

PALEONTOLOGY AND STRATIGRAPHY OF THE MIOCENE SADDLEBACK VALLEY LIMESTONE, ORANGE COUNTY, SOUTHERN CALIFORNIA¹

CAROL J. STADUM² AND KENNETH L. FINGER^{3,4}

ABSTRACT. Although rare in California, Neogene limestone outcrops are well exposed within a 10 km² area of western Saddleback Valley in southern Orange County. These occur as inconsistent, discontinuous sequences of micrite, calcarenite, and limy sands that are informally referred to herein as the Saddleback Valley limestone. Its principal biotic components are cheilostome bryozoans, coralline red algae, and mollusks characteristic of the middle Miocene “Temblor” California Provincial Molluscan Stage (CPMS); hence, previous workers had referred to these beds as the “Temblor” limestone. In the Los Angeles Basin, the shallow-marine “Temblor” macrofauna also occurs in the Topanga Canyon Formation of the Santa Monica Mountains and the Topanga Formation in the Santa Ana Mountains. Nevertheless, geologists mapping the San Juan Capistrano and El Toro quadrangles placed the Saddleback Valley limestone at the base of the local Monterey Formation, presumably on the basis of undescribed field observations. This study combines lithostratigraphic and paleontologic data, including micropaleontology, to determine whether this recently challenged affiliation is justified.

Microfossils (ostracodes, foraminifera, and calcareous nannoplankton) in the Saddleback Valley limestone indicate that its conspicuous shallow-water “Temblor” fauna and associated Topanga-like sediments had been transported downslope in the late Relizian (late early Miocene) at ~16 Ma. ⁸⁷Sr/⁸⁶Sr analyses confirm the age at 15.9–16.5 My. It is therefore interpreted that the depositional history of the Saddleback Valley limestone began with a rich subtropical invertebrate community inhabiting the margins of a channel that existed between the mainland and a high-relief peninsula or island to the west. Increasing tectonic activity along the plate margin caused large amounts of schistose rock to slide off the island’s eastern slope and into the channel, forming the San Onofre Breccia. Continued subsidence of the area created a deep basin into which turbidity currents transported the unconsolidated sediments, including its “Temblor” biota, which settled on the breccia or where “Monterey” muds had started to accumulate. These displaced sediments filled slope channels that were part of a deep-sea fan complex. In the deep-water Monterey realm, the intermittent deposits of limy sands were buried by hemipelagic muds. Diagenesis transformed isolated calcarenite lenses composed predominately of calcareous algae and invertebrates into nearly pure limestone. As the basin emerged in the late Pleistocene, erosion of the overlying strata exposed the Saddleback Valley limestone. Its depositional history and stratigraphy imply that it is the basal “member” of the local Monterey Formation.

INTRODUCTION

LOCATION, GEOLOGIC SETTING, AND HISTORICAL INTEREST

Saddleback Valley is located where the Santa Ana Embayment extended off the southeastern Los Angeles Basin during the Neogene in southern California (Fig. 1). The valley has been geologically described as a transgressive marine sequence of Miocene formations folded into a broad, north-trending syncline (Morton et al., 1974). In the western part of the valley and the adjacent San Joaquin Hills, the stratigraphic succession consists of five geologic units, which, from oldest to youngest, are the Vaqueros Formation, Topanga Formation, San Onofre Breccia, Monterey Formation, and Capistrano Formation (Fig. 2).

Within an area of 10 km², carbonate-rich beds and lenses crop out above the breccia and below the Monterey mudstones. We refer to these limy deposits collectively as the “Saddleback Valley limestone.” The earliest published account of this limestone is that of Bowers (1890:399–400), who described a quarry used to construct Mission San Juan Capistrano in the 1790s (see Figs. 1 and 3):

At this place is a most remarkable bed of fossils. It is about ten miles from the ocean and nearly one and a half miles southwest of El Toro Station. An exposure

has occurred by excavating into the bed of fossil shells in view of burning for lime. At the exposure the stratum is about seven feet thick, dipping to the south, and can be traced for nearly a half-mile. It is composed almost wholly of bivalves, Saxidomus gracilis, largely predominating, with occasional Cardium corbis, pecten, and casts of univalves. The teeth of sharks are occasionally found. The casts are found in a marly substance, which is doubtless the result of the decomposition of their shells. They are easily dislodged with a pick, and the bed of a wagon could be filled with them as readily as coal or gravel. What is especially strange concerning them is that the bivalves lie generally on their side and were fossilized with closed shells. But how did they become heaped up in such vast numbers? Dr. J.G. Cooper suggests that it is probably the result of an earthquake and tidal wave. At present we can advance no more plausible theory to account for this vast accumulation of fossils in this spot.

Still visible in some blocks of the Mission’s buildings are molds of *Lyropecten crassicardo* (Conrad, 1857), *Amussiopecten vanulecki* (Arnold, 1907), *Saxidomus* cf. *S. vaquerosensis* (Arnold, 1910) (*S. gracilis* of Bowers, 1890), and *Turritella ocoyana* Conrad, 1855 (Fig. 3). In addition to these limestone blocks, the limestone was pulverized to make the mortar used in constructing the Mission (Wright, 1950). A century later, tests of Saddleback Valley Limestone showed that it would be a satisfactory source of material for Portland cement, but production never materialized (Logan, 1947).

¹ URL: www.nhm.org/scholarlypublications

² San Diego Natural History Museum, Department of Paleontology, 1788 el Prado, San Diego, California 92101, USA.

³ University of California Museum of Paleontology, 1101 Valley Life Sciences Building, Berkeley, California 94720-4780, USA.

⁴ Corresponding author: Kenneth L. Finger, E-mail: kfinger@berkeley.edu

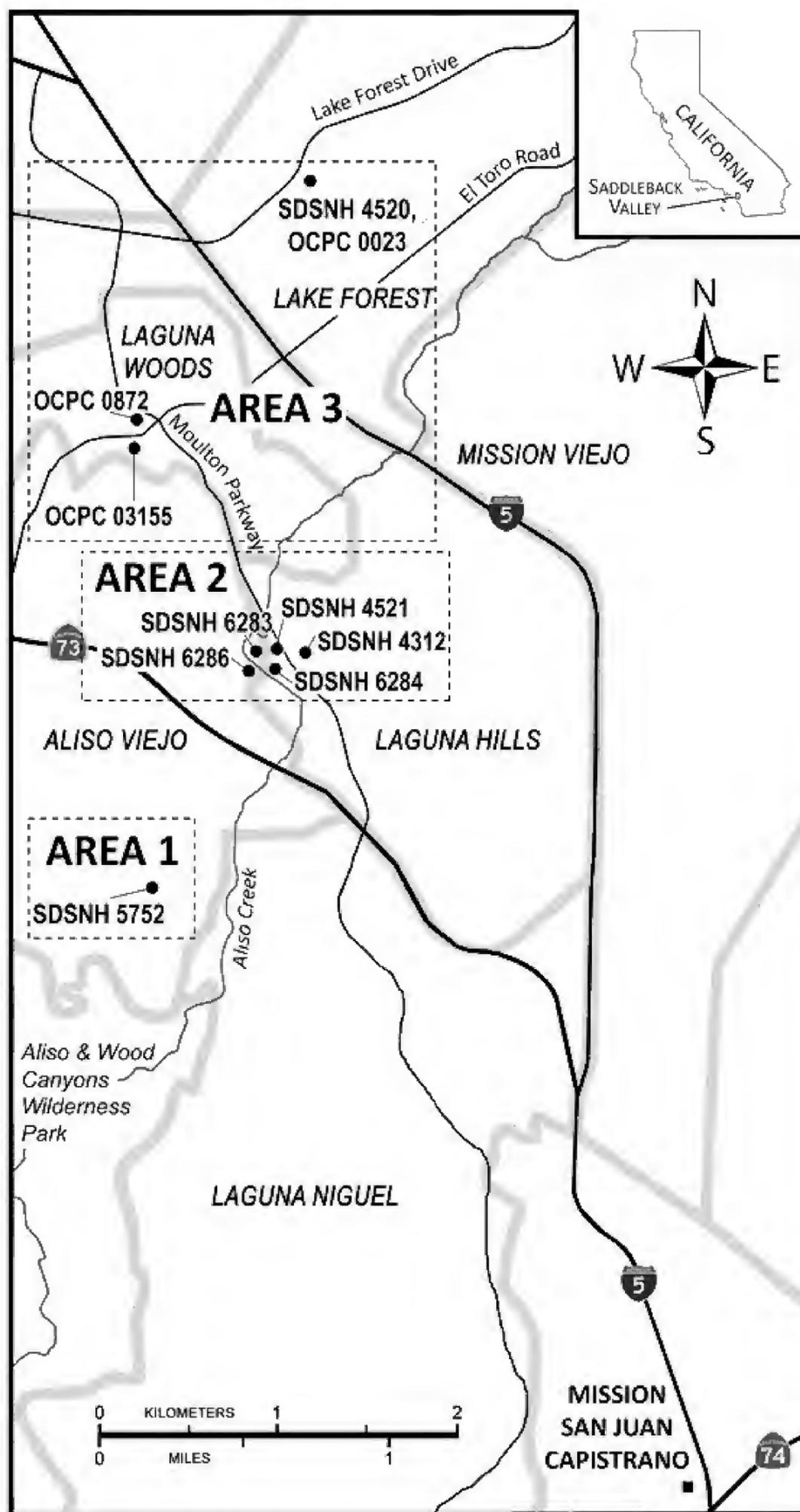


Figure 1 Map of the Saddleback Valley study area delineating city boundaries (thick grey lines) and the three study areas with sample localities.

In the 1920s, the short-lived Moulton Marine Shell Fertilizer Company was formed to mine the limestone as soil enrichment, which it marketed to local farmers (Tucker, 1925). A remnant of their activity is a small quarry that remains visible just northwest of Moulton Parkway, as shown on the geologic map of Morton et al. (1974).

OCCURRENCES OF OTHER LIMESTONES IN THE MIOCENE OF CALIFORNIA

The scarcity of limestone in the thick Tertiary sections of California was noted by Bramlette (1946) in his study of the Monterey Formation, which reported thin beds of impure calcareous and

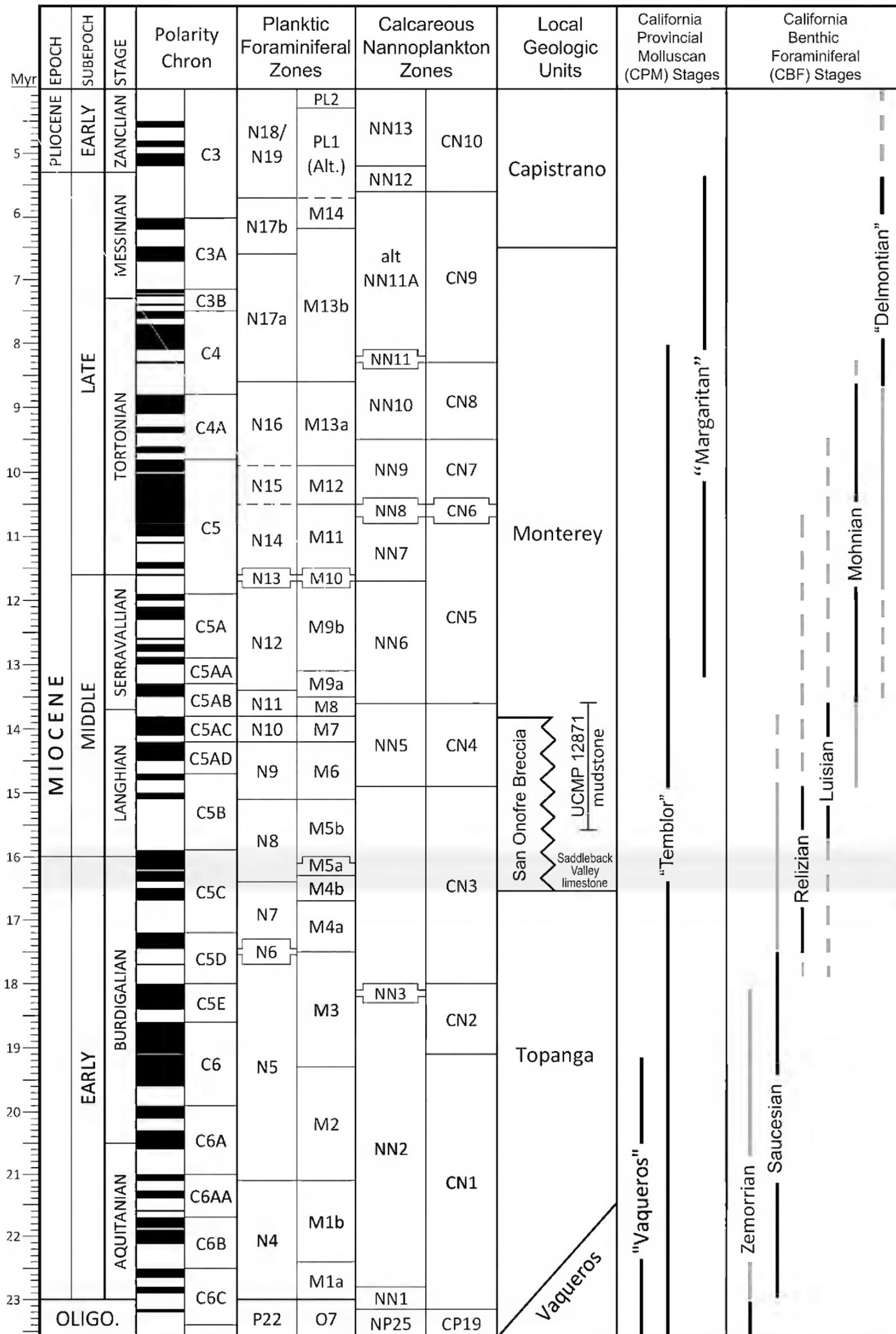


Figure 2 Miocene timescale (derived from Hilgen et al., 2012) with the addition of California biozonations. Shaded horizontal band denotes the age interval of the Saddleback Valley limestone (SVL) and orange sand, and that of younger Monterey mudstone in the present study. Ranges of molluscan stages derived from Prothero (2001) and McCulloh et al. (2002). Intervals of the benthic foraminiferal stages shown as solid black lines are from McDougall (2007); broader correlations with calcareous nannoplankton zones (Crouch and Bukry, 1979:fig. 3) indicated by solid grey extensions for those they range completely through and dashed lines for zones they range into but not beyond.

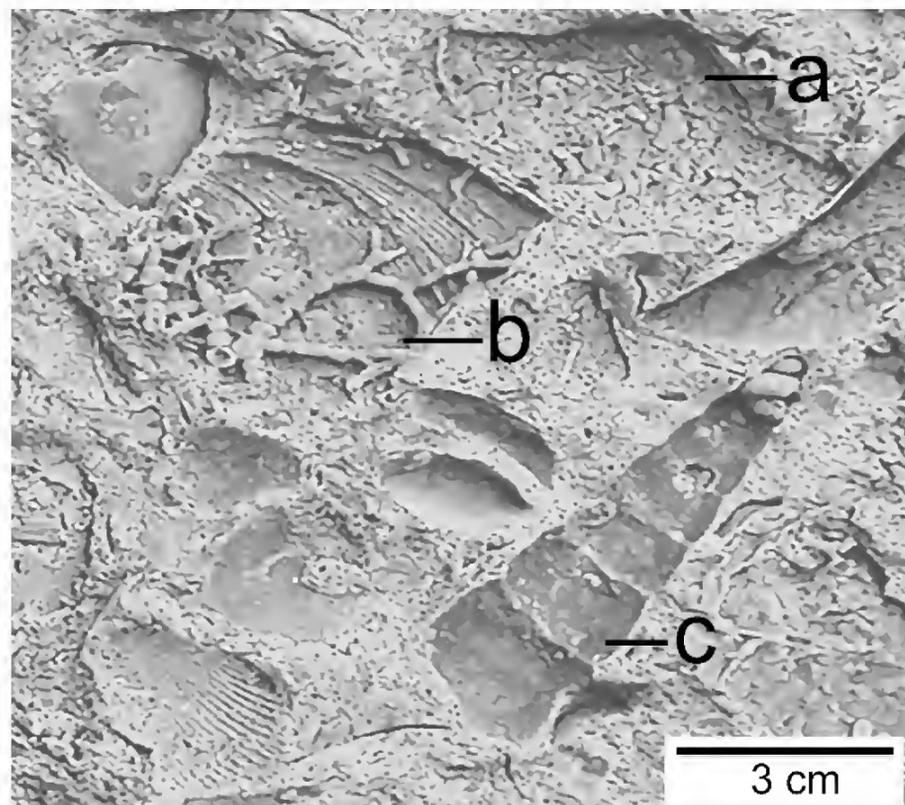


Figure 3 Surface of a limestone block at Mission San Juan Capistrano showing mollusk molds and bryozoans: a, cheilostome bryozoan fragments on *S. vaquerosensis*; b, *Entobia*-bored valve of *Saxidomus vaquerosensis* Arnold, 1910; c, *Turritella ocoyana* Conrad, 1855.

dolomitic rocks, or more commonly as concretions, throughout much of the unit. Bramlette (1946) generalized that limestone occurs at the base of the Monterey Formation in San Luis Obispo, Santa Barbara, Los Angeles, and Orange counties, where it appears as conspicuous carbonate beds. Furthermore, he indicated that these share a fauna similar to that recovered by Arnold and Anderson (1907) in southern Orange County. He also referred to this limestone as a transitional middle Miocene horizon in Santa Barbara County.

In the lower Monterey Formation near Lompoc, Dibblee (1950) encountered limestone lenses over 30 m thick that are composed mostly of calcareous algae. Nevertheless, when shown samples of the Saddleback Valley limestone, he stated (pers. comm., 2001) that its fossil density, diversity, and preservation did not resemble anything he had observed in the decades he devoted to mapping the geology of central and southern California. In the Santa Monica Mountains, Stanton and Alderson (2013) recently described limy deposits that are interbedded with Conejo Volcanics and contain coralline algae, encrusting bryozoans, and the bivalves *L. crassicardo* and *Spondylus scotti* Brown and Pilsbry, 1913.

