. Specialized relationships were especially impacted. Such a conclusion is based on limited, empirical, body-fossil data on Early Triassic plants (Retallack 1995) and insects (Shcherbakov 2000, 2008a; Ponomarenko 2016), but also buttressed by Karoo Basin food-web reconstructions that use trophic network models emphasizing diminished vertebrate ecological response to the P-Tr event that favored generalists (Sidor et al. 2013; Roopnarine and Angielczyk 2007, 2015). This pattern also is consistent with the observation that several major insect lineages experienced extinction at or close to the P-Tr boundary, such as many paleodictyopteroid, odonatopteran and orthopteroid lineages. By contrast, uncommon and inconspicuous lineages such as hemipterans (aphids, psyllids, whiteflies and related forms), coleopterans (beetles) and dipterans (true flies) survived and diversified considerably during the subsequent Triassic (Krzeminski 1992; Shcherbakov 2000, 2008a, b; Béthoux et al. 2005). Significantly, minimal plant–insect associational evidence is available from the Early Triassic Induan and Olenekian stages. The few reports available represent questionable assignment to the Olenekian Stage or describe only a few notable interactions (McLoughlin 2011; Kustatscher et al. 2014). These reports indicate that interactions were more negatively affected than the primary plant and insect extinctions at the P-Tr event. Severe reductions of taxa and improperly functioning ecosystems essentially produced a terrestrial dead zone approximately lasting a 5 million-year-long Early Triassic interval during a very inclement greenhouse world characterized by highly elevated CO_2 levels and temperatures that were excessive in continental interiors (Tong et al. 2007; Krassilov and Karasev 2009; Sun et al. 2012).

During the Middle Triassic there is increasing evidence for a major transformation in the relationships between plant hosts and their insect herbivores. This change began during the Anisian Stage and became more pronounced in the Ladinian Stage. During Anisian times there is an uptick in the number and quality of preservation of vascular plant floras, insect faunas and plant–insect interactions in several regions worldwide, particularly Western Europe. In Western Europe, a major regional flora of Anisian age was the Grès à Voltzia flora from upper Buntsandstein strata of the Röt Formation, located in the Vosges Mountains of northeastern France, with lateral equivalents in western Germany (Grauvogel-Stamm and Kelber 1996). Also in Western Europe, several geographically proximal floras of Anisian age occur in the Dont, Richthofen and Agordo formations from the Dolomites Region of northeastern Italy. Collectively these floras document additional plant communities in Western Europe that harbored a variety of plant–insect interactions prior to the buildup of the Alpine Cordillera (Labandeira et al. 2016). Plant–insect associations from the Italian floras indicate a degree of plant–insect interaction heterogeneity that rival those of Lopingian floras.

It was during the Ladinian Stage that several floras worldwide apparently exceeded the diversity of plant–insect interactions that had occurred during the previous Anisian Stage. This seemingly small but discrete increase in the level of plant–insect interaction activity is evident especially in Western Europe, particularly for Ladinian floras from the Lettenkohle Formation in the Alsace Region of northeastern France, and in the Lower Keuper Formation of Franconia, in south-central Germany. The relevant, plant-yielding beds of the German deposits with insect interactions are somewhat older that those found in France, but both deposits house evidence for some of the same interactions, principally margin feeding, oviposition and galling (Grauvogel-Stamm and Kelber 1996). A similar increase in herbivory also is detected in Ladinian-age floras from the Aquatona, Vulcanites, Fernazza and Wengen formations in the Dolomites Region of Northeastern Italy (Wappler et al. 2015; Labandeira et al. 2016). Compared to nearby Anisian floras of the Dolomites, these pooled Ladinian floras from both regions in Western Europe show elevated percentages of foliage that were herbivorized and a greater proportion of specialized DTs than earlier Anisian floras. Also, some of the earliest examples of leaf mining are absent from the French and German localities, but present in the Italian localities. This presence of leaf-mining DTs in Ladinian northeastern Italy presages expansion of the leaf-mining FFG during the Carnian of Gondwana, as exemplified by Molteno localities such as Aas411.

It was during the Carnian Stage of the Late Triassic that the full recovery and subsequent development of the plant–insect associations apparently becomes evident for the early Mesozoic in the wake of the P-Tr ecological crisis. The prolonged expansion of this plant–insect associational diversity is dramatically manifest in the Molteno Formation of South Africa. In particular, the earliest major deposit of the Molteno sedimentary sequence, the Aas411 site with 20,358 examined specimens, 111 plant form-genera, 14 whole-plant taxa, and representing 10 FFGs, 44 DTs and 11 host-specific associations, displays a qualitative and quantitative quantum increase in associational diversity. In addition, highly diverse, plant–insect component communities were developed, such as the one on *H. elongatum* (Fig. 14.13). Future, additional examination of all 106 plant assemblages in the Molteno Formation as well as earlier Karoo deposits extending to the mid Permian will reveal not only the patterns of insect herbivory within the Molteno Formation based on variables such as site, time, habitat, plant host, FFG, DT, and specialized associations, but also the particularities of response of insect herbivores to the P-Tr ecological crisis approximately 18 million years earlier.

