The "Seeds" on *Padgettia readi* are Insect Galls: Reassignment of the Plant to *Odontopteris*, the Gall to *Ovofoligallites* N. Gen., and the Evolutionary Implications Thereof

THE "SEEDS" ON *PADGETTIA READI* ARE INSECT GALLS: REASSIGNMENT OF THE PLANT TO *ODONTOPTERIS*, THE GALL TO *OVOFOLIGALLITES* N. GEN., AND THE EVOLUTIONARY IMPLICATIONS THEREOF

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ABSTRACT—The Early Permian (Asselian) Euramerican plant *Padgettia readi* Mamay is reassigned to *Odontopteris* Brongniart, as *O. readi* (Mamay) Stull et al. n. comb. Distinctive elongate structures on neuropteroid pinnules of this plant, previously interpreted as fructifications, are herein reinterpreted as foliar histoid galls, structurally analogous to blister or vein galls, and probably induced by an early lineage of hemipterans or mites. These distinctive features are assigned to the new gall ichnogenus *Ovofoligallites* Labandeira, n. ichnogen. n. ichnosp, as *O. padgetti* Labandeira. The Early Permian association between an *Odontopteris* host and *Ovofoligallites* gallers probably originated during the Middle Pennsylvanian as a similar, antecedent association between *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute, and Zodrow and the maker of U-shaped surface features long known as a distinctive, unattributed damage type, but now recognizable as a likely gall. The persistence of this association between the galler and certain medullosan pteridosperms into the Permian adds to the morphological richness of the Permian galler insect fauna. The Permian ecological expansion of galling insects resulted in colonization of new host plants, primarily through a shift from the consumption of entire, mostly pteridophyte axial organs during the Pennsylvanian to the partitioning of seed plant tissues in leaves and small branches in the Permian. The *Ovofoligallites* galler was part of a diverse Permian galler guild involving a variety of plant taxa, organs and tissues that overwhelmingly targeted multiple lineages of seed plants.

INTRODUCTION

PADGETTIA IS a monospecific genus erected by Mamay (1960) based on isolated pinnules of a neuropteroid pteridosperm or seed fern (terms that are used interchangeably) possessing putative seed-like fructifications. Re-examination of these specimens reveals that the previously described seeds actually represent a distinctive type of insect damage similar to late Paleozoic U-shaped surface-feeding lesions that contain necrotic or otherwise histologically altered tissue surrounded by a prominent border of reaction tissue. This distinctive kind of surface feeding has been diagnosed as a Damage Type (DT) 97 (Labandeira et al., 2007), often found on seed-fern taxa during the Pennsylvanian through Permian (Müller, 1982; Beck and Labandeira, 1998; Labandeira, 2006b; Krassilov and Karasev, 2008). While the variously shaped structures described by Mamay (1960) resemble that of DT97, the distinctive damage on *Padgettia* pinnules now is allocated informally to DT239, herein formally recognized morphologically as a new ichnogenus and species: *Ovofoligallites padgetti* n. ichnogen. n. ichnosp. The naming of such ichnogenera is provided for by the latest (fourth) edition of the Code of Zoological Nomenclature (Bertling et al., 2006), including galls (Tubbs, 2003).

Mamay (1960) did not consider that an insect might have been the causative agent of these ovoidal structures. An insect gall would have been an obvious candidate, particularly as a superficially similar insect and possibly fungal damage type, DT97 (Labandeira et al., 2007), occurs commonly on a variety of seed-fern foliage throughout the late Middle Pennsylvanian to Early Permian (Müller, 1982; Labandeira and Beall, 1990) and in the Late Permian (Krassilov and Karasev, 2008) of

Euramerica. However, this distinct type of damage was not well documented at the time and probably not known to Mamay. In addition, it is now well established that various modern gall associations overwhelmingly are species specific, targeting particular organs and tissues and typically occurring in recurring spatial patterns on their host plants (Meyer, 1987; Johnson and Lyon, 1991; Gagné, 1994). This host-plant specificity increasingly has been documented on Permian plants as well (Florin, 1950; Banerjee and Bera, 1998; Beck and Labandeira, 1998; Labandeira and Allen, 2007; Guleva and Raman, 2007; Vasilenko, 2007; Prevec et al., 2009). The "ovoid objects" mentioned by Mamay (1960) also show considerable conformity to a well known type of specialized herbivory, galling. Conspicuous reaction rims (i.e., plant wound responses or cellular proliferations) occur on these ovoidal objects, providing strong evidence that insect damage is present. Furthermore, these structures are variable in shape, size, internal distribution of contents, position, and their effect on adjacent foliar tissues. Ovules embedded in the lamina, or attached to it, as proposed in Mamay's original paper, should have left detectable scars on the leaf surface if attached to the lamina, or, alternatively, be clearly embedded within foliar tissue. Instead, the structures interpreted as ovules or seeds are hollowed-out and extend to the leaf margin, but not beyond. Finally, a pinnule of a typical *Odontopteris* pinna, in Mamay's original Padgett collections, has been found with similar marginal U-shaped disorganized tissue surrounded by reaction rims. When Mamay (1960) considered the origin of these enigmatic structures, virtually nothing was known about Paleozoic plant galls, as indicated by more recent reviews of the topic (Larew, 1992; Scott et al., 1994; Labandeira, 2002). Since the time of these reviews, a significant diversity of

Permian gall material has been documented (Labandeira, 2006a, 2006b), necessitating a reconsideration of the origin of these curious structures.

In addition, the host plant of these distinctive, insect-induced structures is revised. If Mamay's interpretation of these foliar features (now considered as galls rather than seeds) is excluded, the foliar characters shown by *Padgettia readi* Mamay (1960) are similar to those of the pteridosperm genus *Odontopteris* (of the mixoneuroid type) to the extent that this can be determined from disarticulated remains. Nevertheless, the specimens differ from known species of *Odontopteris* in subtle but consistent ways. Therefore, *Padgettia readi* is reassigned to *Odontopteris* Brongniart, as *Odontopteris readi* (Mamay) Stull, DiMichele and Chaney. As a consequence of these changes, the taxonomy of the host plant is emended and a new ichnotaxon for foliar structures, formerly considered as seeds, is erected. These two actions will help to distinguish a distinctive new medullosan leaf type as well as provide an account of a new form of gall, adding to the increasingly diverse inventory of Permian gall morphologies.

THE INSECT GALL

OVOFOLIGALLITES Labandeira new ichnogenus
Figures 1, 2.1, 2.2

Type species.—By monotypy.

Diagnosis.—Flattened ovoidal, ellipsoidal, lenticular, pyriform, or otherwise elongate pinnular structures with a long axis parallel to the major venation of a leaf and characterized by a variously positioned inner chamber and adjacent modified tissue, an encircling rim of plant-host response tissue, and tumescent foliar tissue extending to pinnular margin (Fig. 1).

Etymology.—From the Latin: *ovo*, meaning an egg, *folium*, referring to a plant leaf, and *galla*, signifying a tumor or gall-like structure.

Occurrence.—*Ovofoligallites* n. gen. is known from a single locality in Texas, U.S.A., occurring approximately 3.2 km NW of Padgett in Young County, Texas, U. S. Geological Survey locality 8967 (Mamay, 1960). The stratigraphic position is Lower Permian, within the upper part of the Archer City Formation, below Sandstone 8 (Hentz, 1988), of Asselian age.

Remarks.—In 1960 Mamay put forth the following arguments for his interpretation of *Padgettia readi* as a medullosan fructification. First, approximately 100 ovoidal structures are restricted to the leaves of one plant species, despite the considerable diversity of plants in the deposit. Second, the stereotyped orientation and approximately regular spacing of the foliar structures indicated a reproductive origin rather than the presence of histologically anomalous tissue. Lastly, the shape and size of the ovoid objects are comparable to other small pteridosperm seed types from Permian deposits. From these three categories of evidence, Mamay (1960) concluded that the most parsimonious interpretation of the admittedly unusual structures was that of a seed embedded in the surface tissues of a medullosan leaf that he named *Padgettia readi*. It

now appears that these "seeds" have incongruous features inconsistent with known Carboniferous or Permian seed-plant reproductive structures, and in particular the morphological range of seed morphologies in medullosan seed ferns. As well, the taxonomic affinities of the *P. readi* plant also provide insight into the identity of these seed-like structures. The taxonomic affiliation of *P. readi*, coupled with an evaluation of the Late Carboniferous and Early Permian plant-damage record on earlier medullosan (especially neuropteroid) foliage, now provides a more accurate determination of these curious structures.

OVOFOLIGALLITES PADGETTI Labandeira new ichnospecies
Figures 1, 2.1, 2.2

Diagnosis.—Enclosed ovoid, elliptical or pyriform structures, occasionally U-shaped, from 2.5 to 9.0 mm long and 2.0 to 5.0 mm wide, usually borne one to two, and up to several per pinnule, irregularly spaced in the latter instances. The thickened swellings are oriented lengthwise along the decurrence of lateral veins inclined 20 to 30° to the midrib, always on the pinnule blade, with the rounded, broadest ends oriented toward the midrib, some in contact with midribs, and apparently adnate to and embedded in laminar tissues throughout their length. Swellings surrounded by a prominent ridge of distinctive reaction tissue, often consisting of carbonized material. Some structures have apices that extend as either broad or constricted "beaks" enclosing distinctive necrotic or otherwise altered tissue that terminate acutely near or are abruptly truncated at the pinnular margin.