GEOLOGICAL STUDIES ON THE LIMESTONE IN SADDLEBACK VALLEY

Arnold and Anderson (1907) and Arnold (1909) were the first geologists to suggest an origin for the Miocene limestones that, in some areas, occur between the Vaqueros and the Monterey formations. They interpreted those carbonates as having formed primarily in semi-enclosed basins that accumulated alkaline mud. Corby (1922) described and illustrated articulated *Pecten crassicardo* from what he referred to as the Temblor Formation near El Toro (now Lake Forest). His locality appears likely to be coincidental with the “Pecten Reef” locale (SDSNH loc. 4520) in Lake Forest. Woodford (1925) also assigned these limestone deposits to the Temblor Formation based on faunal similarities. He described the unit as occurring between the San Onofre Breccia and the Monterey Formation throughout the Capistrano–El Toro area

with a stratigraphic thickness exceeding 30 m and extending northward beyond the pinch-out of the breccia between Wood Canyon and Laguna Woods. He also observed the breccia north of Dana Point, where it intercalates with limy mudstone at the base of the Monterey Formation. Loel and Corey (1932:58) considered the limestone fauna as a transition between those of the lower Miocene Vaqueros Formation and middle Miocene Topanga Formation and San Onofre Breccia. They described it as “bryozoan-limestone reefs with *P. crassicardo*, *Ostrea*, and *Scutella merriami*.”

Interest in the Saddleback Valley limestone was rekindled in the late 1960s, when commercial developers in Lake Forest and Laguna Hills began blasting the indurated calcarenite, forming fossil-rich spoils and fresh exposures. In 1972–73, construction east of Interstate 5 and south of Lake Forest Drive exposed limestones rich in fossils. These rocks (Fig. 4) are dominated by the middle Miocene pectinids *L. crassicardo*, *Amusium lomdocensis* (Arnold, 1906), and *A. vanvlecki*, which are characteristic of the “Temblor” California Provincial Molluscan Stage (CPMS). Consequently, the locality became known as the “Pecten Reef” and within a three-month interval in 1973, paleontologists from the Natural History Museum of Los Angeles County (LACM) collected more than 30,000 marine fossils (primarily echinoids, mollusks, and shark teeth) from this locality.

Southwest of the “Pecten Reef,” Morton et al. (1974) mapped fossiliferous limestones in Laguna Woods, Laguna Hills, Aliso Viejo, and Wood Canyon and estimated the composite stratigraphic thickness of that discontinuous lithofacies as more than 120 m. Fife (1974) and Morton et al. (1974) placed the limestone at the base of the Monterey Formation; however, there has been no consensus on whether it belongs to Kleinpell’s (1938) Relizian or Luisian California benthic foraminiferal stage (CBFS). For example, Fife (1979) and consulting micropaleontologist R. Boettcher (pers. comm., 2001) considered the unit to be Relizian, whereas Stadum (1982) and Finger (1988) ascribed it to the Luisian. Kleinpell’s (1938) differentiation of the Relizian and Luisian, however, is dubious, as differences in taxa, species richness, and apparent depth are particularly subtle and interbasinally inconsistent compared with the other stages that subdivide the Miocene (Finger, 1992). It is not surprising that Vedder (1971) referred to the foraminifera present in siltstone interbedded in the San Onofre Breccia in Shell’s Moulton No. 14 well as lower Luisian or Relizian, and that lower Luisian foraminifera occur in strata superjacent to the unit in the Aliso Creek area.

Stadum (1982) wrote a thesis on the Saddleback Valley limestone and its macroinvertebrate fauna and concurred with previous workers by referring to it as the basal Monterey Formation. However, Powell and Stadum (2010) recently refuted that correlation by reassigning the limestone to the Topanga Formation, primarily because of its “Temblor” molluscan faunal affinity. In this present study, stratigraphic affiliations are reconsidered by further investigating the lithostratigraphy and paleontology of the limestone. The primary goal, however, is to derive a better understanding of the depositional history and stratigraphic relationships of this enigmatic unit in the Neogene section of California by integrating all available data.

MATERIALS AND METHODS

ABBREVIATIONS

Abbreviations used in this study are primarily those that prefix sample locality or specimen numbers: LACMIP, Los Angeles County, Invertebrate Paleontology; LACMVP, Los Angeles County, Vertebrate Paleontology; OCPC, Orange County Paleontological Collection (located in Santa Ana at the John D. Cooper Center for Paleontology and Archaeology, which is herein referred to as the Cooper Center); SDSNH, San Diego Society

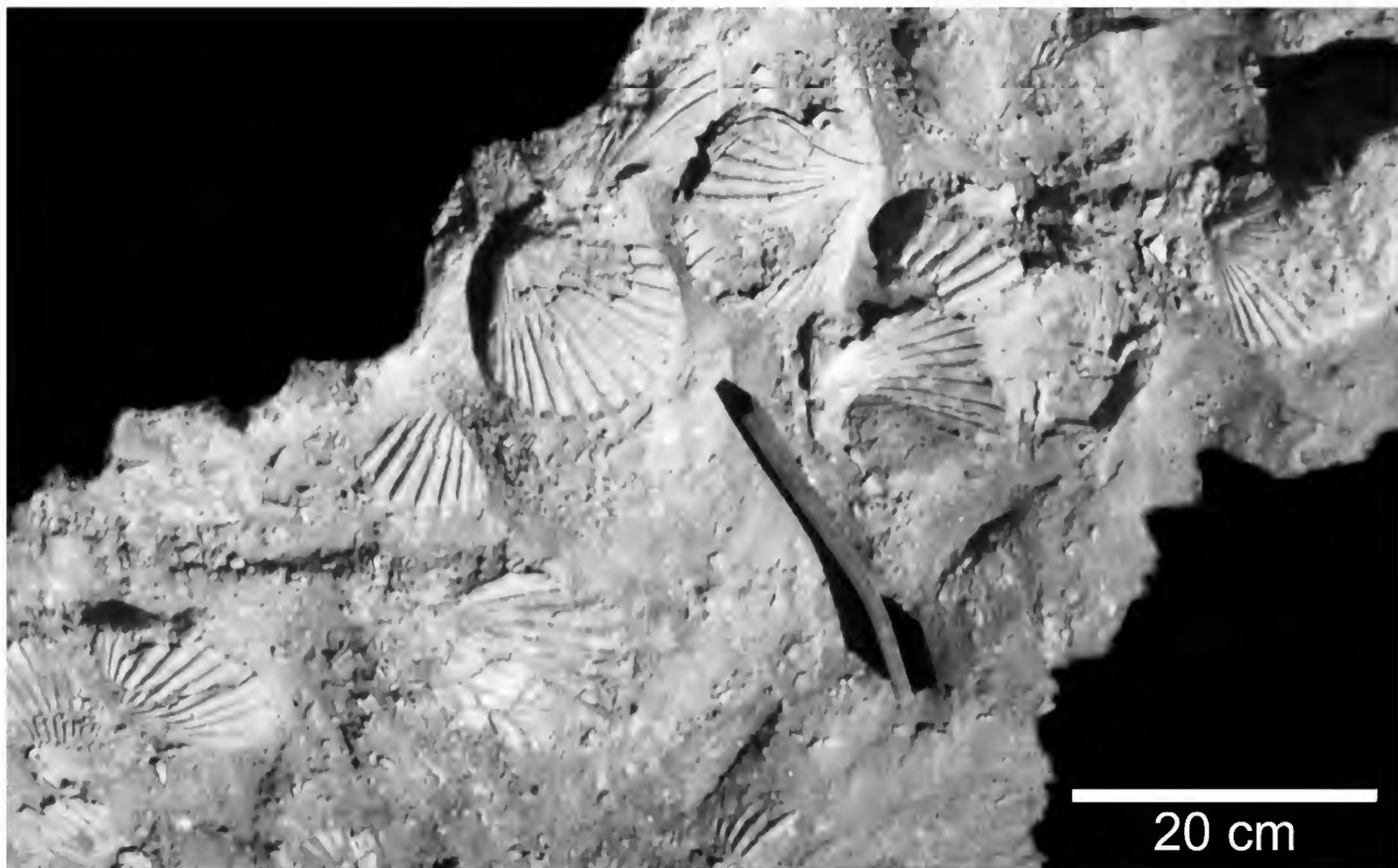


Figure 4 Well-preserved, mostly articulated *Lyropecten crasscardo* (Conrad, 1857) in limestone exposed at Fossil Reef Park (SDSNH loc. 4312). Similar occurrences were found at the original “Pecten Reef” site (SDSNH loc. 4520) and near the base of the measured section in the Moulton Parkway road cut (SDSNH loc. 4521).

of Natural History (San Diego Natural History Museum [SDNHM] paleontological collection).

METHODS

Fieldwork was intermittent during land development that spanned four decades. Lab work included removing matrix from the macrofossils and applying polyvinyl acetate (VinacTM) to repair and stabilize broken and fragile specimens. Unconsolidated sands were dry-sieved through a series of 20-, 32- and 100-mesh screens to isolate minute fossils, including fish bones and teeth, shell fragments, and echinoid spines. To obtain foraminifers and ostracodes, sediment samples were washed over a 200-mesh screen, then dried and picked under the microscope. Calcareous nannoplankton samples were given to consultant Stanley Kling, who used conventional methods to prepare strewn slides. Thin sections of the indurated limestones were also examined, particularly for microfossils that could be useful in interpreting the depositional history of the local geologic sequence. Latex and silicone peels were made from the molds in indurated limestone to facilitate identifications.

FOSSIL LOCALITIES

Development has obscured or obliterated many of the exposures, but 40 acres of limestone outcrops remain preserved in the northern Aliso and Wood Canyon Wilderness Park and, in 1982, community interest in the fossiliferous limestone and the efforts of the senior author led to the preservation of a one-acre outcrop in Laguna Hills as “Fossil Reef Park” (Orange County Historical Site No. 28; Fig. 5). Earth-disturbing activities related to the ongoing development of western Saddleback Valley continue to be monitored for paleontological resources. Orange

County Resolution No. 87-516, passed in 1987, stipulates that all fossils recovered from new county excavations and projects belong to Orange County.

The fossiliferous outcrops in this study are divided into three areas based on their geographic distribution (Fig. 1) and paleontologic and lithostratigraphic differences (Fig. 6), and referred to herein by number: (1) Wood Canyon, (2) Laguna Hills–Aliso Viejo, and (3) Laguna Woods–Lake Forest. Field observations in each of these areas are presented below.

All of the following localities are in the Monterey Formation. The nine SDSNH and OCPC localities are in the Saddleback Valley limestone “member,” whereas the two UCMP localities in Area 2 are not. Geographic coordinates were derived from plotting the localities in Google Earth[®] utilizing “Street View” mode whenever possible for maximum accuracy.

Area 1: Wood Canyon

SDSNH LOC. 5752. North canyon wall off Sheep Hills, southern Aliso Creek and Wood Canyon Wilderness Area; San Juan Capistrano quad., 33°33′20.18″N, 117°44′15.33″W, elevation (elev.) 396 ft (121 m).

Area 2: Laguna Hills–Aliso Viejo

SDSNH LOC. 4312 (OCPC LOC. 0022). One-acre site preserved as Fossil Reef Park, Laguna Hills; San Juan Capistrano quad., 33°35′19.07″N, 117°42′20.24″W, elev. 275 ft (84 m).

SDSNH LOC. 4521. Road cut along west side of Moulton Parkway, ~600 m north of Aliso Parkway, Laguna Hills; San Juan Capistrano quad., 33°35′08.74″N, 117°42′33.77″W, elev. 271 ft (83 m). Site now

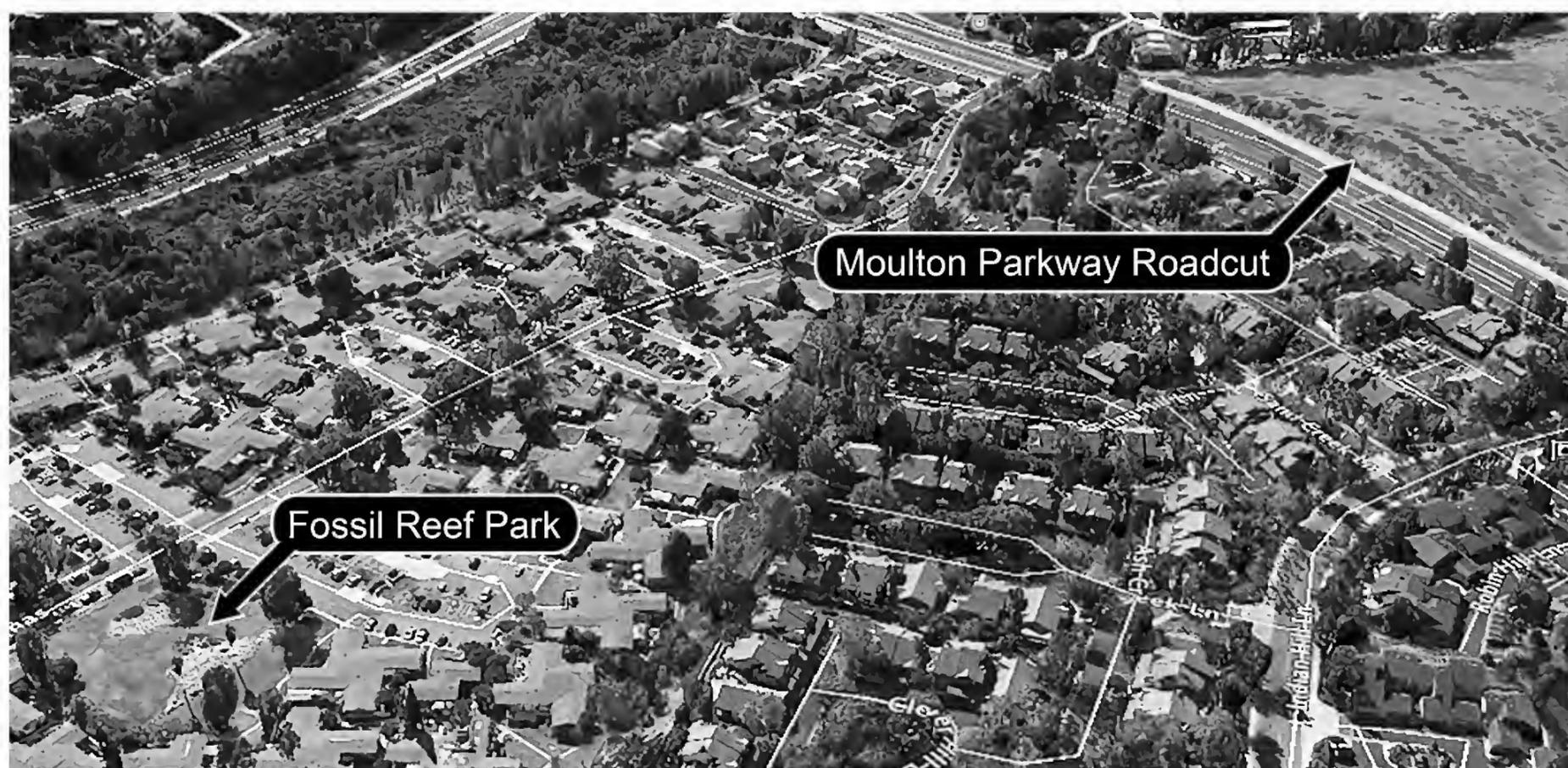


Figure 5 Southward oblique aerial view of part of Area 2 showing Fossil Reef Park (SDSNH loc. 4312 [OCPC loc. 0022]) and the Moulton Parkway road cut (SDSNH loc. 4521).

greatly reduced. In this report, SDSNH loc. 4521 includes sublocalities SDSNH 4521A and LH-1 to LH-4 of Finger (1988, 1992).

UCMP LOC. 12871. Small exposure of steeply dipping dark brown mudstone beds on Aliso Parkway at the east corner of its intersection with Moulton Parkway; Laguna Hills; San Juan Capistrano quad., 33°35′01.07″N, 117°42′23.60″W, elev. 243 ft (74 m). Site no longer exists due to landscaping related to development of adjacent housing community.

UCMP LOC. 12873. Orange sand lens (~4 m³) surrounded by greenish-grey mudstone, ~0.4 km northeast of SDSNH 4521, Laguna Hills; San Juan Capistrano quad., 33°35′12.32″N, 117°42′31.64″W, elev. 289 ft (88 m). MAR-254 in Finger (1988, 1992).

SDSNH LOC. 6283. Weathered outcrops of Saddleback Valley limestone in North Aliso and Wood Canyon Wilderness Park, Aliso Viejo; San Juan Capistrano quad., 33°35′06.90″N, 117°42′40.42″W, elev. 291 ft (89 m).

SDSNH LOC. 6284. Weathered outcrops of Saddleback Valley limestone in North Aliso and Wood Canyon Wilderness Park, Aliso Viejo; San Juan Capistrano quad., 33°35′11.01″N, 117°42′42.65″W, elev. 294 ft (90 m).

SDSNH LOC. 6286. Weathered outcrops of Saddleback Valley limestone in North Aliso and Wood Canyon Wilderness Park, Aliso Viejo. San Juan Capistrano quad., 33°35′02.69″N, 117°42′47.16″W, elev. 295 ft (90 m).

Area 3: Laguna Woods and Lake Forest

OCPC LOC. 0872. Laguna Woods Self Storage, 24151 Moulton Parkway; Laguna Woods, San Juan Capistrano quad., 33°36′37.29″N, 117°43′34.58″W, elev. 389 ft (119 m). Not collected. Site destroyed in 1998.

OCPC LOC. 03155. Home Depot, 24332 El Toro Road, Laguna Woods, San Juan Capistrano quad., 33°36′26.52″N, 117°42′67″W, elev. 447 ft (136 m). Site buried in 1997.