14.11 Summary and Conclusions

This study represents one installment of a continuing study that will examine the consequences of the end-Permian (P-Tr) ecological crisis in the Karoo Basin of South Africa. To partially address this issue, the Aasvoëlberg 411 (Aas411) site of the Late Triassic Molteno Formation was selected in this report to determine the extent and intensity of insect herbivory on all plant material collected toward the beginning of the Molteno depositional sequence. Although preliminary comparisons are made to other, unstudied Molteno localities, the principal focus of this study is to understand how plant hosts, their arthropod herbivores and particularly their shared interactions responded to the ecologically catastrophic events of the P-Tr event approximately 18 million years earlier. Seven general points summarize this study.

1. Response of plant–insect interactions to the end-Permian extinction. Tentative data indicates that by 18 million years after the P-Tr event, herbivory levels were equivalent to or surpassed those of the Late Permian. During the early Carnian Stage of the Late Triassic, insect herbivory had surpassed the level that was established during the Late Permian of southeastern Gondwana and southern Euramerica. This conclusion is based on an evaluation of plant–insect interactions at the Aas411 site from the Molteno Formation, Karoo Basin of South Africa.

2. The spectrum of arthropod herbivory at the Aasvoëlberg 411 (Aas411) site. The Aas411 site has a diverse spectrum and moderately elevated levels of herbivory within the Molteno Biome. At the Aas411 site, 20,358 plant specimens, including foliage, stems and reproductive material was examined representing 111 plant form-genera that includes 14 whole-plant taxa, 11 functional feeding groups (FFGs), and 44 arthropod herbivore damage type (DT) categories and 1127 individual DT feeding occurrences on specimens that were assessed using version 3 of the *Guide to Insect (and Other) Damage Types on Compressed Plant Fossils* (Labandeira et al. 2007). The Aas411 site is one of the more intensely herbivorized localities in the Molteno Biome.

3. The most herbivorized plant hosts at Aas411. The seven most herbivorized hosts at Aas411 are a broad representation of the vascular-plant taxa present at Aas411. Although 39 taxa showed DT evidence of arthropod herbivory on some plant tissue, the seven most herbivorized taxa, in decreasing rank order were the conifer *Heidiphyllum elongatum*; the corystosperm *Dicroidium crassinervis*; the ginkgophyte *Sphenobaiera schenckii*, the peltasperms *Lepidopteris stormbergensis* and *L. africana* and the horsetail *Zonulamites viridensis*. The spectrum of herbivory on these targeted and other less herbivorized plants at Aas411 includes generalized and specialized damage.

4. Specialized insect-herbivore interactions on whole-plant taxon hosts at Aas411. A broad spectrum of generalized feeding damage as well as 11 host-specialized associations were present at Aas411 that targeted 39 of the 111 plant species or morphotype taxa at the site. Host-specialized associations were particular damage types (DTs) of hole feeding, piercing and sucking, oviposition, mining, galling and seed predation that variously targeted whole-plant taxa. The most herbivorized whole-plant taxa with specialized herbivores are: (i), the *Heidiphyllum elongatum–Telemachus acutisquamus–Odyssanthus crenulata* conifer; (ii), the *Dicroidium crassinervis–Fanerotheca papilioformis–?Pteruchus matatimajor* corystosperm; (iii), the *Sphenobaiera schenckii–Sphenobaiera* short shoot–*Hamshawvia longipeduncula–Stachyopitys gypsianthus* ginkgophyte; (iv) the *Ginkgoites matatiensis–Avatia bifurcata– Eosteria eosteranthus* ginkgophyte; and (v) the *Zonulamites viridensis*–nodal diaphragm A–*Viridistachys gypsensis–Paraschizoneura fredensis* horsetail.

5. The *Heidiphyllum elongatum* component community at Aas411. The *Heidiphyllum elongatum* whole-plant-taxon is the most herbivorized plant at Aas411. The component herbivore component community is extensive compared with other highly herbivorized whole-plant taxa at the site and is trophically well balanced across FFGs with arthropod herbivores. This Aas411 plant host contains 81.8% (9/11) of all FFGs (including fungal damage), 63.6% (28/44) of all DT feeding categories, 40.9% (461/1127) of all individual DT occurrences, and 36.4% (4/11) of all specialized interactions.

6. Biology of the mite gall DT70. The gall DT70 has a host-specialized association with *Dicroidium crassinervis* at Aas411. At Aas411, DT70 constitutes 70.1% of all feeding occurrences in the 11 other localities throughout the Molteno Biome where this host-specialist association occurs. The 117 occurrences of DT70 at Aas411 provides sufficient material that allows determination of the plant-host association, anatomical structure, and developmental ontogeny of this distinctive mite gall. This gall is consistent with an assignment to an eriophyioid gall mite culprit.

7. Future work on plant–insect interactions of the Molteno Biome. Future work will evaluate the relationships that the variables of time, habitat, host-plant abundance, insect herbivore abundance, FFG occurrence, DT occurrence and host-specialist associations. Such an assessment will span an interval from the mid Permian to the early Late Permian, including the Molteno Formation. These works will allow better understanding of the evolutionary and ecological dynamics of plant–insect interactions in the wake of the P-Tr event.

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