Description.—Structures numbering approximately 100, distributed on 52 pinnules, varying from one to nine (perhaps 10) per pinnule. Structures flattened, retaining significant three-dimensionality revealing subepidermal emplacement of thickened tissues (Fig. 1); evidence lacking for pedicellate attachment (Baxter, 1978). Structures occur on the lower pinnular surface, frequently concentrated toward the pinnular base, occurring independently at varying intervals along each side of midrib (Fig. 1.1, 1.2, 1.4), not in paired, opposite fashion, never extending beyond the leaf margin, unlike seeds (Cridland and Morris, 1960). Larger, pyriform variants have featureless beak-like apices or constrictions (Fig. 1.1–1.4, 1.5, 1.8, 1.9, 1.11) truncated at pinnular edge (Fig. 1.1, 1.2, 1.4, 1.10, 1.11); smaller variants broadly ellipsoidal lacking beaks or extended necrotic areas toward the pinnular margin (Fig. 1.2, 1.6, 1.7). All structures lack reproductive features such as spores, sporangial tissues, or seed membranes.

Structures consist of four recurring, major features: 1) outer encompassing wall; 2) internal chamber; 3) irregular tumescenses of tissue adjacent to the internal chamber; and 4) histologically altered zone extending as a beak distally toward the pinnular margin (Fig. 1.9), a narrowing (Fig. 1.3), or broader area ending at margin (Fig. 1.5). Structures enclosed by a distinctive bordering wall preserved as a ridge or furrow, in turn, surrounded by zone of altered tissue extending outward to unaffected pinnular tissue. This wall lacks typical, irregular, botryoidal appearance of

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FIGURE 1—The gall *Ovofoligallites padgetti* (Mamay) Labandeira (2012), n. ichnogen. n. ichnosp., corresponding to DT239, on *Odontopteris readi* (Mamay) Stull, DiMichele and Chaney, n. comb., from the Lower Permian (Asselian) locality of Padgett, in north-central Texas. *1*, rephotographed image of *O. readi* (Mamay, 1960), showing nine or possibly 10 galls, and illustrating their variation in size, shape and contents on the same pinnule, USNM 41165a; *2*, camera lucida drawing of specimen in *1*, showing variation in individual gall histology; *3*, camera lucida drawing of the detail in the encircled, upper-right gall in *1* and *2*, exhibiting a central chamber and adjacent nutritive tissue, necrotic tissue extending to the pinnular margin, and an outer, encapsulating wall; the circular structure in the lower left may be a hemipteran scale mark; *4*, counterpart of specimen in *1*, USNM 41165b; *5*, enlargement of two galls with prominent outer walls outlined in the rectangular template at *4*, the top one showing a contracted necrotic zone and the bottom one displaying an extended, necrotic swath; *6*, immature ovoidal galls at top (arrow) and bottom (square outline), USNM 546100; *7*, enlargement of lower-right gall in *6*, showing a thick outer wall and featureless interior; *8*, rephotographed image of *O. readi* of Mamay (1960), showing an urn-shaped gall, USNM 42179; *9*, camera lucida enlargement of encircled gall in (H), displaying a central chamber, surrounding nutritive tissue, and outer wall; *10*, another *Ovofoligallites* gall on *Odontopteris readi*, but bearing a resemblance to U-shaped galls on *Macroneuropteris scheuchzeri* in *2.3* and *2.4*; *11*, two pinnules, rephotographed from Mamay (1960), attached to a rachis at right, with each bearing an *Ovofoligallites* gall, indicated by arrows, USNM 546101. Scale bars: solid=1 cm; striped=1 mm.
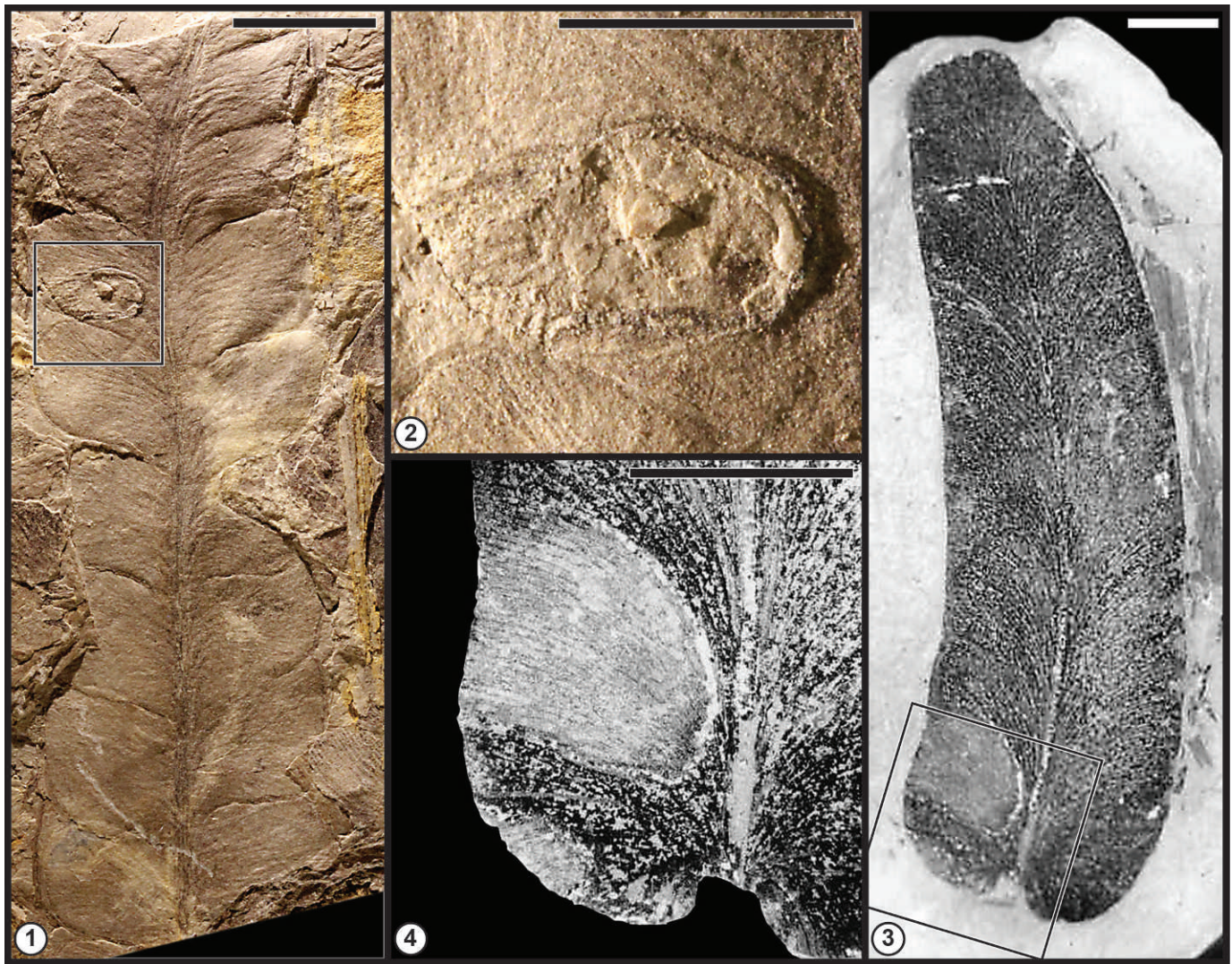
Figure 2—Comparison of *Ovofoligallites padgetti* galls (Mamay) Labandeira (2012), n. ichnogen. n. ichnosp., on hosts other than *Odontopteris readi* (Fig. *1*); *1*, an *Ov. padgetti* gall on a Padgett *Odontopteris* sp. host other than *Ov. readi*, USNM 546102; *2*, enlargement of gall outlined in the square at *1*, showing a thickened outer wall, bulbous internal contents and possible incipient necrotic tissue toward the pinnular margin; *3*, a *Macroneuropteris scheuchzeri* pinnule from the late Middle Pennsylvanian Mazon Creek locality of northeastern Illinois, FMNH PP 31384; *4*, enlargement of U-shaped, gall-like structure (DT97) from the outlined square in *3*, showing a poorly developed outer border, structureless inner contents, and absence of necrotic tissue. Scale bar=10 cm.

callus tissue, appearing well organized as curvilinear structures of relatively constant width (Fig. 1.3, 1.5, 1.7, 1.9). In central part of structure is single, central, irregularly shaped chamber with smooth surface and embayed margins (Fig. 1.3, 1.5, 1.9). Surrounding this chamber are one or more variously shaped clusters of prominent, puffy areas extending to walls (Fig. 1.1–1.5). Between the ovoidal central body and distal pinnular margin is a histologically disorganized area of epidermal and subepidermal tissues.

Etymology.—From the sole locality where this ichnospecies is known at present, Padgett, in Young County, Texas.

Holotype.—USNM-41165a and USNM-41165b, as part and counterpart (Fig. 1.1–1.3). All specimens are deposited in the Paleobotanical Type and Illustrated Collection, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

Material.—Figure 1.1–1.11: USNM-4115a,b; USNM-546100; USNM-42179: USNM-546101; Figure 2.1, 2.2: USNM-546192; and Figure 3: USNM-544639.

Plant host.—*Odontopteris readi* (Mamay) Stull, DiMichele and Chaney (Tracheophyta, Spermatopsida, Medullosales, Medullosaceae).

Occurrence.—*Ovofoligallites padgetti* n. gen. n. sp. is known from a single locality in Texas, U.S.A., occurring approximately 3.2 km NW of Padgett in Young County, Texas, U.S. Geological Survey locality 8967 (Mamay, 1960). The stratigraphic position is Lower Permian, within the upper part of the Archer City Formation, below Sandstone 8 (Hentz, 1988), of Asselian age.