SDSNH LOC. 4520 (OCPC 0023). Original “Pecten Reef” site. El Toro Quad., 33°37′49″N, 117°42′46″W, elev. ~95 m (311.6′). Site destroyed in 1974.

STRATIGRAPHY AND PALEONTOLOGY

Fossils characteristic of the outcrops are noted in this section. A total of 106 macroinvertebrate taxa were recovered from nine outcrops of the Saddleback Valley limestone (Table 1): 48 gastropods, 45 bivalves, 4 bryozoans, 4 echinoids, 1 poriferan, 1 polychaete, 1 cirriped, 1 ichnotaxon, and 1 coralline alga. Also present are teeth of cartilaginous and bony fish. Samples from two of the limestone localities in Area 2 were processed for microfossils—SDSNH 4312 for calcareous nannoplankton and SDSNH 4521 for both foraminifera and ostracodes. In addition, microfossil samples were collected from two non-limestone localities in Area 2 for comparative study. Photographs of 38 macroinvertebrate taxa found in this study are shown in Figures 7–52.

Area 1: Wood Canyon

To the west of the junction of Aliso Creek and Wood Canyon Creek near Laguna Niguel, the Saddleback Valley limestone cropped out as lenses in the north wall of Wood Canyon (Morton et al., 1974). All the Wood Canyon outcrops have been destroyed by development, including the section of five lithofacies at SDSNH loc. 5752 (Fig. 1) that greatly contributed to our understanding of the limestone unit. From top to bottom (Fig. 6), these lithofacies are described below.

The sequence begins with Lithofacies A, a 1.2-m-thick lag deposit of subrounded quartz and blueschist pebbles and cobbles, and abraded mollusk fragments cemented by calcium carbonate. This lithofacies unconformably overlies the >1,000-m-thick San Onofre Breccia, which is subjacent to the limestone in Area 1 and extends northward into western Area 2. Cooper (pers. comm., 1987) described the outcrop in Area 1 as flat-topped with a spoon-shaped base, indicating that it was a channel-fill deposit.

From 1.2–5.7 m, Lithofacies B is a 5.4-m-thick layer of bioclast-supported limestone (Fig. 53). Cooper (pers. comm., 1987) described this bed as ranging from coarse limestone (grainstone) to a fine carbonate mud (rudstone) with steinkerns of *Saxidomus* cf. *S. vaquerosensis*. The geotetal steinkerns of this lithofacies readily weather, and the fossils, which are elements of a marine shelf fauna, appear to have experienced pre-mortem

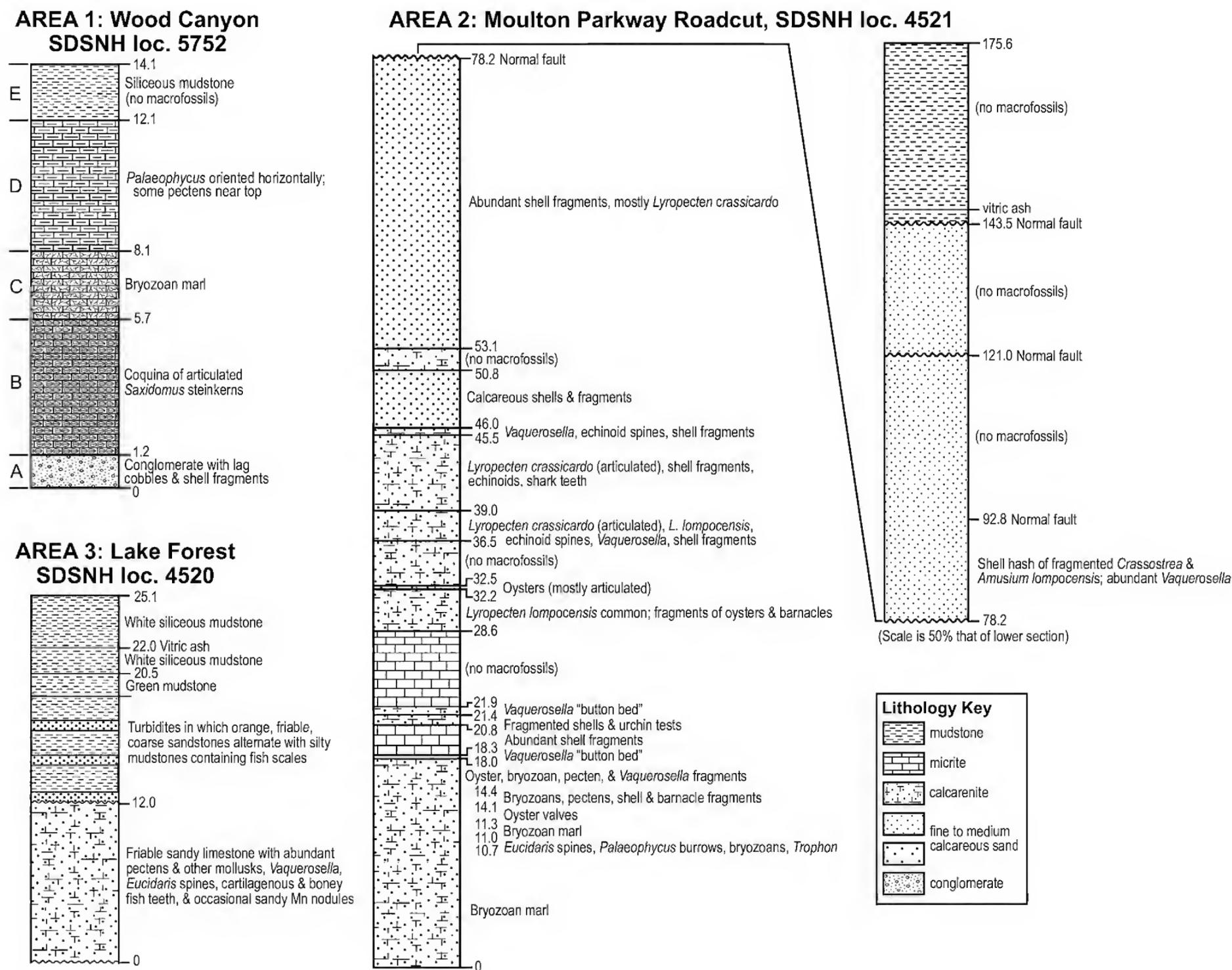


Figure 6 Examples of stratigraphic columns from each of the three designated areas in Saddleback Valley. Letters on left side of Area 1 column refer to lithofacies described in text. The heterogeneity in and between the sequences supports the hypothesis of localized pulses of transport and deposition.

transportation, concentration, and resedimentation in a deeper water environment. A thin section of the limestone reveals foraminifera similar to those found in Area 2 (Fig. 54). Although Cooper's interpretation of the transport and deposition of the fossil mollusks is admissible, his suggestion that they were transported postmortem is questioned. The *Saxidomus vaquerosensis* steinkerns are from articulated shells, which indicates that these bivalves were alive when suddenly displaced and rapidly buried by a turbidity current. Soon after death, their internal soft parts decomposed and the surrounding matrix of limey mud and bryozoan fragments infiltrated the shells and filled the voids, forming internal molds that preserve the smooth impressions of distinct muscle scars after the shells dissolved.

From 5.7–10.1 m, Lithofacies C is a biosparite recognized in all three areas of Saddleback Valley as a 1.5-m-thick cheilostome bryozoan rudstone with an irregular, somewhat erosional, basal contact. Cheilostome bryozoans typically form thickets or dense patches at outer-neritic (50–150 m) depths on sediment-starved hard substrates where weak bottom currents limit lateral transport (Cuffey et al., 1981). Bryozoan fragments are a major component of the Saddleback Valley limestone, but they are less apparent in the dense biosparite than in the weakly cemented limey sandstone. Broken shells of *L. crasscardo* and *A. vanvlecki* are scattered infrequently in the uppermost bryozoan biosparite, whereas whole

pectinids and *Crassostrea titan* (Conrad, 1853) are common throughout the limestones of Areas 2 and 3.

Cuffey et al. (1981) referred to the cheilostome bryozoan in the Saddleback Valley limestone as *Gemelliporella* aff. *G. punctata* Canu and Bassler, 1919, which was described from outer-neritic depths in the warm waters of the Caribbean. The Saddleback Valley taxon may be its descendant, as the limestone was deposited prior to the closing of the Panama seaway in the Pliocene. Also occurring in this limestone are the encrusting bryozoans *Conopeum barbarensis* (Gabb and Horn, 1862) and *Smittina maccullochae* Osborn, 1952, extant taxa previously unknown as fossils. Cuffey et al. (1981:70–71) stated that in "contrast to all the abundant *Gemelliporella* aff. *G. punctata*, which is a Caribbean form, these two are more expectable 'local' species in the southern California area." In reference to this limestone, they also noted "few other Cenozoic deposits exhibit as high a bryozoan content as do certain of these lenses." Living *S. maccullochae* inhabits shallow substrates at depths down to 35 m off the coasts of southern California and Baja California, México. The presence of *Gemelliporella* in the Saddleback Valley limestone appears to be the first fossil occurrence of this genus in the eastern Pacific.

A rhodophytic biosparite at 10.1–12.1 m is Lithofacies D. Thin sections of this limestone contain abundant thalli of the red coralline alga

Table 1 Taxonomic checklist of macrofossil taxa in the Saddleback Valley limestone. Equivalent locality numbers: SDSNH loc. 4312 = OCPC loc. 0022; SDSNH loc. 4520 = OCPC loc. 0023.

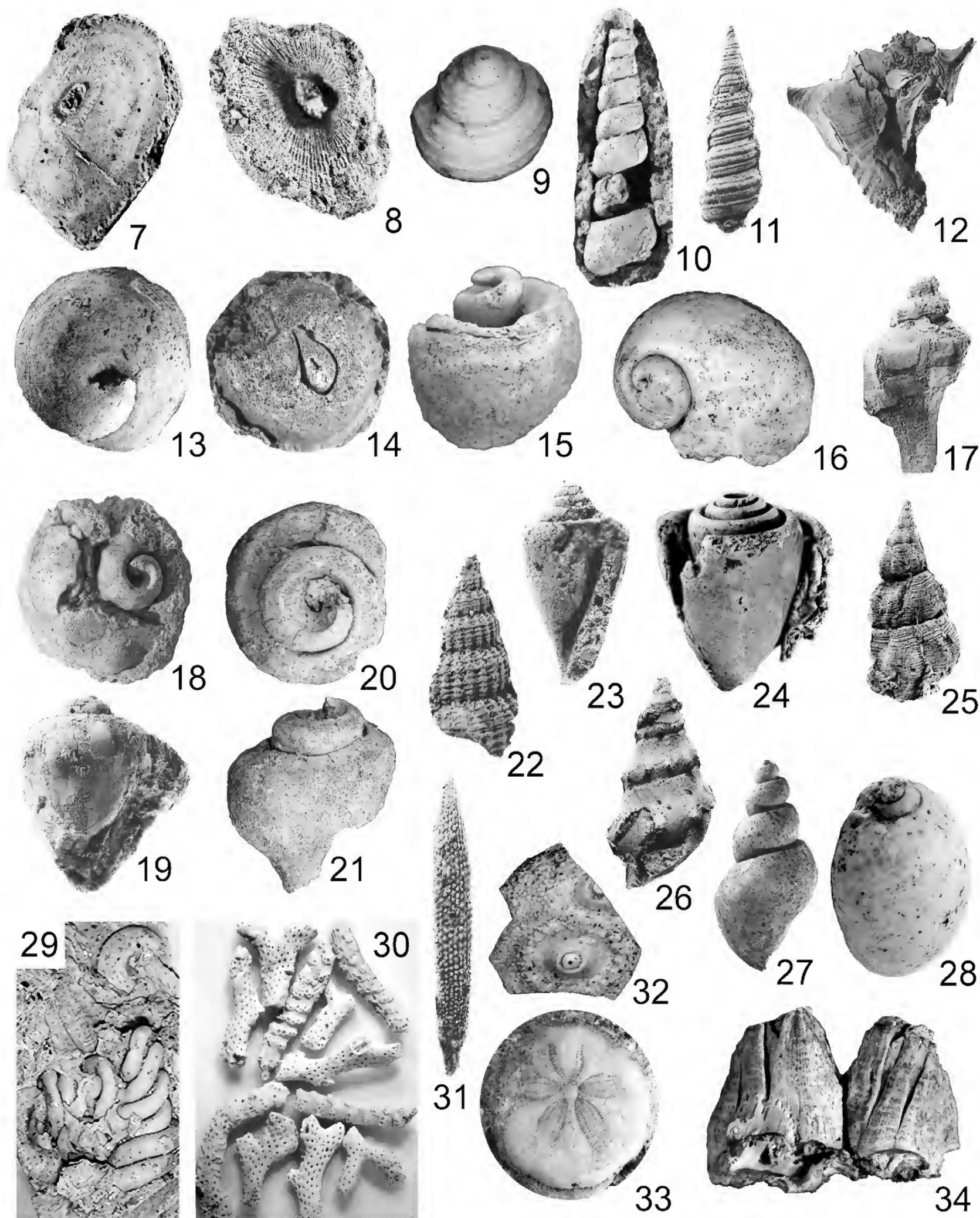
	Area 1		Area 2				Area 3		
	SDSNH 5752	SDSNH 4312	SDSNH 4521	SDSNH 6283	SDSNH 6284	SDSNH 6286	OCPC 0872	OCPC 03155	SDSNH 4520
Rhodophyta: Corallinales									
<i>Lithophyllum</i> cf. <i>L. profundum</i> Johnson, 1954	X								
Bryozoa: Cheilostomatida									
<i>Conopeum barbarentis</i> (Gabb and Horn, 1862)		X	X						X
<i>Gemelliporella</i> aff. <i>G. punctata</i> Canu and Bassler, 1919		X	X					X	
<i>Smittina maccullochae</i> Osborn, 1952			X						
Indeterminate bryozoan	X								
Mollusca: Gastropoda									
<i>Antillophos woodringi</i> Addicott, 1970		X							
<i>Calyptrea</i> sp.		X							
<i>Cancellaria dalliana</i> Anderson, 1905		X							
<i>Cancellaria ocoyana</i> Addicott, 1970		X							
<i>Cancellaria</i> sp.		X							
<i>Chlorostoma</i> sp.		X							
Columbellidae (indeterminate)		X							
<i>Conus</i> sp.		X							
<i>Crepidula</i> sp.		X							
<i>Crucibulum</i> sp.		X							
Cypraeidae									X
<i>Diodora</i> sp.		X							
Fascioliidae		X							
<i>Felaniella harfordi</i> (Anderson, 1905)		X							
<i>Ficus</i> sp.		X							
<i>Fissurella rixfordi</i> Hertlein, 1928		X							
<i>Forreria bartoni</i> (Arnold, 1910)		X	X						X
<i>Fusinus</i> sp.		X							
<i>Hexaplex</i> sp.		X							
<i>Kelletia lorata</i> Addicott, 1970		X							
cf. <i>Leporimetis</i> sp.		X							
cf. <i>Macrarenne</i> sp.		X							
<i>Megasurcula keepi</i> (Arnold, 1907)		X							
<i>Melongena californica</i> Anderson and Martin, 1914		X							
Mitridae		X							
<i>Morula</i> cf. <i>M. granti</i> Addicott, 1970		X							
Nassariidae (indeterminate)		X							
Naticidae (indeterminate)		X							
cf. <i>Odostomia sequoiana</i> Addicott, 1970		X							
<i>Ophiodermella</i> cf. <i>O. temblorensis</i> (Anderson and Martin, 1914)		X							
<i>Pleuroploca</i> sp.		X							
<i>Priscofusus geniculus</i> (Conrad, 1849)		X							
<i>Pyruconus</i> cf. <i>P. hayesi</i> (Arnold, 1909)		X							
<i>Pyruconus</i> cf. <i>P. owenianus</i> (Anderson, 1905)		X		X					
<i>Scaphander</i> cf. <i>S. jugularis</i> (Conrad, 1855)		X							
<i>Sinum</i> cf. <i>S. scopulosum</i> (Conrad, 1849)		X							
<i>Strombus</i> sp.		X							
<i>Terebra cooperi</i> Anderson, 1905		X							
Teredinidae		X							
<i>Thais edmondi</i> (Arnold, 1907)		X							
<i>Trophon kernensis</i> Anderson, 1905		X	X					X	
Turridae		X							X
<i>Turritella ocoyana</i> Conrad, 1855		X							
<i>Turritella temblorensis</i> Wiedey, 1928		X							X
<i>Turritella</i> spp.		X							
<i>Vernicularia</i> sp.		X							
Mollusca: Bivalvia									
<i>Amusium lompocensis</i> (Arnold, 1906)		X	X						
<i>Amussiopecten vanvlecki</i> (Arnold, 1907)		X	X						
<i>Anodontia</i> sp.		X							
<i>Batillaria</i> sp.		X							
<i>Chlamys sespeensis</i> (Arnold, 1906)		X							
<i>Chione</i> cf. <i>C. richthofeni</i> Hertlein and Jordan, 1927		X							

Table 1 Continued.