Comparisons.—*Ovofoligallites padgetti* represents a histoid gall in which certain localized tissues are affected rather than entire organs of the plant's axial vascular system. Histoid galls form at the site of gall induction and produce cells that display abnormal histology such as cellular hypertrophy and hyperplasia, forming tumor-like malformations and affecting only particular tissues of an organ (Küster, 1911; Roskam, 1992). Histoid galls affect at most a few local tissue types of an organ and are made typically by holometabolous insects such as sawflies, beetles, wasps, and flies (Meyer, 1987). By contrast, organoid galls are induced at a site remote from gall induction, display a histology of normal cells but otherwise producing abnormal modifications resulting in a more systemic co-optation of the host's
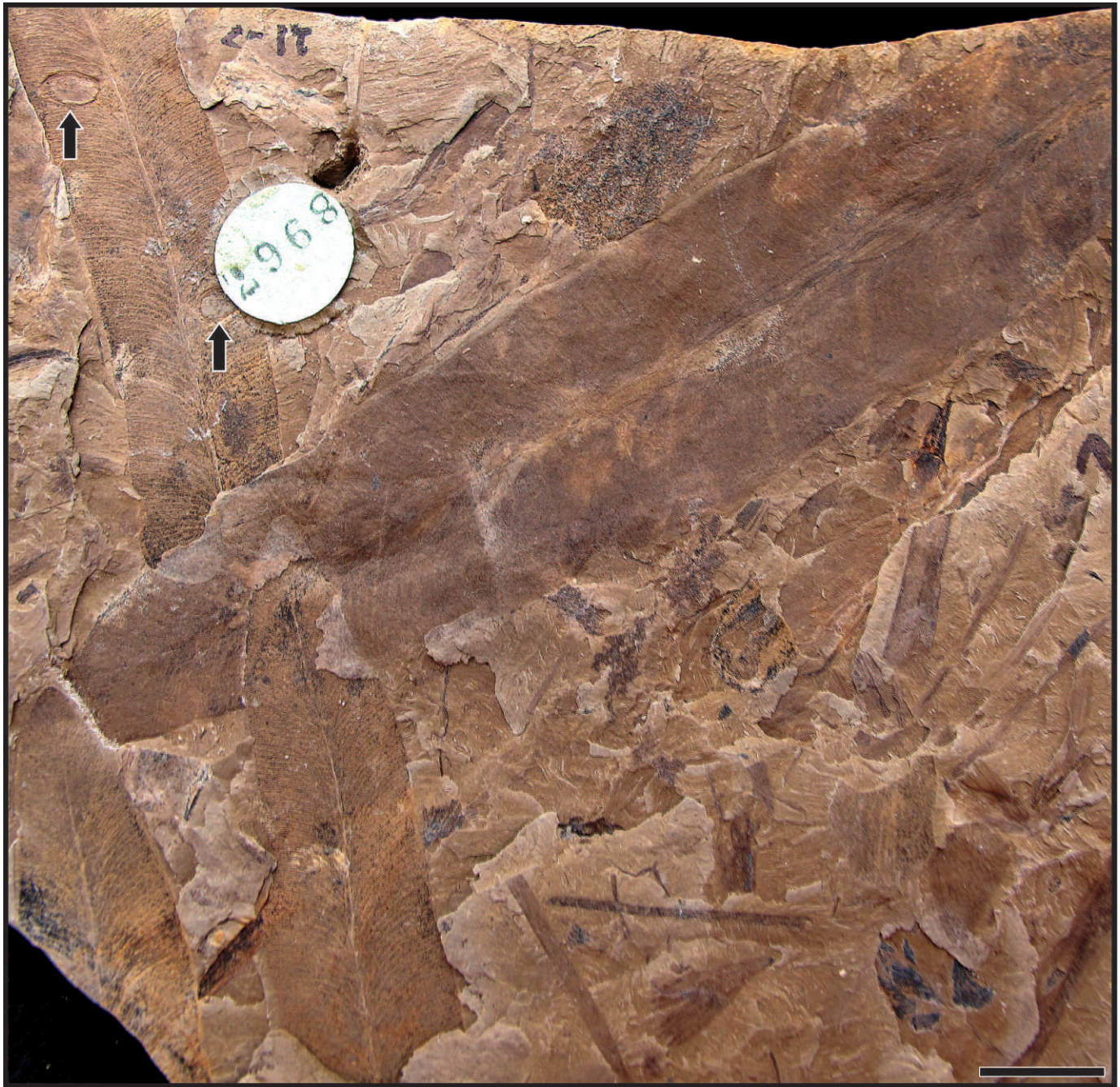
FIGURE 3—*Odontopteris readi* (Mamay) Stull, DiMichele and Chaney n. comb. Several overlapping neuropteroid pinnae/pinnules of the type originally attributed to *Padgettia*. Note coarseness of lateral veins, thickness of midvein, tapering pinna apex and relatively narrowness compared to length. Arrows point to galls of the *Ovofoligallites padgetti* Labandeira 2012, n. ichnogen. n. ichnosp. type, USNM 544639. Scale bar=1 cm.

developmental and metabolic machinery (Küster, 1911; Roskam, 1992). Organoid galls are broad-spectrum galls, such as witches' brooms, formed by fungi, mites and aphids that result in conspicuous, three-dimensional teratologies typically affecting stems and buds (Meyer, 1987). In addition, *O. padgetti* represents a particular type of histoid gall, a prosoplasmic histoid gall in which there is a definite size, shape and differentiation into multiple anomalous tissue layers, in contrast to a cataplasmic histoid gall, which displays amorphous, poorly differentiated galled tissues variable in size and shape (Meyer, 1987). Because of these two, important developmental and morphological gall distinctions—histoid versus organoid galls, and within histoid galls, prosoplasmic versus cataplasmic versions—in addition to

other structural peculiarities, *O. padgetti* can be distinguished from all other fossil galls.

Most Paleozoic and some early Mesozoic galls are organoid in nature and typically are deployed as large tumescenses of the axial portion of the plant, particularly affecting the vasculature and surrounding tissues. Conspicuous organoid galls from the Euramerican late Paleozoic include the Middle Pennsylvanian gall *Acrobulbilites* sp., consisting of large teratological expansions on sphenopsid cones of northern Europe (Weiss, 1876; Thomas, 1969; Van Amerom, 1973); the Late Pennsylvanian gall *Pteridoichnos stipitopteri*, on the basal petiole of a marattialean tree-fern host, consisting of hyperplasic and hypertrophic

alteration of mostly inner parenchyma induced by a holometabolous galler (Labandeira and Phillips, 1996, 2002); and an Early Permian gall, assigned to DT121 (Labandeira et al., 2007), consisting of a distinctive bud gall on vegetative branchlets of a walchian conifer (Labandeira and Allen, 2007), similar to galls of modern aldegid hemipterans on pinaceous conifers (Plumb, 1953). Triassic organoid galls similarly are broadly different from *O. padgetti*, the best example of which is the Middle Triassic "cone gall" on an herbaceous voltzialean conifer (Grauvogel-Stamm, 1978; Grauvogel-Stamm and Kelber, 1996), consisting of petiolar swellings of short axes that give rise to female cones, resembling modern sawfly damage. Other formally described or figured organoid galls from the later Mesozoic and Cenozoic can be separated from *O. padgetti* by noticeable organoid features.

Histoid galls appear in the fossil record during the Permian and, like *O. padgetti*, occur overwhelmingly on seed-plant foliage. The most commonly described foliar galls are small, hemispheroidal, and circular to somewhat ovoidal in outline, of the same regular shape, and display a modest variation in size, indicating a prosoplasmic histoid origin. Such galls are significantly different from the larger ovoidal to elongate-lenticular shapes that characterize *O. padgetti*, and include formally described and informally mentioned galls on various glossopterid leaf taxa of Late Permian age (Pant and Srivastava, 1995; Banerjee and Bera, 1998; Banerjee, 2004; Prevec et al., 2009). A similar prosoplasmic gall, from the Early Permian of Texas (Labandeira and Allen, 2007), is elliptical in shape and occurs in the midveinal area of a peltasperm leaf (Labandeira and Allen, 2007) but, like the above-mentioned glossopterid galls, is different in size, shape, surface texture and position compared to the galls of *O. padgetti*. Similarly, Triassic galls from Gondwana, Euramerica and Angara are morphologically differentiated from *O. padgetti*, such as broom-like galls on the vegetative branches of *Voltzia* conifers from the Middle Triassic of France and Germany (Grauvogel-Stamm and Kelber, 1996; Rothwell et al., 2000); the prominent, bulbous to hemispheroidal pouch galls on distorted leaves of *Dechellyia*, a probable gnetalean seed plant from the Late Triassic of Arizona (Ash, 1997); and the very different, cataplasmic histoid galls on the pinnules on various species of the corystosperm *Dicroidium*, in the Molteno Formation of South Africa, consisting of pinnular irregular thickenings of miniscule chambers that exhibit a pockmarked surface texture, similar to modern erineum mite galls (Labandeira, 2006b). Other gall types on gymnospermous foliage occur from the Jurassic to Early Cretaceous, such as distinctively clustered, hemispheroidal to bulbous to occasionally pedicellate galls of *Wonnacottia* on bennettitalean *Anomozamites* leaves from the Middle Jurassic of Yorkshire, United Kingdom (Harris, 1942, 1969); and notably two small, hemispheroidal gall types from the Jurassic–Cretaceous boundary from the Chita Region of Russia, *Paleogallus porusoformis*, 1–2 mm in diameter on the bennettitalean leaf *Pityophyllum*, and the other, *Paleogallus zherichini*, 2–4 mm in diameter on the leaf of the podocarpalean *Desmophyllum* (Vasilenko, 2005).