	Area 1		Area 2				Area 3		
	SDSNH 5752	SDSNH 4312	SDSNH 4521	SDSNH 6283	SDSNH 6284	SDSNH 6286	OCPC 0872	OCPC 03155	SDSNH 4520
<i>Chione schencki</i> Loel and Corey, 1932		X							
<i>Clementia</i> cf. <i>C. conradiana</i> (Anderson, 1905)		X							
<i>Crassadoma</i> cf. <i>C. gigantea</i> (Gray, 1825)		X							
<i>Crassostrea titan</i> (Conrad, 1853)		X	X			X	X	X	
cf. <i>Crassostrea</i> sp.									X
<i>Crenomytilus expansus</i> (Arnold, 1907)			X						
<i>Dosinia</i> sp.		X							
<i>Felaniella</i> cf. <i>F. barfordi</i> (Anderson, 1905)		X							
cf. <i>Gari</i> sp.		X							
<i>Glycymeris</i> sp.		X							
<i>Lima</i> sp.		X							
<i>Limaria</i> sp.		X							
<i>Lithophaga</i> sp.		X							
Lucinidae		X							
<i>Lyropecten crassicardo</i> (Conrad, 1857)		X	X				X	X	X
Mactridae		X							
<i>Modiolus ynezensis</i> Arnold, 1907		X							
<i>Mytilus</i> cf. <i>M. coalingensis</i> Arnold, 1910			X						
<i>Mytilus</i> cf. <i>M. expansus</i> Arnold, 1907		X							
<i>Mytilus</i> sp.		X							X
<i>Pacipecten andersoni</i> (Arnold, 1906)		X							
<i>Panopea abrupta</i> (Conrad, 1849)		X							
<i>Panopea tenuis</i> (Wiedey, 1928)		X							
<i>Panopea</i> sp.		X							X
<i>Pycnodonte</i> cf. <i>P. howelli</i> (Wiedey, 1928)		X				X			
<i>Pycnodonte</i> cf. <i>P. wiedeyi</i> (Hertlein, 1928)		X				X	X		
<i>Penitella</i> sp.						X			
<i>Protothaca</i> sp.						X			
<i>Saxidomus vaquerosensis</i> Arnold, 1910		X							
<i>Saxidomus</i> sp.	X								X
Solecurtidae?		X							
<i>Spondylus perrini</i> Wiedey, 1928				X					
<i>Spondylus scotti</i> Brown and Pilsbry 1913									X
<i>Spondylus</i> sp.		X							
<i>Trachycardium</i> cf. <i>T. vaquerosensis</i> (Arnold 1908)		X							
<i>Trachycardium</i> sp.		X		X					X
<i>Tresus</i> sp.		X							
Solencurtidae (indeterminate)		X							
Veneridae		X							X
Annelida: Polychaeta									
<i>Spirorbis</i> sp.		X							
Arthropoda: Crustacea: Cirripedia									
<i>Megabalanus tintinnabulum</i> (Linnaeus, 1758)		X	X						
Echinodermata: Echinoidea									
<i>Eucidaris</i> cf. <i>E. thouarsii</i> (Valenciennes, 1846)		X	X					X	X
<i>Strongylocentrotus</i> sp.									X
<i>Vaquerosella</i> cf. <i>V. andersoni</i> (Twitchell, 1915)			X						
<i>Vaquerosella merriami</i> Anderson, 1905		X	X	X	X	X		X	X
Ichnotaxa									
<i>Entobia</i> isp (burrows)		X							
<i>Palaeophycus</i> isp.	X	X	X					X	X
Chordata: Vertebrata									
Chondrichthyes		X	X					X	X
Osteichthyes		X	X						

Lithophyllum cf. *L. profundum* Johnson, 1954 (Fig. 55), as well as benthic foraminifers, ostracodes, echinoid spines, and mollusk shell fragments. Another feature of Lithofacies D are clusters of linear bioturbations (Fig. 56) that Cuffey et al. (1981) described as burrows of polychaete colonies composed of cylindrical, micrite-filled tubes arranged parallel to bedding and each other. Loel and Corey (1932:275) referred to these as *Serpula coreyi* Wiedey, 1928, recognizing that its original designation as *S. careyi* was a typographical error. Loel and Corey also reported large colonies of "worms" in the Vaqueros and Temblor formations in the San Joaquin Hills in Orange County, the Santa Monica Mountains in Los Angeles

County, the Ventura River "Reef" beds in Ventura County, and the western Santa Ynez Mountains in Santa Barbara County. Lithofacies D burrows are herein referred to *Palaeophycus* isp. These parallel bioturbations range from 2 to 4 mm in diameter and up to 20 cm in length and are straight or, more rarely, slightly curved. There is no evidence of backfilling or setae impressions in any of the burrow walls; however, faint concentric rings, possibly from somite segments, with a thin linear ridge, extend the length of the burrow. Sullwold (1940) also noted thin rings on the internal walls of his specimens from Wood Canyon (LACMIP loc. 22004). Having examined specimens from Area 1, A. Myra Keen (pers.



Figures 7–34 Saddleback Valley limestone gastropods (Figs. 7–29) and other invertebrates (Figs. 30–34). SDSNH numbers are locality/specimen; H=height, W=width, L=length. 7, 8. *Fissurella rixfordi* Hertlein, 1928: 7, internal mold, SDSNH 4312/136497, L=35 mm, W=24 mm; 8, external mold, SDSNH 4312/140187, L=30 mm, W=20 mm; 9. *Chlorostoma* sp., external cast, SDSNH 4312/93707, H=10 mm, W=10 mm; 10. *Turritella ocoyana* Conrad, 1855, internal mold, SDSNH 4312/140188, H=75 mm, bottom whorl W=20 mm; 11. *Turritella* sp., latex peel of external cast, SDSNH 4312/85244, H=33 mm, W=10 mm; 12. *Forreria bartoni* Arnold, 1910, original shell (missing upper part of spire), SDSNH 4521/83243, H=24 mm, W=33 mm; 13. *Calyptrea* sp., internal mold, SDSNH 4312/85244, H=25 mm, W=35 mm; 14. *Crucibulum* sp., apical view of internal mold showing septum partially attached to shell; 15. naticid, internal mold, SDSNH 4312/140186, H=35 mm, ultimate whorl W=32 mm; 16. *Sinum* cf. *S. scopulosum* (Conrad, 1849), internal mold, SDSNH 4312/93721, H=25 mm, ultimate whorl W=28 mm; 17. *Trophon kernensis* Anderson, 1905, latex peel of

comm., 1979) commented that the "Reef" looks like a stratum of lime mud in which these annelids were burrowing, and as the deposit thickened, they moved upward to form long tubes.

The upper part of the section, from 12.1–14.1 m, is Lithofacies E, a white Monterey mudstone unconformably above the biosparite of Lithofacies D. It was exposed on a grassy hillside that extended downward for more than 6 m.

Area 2: Laguna Hills-Aliso Viejo

Area 2 is 5.2 km north of Wood Canyon and extends west from Via Lomas in Laguna Hills (SDSNH loc. 4312) and into Aliso Viejo (SDSNH locs. 4521, 6283, 6284, 6286) (Figs. 1, 57). In this area, the Saddleback Valley limestone consists primarily of highly indurated fossiliferous limestone and friable calcareous sandstone.

Mollusk molds (Fig. 58) are visible in the limestone at Fossil Reef Park (SDSNH loc. 4312; Fig. 5), which is part of a small fault block displaced 300 m southward from an east–west ridge (Morton et al., 1974). The ridge structure is characterized by minor east–west normal faults along both its northern and southern flanks. The nearby Moulton Parkway road cut (SDSNH loc. 4521; Fig. 5) exposed a 201-m-long cross section of the ridge. South of the first fault, 88.2 stratigraphic meters of the Saddleback Valley limestone are exposed. It comprises 15 beds differentiated by lithology and fossils (Fig. 6). Most of the beds are calcareous sands to friable calcarenites, but also present are two marls composed almost entirely of abraded cheilostome bryozoan fragments, two "button beds" (*sensu* Anderson, 1905) densely packed with the small sand dollar *Vaquerosella merriami* Anderson, 1905, and two beds of highly indurated limestone composed of 93–95% calcium carbonate (Morton et al., 1974). From 0 to 21.9 m, the fauna is characterized by intermittent appearances of *Eucidaris* cf. *E. thouarsii* (Valenciennes, 1846), *Palaeophycus* isp. burrows preserved as biosparite intraclasts, bryozoans, oysters, pectens, gastropods, echinoids, and barnacles. The 28.6–45.5-m interval is characterized by articulated pectens and oysters and include large well-preserved *L. crassicardo* in preferred orientation, similar to their occurrence in fine calcarenite near Fossil Reef Park in Area 2 (Fig. 4). The road cut section is then dominated by unconsolidated calcareous sand with shell fragments. Sands between the first and second fault are finer, and between the second and fourth fault they are devoid of macrofossils. The latter fault separates the calcareous sands of the Saddleback Valley limestone from the mudstone that is most characteristic of the lower Monterey Formation. A thin layer of vitric volcanic ash is present in the northernmost mudstone block, but attempts in this study to isotopically date it were unsuccessful.

The "Temblor" molluscan fauna in Area 2 is characterized by the bivalves *S. vaquerosensis*, *L. crassicardo*, *Crenomytilus expansus* (Arnold, 1907), *Panopea abrupta* (Conrad, 1849), *Modiolus ynezensis* Arnold, 1907, and *C. titan*, and the gastropods *T. ocoyana*, *Turritella temblorensis* Wiedey, 1928, and *Pyruconus* cf. *P. hayesi* (Arnold, 1909). Throughout Area 2, molds account for the highest numbers of specimens and species of any molluscan assemblage collected in this study.

A hillside outcrop immediately west of Moulton Parkway displays what appears to be a series of channelized, partial turbidite sequences in which dense limestone alternates with friable sandy limestone (Fig. 59). The sandy limestone contains *V. merriami*, echinoid spines, *Gemelliporella* aff. *G. punctata*, and *Megabalanus tintinnabulum* (Linnaeus, 1758). In contrast, 90% of the dense limestone consists of unsorted invertebrates, predominately the bivalves *C. titan*, *L. crassicardo*, *Pycnodonte* cf. *P. howelli* (Wiedey, 1928), *S. vaquerosensis*, and *Tresus* sp. This sequence was apparent in western Area 2 localities SDSNH 4521, 6283, 6284, and 6286.

On the west side of the northern Aliso and Wood Canyon Wilderness Park, south of the intersection of Aliso Viejo Parkway, a paved path leads

up from Cedarbrook past weathered dense limestone to an undeveloped outcrop where mudstone unconformably caps the limestone. Morton et al. (1974) mapped similar contacts elsewhere in the area, but this is the only one that remains visible.

Three exploratory wells drilled in the mid-20th century encountered limestone in the subsurface of western Saddleback Valley. In Shell Oil's Moulton No. 88-4, adjacent to SDSNH loc. 6283 in Area 2, a thick coquina of megafossil fragments that includes some blueschist clasts is at 0–300 ft, and a much thinner calcareous bed containing shell fragments, small bivalves, and echinoid spines is at 488–491 ft. About a quarter-mile north-northeast of the Area 2 fossil localities, South Fullerton Oil's No. 1 well has a hard shell bed at 840–895 ft. In the vicinity of Area 1, Shell's Moulton No. 14 well drilled through Monterey mudstone and into a fossiliferous limestone 239–253 ft above the San Onofre Breccia.

Area 3: Laguna Woods and Lake Forest

Limestone localities in Area 3 include the original "Pecten Reef" in Lake Forest (SDSNH loc. 4520/OCPC loc. 0023) and the Home Depot (OCPC loc. 03155) and Laguna Woods Self-Storage (OCPC loc. 0872) sites. No basal contacts of the limestone were exposed in this area, but infrequent blueschist and quartz cobbles in the sandy limestone reveal that the San Onofre Breccia extended into OCPC loc. 03155.

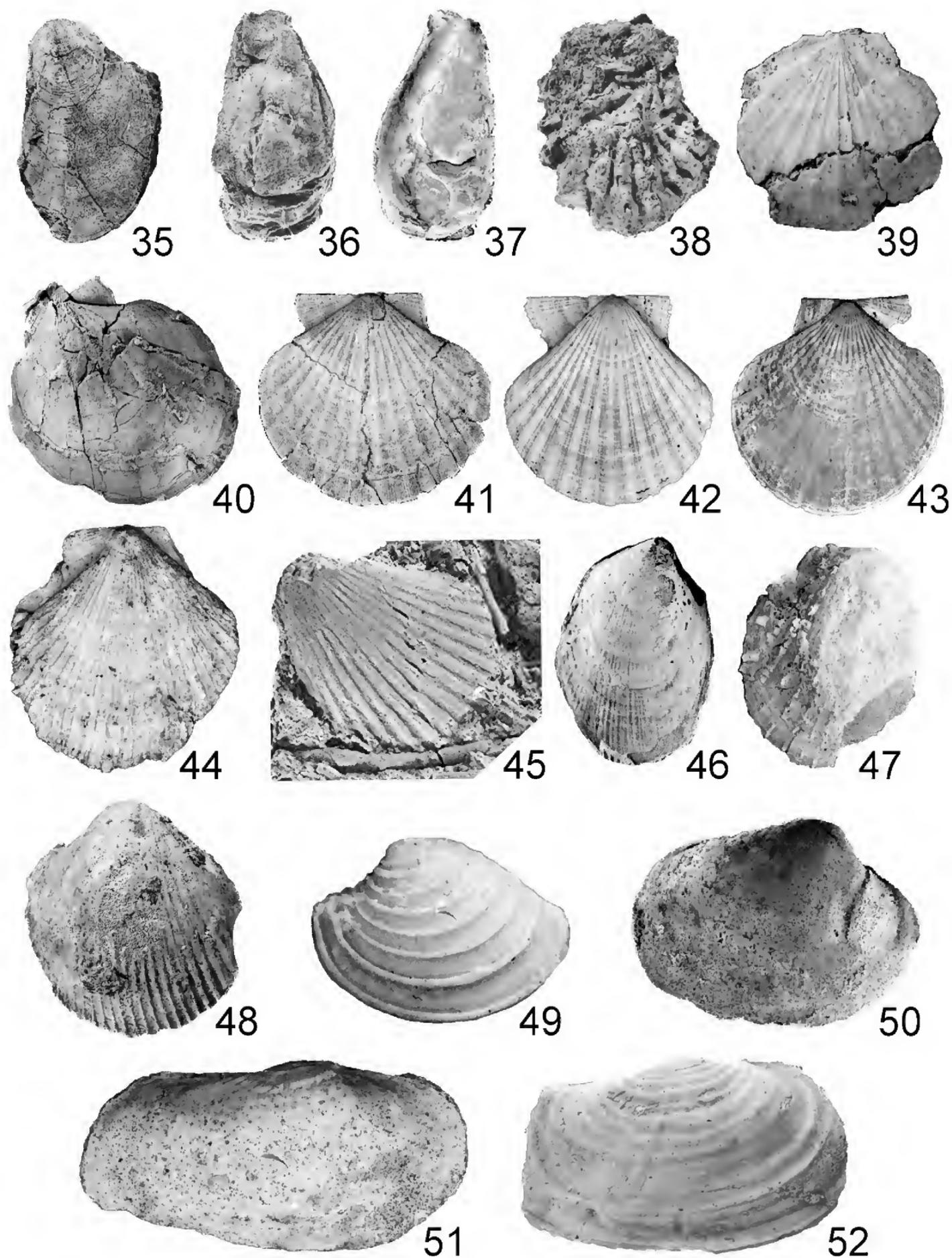
Narrow lenses of friable calcareous sandstone in Lake Forest (SDSNH loc. 4520), containing echinoids ("button" sand dollars, eucidarid spines), cartilaginous and boney fish teeth, and occasional sandy manganese nodules up to 6 cm in width, exuded a strong petroliferous odor when exposed. Bonatti and Nayudu (1965:26) contend that the rate of manganese oxide deposition can vary, and although manganese nodules generally represent low rates of growth in the deep sea, nodules have also been found in several localities where sedimentation rates are relatively high, such as the Gulf of California, and at shallow depths (Calvert and Price, 1977). The friable calcareous sandstones are overlain by a sequence of three turbidites in which 60–72-cm-thick, orange, friable, coarse sandstones alternate with 200–210-cm-thick greenish-gray silty mudstones containing scattered fish scales. The sandstones (SDSNH loc. 4964; LACMVP loc. 3414) yielded abundant fish teeth, as well as a crocodile tooth. In 1973, development of a housing tract that includes Mountain View Park covered the limestone and sandstone, although a few boulders of the indurated limestone remain as decorative features of the community landscape, and a small cut-slope east of the park exposes the mudstones.

West of Lake Forest, in Laguna Woods, grading for the Leisure World community in the 1960s exposed an orange, friable, coarse sandstone that yielded fish, sea turtle, and bird fossils at three localities north of Aliso Creek. A rich marine vertebrate fauna recovered from a later exposure (LACMVP loc. 1945) includes 19 bird and 20 shark species dated at 12–14 Ma (Howard, 1968; Howard-Wylde, 1980), which is younger than the limestone. Howard-Wylde (1980) characterized this sandstone as having the densest concentration of shark teeth in western North America.

Grading for the Laguna Woods Home Depot (OCPC loc. 03155; 3.3 km west of SDSNH loc. 4520) exposed a limestone with poorly preserved mollusks, notably *L. crassicardo* and *C. titan* and fragments of *S. vaquerosensis*, *Pyruconus* cf. *P. hayesi*, *Forreria bartoni* (Arnold, 1910), cheilostome bryozoans, and *Palaeophycus* isp. Also present are unbroken *V. merriami* and random small shark teeth.

Along the north side of the Home Depot site (OCPC loc. 03155), there was a small outcrop of gritty, poorly consolidated Topanga siltstone that Morton et al. (1974) mapped as the Vaqueros Formation. The unit contains *Acila* sp., *Scapharca* sp., *A. lomdocensis*, and well-preserved clusters of translucent brown brachiopods identified as a *Glottidia* sp. This association was also seen in a dark siltstone laterally adjacent to

← external cast; 27, internal mold; 28. *Calyptraea* sp., internal mold, SDSNH 4520/98688, L=21 mm, W=15 mm; 29. vermetid, internal mold, SDSNH 4512/142016, image H=30 mm; 30. *Gemelliporella* aff. *G. punctata* Canu and Bassler, 1919, fragments, SDSNH4521/98668, image H=63 mm; 31, 32. *Eucidaris* cf. *E. thouarsii* (Valenciennes, 1846): 31, original spine with regularly spaced knobs, SDSNH 4521/140192, L=30 mm; 32, original test fragment, SDSNH 4521/98680, L=19 mm; 33. *Vaquerosella merriami* (Anderson, 1905), external dorsal view, SDSNH 4521/83249, H=18 mm, W=18 mm; note anal aperture (notch) at ventral margin; 34. *Megabalanus tintinnabulum* (Linnaeus, 1758), original shells, side view of attached pair, SDSNH 4312/140191, H=25 mm, W=20 mm.