For the Late Cretaceous and Cenozoic, various galls on angiosperm hosts have been described, but with one possible exception, none are similar to *O. padgetti*. Lesquereaux (1992) and Berry (1923) provided cursory descriptions of an "oak gall," presumably attributable to a gall wasp inducer and on unknown dicot leaves, from the Dakota Formation of the western United States. However, the morphology of these bulbous, hemispheroidal galls lack any known resemblance to *O. padgetti*. Krassilov et al. (2008) described and illustrated an irregularly shaped, polygonal gall housing an unusually small central chamber, of probable cataplasmic histoid origin, on *Dewalquea gerofitica* (Dobuskina) Krassilov 2005 (Krassilov et al., 2005), from the early Late Cretaceous of Gerofit, Israel. From the same site, Krassilov and Rasnitsyn (2008) erected two ichnogroups, three ichnosubgroups, 10 ichnogenera and 25 ichnospecies of galls, categorized by: 1) whether they represent anomalous proliferation of surface tissues associated with oviposition scars or alternatively are true galls; 2) if the galls are organoid or histoid; and 3) the histoid galls are cataplasmic or prosoplasmic in histological features. The gall morphologies represent 10 basic morphologies: cupulate scars bordered by an encircling callus rim (*Cupleon*); unenclosed pit galls (*Foveon*); minutely chambered, scabrate, pitted galls (*Emergeon*); small, ostiolate, pustulate galls (*Pustleon*); lenticular to fusiform blister galls (*Lenticeon*); nonostiolate, spheroidal, pustular galls (*Cephaloneon*); horned, conical, ostiolate galls that abscise from the leaf surface (*Ceratoneon*); petiolar galls (*Petioleon*); midrib and primary vein galls (*Costaeon*); and leaf-margin roll galls (*Involuteon*). These gall-like structures and true galls are highly host-specific, typically occurring on one host or occasionally on two hosts, and colonizing a variety of early dicot lineages. None of these galls resemble *O. padgetti*. Also dissimilar from *O. padgetti* are highly host-specific, histoid-prosoplasmic, and distinctive galls from the Cenozoic, such as petiolar *Pemphigus* galls on species of poplars (Salicaceae, *Populus*) (Mädler, 1936), representing a significant modern association; and various deciduous cynipid spindle galls, such as *Antronoides*, on species of oak (Fagaceae, *Quercus*) (Waggoner and Poteet, 1996; Waggoner, 1999; Erwin and Schick, 2007), both of which survive as prominent associations in the modern flora (Aoki and Moran, 1996; Russo, 2006). These two later galls, and almost all other documented Cenozoic galls (Scott et al., 1994) lack features that characterize *O. padgetti*, with one exception.

The only described or otherwise figured gall in the fossil record that could be confused with *O. padgetti* is *Mikiola pontiensis* Villalta (1957), a distinctive cecidomyiid (gall midge) swelling on a leaf of the beech *Fagus pristina* Saporta (1867) (Fagaceae), from the late Miocene of Spain (Diéguez et al., 1996). This distinctive gall consists of histoid thickening of epidermal and inner parenchymatic tissues, typical of galls made by some extant gall-midge species of *Mikiola*, such as *M. fagi* Hartig (1839) on *Fagus sylvatica* L. (1753). The broadly lenticular-shaped galls are inclined along the intercostal area between the secondary veins of the central leaf blade region, and do not contact the midrib nor the leaf edge. *Ovofoligallites padgetti* differs from *M. potiensis* in that the former has a much larger, ovoidal central chamber, the distal gall region has a constriction, and the mature gall extends to the leaf margin. It also is notable that the Cecidomyiidae probably had an origin during the Early Cretaceous (Blagoderov and Grimaldi, 2004), postdating *O. padgetti* by ca. 190 million years and the end-Permian extinctions.

Remarks.—The *O. padgettii* structures are interpreted as insect galls on the basis of three essential features: an outermost wall, an internal chamber, and adjacent thickenings of nutritive or similar consumable tissue. In addition, these features bear evidence of plant response in the form of a disorganized, necrotic area "downstream" of the primary supplying vasculature, toward the pinnular margin that reveals plant-host containment of the gall.

The three reasons offered by Mamay (1960, p. 54) in support of the fructification interpretation of the U-shaped structures on the pinnule surfaces also equally support a gall interpretation. The first of these reasons was the "…complete restriction [of these features] to one species of plants in a reasonably diverse flora…." Insect galls are widely understood to be overwhelmingly host specific and are typically confined to particular organs and often

tissues of their host plants (Johnson and Lyon, 1991; Gagné, 1994). Consistent with this assertion of Mamay's and with the taxonomic reassignment of the suite of Padgett specimens to one species of *Odontopteris*, inspection of the larger Padgett collection did uncover a specimen of a pinnate pinna of *Odontopteris readi* (Fig. 2.1, 2.2) that bears *Ovofoligallites padgetti* marginal damage, although it is noteworthy that the vast majority of damage is confined to the neuropteroid pinnules of *O. readi*.

Secondly, Mamay mentioned that the "... strict conformity of the long axes of the objects with the decurrence of the lateral veins of the supporting pinnules indicates a preferential orientation along the ultimate vascular strands." Whereas Mamay correctly suggested that reproductive tissues such as ovules are necessarily connected to a vascular tissue supply, such a nourishing role also is true for galls (Meyer, 1987). Insect galls on plants require continual input of nutrients, lipids, essential elements, and other fluids from vascular tissue necessary to produce tissue consumed by developing gall occupants. This delivery system involves hormonal control by the insect galler of the plant host's developmental machinery, including in many instances the production of nutritive tissue, an anomalous tissue mimicking meristematic growth, consumed by the subadult gall occupant. Thirdly, Mamay suggested that the "...shape of these structures is seed-like and their size is comparable to that of any number of smaller pteridospermous seeds." However, the highly variable size, shape and arrangement of these structures and their internal features are within the typical range of foliar galls among a wide variety of candidate arthropod galler groups, including eriophyoid mites; hemipterans comprising aphids, adelgids, phylloxerids and psyllids; thrips; sawflies; and perhaps beetles (Meyer, 1987; Johnson and Lyon, 1991), all of whose ancestral lineages were present during the Permian (Labandeira, 1998, 2006b, 2011; Shcherbakov, 2000, 2008). Also noteworthy are the gross and subtle morphological aspects found in these structures. If these were seeds, both a greater uniformity in size as well as consistency of fine morphological details would be expected. By contrast, galls typically are more morphologically variable, given their more complex origins and expression of variably deployed patterns of plant-host reaction. Lastly, the apices of the presumptive seeds are abruptly truncated along the leaf margin, a feature mentioned in passing by Mamay. Such a termination suggests a cecidogenous origin, as most shallow-tissue galls, such as blister galls and vein galls, do terminate at the leaf edge, whereas projecting seed structures would be expected to extend beyond the leaf margin without interruption (Cridland and Morris, 1960).

The variability of these morphological features (Fig. 1) and the high sample size of *O. padgetti* galls suggest a developmental sequence. Cecidogenesis commenced as small, ovoidal, walled galls lacking clear differentiation of internal features and the absence of adjacent necrotic tissue (Fig. 1.6, 1.7). This was followed by histogenesis of several clusters of anomalous tissue occurring next to a variously positioned chamber with limited production of necrotic tissue (Fig. 1.5 top, 1.9, 1.11 bottom). The process ended with the largest, most elongate galls characterized by robust development of a wall and extension to the pinnule margin of a broad swath of disorganized host-plant tissue (Fig. 1.1, 1.2, 1.5 bottom). These phases of cecidogenesis parallel those of many modern insect galls (Meyer, 1987).

The morphology, association with a particular host plant, and physical location on the plant organ strongly suggest that these ovoid structures are insect galls, herein described as *Ovofoligallites padgetti*, and permit attribution to a modern gall type, though less reliably to a specific galler clade. Of the wide variety of gall morphologies present in a variety of habitats, both modern (Meyer, 1987; Johnson and Lyon, 1991; Gagné, 1994) and fossil (Larew, 1992; Scott et al., 1994; Labandeira, 2002; Labandeira et al., 2007), there are two obvious gall types to which *O. padgetti* bears closest resemblance. One is a foliar blister gall, commonly formed by mites, aphids, sawflies and gall midges (Nyman et al., 2000; Maia and Fernandes, 2004; Stireman, 2009), which usually consists of puffed epidermal tissue and anomalous hyperplasic and hypertrophic proliferation of relatively shallow tissue, such as palisade parenchyma, all of which may be encapsulated by a variously hardened response tissue, such as corky parenchyma (Meyer, 1987; Johnson and Lyon, 1991). A second attributable gall type is a foliar vein gall. Histologically deeper-seated vein galls occur along the primary and especially secondary veins of leaves where the vasculature and surrounding tissue is galled, expressed on the surface as an elongate, often ellipsoidal, epidermal thickening that follows a secondary vein course and extends on each side of the vein (Yukawa, 1978; Johnson and Lyon, 1991). Vein galls are significantly thicker than the ungalled leaf blade and are prominent; like the reaction tissue of mature blister galls, they would be expected to be highly recognizable if fossilized. Although blister and vein galls are made by a wide variety of extant organisms, and occasionally fungi, it was especially mites and hemipteroid insects that were the likely fabricators during the Early Permian. The most likely culprit was an early ancestral lineage of Hemiptera that currently encompasses aphids, scale insects, whiteflies, and psyllids, or alternatively, and more remotely, eriophyoid mites (Labandeira, 1998, 2006b). A hemipteran or a mite culprit for the gall would be consistent with the absence of coprolites or chewed tissue fragments in *O. padgetti* gall chambers, indicating that the fabricator was not a mandibulate insect.

THE HOST PLANT

Division TRACHEOPHYTA
Class SPERMATOPSIDA
Order MEDULLOSALES
Family MEDULLOSACEAE
Genus ODONTOPTERIS Brongniart
ODONTOPTERIS READI (Mamay) Stull, DiMichele and Chaney
Figures 3–6

Basionym.—*Padgettia readi* Mamay (1960).
Diagnosis.—Fronds at least twice pinnate. Ultimate pinnae bearing pinnules with varying degrees of lateral fusion, completely free to completely fused. Free pinnules from 5 mm high × 4 mm wide to 12 mm high × 8 mm wide. Small free pinnules with straight, nearly parallel, lateral margins, broad, slightly rounded apices and broad basal attachments to pinna rachises. No midvein, all veins originating from common strongly decurrent basal vein inserted in pinna rachis at pinnule base. Veins strongly upwardly arced, in lower third of length and then sub-perpendicular to pinnule margin, forking two, rarely three times, meeting pinnule margin in upper two-thirds, majority reaching rounded apex. Large free pinnules with subparallel to slightly convex lateral margins, broadly triangular apex, broad, attachment to pinna rachis with both basipetal and acropetal constriction. No midvein. Veins entering pinnules in central and basiscopic portions at several points, resulting in concentration of veins in middle portions. Veins in acroscopic half of laminae proceed more directly to pinnule margins than those in basiscopic half, which are more curved. Veins fork up to four times and contact pinnule margins along entire lengths. Pinnae terminate with various degrees of pinnule fusion, leading to small undifferentiated terminal pinnules or elongate neuropteroid pinnules. Large neuropteroid pinnules caducous, mostly
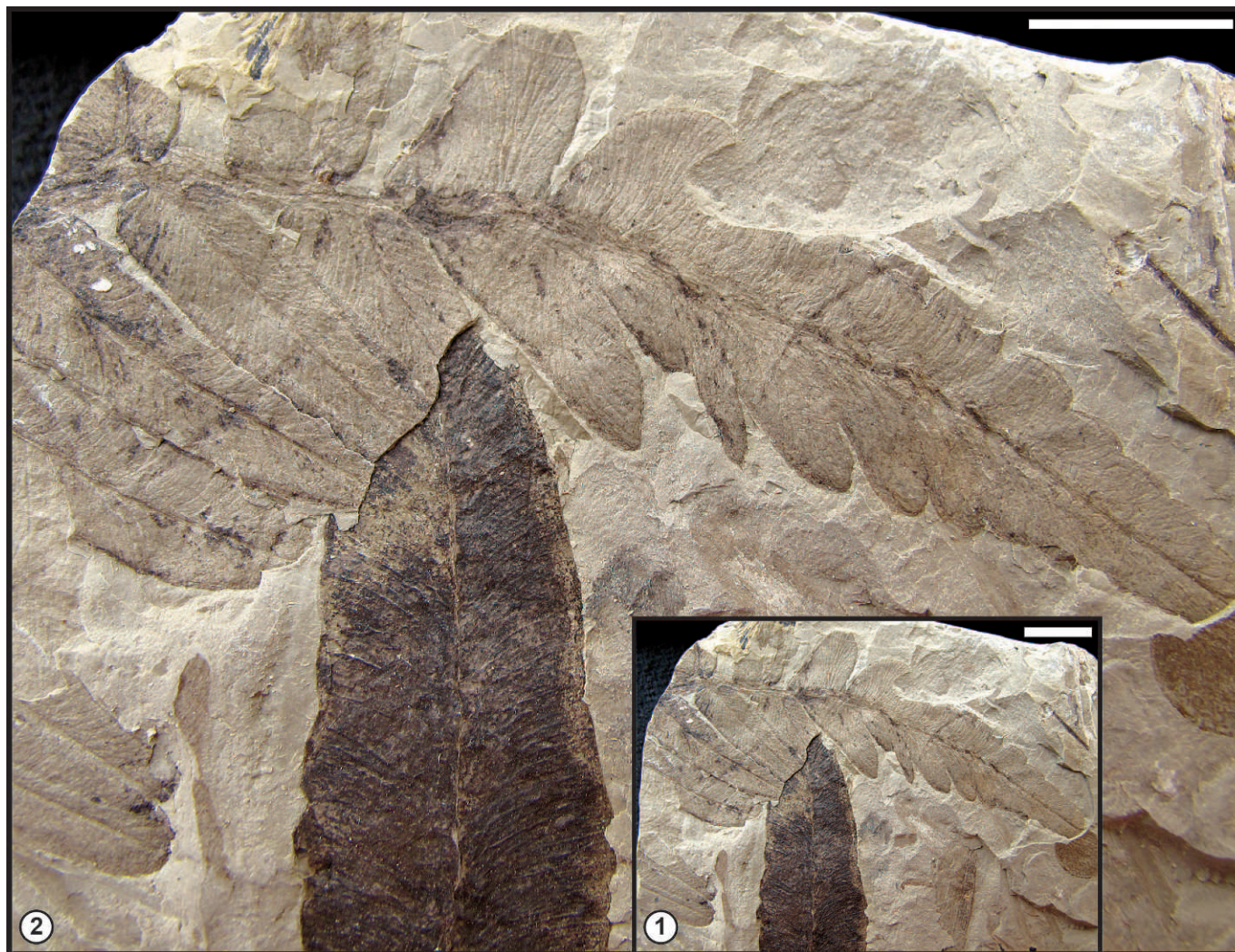
FIGURE 4—*Odontopteris readi* (Mamay) Stull, DiMichele and Chaney n. comb., two specimens, USNM 544633. *1*, natural size; *2*, ×3 magnification. Upper specimen is a pinna bearing elongate, neuropteroid pinnules that become more typically odontopterid toward the apex. Lower specimen is a larger neuropteroid pinnule with slight undulations of a generally entire margin. Scale bars=1 cm.

isophyllous, variable in length, <1.5 cm to >12 cm, and width to 3 cm wide, with entire margins and cordate bases, rarely lobed at base or bearing paired, opposite, basal ovoid pinnules. Laminae taper gently to apices varying from bluntly to sharply acute. Pinnule midribs to 3 mm wide, finely striate, extending nearly to pinnule apices. Lateral veins decurrent, depart midrib at an angle of approximately 30°, arching, becoming sub-perpendicular by laminae midpoints to meet pinnule margins nearly perpendicularly, usually forking once within a short distance of midribs. Leaf surfaces may bear short, irregularly directed adpressed hairs most commonly on abaxial sides.

Description.—The specimens from the Padgett locality in Texas are fragmentary remains of once larger fronds. It is virtually impossible to reconstruct the frond, with any confidence, from such material, and the property is no longer accessible for additional collection. Thus, the taxonomic determinations made here must be a hypothesis—not only that there was a biological species in the Early Permian that bore leaves of the type assigned to *Odontopteris readi*, but that the various disconnected pinnae and frond bits of the forms illustrated and described herein belong to this same species.

In his original description, Mamay (1960) provided a combined generic and specific diagnosis, a practice that makes descriptions of new species difficult, essentially requiring re-diagnosis of the genus. It also turns species emendation into an effective re-diagnosis. The practice of combined generic-specific diagnoses should be discouraged. Mamay (1960) also did not link the morphologies of the large, mixoneuroid pinnules, on which insect damage is prominent, to the more typically odontopterid pinnae and their somewhat falcate, broadly attached, decurrent pinnules, describing the plants (p. 53) as having "large neuropteroid pinnules... apparently isophyllous, long (12 cm or more) and relatively narrow (to 3 cm wide) with entire margins and cordate bases". On this basis, Mamay (1960) concluded conservatively that the fronds were at least once pinnate.