Figures 35–52 Saddleback Valley limestone bivalves. Figured specimens are external casts unless indicated otherwise. LV=left valve, RV=right valve; SDSNH numbers are locality/specimen; H=height (dorsal to ventral), L=length (anterior to posterior). 35. *Crenomytilus expansus* (Arnold, 1907), LV, SDSNH 4312/83246, H=130 mm, L=75 mm; 36, 37. *Crassostrea titan* (Conrad, 1853), RV, SDSNH 4312/83238, H=97 mm, L=52 mm: 36, exterior; 37, interior; 38. *Pycnodonte* cf. *P. howelli* (Wiedey, 1928), SDSNH 4312/83234, H=70 mm, L=70 mm; 39. *Amusiopecten vanvlecki* (Arnold, 1907), LV with faintly raised ribs, SDSNH 4312/83232, H=70 mm, L=75 mm; 40. *Amusium lomdocensis* (Arnold, 1906), crushed shell with smooth surface, SDSNH 4512/98676, H=104 mm, W=68 mm; 41, 42. *Lyropecten crassicardo* (Conrad, 1857), original shells, external views: 41, LV, SDSNH 4521/98672, H=97 mm, L=107 mm; 42, juvenile, LV, SDSNH 4521/98671, H=30 mm, L=30 mm; 43. *Pacipecten andersoni* (Arnold, 1906), original shell, RV, external view, SDSNH 4312/140181, L=30 mm, W=30 mm; 44. *Crassadoma* cf. *C. gigantea* (Gray, 1825), external cast, LV, SDSNH 4312/140354, H=42 mm, W=32 mm; 45. *Lima* sp., external cast in bioturbated matrix, RV, SDSNH 4312/140182, L=47 mm, W=35 mm; 46. *Limaria* sp., external cast, RV, SDSNH 4312/121368, L=30 mm, W=21 mm; 47. *Spondylus scotti* (Brown and Pilsbry, 1913), external cast, SDSNH 4520/83235, L=124 mm, W=100 mm; 48. *Trachycardium* sp., LV, external cast, SDSNH 4312/93837, L=86 mm, W=80 mm; 49. *Chione* cf. *C. richthofeni* Hertlein and Jordan, 1927, latex peel of external cast, LV, SDSNH 4312/83248, L=20 mm, W=25 mm; 50. *Saxidomus vaquerosensis* Arnold, 1910, RV view of steinkern, SDSNH 4312/180184, L=70 mm, W=100 mm. Note anterior and posterior muscle scars (light patches); 51. *Panopea tenuis* (Wiedey, 1928), external cast, LV, SDSNH 4312/140185, L=45 mm, W=85 mm; 52. *Panopea abrupta* (Conrad, 1849), external cast, LV, SDSNH 4312/83237, L=40 mm, W=58 mm.



Figure 53 Thick limestone of Lithofacies B dominated by steinkerns of *Saxidomus vaquerosensis* in Wood Canyon (SDSNH loc. 5752). W.J. Edgington stands on a lag deposit (Lithofacies A) consisting of abraded and broken mollusk shells and blueschist cobbles derived from the San Onofre Breccia. Image taken in 1976 before site was destroyed by development.

indurated limestone, 15 km to the south near the junction of Wood Canyon and Aliso Canyon in Area 1 (Sullwold Collection, LACMIP loc. 21981). Thin sections of this sandy limestone display articulated ostracodes.

In the vicinity of the Home Depot site is the Laguna Woods Self Storage facility (OCPC loc. 0872), located at the northwest junction of El Toro Road and Moulton Parkway. Grading on this site in 1997 exposed an indurated sandy limestone containing abraded fragments of *L. crassiscardo* and *C. titan*. East of SDSNH loc. 4520, grading in 1975 had also revealed a small limestone lens near Muirlands Boulevard and Lake Forest Drive. No fossils or data were collected from either of these two localities.

DISCUSSION

DEPOSITIONAL PALEOENVIRONMENT

The fossils of Saddleback Valley limestone (Table 1) indicate that around 16 Ma, middle Miocene coastal waters were warmer than those off southern California today. Fife (1979) suggested that the

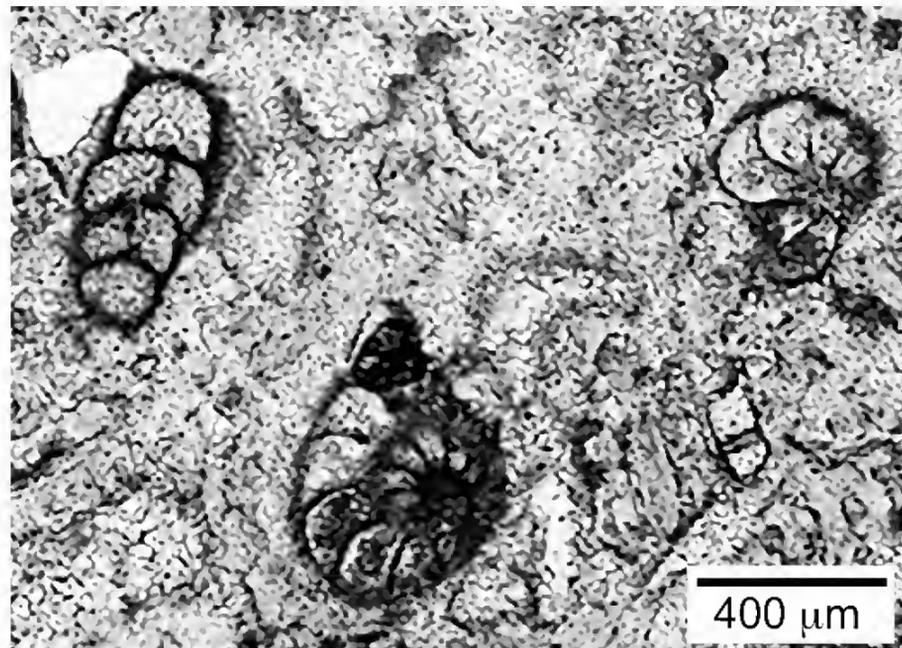


Figure 54 Microphotograph of thin-sectioned biosparite from Lithofacies B in Wood Canyon (Area 1, SDSNH loc. 5752). Faint microcrystalline calcite surrounds benthic foraminifera that are likely among those taxa isolated from the matrix of SDSNH loc. 4521 in Area 2. Plausible identifications based in Finger (1990) are *Bolivina* sp., (upper left), *Anomalinoides salinasensis* (Kleinpell, 1938) (below center), and *Valvulineria miocenica* Cushman, 1926 (upper right).

limestone was an “allochthonous fossiliferous deposit” in which marine benthic organisms were transported by longshore currents, storm waves, and gravity to lower areas on the shallow substrate. However, the microfossil component described in the present study reveals that the shallow-water benthos were redeposited at much greater depths, most likely due to subsidence and turbidity currents. Those phenomena are responsible for much of the deep-water deposition off the coast of California during the Miocene, particularly that of the Monterey Formation and its equivalent units in the Los Angeles Basin.

Woodford (1925) interpreted the depositional environment as a gulf or strait bounded on the west by a region of high relief, with an arid climate that permitted the thick, poorly sorted San Onofre Breccia to accumulate without muddying the waters.

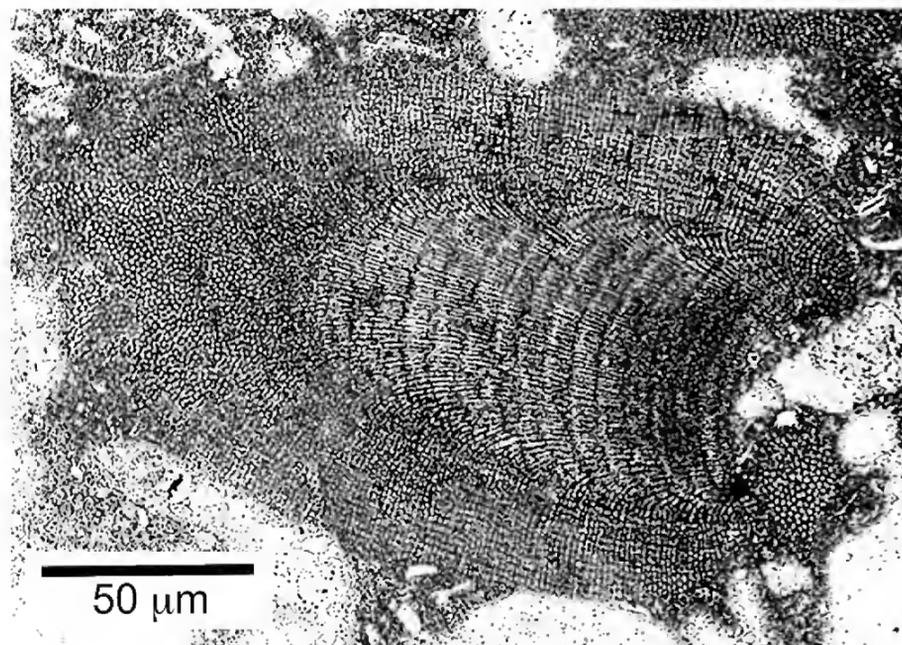


Figure 55 Thallus of the red coralline algae *Lithophyllum* cf. *L. profundum* Johnson, 1954. Photomicrograph of thin-sectioned biosparite of Lithofacies D, SDSNH loc. 5752.

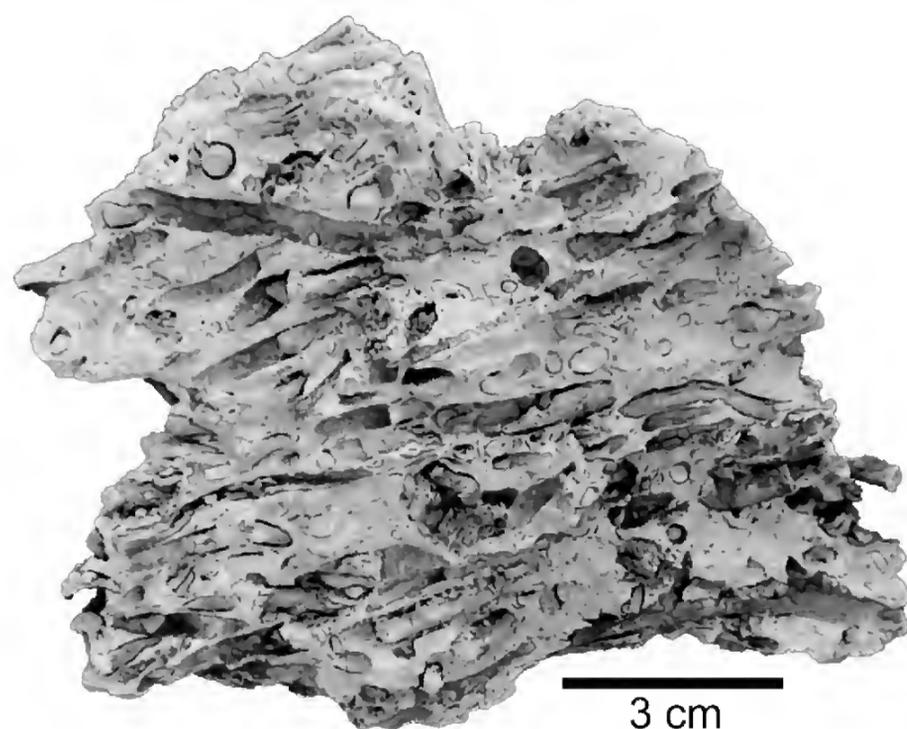


Figure 56 *Palaeophycus* isp. (SDSNH 93703) in limey mudstone of Lithofacies D, SDSNH loc. 4512.

Loel and Corey (1932) proposed that the widespread uniformity of marine conditions that characterize the “Temblor” CPMS resulted from an abrupt subsidence of the California coast and that the resulting transgression that modified the coastline was accompanied by a rapid increase in the number and diversity of invertebrates as tropical species expanded their ranges northward.

Similar to the rhodophytic rudite described from Wood Canyon, Johnson and Kaska (1965) found abundant red coralline algae in the Miocene El Petén Limestone of Guatemala, which they described as a biosparite with a rich megainvertebrate fauna of mollusks, echinoids, and bryozoans. Modern colonies of coralline red algae inhabit the photic zone of calm waters, such as those in the Gulf of California, around Cedros Island west of central Baja

California, and on the leeward side of Santa Catalina Island in the San Pedro Channel off Los Angeles.

Cuffey et al. (1981:65) suggested that the Saddleback Valley limestone “developed on the shallow part of a submarine slope, from a gravel flanked offshore island, down into a mud-floored deep-marine basin to the east.” They noted that foraminifers and nannofossils in the limestones (from all three areas referred to in the present study) indicate deposition at outer-neritic to upper-bathyal depths, but the associated ostracodes and mollusks are characteristic of intertidal to inner-neritic depths. These mixed-depth associations confirm that the limestone was formed mostly from sediments that had been displaced downslope.

Finger (1988) documented the occurrence of shallow-marine ostracodes in Laguna Hills and interpreted them also as having been displaced downslope based on their association with deep-water foraminifera in accordance with the upper depth limits (UDLs) assigned by Ingle (1980). Finger (1992) later provided a list of those foraminiferal assemblages, three of which were from the original Moulton Parkway road cut (SDSNH loc. 4521). The composite foraminiferal assemblage in the road cut consists of 35 species. Each of the three assemblages are similarly mixed, as indicated by the association of multiple species representing four paleobathymetric biofacies ranging from inner-neritic to upper-middle bathyal depths (Table 2). The deepest dwelling species indicate that final deposition of the Saddleback Valley limestone sediments was at upper middle-bathyal depths.

In association with the foraminifera are nine species of ostracodes that Finger (1988) assigned to seven genera characteristic of a shallow-marine biofacies: *Aurila* (3 species), *Cytherella*, *Hermanites*, *Loxoconcha*, *Loxocorniculum*, “*Paijenborchella*,” and *Paracytheridea*. About 0–.4 km northeast of, and stratigraphically above, the road cut section, an orange sand lens (~4 m²) within a greenish-grey silty mudstone (UCMP loc. 12873) yielded a similar microfauna. Ostracodes were also observed in thin sections from Area 1, but none have been recorded from Area 3.

Finger (1988, 1992) also sampled the mudstone that was exposed across the nearby intersection of Alicia and Moulton parkways, and they yielded Luisian foraminiferal assemblages more typical of the deeper water Monterey Formation, with the

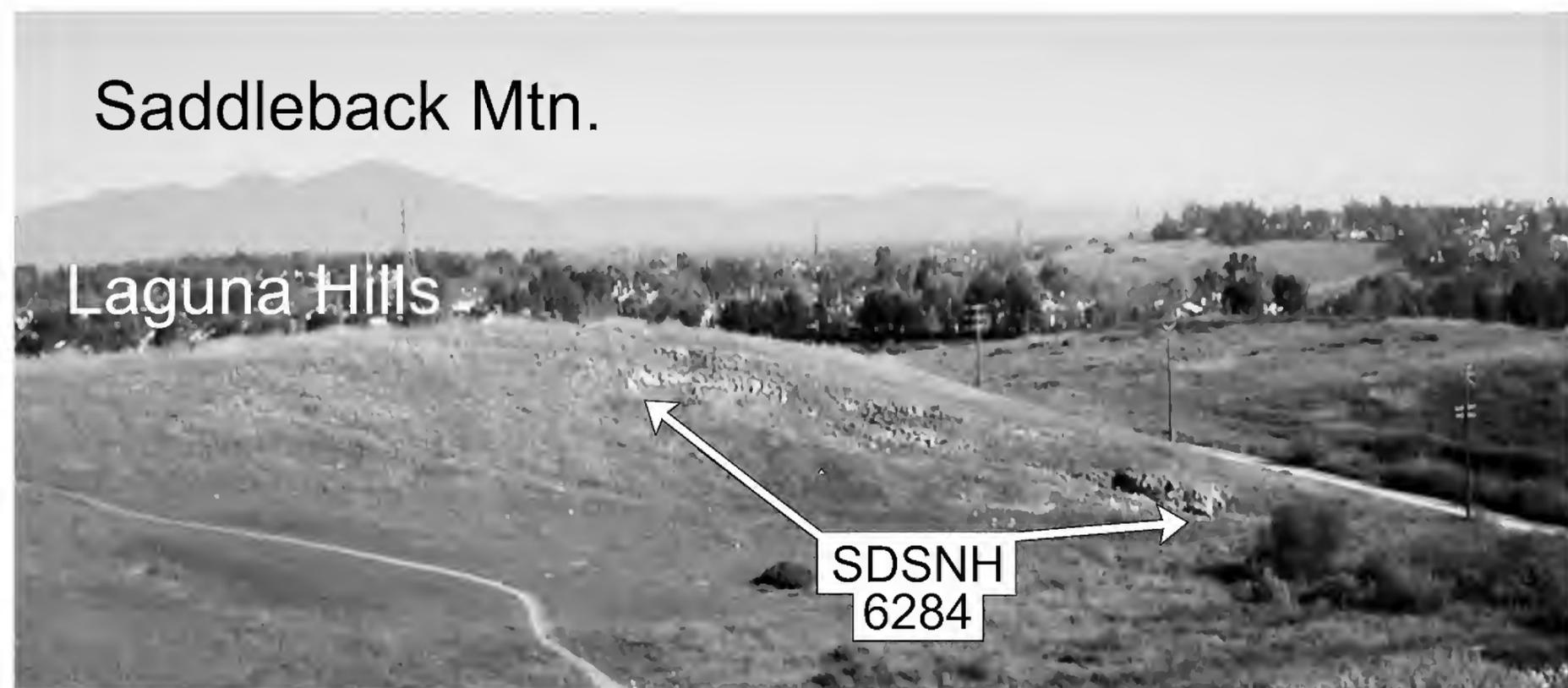


Figure 57 Saddleback Valley looking N79E from Aliso and Wood Canyons Wilderness Park (Area 2). The Santa Ana Mountains are visible on the horizon.