Within the larger Padgett collection, a specimen typical of *Odontopteris* (Fig. 2.1) was discovered with an *Ovofoligallites padgetti*-type gall (Fig. 2.2), identical in form to the kind found on the large, neuropteroid pinnules upon which the genus *Padgettia* was based. This ultimate pinna bore small, bluntly rounded pinnules and raised the possibility that the original *Padgettia* specimens were, in fact, part of a morphologically variable *Odontopteris* frond, possibly terminal pinnules of lateral pinnae or from terminal parts of the frond where pinnule fusion had taken place. Morphological variability of this kind is known
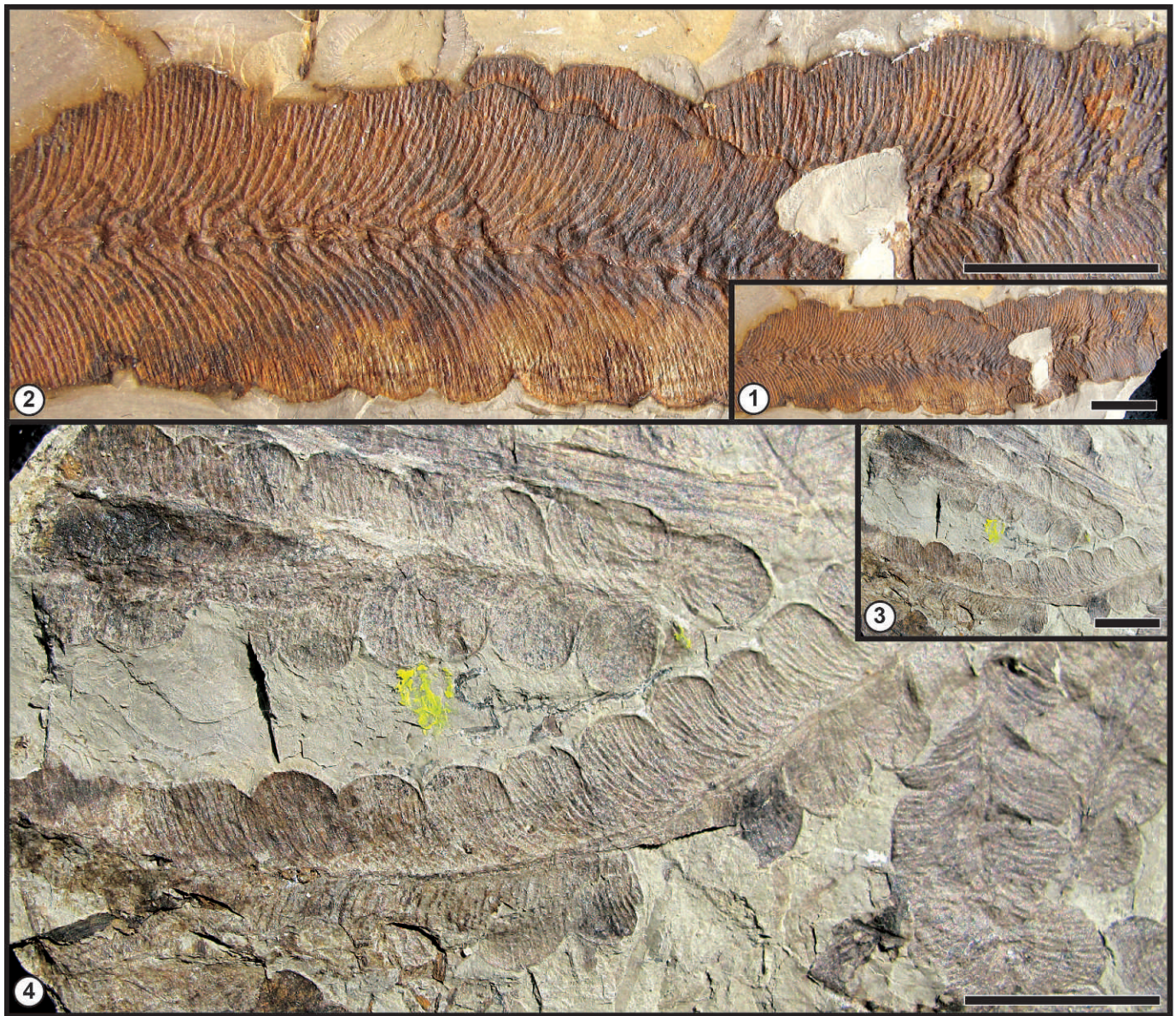
FIGURE 5—*Odontopteris readi* (Mamay) Stull, DiMichele and Chaney n. comb. *1, 2*, two overlapping pinnae with slight marginal lobing, USNM 544638; *3, 4*, pinna with deeply incised margins that define confluent, but relatively distinct pinnules, USNM 544632. Scale bars=1 cm.

in many *Odontopteris* species (e.g., Barthel and Amelang, 2011). In the Padgett collection, a continuum is found in shape from neuropteroid pinnae with entire margins to pinnae consisting of entirely free odontopterid pinnules, illustrated in Figures 3 through 7. This series begins with the typical "*Padgettia*" of the type originally described by Mamay (1960) (Fig. 3). Figure 4 illustrates a pinna composed of small, but tongue-shaped pinnules, with an elongate, terminal portion composed of progressively more fused pinnules, becoming more odontopterid in shape closer to the apical area. Some of the larger pinnae show marginal undulations, as illustrated by two overlapping pinnae in Figure 5.1 and 5.2. These marginal undulations become deeper in other pinnae (Fig. 5.3, 5.4), revealing more odontopterid pinnule shapes of a somewhat rounded form with broad, flat apices. Continued lobing leads to mostly free but still basally fused pinnules (Fig. 6.1). Ultimately, pinnae bearing free pinnules can be found, with broad but slightly constricted bases that are weakly confluent (Fig. 6.2) or completely free and distinct (Fig. 7). In all

of these forms, the venation is essentially the same: coarse, relatively sparse, somewhat fasciculate, and extending to the distal margin of the pinna or pinnule. This is illustrated in a series of camera-lucida line drawings (Fig. 8) that follows the same trajectory as illustrated in the photographic plates, beginning with typical "*Padgettia*"-type pinnules of various widths, some with slight marginal undulation (Fig. 8.1–8.4), then showing various degrees of pinna to free pinnule transition (Fig. 8.5–8.9).

Etymology.—Mamay (1960) named the species in honor of Charles B. Read, paleobotanist with the U.S. Geological Survey.

Holotype.—USNM 41165a and USNM 41165b, as part and counterpart (Fig. 1.1, 1.4). All specimens are deposited in the Paleobotanical Type and Illustrated Collections, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

Occurrence.—*Odontopteris readi* is known from a single locality in Texas, U.S.A. This location was given in Mamay (1960) as lying approximately 3.2 km NW of Padgett in Young County, Texas, as U.S. Geological Survey locality 8967. It is
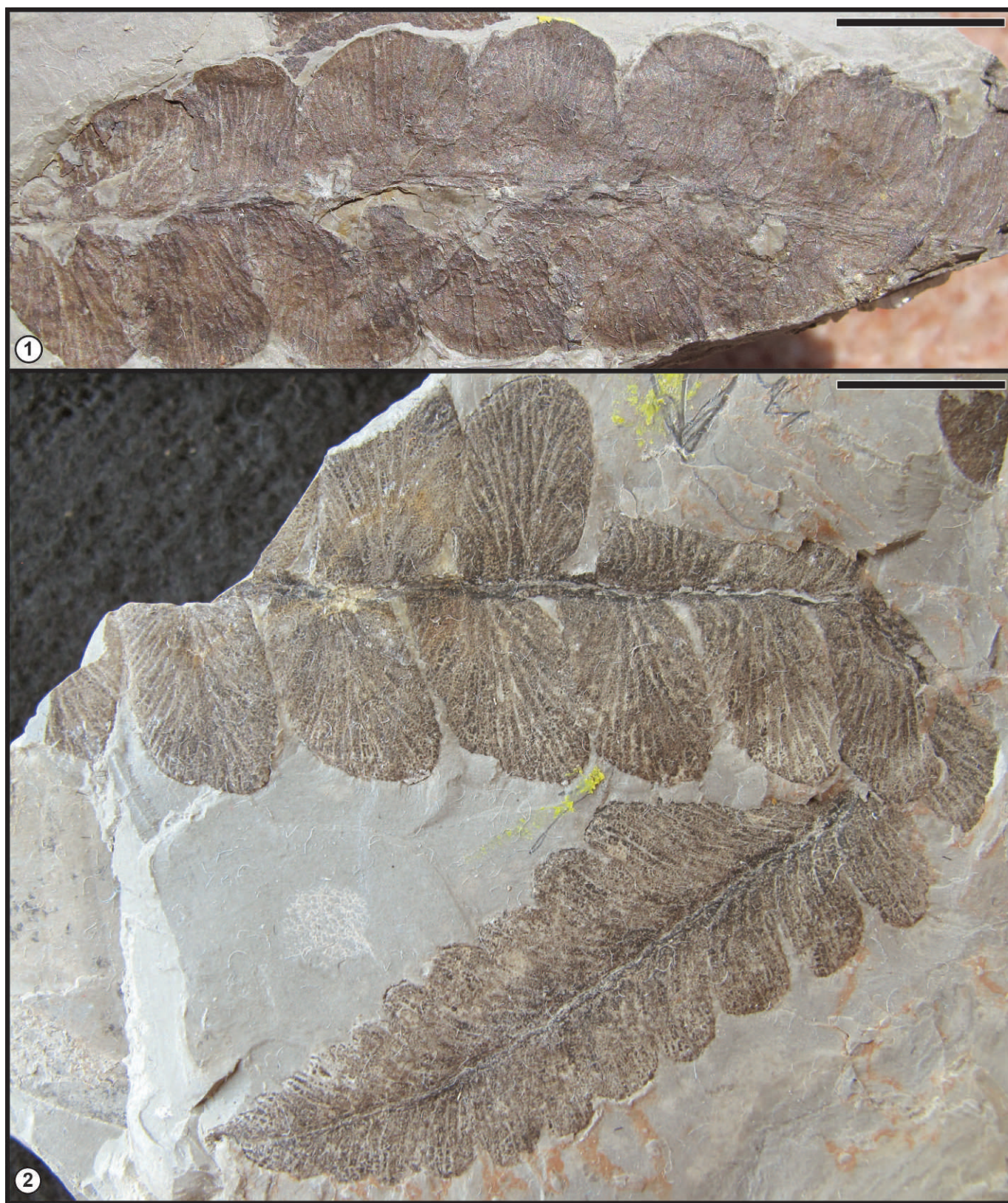
FIGURE 6—*Odontopteris readi* (Mamay) Stull, DiMichele and Chaney n. comb. *1*, pinna with confluent pinnae, USNM 544636; *2*, pinna with free pinnules (top specimen) showing slight basal confluence, and pinna (lower specimen) of same order with pinnules fused in proximity to the pinna apex, USNM 544637. Scale bars=1 cm.
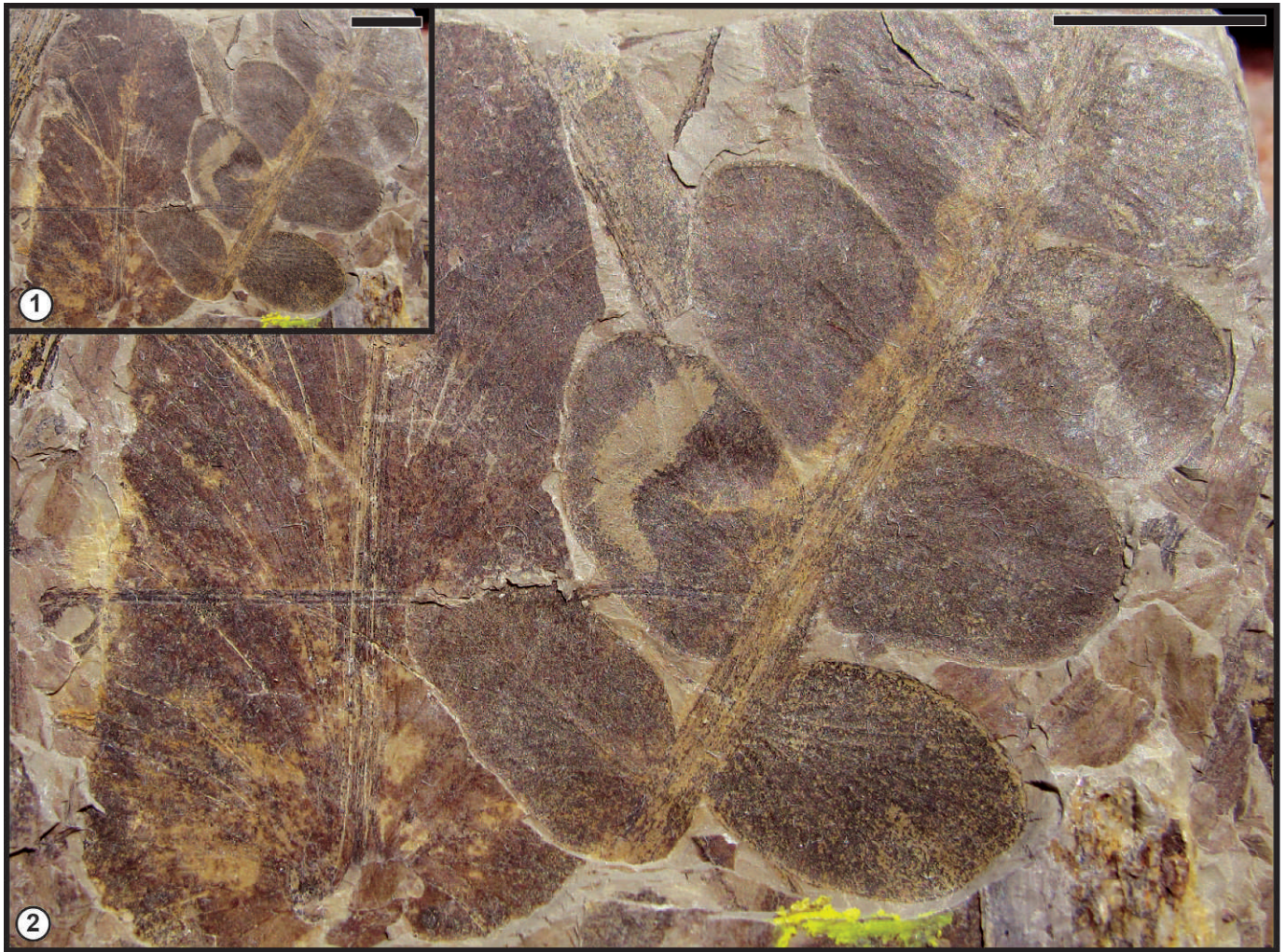
FIGURE 7—*Odontopteris readi* (Mamay) Stull, DiMichele and Chaney n. comb., USNM 544635. *1*, natural size; *2*, ×3 magnification. Pinnae (right-hand specimen) with completely free pinnules of odontopterid aspect. Note constricted base and rounded shape. The left hand specimen is an entire, large neuropteroid pinnule with thick midvein, sparse, coarse lateral venation and entire margin. Note the cordate base. Scale bars=1 cm.

stratigraphically in the Lower Permian, at the time assigned to the Moran Formation, of Asselian age. In the revised stratigraphic terminology of Hentz (1988), the Padgett locality is in the upper part of the Archer City Formation, below Sandstone 8.

Remarks.—When considered in terms of this pattern of variability in form, *Odontopteris readi* compares closely with several species of *Odontopteris* from the latest Pennsylvanian and Early Permian of equatorial Pangaea, variously classified as part of the *Mixoneura* Weiss group of odontopterids. There is considerable confusion surrounding the use of the name *Mixoneura*, however, a matter that is cogently discussed in Wagner and Castro (1998). Laveine and Delbecque (2011) argue for a natural biological distinction between *Odontopteris* and *Mixoneura* on the basis of frond architecture. However, as they note, this complex is in need of detailed taxonomic revision. The name *Odontopteris* was chosen for the Padgett material, in part because of the present state of understanding of *Mixoneura* and, in part, because of the fragmentary nature of the specimens, preventing reconstruction of the frond architecture.

The species to which *O. readi* compares most closely include *Odontoperis lingulata* Goeppert and *O. subcrenulata* Rost, which are possibly synonymous. These species are characterized by pinnule shape variation similar to that of *O. readi*, including forms intermediate between more typically pinnulate pinnae and

entire-margined, neuropteroid pinnae. Free to basally confluent pinnules are mostly rounded and often with squarish apices; entire margined, neuropteroid pinnae have wide, well marked midveins. Venation, however, appears to be considerably finer than that typical of *O. readi* specimens. Furthermore, in the Padgett population of *O. readi* specimens, no pinnae were found that show a clear transition from free or mostly free pinnules to large terminal pinnules of neuropteroid aspect, which implies that such transitions may have been disposed differently in *O. readi* than in these other species, or that the *O. readi* frond might have been small and zones of such transitions limited or non-existent.

The morphological variation proposed here to exist in *Odontopteris readi* may find a parallel in *Odontopteris schlotheimii* Brongniart, recently redescribed by Barthel and Amelang (2011), who propose frond dimorphism, possibly sexual in origin, between polleniferous and ovuliferous plants. The nature of the variation in shape that they illustrate for this species is similar to that seen in *O. readi*. The similarity extends to details such as the coarseness of the venation, the strong differentiation of pinnule-bearing pinnae and entire, neuropteroid pinnae, strong midveins in neuropteroid pinnae, and the presence of "intermediate" forms with various degrees of marginal undulation. Free pinnules of *O.*
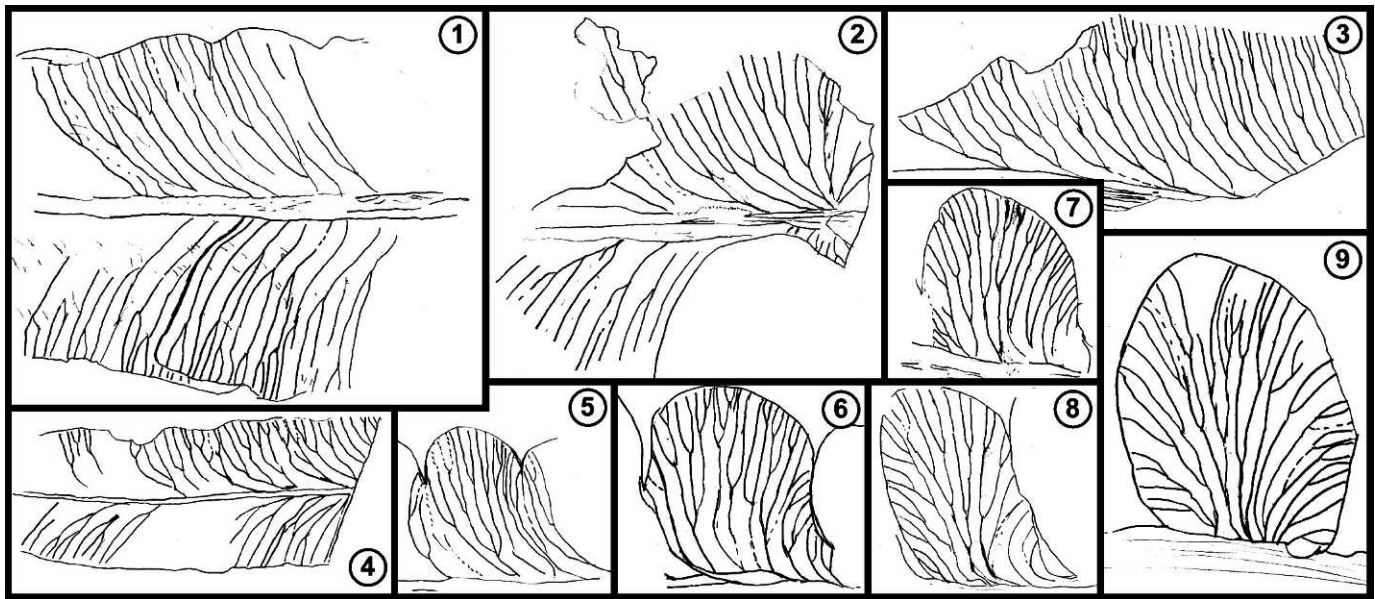
FIGURE 8—*Odontopteris readi* (Mamay) Stull, DiMichele, and Chaney n. comb. Series of camera lucida drawings of the venation of proceeding from neuropteroid pinnae with entire margins, progressively through neuropteroid pinnae with undulate to lobed margins to free pinnules. In all specimens, the venation shows the same pattern of coarseness, and multiple, upwardly directed vein bifurcations. *1*, USNM 544634; *2*, USNM 544630; *3*, USNM 544631; *4*, USNM 544633, Figure *4.1*, *4.2*; *5*, USNM 544632, Figure *5.3*, *5.4*; *6*, USNM 544636, Figure *6.1*; *7*, USNM 544633, Figure *4.1*, *4.2*; *8*, USNM 544637, Figure *6.2*; *9*, USNM 544635, Figure *7.1*, *7.2*. All magnifications ×3.

schlothemii, however, are somewhat more angular than those of *O. readi*, which tend to be rounded in most forms of development.