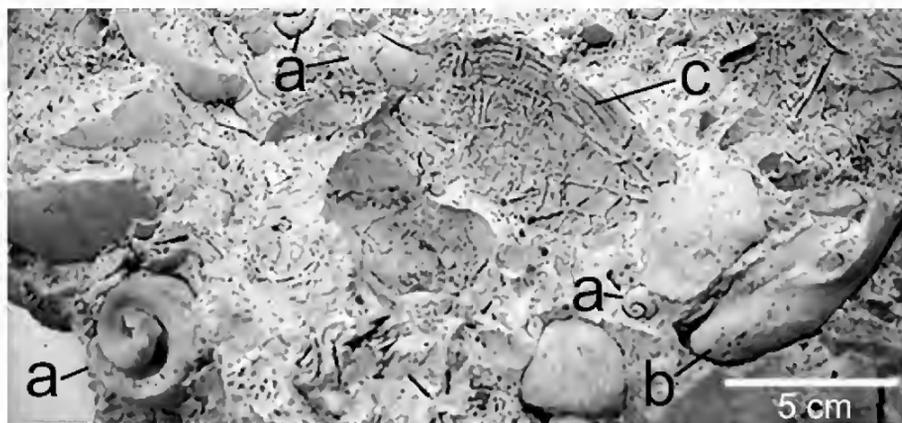


Figure 58 Fossiliferous biosparite (OCPC 50310) salvaged in 1979 from a spoils pile at SDSNH loc. 4312 (OCPC loc. 0022) in Laguna Hills (Area 2). Note the fossils are molds not in preferred orientation or size-sorted. Visible in this photograph: a, gastropods; b, *Saxidomus vaquerosensis* (steinkern, hinge-up); c, mold of *S. vaquerosensis* valve with calcite-filled *Entobia* isp. burrows.

inclusion of species such as *Rectuwigerina branneri* (Bagg, 1905) and *Pullenia miocenica* Kleinpell, 1938, and a much lower component of shallow-water species. No ostracodes were recovered from these mudstones.

Although they did not analyze microfossils, Stanton and Alderson (2013) concluded that the limestone interbedded with the Conejo Volcanics in the Santa Monica Mountains is similar to the limestone in Saddleback Valley, in that both formed from shallow-water sediments displaced into deep water during the early to middle Miocene.

Hall (2002) considered the bivalve *L. crassicardo* and the gastropod *Trophosycon kerniana* (Cooper, 1894), both of which are abundant in some of the Saddleback Valley limestone outcrops, as representatives of his middle Miocene “outer tropical range.” He placed the region approximately 750 km to the south, in subtropical waters where Cedros Island is today, during the global Middle Miocene Climate Optimum (MMCO) at 17–15 My (Flower and Kennett, 1994; Zachos et al., 2001). This



Figure 59 Alternating beds of indurated limestone and friable sandy limestone, North Aliso and Wood Canyon Wilderness Park (Area 2, SDSNH loc. 6283). The more resistant limestone that forms the ledges shown here correlates with the indurated limestone exposed along Moulton Parkway (SDSNH loc. 4521), which is on the east side of this hill (to the left of photo).

Table 2 Upper depth limits of benthic foraminifera recovered from the Saddleback Valley limestone in the Moulton Parkway road cut (SDSNH loc. 4521).

Inner neritic (50–150 m)	
	<i>Buccella oregonensis</i> (Cushman, Stewart and Stewart, 1948)
	<i>Buliminella elegantissima</i> (d’Orbigny, 1839)
	<i>Elphidium granti</i> Kleinpell, 1938
	<i>Gaudryina pliocenica</i> Cushman, Stewart and Stewart, 1949
	<i>Gaudryina subglabrata</i> Cushman and McCulloch, 1939
	<i>Nonionella miocenica</i> Cushman, 1926
	<i>Pseudononion costiferum</i> (Cushman, 1926)
Outer neritic (50–150 m)	
	<i>Bolivina advena ornata</i> Cushman, 1925
	<i>Buliminella subfusiformis</i> Cushman, 1925
	<i>Islandiella modeloensis</i> (Rankin, 1934)
	<i>Marginulinopsis beali</i> (Cushman, 1925)
	<i>Valvulineria californica</i> Cushman, 1926
	<i>Valvulineria miocenica</i> Cushman, 1926
Upper bathyal (150–500 m)	
	<i>Baggina californica</i> Cushman, 1926
	<i>Bolivina brevior</i> Cushman, 1925
	<i>Bolivina tumida</i> Cushman, 1925
	<i>Cancris baggi</i> Cushman and Kleinpell, 1934
	<i>Pseudoparrella subperuviana</i> (Cushman, 1926)
	<i>Kleinpella californiensis</i> (Cushman, 1925)
	<i>Uvigerinella californica ornata</i> Cushman, 1926
Upper-middle bathyal (500–1,500 m)	
	<i>Bolivina californica</i> Cushman, 1925
	<i>Bolivina imbricata</i> Cushman, 1925

MMCO was the warmest interval in the Neogene, as evidenced by the many molluscan ranges that extended their farthest north since the middle Eocene (Oleinik et al., 2008).

BIOSTRATIGRAPHIC AGE

The shallow-marine invertebrate fauna of the Saddleback Valley limestone represents the “Temblor” CPMS, which Smith (1991) placed at approximately 19.5–12 My, an interval spanning the middle Saucelian to early Mohnian benthic foraminiferal stages of Kleinpell (1938) (see Fig. 2). McCulloch et al. (2002) shortened this CPMS in the Los Angeles Basin to approximately 16.65–14.2 (late Saucelian to late Luisian). Among the mollusks, the bivalve *Pacipecten andersoni* and the gastropods *Pyruconus* cf. *P. hayesi*, *Megasurcula keepi* (Arnold, 1906), and *Priscofusus geniculus* (Conrad, 1849) are restricted to the “Temblor” CPMS. Although most of the species in the Saddleback Valley limestone are known to occur in the “Temblor” CPMS, *P. geniculus* and the bivalve *Pycnodonte* cf. *P. wiedeyi* (Hertlein, 1928) had not been previously recognized above the Vaqueros CPMS.

The benthic foraminiferal fauna recovered from the limestone at Moulton Parkway (Area 2) characterizes the Relizian–Luisian interval, while the absence of species that first appear in the Luisian Stage favors the older part of that range. Also, in Area 2 (SDSNH 4312), Kling (pers. comm., 2002) identified coccoliths of *Calcidiscus leptoporus* (Murray and Blackman, 1898), *Coccolithus pelagicus* (Wallich, 1877) Kamptner 1954, *Dictyococcites minutus* (Haq, 1971), *Helicosphaera carteri* (Wallich 1877), and *Helicosphaera scissura* Miller, 1981. The concurrent calcareous nannoplankton zonal range is delimited by the range of *H. scissura* at calcareous nannofossil (CN) zones CN1–CN3 (late Saucelian–late Relizian). The concurrent biostratigraphic data therefore place the limestone in the Relizian and within CN3. The Monterey Formation mudstones at the intersection of Alicia and Moulton parkways (just south of the Moulton Parkway road cut) yielded a

Table 3 Strontium isotope data and ages for the Saddleback Valley limestone (three SDSNH localities), the orange sand lens in mudstone (UCMP loc. 12873), and dark brown mudstone (UCMP loc. 12871). Ages interpreted from unpublished reference data provided by J. McArthur (LOWESS 5) and D. DePaolo.

Sample	$^{87}\text{Sr}/^{86}\text{Sr}$ normalized ± 2 SE			Age	
	Minimum	Mean	Maximum	LOWESS 5	DePaolo
UCMP 12871	.708830	.708837	.708844	12.00 \pm 2.5	13.5 \pm 2.0
SDSNH 4521A	.708764	.708774	.708784	15.00 \pm 0.7	15.9 \pm 0.1
UCMP 12873	.708756	.708765	.708774	15.40 $-0.7/+0.5$	16.0 \pm 0.1
SDSNH 4521	.708722	.708730	.708738	15.92 \pm 0.6	16.3 \pm 0.1
SDSNH 4312	.708717	.708727	.708737	15.96 \pm 0.6	16.3 \pm 0.1

distinctly Luisian foraminiferal fauna, which suggests that the older limestone could be within the late Relizian Stage, but that interval overlaps with the Luisian Stage (Fig. 2). Although McCulloh et al. (2002) places the Relizian/Luisian boundary at 15.6 Ma, just above the 15.97 Ma boundary between the early and middle Miocene, Crouch and Bukry (1979) had previously indicated that the Relizian ranges into CN5 (13.6–11.7 My). For the most part, the relative age, lithology, and paleontology of the Saddleback Valley limestone are consistent with the “Temblor” CPMS in the Topanga Formation. Coccoliths are elements of oceanic plankton that are more likely to be deposited in a deep marine embayment than along the shallow margin of a restricted fluvio-marine inlet or channel. Hence, it is unlikely that *H. scissura* was deposited in the Topanga sediment before its down-slope displacement, implying that deposition of the Monterey Formation in the study area commenced in the Relizian. It is unfortunate that the Wood Canyon exposure (Area 1) was among the first destroyed by development; had microfossil samples been taken at or just below the level of its limestone lenses, they could have added credence to the late Relizian age of the limestone.

The California Miocene benthic foraminiferal zonation of Kleinpell (1938) began morphing in the 1970s with the development of global planktic microfossil zonations. Local studies on planktic microfossils (i.e., foraminifera, diatoms, radiolarians, calcareous

nannofossils) associated with “stage-diagnostic” benthic foraminiferal assemblages evidenced the time-transgressive nature of the Opeelian-based benthic stages (see introduction in McDougall, 2007, for elaboration). The implied geographical inconsistency is simply because benthic organisms are controlled by local bottom facies. Problems with the CBFS are most evident when attempting interbasinal correlation (Finger, 1992), and a similar situation restricts the utility of the CPMS. The biostratigraphic placement of the Saddleback Valley in the late early Miocene therefore needed to be assessed by a geochronologic method that could produce high-resolution dates, as reported in the following section.

CHRONOSTRATIGRAPHIC AGE

Five well-preserved samples of biogenic calcite from Area 2 were sent to the Pacific Centre for Isotopic and Geochemical Research (PCIGR) at the University of British Columbia for strontium isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) analysis. These were bivalve (*L. crasscardo*) shells from SDSNH 4312 (Fossil Reef Park), gastropod (*F. bartoni*) spines from SDSNH 4521, and cheilostome bryozoans (*Gemelliporella* aff. *G. punctata*) from SDSNH 4521A (both in the Moulton Parkway road cut), foraminifera (*Valvulineria miocenica* Cushman, 1926) from UCMP loc.12873 (orange sand lens in Monterey mudstone), and foraminifera (*R. branneri*) from UCMP loc.12871 (dark brown mudstone of Monterey Formation that was exposed at the eastern corner of Moulton and Alicia parkways).

Table 3 presents the analytical data ($^{87}\text{Sr}/^{86}\text{Sr}$ ratios) and two sets of age interpretations according to McArthur’s LOWESS 5 curve (unpublished version “LOWESS 5 Fit 26 03 13” of the LOWESS 3 curve in McArthur et al., 2001) and DePaolo’s revision (unpublished) of the Miocene $^{87}\text{Sr}/^{86}\text{Sr}$ curve of Richter and DePaolo (1988) that DePaolo and Finger (1991) used to evaluate the biostratigraphic correlations in the Monterey Formation of central California. That $^{87}\text{Sr}/^{86}\text{Sr}$ curve is offset from the more commonly used LOWESS curve that indicates younger ages for the same values. DePaolo’s curve is favored here as the more accurate of the two, because the pertinent part of it was derived solely from the datasets of two Deep Sea Drilling Project (DSDP) cores (575B and 590B), and diagenetic effects, which were evident in the poor match of the original datasets, were corrected with the methods described by Richter and DePaolo (1988). This correction can only be done on a continuous section that has both pore-water and carbonate fossil data; hence, most $^{87}\text{Sr}/^{86}\text{Sr}$ data incorporated into the LOWESS curve is uncorrected. Data from the 13–18 My interval, within which the curve is kinked at about 15 Ma, are particularly susceptible to shifting by diagenesis. The inaccuracy of the LOWESS curve was most evident in the impossible age of 12.0 Ma it indicated for *Rectuvigerina* tests from the Monterey mudstone (UCMP loc. 12871), as that genus had disappeared from California at the mid-Miocene cooling event that triggered the biotic turnover demarcating the Luisian/Mohnian boundary at 13.6 Ma.

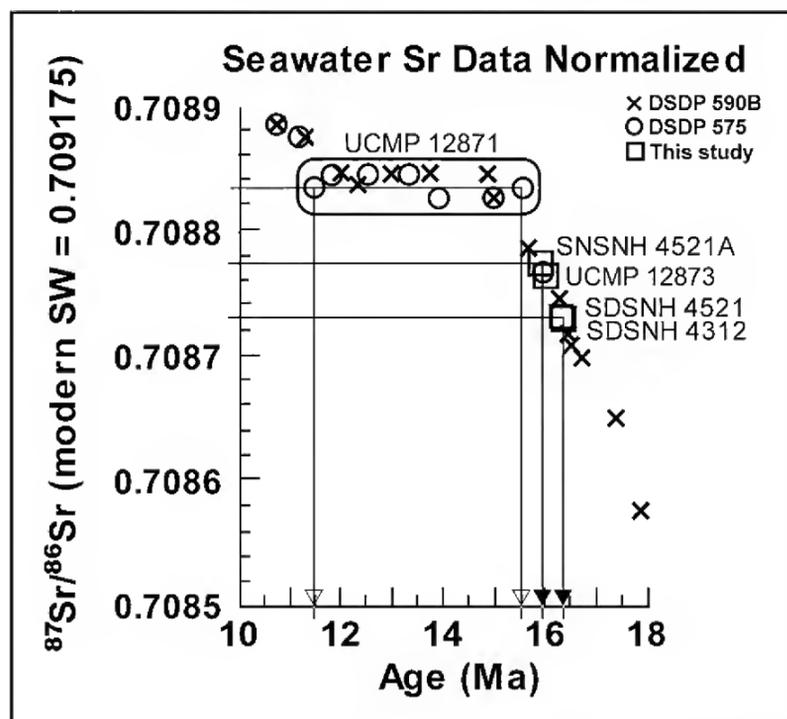


Figure 60 Determination of Miocene isochronologic ages for five samples of the Monterey Formation in Saddleback Valley using DePaolo’s latest (unpublished) version of the Richter and DePaolo (1988) $^{87}\text{Sr}/^{86}\text{Sr}$ curve for the Miocene. The three SDSNH samples are from limestones, UCMP 12873 is an orange sand lens within mudstone, and UCMP 12871 is mudstone.

Correlation with DePaolo's curve (Table 3; Fig. 60) age-dates the "Temblor" fauna in the Saddleback Valley limestone within the interval $16.3\text{--}15.9 \pm 1.0$ My (see Fig. 2). Determination of this relatively narrow age interval is possible because the $^{87}\text{Sr}/^{86}\text{Sr}$ values correlate with the steepest part of the Cenozoic curve. In contrast, the higher ratio of the mudstone from UCMF loc. 12871 is within the flattest section of the curve and yields an imprecise age of $15.4\text{--}11.4$ My, but its Luisian foraminiferal assemblage indicates that it is unlikely to be younger than 13.6 Ma, refining the age of the mudstone to 14.5 ± 0.9 Ma. The part of the DePaolo curve relative to this study remains intact despite the latest revision (Hilgen et al., 2012) of the geologic time scale and its CN zonation in particular.

TAPHONOMY

Thin sections of the indurated limestone exhibit a microcrystalline calcite matrix with foraminifers, ostracodes, coccoliths, siliceous sponge spicules, echinoid spines, coralline red algae thalli, and fragments of mollusks and bryozoans. Recrystallization has degraded the preservation quality of the calcareous microfossils with the exception of the coralline red algae thalli. In all three areas, indurated biosparite has mollusk molds displaying detailed internal and exterior shell structures. Distinctive chains of round chambers ascribed to *Entobia* isp. occur in molds of *Saxidomus vaquerosensis*. As the biosparite grades into a sandy limestone, the form of preservation changes from molds to well-preserved, articulated shells that are primarily pectinids but also include *C. titan*, *Pycnodonte* cf. *P. howelli*, and *Pycnodonte* cf. *P. wiedeyi*. The limy sandstones of Area 2 contain scattered shell fragments of *S. scotti*, *Trachycardium* sp., and *F. bartoni*; spines of the latter species retain some original pigmentation visible as a faint pink. In sandier limestone matrices, abundant well-preserved echinoids (*Eucidaris* sp., *V. merriami*) occur with shark teeth and red-tinted barnacles (*M. tintinnabulum*). Also common in the limy sandstone are bryozoan branches, especially in Lithofacies C of Area 1 (SDSNH loc. 5752) and in the upper friable limy sandstone beds of Area 2 (SDSNH loc. 4521). The poor preservation of fossils in limestone at the western Area 3 site (OCPC loc. 03155) is attributed to groundwater infiltration along a fault that extends across the development; for example, articulated pectinids, well preserved in other limestone localities, are crumbly and stained orange.