There are other species that belong in this mixoneuroid group of plants, at least based on the spectrum of variation displayed by their dispersed remains. This includes such forms as *Odontopteris gimmi* Remy (Wagner and Castro, 1998), *Mixoneura wagneri* Lorenzo (Castro, 2005), and *Odontopteris pseudoschlothemi* de Maistre (Doubinger et al., 1995). These all differ from one another and from *O. readi* in various details regarding the shape of pinnules, the commonness of specimens displaying transitions from pinnulate pinnae to entire-margined neuropteroid pinnae/pinnules, and aspects of venation.

In his original description of *Padgettia*, Mamay (1962) noted that his new plant "bears a close resemblance to *Neuropteris permiana* Sellards (1908) . . . and the two species would possibly be regarded as conspecific if the fructifications of the Padgett material were not known" (p. 55). Sellards (1908) original description of this Early Permian species is accompanied only by line drawings, which show large, neuropteroid pinnules with an unusually strong midvein that goes all the way to the pinnule apex, relatively coarse lateral venation that curves steeply to meet the margin, a cordate base without transition to small, free pinnules, and entire margins. The pinnules are described as long and sloping gradually to an obtuse apex. This certainly appears to be similar to the non-divided pinnae/entire pinnules of *Odontopteris readi*. In addition, Sellards (1908) also describes and illustrates, as *O. reichiana*, an *Odontopteris* of typical aspect in the same flora as the large pinnules—the Banner City locality in the Wellington shales (Wellington Formation). Based on the illustrations, the pinnules of this plant are somewhat more angular than those of *O. readi*. Yet, the entire suite from this locality suggests the possibility of a mixoneurid odontopterid not unlike *O. readi*, if not identical to it. Unless better material can be obtained of both *O. readi* and *N. permiana*, this matter may be impossible to resolve further.

Sellards' (1908) attribution of mixoneurid-like material to *Neuropteris* brings to mind a more distant comparison between *Padgettia readi* and similar neuropterids, in this instance *Macroneuropteris scheuchzeri*, a specimen of which is illustrated in Figure 2.3, and is important in the context of this paper because of the nature of arthropod damage it demonstrates (Fig. 2.4). *Odontopteris readi* is vaguely similar to *M. scheuchzeri* in several features (illustrated in Figs. 1.10, 3, 4), including the large pinnule size in many specimens, elongate pinnule shape, generally much longer than wide, the bluntly acute apices, a midrib that runs nearly to the pinnule apex with arching lateral veins, and surface hairs (Laveine and Legrand, 2008). However, the pinnules of *O. readi* (Fig. 1.10, 3, 4) can be far more elongate than reported for any *Macroneuropteris* Cleal, Shute and Zodrow species and narrow relative to their length. The pinnule midveins are wide, more than 3 times wider than is typical of virtually any medullosan, and are solid in appearance, not a bundle of independent fine veins (Fig. 1.10, 3). The lateral veins are relatively heavy and sparse (Fig. 5). In addition, the surface ramentum is different from that of *M. scheuchzeri*, consisting of variably dense, nearly triangular hairs directed mostly toward the margins, rather than the fine, elongate, apically directed hairs typical of *M. scheuchzeri* (Darrah, 1969; Cleal et al., 1990; Laveine and Behlis, 2007).

DISCUSSION

The reassignment of *Padgettia* to *Odontopteris* reduces the number of plant genera thought to be endemic to western North America and provides another link with the Permian equatorial regions of central Pangaea. In addition, the *Ovofoligallites* gall is of particular importance when considering the expansion of the galler insect functional feeding group during Permian time. Thus, the reassignment of *Padgettia readi* to both a new host-plant as well as to a new type of gall has implications that extend beyond taxonomy and systematics, providing insight on biogeography and the ecological context of plant–insect associations during the late Paleozoic.

Although previously unrecognized in the Paleozoic (Larew, 1992; Scott et al., 1994), insect galls have been documented

from Pennsylvanian (Van Amerom, 1973; Labandeira and Phillips, 1996, 2002) and especially Permian (Pant and Srivastava, 1995; Banerjee and Bera, 1998; Beck and Labandeira, 1998; Labandeira, 1998, 2002, 2006a; Guleva and Raman, 2007; Labandeira and Allen, 2007; Labandeira et al., 2007; Krassilov and Karasev, 2008; Prevec et al., 2009) deposits. This recent flurry of documentation contrasts with older references that mentioned unusual teratologies for plant tissues that were unexplainable based on known plant anatomy (Florin, 1945; Thomas, 1969), and before insect damage had become a widely recognized phenomenon in late Paleozoic plants. Some of these older reports now have been reinterpreted as galls (Van Amerom, 1973; Labandeira and Allen, 2007), but also there have been new descriptions of galls based on the discovery of additional fossil deposits. In the Permian, several types of galls now have been documented on a variety of plant hosts. Examples include the cone-mimicking bud gall on shoots of the conifer *Walchia piniformis* Sternberg (Florin, 1945; Labandeira and Allen, 2007); small, circular galls on *Glossopteris browniana* Brongniart (Banerjee and Bera, 1998) and other glossopterid leaves (Prevec et al., 2009); elongate, midrib galls on the leaves of the callipterid *Autunia conferta* (Sternberg) Kerp (Labandeira and Allen, 2007); smooth-walled lenticular and tiny, irregular pock galls on the probable peltasperms *Vijanikopteris rigida* Naugolnykh and *Pursongia* sp. of Russia (Vasilenko, 2007; Krassilov and Karasev, 2009); and perhaps blister-like, epidermal "Runzelgallen" on the medullosan *Odontopteris* sp. from Germany (Potonié, 1893). The comparatively large, blister-like *Ovofoligallites padgetti* galls on *Odontopteris readi* foliage adds to the structural diversity of this increasing number of distinctive Permian galls.

Several patterns are notable in the diversity of late Paleozoic galls. First, is the broad galler plant-host shift from Pennsylvanian sphenopsid and pteridophyte taxa to Permian seed-plant taxa, which undoubtedly reflected major changes in plant community development, particularly in Euramerica. Climatic changes during the Pennsylvanian–Permian transition brought to the fore non-wetland vegetation types, dominated by seed plants and characteristic of seasonally dry habitats (DiMichele et al., 2009). Such seasonally dry floras had existed since at least the Middle Pennsylvanian, if not earlier (Mapes and Gastaldo, 1989; Broutin et al., 1990; DiMichele and Aronson, 1992; Plotnick et al., 2010; Falcon-Lang et al., 2010). They grew largely in extrabasinal settings (Pfefferkorn, 1980), or in basins during periods of drier climate (Falcon-Lang and DiMichele, 2010; DiMichele et al., 2010), associated with the glacial–interglacial fluctuations that characterized this time interval (Fielding et al., 2008). Consequently, these floras, dominated by seed plants, rarely appeared in the fossil record until the lowland basins became more persistently and seasonally dry, even during the wettest time periods. Because these floras are so poorly known, it is possible that the movement of insect gallers into them occurred much earlier than presently understood from the known fossil record.

The second pattern of note is the shift from organoid galls, which induce anomalous growth affecting segments of the stem and axial reproductive organs in Carboniferous plant hosts, to histoid galls, which target specific tissues within leaves and terminal branches in Permian plants. The similarity of the distinctive damage pattern on *O. readi* with that found on the Pennsylvanian plant *Macroneuropteris scheuchzeri* (DT97) may, however, necessitate a re-evaluation of the associational affinities of the earlier occurring, U-shaped, Pennsylvanian-age damage (Müller 1982; Labandeira and Beall, 1990) as a less developed blister or vein gall. These gall-like, apparently internally featureless structures (Fig. 2.3, 2.4), characteristically occur on *M. scheuchzeri* across the equatorial belt of Euramerica in a variety of environments, and may have originated in relatively xeric environments.

The third pattern is the ecological movement of the galling functional feeding group from Pennsylvanian plants such as calamites and marattialean ferns that occupied wetland environments, to a much broader range of seed-plant lineages during the Permian. Seed plants were the most herbivorized group of land plants that occupied better drained sites of the Permian, and would have been an attractor to a variety of herbivorous insect functional feeding groups, including gallers (Fernandes and Price, 1988). The taphonomy of this transition is affected by the same matters discussed above regarding the general galler host shift. Evidently, the floral transition provided opportunities for greater resource exploitation by emerging insect lineages of new plant-host taxa and tissues, as shown in the broader fossil record of galls. For the Permian, most of these new lineages were homopterous Hemiptera, which diversified throughout the Permian, including the Aphidoidea (currently, aphids, adelgids and phylloxerids), Psylloidea (psyllids), both extant galler groups, and the extinct Paleorrhyncha during the Early Permian (Shcherbakov, 2000). By the end of the Permian, several extinct lineages of the Cicadomorpha additionally were present (Shcherbakov, 2000), some of which may have been gallers. In addition, eriophyoid mites also occurred (Krantz and Lindquist, 1979), as well as early holometabolous insect lineages (Labandeira, 2011), possibly including gallers. There also were holdover associations from the Pennsylvanian— perhaps, for example, the galler of *Macroneuropteris*—that survived into the Early Permian, in refugial habitats.

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