COMPARISON WITH "TEMBLOR" FAUNA IN THE LOS ANGELES BASIN

The "Temblor" fauna in the Saddleback Valley limestone differs from those of the Topanga Formation in the northern foothills of the Santa Ana Mountains (Schoellhamer et al., 1981) and the Cold Creek Member of the Topanga Canyon Formation in the Santa Monica Mountains (Alderson, pers. comm., 2014) by having abundant coralline algae, cheilostome bryozoans, common small gastropods, and isolated concentrations of pectinids. Additionally, *V. merriami*, which is abundant in all three Saddleback Valley limestone areas, has not been reported from the Santa Monica Mountains, but it occurs in the northern Santa Ana Mountains (SDSNH loc. 4308A) in association with *T. ocoyana*, *T. temblorensis*, *Dosinia* sp., and *Antillophos posunculensis* (Anderson and Martin, 1914).

Although no bioturbated mudstones have been reported in the Topanga and Topanga Canyon formations, clusters of *Palaeophycus* isp. were observed in Topanga Formation siltstone along the eastern flank of SDSNH loc. 4312 in Area 2. Similar parallel burrows with internal ringlike impressions also occur in gray

biosparite in Wood Canyon (LACMIP loc. 22004) and in the San Joaquin Hills just south of Saddleback Valley in the Bommer Member of the Topanga Formation (SDSNH loc. 6836). These burrows are also in the Topanga Formation near Ortega Highway in southern Rancho Mission Viejo (OCPC loc. 3266) associated with cheilostome bryozoans and the majority of mollusk species found in the Saddleback Valley limestone.

Foraminifera do not appear to be abundant in the Topanga Formation in the San Joaquin Hills, as first noted by Vedder et al. (1957) when they split it into, from oldest to youngest, the Bommer, Los Trancos, and Paularino members. Their only mention of foraminifera referred to them as sparse in the Los Trancos Member. Smith's (1960) foraminiferal study focused on the Santa Ana Mountains but included the San Joaquin Hills. She reported four assemblages in the Topanga Formation of the Santa Ana Mountains that yielded a total of 11 species and noted that foraminifera are abundant but highly dominated by *Bolivina advena* Cushman, 1925, var.; *Nonion costiferum* Cushman, 1926; N. aff. *N. costiferum*; and *Valvulineria depressa* Cushman, 1926. Smith (1960) documented Luisian foraminiferal assemblages from the Monterey Formation overlying the San Onofre Breccia in the San Joaquin Hills. Although she noted that the Monterey Formation exposed west of Oso Creek consists of diatomaceous shale and siltstone containing abundant foraminifera, there was no mention of limestone, Relizian foraminifera, or the foraminifera from Shell's Moulton No. 14 well, which was located almost 1 mi (1.6 km) south of Area 2 and revealed the Luisian/Mohnian boundary at a depth of 410 ft.

A paucity of foraminifera in the Topanga Formation in the Santa Ana Mountains was noted by Yerkes and Campbell (1979) and Schoellhamer et al. (1981). Their reports indicated that the foraminifera are represented by relatively few species, all of which indicate shelf-depth environments. This is in stark contrast with the four assemblages recorded by Finger (1992) from the limestone section in the Moulton Parkway road cut. Ostracodes probably occur in the Topanga Formation in Orange County, but none have been reported.

CONCLUSIONS

The Saddleback Valley limestone occurs only in western Saddleback Valley. It does not represent a reef, biostrome, or bioherm as had been reported previously. Rather, it comprises related but inconsistent and discontinuous sequences of calcareous beds that locally vary in lithology, lithification, paleontology, and stratigraphy. Its lithologies range from unconsolidated limy sands to calcarenites and micrites. Conspicuous "Temblor" CPMS macrofauna and sandy layers in the Saddleback Valley limestone resemble those of the Topanga Formation and indicate a warm, shallow-marine environment. Accordingly, microfossils correlate the limestone with the late Relizian Stage and MMCO between 17 and 15 My, and $\text{Sr}^{87}/\text{Sr}^{86}$ analysis refines its age within the interval of $16.5\text{--}15.9$ My, with a maximum mean age of 15.85 Ma, which is at the base of the middle Miocene. Mixed-depth benthic foraminiferal assemblages, however, indicate that these bioclastic sediments had been dislodged from their provenance and transported to bathyal depths. The limy deposits thus represent the basal Monterey Formation, which is supported by field observations of limestone lenses within Monterey Formation mudstones and channel structures. A summarization of the geologic history of the limestone is as follows:

At the end of the early Miocene, the Saddleback Valley area was located about 750 km south of its present location, at shallow depths in a marine channel between the mainland and a high-relief island or peninsula. Its rich subtropical "Temblor" biota included

dense bryozoan patches that were baffles against which invertebrates, in particular, accumulated in shoals. Coastal tectonics related to the San Andreas fault system caused landslides off the schistose highlands, which migrated across the subsiding channel and formed the San Onofre Breccia. Subsequent high-energy events (i.e., earthquakes and storms) triggered gravity flows (e.g., turbidity currents) that displaced the shallow-water Topanga-like sediments with live and dead elements of the “Temblor” biota down the slope of the newly created and otherwise sediment-starved basin, part of which had already started accumulating the characteristic hemipelagic muds of the Monterey Formation. Diagenesis transformed some of the richest carbonate deposits into an indurated and nearly pure limestone, while others formed unconsolidated calcarenites with macrofossils that are often highly concentrated and well preserved.

In conclusion, recognition of channel-fill structures and mixed-depth microfossil assemblages support the long-held but recently challenged notion that the Saddleback Valley limestone is the basal subunit or informal member of the local Monterey Formation. Despite its affinities with the “Temblor” CPMS fauna and Topanga Formation, the limestone represents the initial subsidence of the basin into the deep-water realm associated with the Monterey Formation.

ACKNOWLEDGMENTS

This study is dedicated to our late colleagues Drs. John D. Cooper (California State University, Fullerton) and Takeo Susuki (University of California, Los Angeles), who assisted in both the field study and the effort that succeeded in preserving two limestone exposures as parklands. Charles L. Powell II (U.S. Geological Survey, Menlo Park) generously assisted in molluscan taxonomy, informed us of his observations in the study area, and provided provocative comments that enhanced the focus of this study. We thank independent consultants Richard S. Boettcher and Stanley A. Kling for providing supplementary micropaleontologic data, John McArthur (University College London) for his unpublished Sr data table, and Donald J. DePaolo (University of California, Berkeley) for assisting in the Sr age determinations. The University of California Museum of Paleontology (UCMP) granted funding for the Sr analyses, which were arranged through Dominique Weis and performed by Bruno Kieffer (University of British Columbia). We are also grateful to our many other colleagues who discussed various aspects of the Saddleback Valley limestone with us: Thomas A. Deméré, Patricia Don Vito, and N. Scott Rugh (San Diego Natural History Museum), Paul K. Morton (TerraMins Inc.), Jere H. Lipps (John D. Cooper Archaeological and Paleontological Center), Richard L. Squires (California State University Northridge), the late Thomas W. Dibblee Jr. (Dibblee Institute), the late A. Myra Keen (Stanford University), Mark A. Roeder (Archaeological Resource Management Corporation), and John M. Alderson, Lindsey T. Groves, Austin J.W. Hendy, and LouElla R. Saul (Natural History Museum of Los Angeles County). Groves and Hendy also reviewed the manuscript and provided many useful comments and suggestions. The former Natural History Foundation of Orange County, community residents, and local geologists generously provided specimens, data, and discussions representing more than 40 years of gathering knowledge about Saddleback Valley.

LITERATURE CITED

- Anderson, F.M. 1905. Stratigraphic study in the Mount Diablo Range of California. *California Academy of Sciences proceedings, 3rd series*, 2:156–248.
- Anderson, F.M., and B. Martin. 1914. Neocene record in the Temblor Basin, California, and Neocene deposits of the San Juan district, San Luis Obispo County. *California Academy of Sciences Proceedings, 4th series*, 4:15–112.
- Arnold, R. 1909. Environment of the Tertiary faunas of the Pacific Coast of the United States. *Journal of Geology* 17:509–533.
- Arnold, R., and R. Anderson. 1907. *Geology and oil resources of the Santa Maria oil district, Santa Barbara County, California*. University of California, Berkeley: U.S. Geological Survey Bulletin 322, 161 pp.
- Bonatti, E., and J.R. Nayudu. 1965. The origin of manganese nodules on the ocean floor. *American Journal of Science* 263:26.
- Bowers, S. 1890. Orange County [California]. *California Mining Bureau, Tenth Annual Report of the State Mineralogist*. Sacramento: California State Mining Bureau, 758–762.
- Bramlette, M.N. 1946. *Monterey Formation of California and origin of its siliceous rocks*. US Government Printing Office, Washington, DC: U.S. Geological Survey Professional Paper 212, 57 pp.
- Calvert, S.E., and N.B. Price. 1977. Shallow marine, continental margin, and lacustrine nodules: distribution and chemistry. In *Marine manganese deposits*, ed. G.P. Glasby, 45–86. Amsterdam: Elsevier.
- Canu, F., and R.S. Bassler. 1919. Fossil bryozoa from the West Indies. *Carnegie Institute of Washington Publication* 291:73–102.
- Corby, G.W. 1922. *The geology and paleontology of the San Joaquin and Niguel Hills, Orange County, California*. M.A. thesis. Stanford, CA: Leland Stanford Junior University, 69 pp.
- Crouch, J.K., and D. Bukry. 1979. Comparison of Miocene provincial foraminiferal stages to coccolith zones in the California Continental Borderland. *Geology* 7:211–215.
- Cuffey, R.J., C.J. Stadum, and J.D. Cooper. 1981. Mid-Miocene bryozoan coquinas on the Aliso Viejo Ranch, Orange County, California. In *Recent and fossil bryozoa*, ed. G.P. Larwood and C. Nielsen, 65–72. Fredensborg, Denmark: Olsen & Olsen.
- DePaolo, D.J., and K.L. Finger. 1991. High resolution strontium isotope stratigraphy and biostratigraphy of the Miocene Monterey Formation, central California. *Geological Society of America Bulletin* 103 (1):112–124.
- Dibblee, T.W., Jr. 1950. Geology of southwestern Santa Barbara County, California: Point Arguello, Lompoc, Point Conception, Los Olivos, and Gaviota quadrangles. *California Division of Mines Bulletin* 150, 95 pp.
- Fife, D.L. 1974. Geology of the south half of the El Toro Quadrangle, Orange County, California. *California Division of Mines and Geology Special Report* 110:22–23.
- Fife, D.L. 1979. The “basal member of the Monterey Formation,” lower Aliso Creek area, Orange County, California. In *Geologic guide to the San Onofre Nuclear Generating Station and adjacent regions of southern California*, ed. J.R. Keaton. South Coast Geological Society, October 20, 1979, field trip guide. American Association of Petroleum Geologists Guidebook 46, 18–24.
- Finger, K.L. 1988. Depositional paleoecology of Miocene ostracodes in the Monterey Formation, Laguna Hills, southern California, U.S.A. In *Evolutionary biology in Ostracoda. Proceedings of the Ninth International Symposium on Ostracoda, held in Shizuoka, Japan*, ed. T. N. Hanai, N. Ikeya, and K. Ishizaki, 1101–1111. Tokyo: Kodansha; Amsterdam: Elsevier.
- Finger, K.L. 1990. *Atlas of California Neogene foraminifera*. Washington, DC: Cushman Foundation Special Publication 28, 271 pp.
- Finger, K.L. 1992. *Biostratigraphic atlas of Miocene foraminifera from the Monterey and Modelo formations, central and southern California*. Washington, DC: Cushman Foundation Special Publication 29, 179 pp.
- Flower, B.P., and J.P. Kennett. 1994. The middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. *Paleogeography, Palaeoclimatology, Palaeoecology* 108:537–555.
- Hall, C.A., Jr. 2002. *Nearshore marine paleoclimatic regions, increasing zoogeographic provinciality, molluscan extinctions, and paleoshorelines, California: Late Oligocene (27 Ma) to Late Pliocene (2.5 Ma)*. Washington, DC: Geological Society of America Special Paper 357, 489 pp.
- Hilgen, F.J., L.J. Lourens, and J.A. Van Dam. 2012. The Neogene period. In *The geologic time scale 2012*, ed. F.M. Gradstein, J.G. Ogg, M. Schmitz, and G. Ogg, 923–978. Amsterdam: Elsevier.
- Howard, H. 1968. Tertiary birds from Laguna Hills, Orange County, California: *Natural History Museum of Los Angeles County Contributions in Science* 142:1–21.
- Howard-Wylde, H. 1980. There was life here millions of years ago. *Journal of the Leisure World Historical Society of Laguna Hills, Calif.*, Spring 1980:62–71.
- Ingle, J.C., Jr. 1980. Cenozoic paleobathymetry and depositional history of selected sequences within the southern California continental borderland. In *Studies in marine micropaleontology and paleoecology*. A

- memorial volume to Orville L. Bandy, ed. W.V. Sliter, 163–195. Washington, DC: Cushman Foundation for Foraminiferal Research Special Publication 19.
- Johnson, J.H., and H.V. Kaska. 1965. Fossil algae from Guatemala. Boulder, CO: Colorado School of Mines Professional Contributions 1, 152 pp.
- Kleinpell, R.M. 1938. *Miocene stratigraphy of California*. Tulsa, Oklahoma: American Association of Petroleum Geologists, 450 pp.
- Loel, W., and W.H. Corey. 1932. The Vaqueros Formation, Lower Miocene of California, Paleontology. 1, Paleontology. *University of California Publications, Bulletin of the Department of Geological Science* 22(3):31–410.
- Logan, C.A. 1947. Limestone in California. *California Journal of Mines and Geology* 43:175–357.
- McArthur, J.M., R.J. Howarth, and R.T. Bailey. 2001. Strontium isotope stratigraphy: LOWESS Version 3: Best fit to the marine Sr-isotope curve for 0–509 Ma and accompanying look-up table for deriving numerical age. *The Journal of Geology* 109:155–170.
- McCulloh, T.H., R.J. Fleck, R.E. Denison, L.A. Beyer, and R.G. Stanley. 2002. *Age and tectonic significance of volcanic rocks in the northern Los Angeles Basin, California*. Sacramento, CA: U.S. Geological Survey Professional Paper 1669, 24 p.
- McDougall, K. 2007. California Cenozoic Biostratigraphy—Paleogene. In *Petroleum Systems and Geologic Assessment of Oil and Gas in the San Joaquin Basin Province, California*, ed. A.H. Scheirer, 1–56. United States Government Printing Office, Washington, DC: U.S. Geological Survey Professional Paper 1713.
- Morton, P.K., W.J. Edgington, and D.L. Fife. 1974. *Geology and engineering geologic aspects of the San Juan Capistrano Quadrangle, Orange County, California*. Sacramento, CA: California Division of Mines and Geology Special Report 112, 64 pp.
- Morton, P.K., and R.V. Miller. 1981. *Geologic map of Orange County, California, showing mines and mineral deposits*. Sacramento, CA: California Division of Mines and Geology Bulletin 204. Scale 1:48,000.
- Oleinik, A., L.N. Marincovich Jr., K.B. Barinov, and P.K. Swart. 2008. Magnitude of middle Miocene warming in North Pacific high latitudes: Stable isotope evidence from *Kaneharaia* (Bivalvia: Dosiniinae). *Bulletin of the Geological Survey of Japan* 59:339–353.
- Powell, C.L., II, and C.J. Stadum. 2010. Unique middle Miocene limestone deposits assigned to the “Topanga” Formation in southern Orange County, California: Its molluscan fauna and geology. In *Program and Abstracts for the Joint 76th American Malacological Society and 43rd Western Society of Malacologists Annual Meeting*, ed. EDITORS, 77–78. San Diego, CA: San Diego State University.
- Prothero, D.R., 2001. Chronostratigraphic calibration of the Pacific Coast Cenozoic: A summary. In *Magnetic Stratigraphy of the Pacific Coast Cenozoic*, ed. D.R. Prothero, 377–394. Washington, DC: Pacific Section SEPM Special Publication 91.
- Richter, F.M., and D.J. DePaolo. 1988. Diagenesis and strontium isotopic evolution of seawater using data from DSDP 590B and 575. *Earth and Planetary Sciences Letters* 90:382–394.
- Schoellhamer, J.E., J.G. Vedder, R.F. Yerkes, and D.M. Kinney. 1981. *Geology of the northern Santa Ana Mountains, California*. United States Government Printing Office, Washington, DC: U.S. Geological Survey Professional Paper 420-D, 106 pp.
- Smith, J.T. 1991. *Cenozoic giant pectinids from California and the Tertiary Caribbean Province: Lyropecten, “Macrochlamis,” Vertipecten, and Nodipecten species*. United States Government Printing Office, Washington, DC: U.S. Geological Survey Professional Paper 1391, 137 pp.
- Smith, P.B. 1960. *Foraminifera of the Monterey Shale and Puente Formation, Santa Ana Mountains and San Juan Capistrano area, California*. United States Government Printing Office, Washington, DC: U.S. Geological Survey Professional Paper 294-M, pp. 463–495.
- Stadum, C.J. 1982. *The development and analysis of a paleontological park in the “pecten reef” of the Monterey Formation, Orange County, California*. M.A. thesis. Long Beach: California State University at Long Beach, 113 pp.
- Stanton, R.J., Jr., and J.M. Alderson. 2013. Limestone interbedded with submarine volcanics: The early–middle Miocene Conejo volcanics, California. *Facies* 59:467–480.
- Sullwold, H.H., Jr. 1940. *Geology of a portion of the San Joaquin Hills, Orange County, California*. M.A. thesis. Los Angeles: University of California, Los Angeles, 57 pp.
- Tucker, W.B. 1925. Orange County. *California Mining Bureau Report* 21:58–71.
- Vedder, J.G. 1971. The San Onofre Breccia in the San Joaquin Hills. In *Geologic guide book Newport Lagoon to San Clemente, California. Coastal exposures of Miocene and early Pliocene rocks*, ed. F.T. Bergen et al., 12–21. Pacific Section SEPM Field Trip, October 23, 1971.
- Vedder, J.G., R.F. Yerkes, and J.E. Schoellhamer. 1957. *Geologic map of the San Joaquin Hills-San Juan Capistrano area, Orange County, California*. U.S. Geological Survey Oil and Gas Investigations, Map OM 193, map scale 1:24,000.
- Wiedey, L.H. 1928. Notes on the Vaqueros and Temblor formations of the California Miocene with descriptions of new species. *San Diego Society of Natural History Transactions* 5(10):95–182.
- Woodford, A.O. 1925. The San Onofre Breccia. *University of California Publications, Bulletin of the Department of Geological Sciences* 15:159–280.
- Wright, R.B. 1950. *California’s missions*. Los Angeles: California Mission Trails Association, 96 pp.
- Yerkes, R.F., and R.H. Campbell. 1979. *Stratigraphic nomenclature of the central Santa Monica Mountains, Los Angeles County, California*. United States Government Printing Office, Washington, DC: U.S. Geological Survey Bulletin 1457-E, 39 pp.
- Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292:686–693.

Received 1 September 2015; accepted 14 March 2016.

ERRATA

PALEONTOLOGY AND STRATIGRAPHY OF THE MIOCENE SADDLEBACK VALLEY LIMESTONE, ORANGE COUNTY, SOUTHERN CALIFORNIA¹CAROL J. STADUM² AND KENNETH L. FINGER^{3,4}

PAGES 40–41 CORRECTED FIGURE CAPTION

Figures 7–34 Saddleback Valley limestone gastropods (Figs. 7–29) and other invertebrates (Figs. 30–34). SDSNH numbers are locality/specimen; H=height, W=width, L=length. **7, 8.** *Fissurella rixfordi* Hertlein, 1928: **7**, internal mold, SDSNH 4312/136497, L=35 mm, W=24 mm; **8**, external mold, SDSNH 4312/140187, L=30 mm, W=20 mm; **9.** *Chlorostoma* sp., external cast, SDSNH 4312/93707, H=10 mm, W=10 mm; **10.** *Turritella ocoyana* Conrad, 1855, internal mold, SDSNH 4312/140188, H=75 mm, bottom whorl W=20 mm; **11.** *Turritella* sp., latex peel of external cast, SDSNH 4312/83244, H=33 mm, W=10 mm; **12.** *Forreria bartoni* Arnold, 1910, original shell (missing upper part of spire), SDSNH 4521/83243, H=24 mm, W=33 mm; **13.** *Calyptrea* sp., internal mold, SDSNH 4312/136498, H=21 mm, W=53 mm; **14.** *Crucibulum* sp., apical view of internal mold showing septum partially attached to shell, SDSNH 4312/93719; **15.** naticid, internal mold, SDSNH 4312/140186, H=35 mm, ultimate whorl W=32 mm; **16.** *Sinum* cf. *S. scopulosum* (Conrad, 1849), internal mold, SDSNH 4312/93721, H=25 mm, W=28 mm (ultimate whorl); **17.** *Trophon kernensis* Anderson, 1905, latex peel of external cast, SDSNH 4312/93835, H=24 mm, W=14 mm; **18, 19.** *Trophosyon* sp., internal mold: **18**, apical view, SDSNH 4520/98691, W=62 mm; **19**, side view, SDSNH 4312/83239, H=68 mm, penultimate whorl W=66 mm; **20, 21.** fascioliid, internal mold, SDSNH 4312/93739: **20**, apical view, W=80 mm; **21**, side view H=97 mm; **22.** *Antillophos woodringi* Addicott, 1970, latex peel of external cast, SDSNH 4312/83242, H=15 mm, W=9 mm; **23.** *Pyruconus* cf. *P. owenianus* (Anderson, 1905), SDSNH 4312/83241, H=36 mm, W=11 mm; **24.** *Pyruconus* cf. *P. hayesi* (Arnold, 1909), internal mold, SDSNH 4312/

140190, H=42 mm, W=30 mm; **25.** *Priscofusus geniculus* (Conrad, 1849), peel of exterior cast, SDSNH 4312/83245, H=44 mm, W=23 mm; **26, 27.** *Megasurcula keepi* (Arnold, 1907), internal mold, SDSNH 4312/83240, H=60 mm, W=30 mm: **26**, latex peel of external cast; **27**, internal mold; **28.** cypræid, internal mold, SDSNH 4520/98688, L=21 mm, W=15 mm; **29.** vermetid, internal mold, SDSNH 4512/142016, image H=30 mm; **30.** *Gemelliporella* aff. *G. punctata* Canu and Bassler, 1919, fragments, SDSNH4521/98668, image H=63 mm; **31, 32.** *Eucidaris* cf. *E. thouarsii* (Valenciennes, 1846): **31**, original spine with regularly spaced knobs, SDSNH 4521/120893, L=30 mm; **32**, original test fragment, SDSNH 4521/140192, L=19 mm; **33.** *Vaquerosella merriami* (Anderson, 1905), external dorsal view, SDSNH 4521/83249, H=18 mm, W=18 mm, note anal aperture (notch) at ventral margin; **34.** *Megabalanus tintinnabulum* (Linnaeus, 1758), original shells, side view of attached pair, SDSNH 4312/140191, H=25 mm, W=20 mm.

PAGE 42 CORRECTIONS IN CAPTION FOR FIGURES 35–52

- 40.** SDSNH 4521/98676 should read SDSNH 4312/98676.
42. SDSNH 4521/98671 should read SDSNH 4521/140355.
49. SDSNH 4312/83248 should read SDSNH 4312/93791.
50. SDSNH 4312/180184 should read SDSNH 4312/140184.

PAGE 44 CORRECTED FIGURE CAPTION

Figure 56 *Palaeophycus* isp. (SDSNH 137452) in limey mudstone of Lithofacies D, SDSNH loc. 4312.

¹ URL: www.nhm.org/scholarlypublications

² San Diego Natural History Museum, Department of Paleontology, 1788 El Prado, San Diego, California 92101, USA.

³ University of California Museum of Paleontology, 1101 Valley Life Sciences Building, Berkeley, California 94720, USA.

⁴ Corresponding author: Kenneth L. Finger, e-mail: kfinger@berkeley.edu

REVISION OF *AEROPHILUS* SZÉPLIGETI (HYMENOPTERA, BRACONIDAE, AGATHIDINAE) FROM EASTERN NORTH AMERICA, WITH A KEY TO NEARCTIC SPECIES NORTH OF MEXICO¹

MICHAEL J. SHARKEY,^{2,4} ERIC G. CHAPMAN,² AND GIULIA IZA DE CAMPOS³

ABSTRACT. The Nearctic species of *Aerophilus* Szépligeti, 1902, are revised with an emphasis on the fauna of the eastern USA. The generic name *Lytopylus* Förster, 1862, is shown to have been misapplied to the group revised here and it is replaced by *Aerophilus*. The following genera are synonymized with *Aerophilus*: *Neomicrodus* Szépligeti, 1908, syn. n.; *Aerophilopsis* Viereck, 1913, syn. n.; *Aerophilina* Enderlein, 1920, syn. n.; *Ioxia* Enderlein, 1920, syn. n.; *Hormagathis* Brues, 1926, syn. n.; *Obesomicrodus* Papp, 1971, syn. n.; *Facilagathis* van Achterberg and Chen, 2004, syn. n. The type species of *Lytopylus* (*L. azygos* Viereck, 1905) fits the generic concept of *Austroearinus* Sharkey, 2006; the latter is therefore synonymized with *Lytopylus*, and all species included in *Austroearinus* are transferred to *Lytopylus* as new combinations. *Agathellina* Enderlein, 1920, and *Ditropia* Enderlein, 1920, are synonymized with *Lytopylus*, syn. n. A list of all new combinations is included.

Thirty-five species of *Aerophilus* are treated, with 16 described as new (i.e., *A. arthurevansi*, *A. chapmani*, *A. davidsmithi*, *A. hopkinsensis*, *A. jdherndoni*, *A. klastos*, *A. kowlesae*, *A. malus*, *A. minys*, *A. pookae*, *A. rayfisheri*, *A. reginae*, *A. robertcourtneyi*, *A. stoelbae*, *A. terrymoyeri*, *A. tommurrayi*). The senior author (M.J.S.), is the sole authority of these species. All 19 previously described species have new combinations (i.e., *A. abdominalis*, *A. aciculatus*, *A. acrobasisidis*, *A. bakeri*, *A. binominatus*, *A. buttricki*, *A. calcaratus*, *A. crassicornis*, *A. difficilis*, *A. erythrogaster*, *A. nigripes*, *A. ninanae*, *A. mucicola*, *A. perforator*, *A. reticulatus*, *A. rugareolatus*, *A. tenuiceps*, *A. usitatus*, *A. wyomingensis*). Several new synonyms are proposed (i.e., *Agathis atripes* Cresson is synonymized under *Agathis nigripes* Cresson, *Bassus pini* Muesebeck is synonymized under *Aerophilopsis erythrogaster* Viereck, and *Agathis wyomingensis* Viereck is removed from synonymy with *Agathis nigripes* Cresson).

An illustrated key, image plates, and distribution maps are included for each species. The revision is primarily based on newly collected material from Kentucky, Virginia, and West Virginia, for which molecular data were available. A phylogenetic analysis of *Aerophilus*, based on 28S and cytochrome *c* oxidase subunit I (COI), with representatives from all major biomes, is included. Another tree, based solely on COI data is included to show species divergences, which was used in conjunction with morphological data to delimit species.

INTRODUCTION

Agathidinae are a moderately diverse subfamily of Braconidae with about 1,200 described species (Yu et al., 2015), and many times that number are yet to be named. Larvae are parasitoids of lepidopteran caterpillars of a multitude of families. Most agathidine genera, including *Aerophilus*, attack an early instar caterpillar and are quiescent until the host has reached the final instar and is ready to spin a cocoon. At this point in time the parasitoid larva becomes active and quickly consumes the host, i.e., they are koinobiont endoparasitoids. *Aerophilus* is world-wide in distribution, with the exception of Antarctica.

Aerophilus is an unusual genus of Agathidinae in that host Lepidoptera are in a wide range of higher taxa. Most genera of Agathidinae seem to be restricted to one or a few closely related families of Lepidoptera. The collective set of *Aerophilus* species attack a wide range of host families. Even within the small sample of 10 reared species of *Aerophilus* represented in the revision of Costa Rican species (Sharkey et al., 2011), five host families are attacked (i.e., Crambidae, Elachistidae, Pyralidae, Thyrididae, and Tortricidae). However, all of these are leaf-rolling and leaf-tying small caterpillars. Members of *Aerophilus* are conspicuous in not using species of caterpillars that feed exposed on leaf surfaces (e.g., butterflies and macro-moths). Individual species of *Aerophilus* tend to be host specific. Of the

10 species treated from Costa Rica, all but one, *A. jessiehillae*, are host specific (i.e., each attacks only one host species). And even the hosts of *A. jessiehillae* are very closely related to each other. The results of the phylogenetic analyses (fig. 1 in Sharkey et al., 2011) show that host family is constrained by phylogenetic history, with sister species of *Aerophilus* sharing the same host family in every case (three). Several species of *Aerophilus* have been employed in biological control attempts. *Aerophilus rufipes* (as *Bassus diversus*) was introduced into the eastern USA from Japan to combat the oriental fruit moth, *Grapholitha molesta* (Busck), Tortricidae, over a period of a number of years in the 1930s (Allen and Yetter, 1949). Despite initial signs of success it does not appear to have become established. *Aerophilus rufipes* was also imported to California in the 1990s to control the codling moth, *Cydia pomonella* L., Tortricidae. However it too failed to become established (Mills, 2005). *Aerophilus acrobasisidis* has been used in the biocontrol of *Acrobasis nuxvorella* (the pecan nut casebearer) and *Cydia caryana* (the hickory shuckworm) (Ellington et al., 1995; Romero et al., 2001) with unknown results.

Although this revision is primarily based on newly collected material from Kentucky, Virginia, and West Virginia, all Nearctic species are included in the key. There are two principal reasons for the emphasis on eastern species. The first is that there are very few if any species with distributions that span the USA or Canada from east to west, therefore including both faunas would pointlessly complicate the key. The second reason for the emphasis on eastern species is that many species are difficult to separate on morphological grounds and molecular data from fresh specimens was necessary. Intensive Malaise trap collecting has been conducted over the past decade in Kentucky by members of the Sharkey lab at the University of Kentucky and

¹ URL: www.nhm.org/scholarlypublications

² Department of Entomology, University of Kentucky, Lexington, Kentucky 40506, USA.

³ Universidade Federal de São Carlos–UFSCar, Departamento de Ecologia e Biologia Evolutiva, São Carlos, SP, Brasil.

⁴ Corresponding author: Michael J. Sharkey, E-mail: msharkey@uky.edu

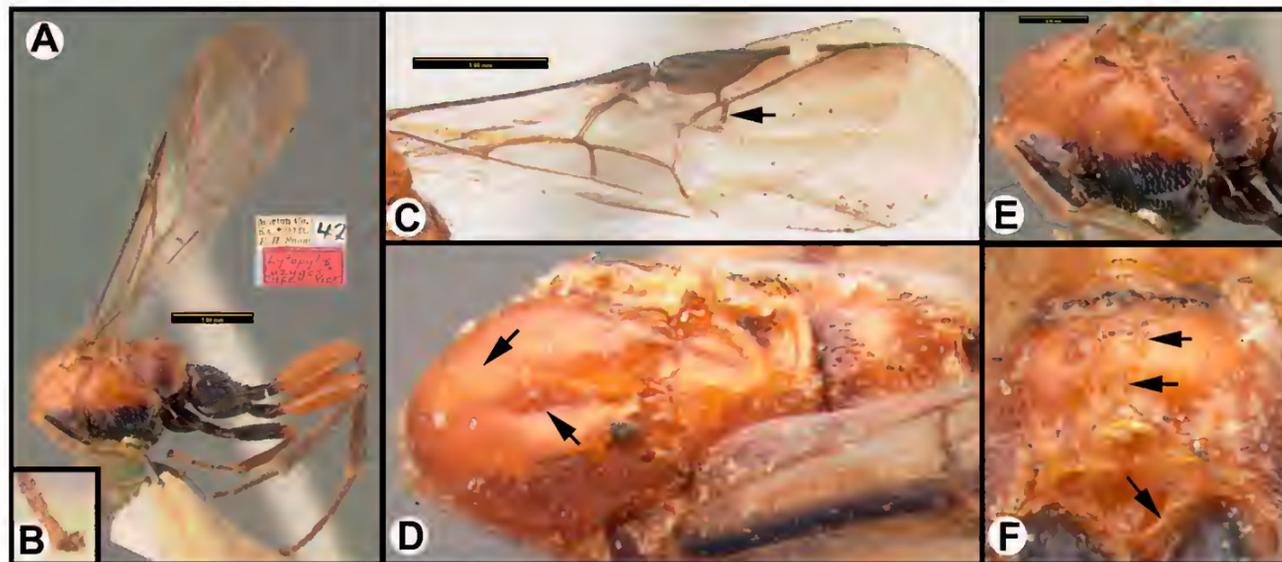


Figure 1 *Lytopylus azygos*, holotype: A. lateral habitus, B. tarsal claw, C. forewing, D. dorsal mesosoma, E. lateral mesosoma, F. propodeum showing sculpture and narrow sclerite between metasomal and hind coxal foramina.

by Dr. David Smith and colleagues in Virginia and West Virginia. Therefore, we have a fair representation of some eastern species, especially those at mid-latitudes, for which molecular data were obtained.

The previously described western species are included in the key, but they are clearly noted as being western, so they can be quickly passed over in most cases. There are many more undescribed western species, some of which are included in the cladograms (Figs. 1 and 2), and a separate revision on these is in preparation (Sharkey and Chapman, in prep.). The species with the widest east–west distribution confirmed here is *A. rayfisheri*, which occurs in North Dakota and Kentucky. It is likely that a good number of species are midwestern with this magnitude of range. Other species such as *A. nigripes* have a wider published distribution; however, in these cases the species identifications are suspect.

Six of the new eastern species are represented by singletons, and several more species are known from fewer than four specimens. These data suggest, despite adding 16 species to the eastern fauna, that there are many more eastern species yet to be discovered.

New World members of *Aerophilus* may be distinguished from other agathidines by the almost universal presence of longitudinal striae on the third metasomal median tergite, at least in some transverse depressions, and by the structure of the propodeal foramen (i.e., a relatively wide space between the metasomal and hind coxal foramina and a strong transverse carina connecting the dorsal margins of the coxal foramina). A key to the Nearctic genera of Agathidinae is provided in Sharkey and Chapman (2015); unfortunately, in this key, the name *Lytopylus* must be replaced by *Aerophilus* and *Austroearinus* must be replaced by

Lytopylus to conform to the corrections made here. The sister group to *Aerophilus* is *Braunsia* Kriechbaumer, which is restricted to the Old World and is mostly tropical or subtropical (Sharkey et al., 2006; Sharkey and Chapman, 2015).

Muesebeck (1927) revised the species of *Aerophilus* (as members of *Bassus*) in his revision of the species of Agathidinae north of Mexico. He treated 16 nominal species in this revision and described several more in subsequent publications (Muesebeck, 1932, 1940). No Nearctic species has been described since 1940. Because Muesebeck's (1927) key includes what are now considered other genera (i.e., *Alabagrus*, *Agathis* s.s., *Aphelagathis*, *Lytopylus*, *Pneumagathis*, *Therophilus*, and *Neothlipsis*), it is unduly complicated; it is also missing the species described since 1927. Simbolotti and van Achterberg (1992) included the six species of *Aerophilus* from the western Palearctic under the umbrella of *Bassus*. Sharkey (1996) included two species from Japan, and Sharkey et al. (2009) recorded two species occurring in Thailand. Van Achterberg and Long (2010) recorded two species for Vietnam, one under *Lytopylus* and one under *Facilagathis*. Farahani et al. (2014) described a new species from Iran and included a key to the West Palearctic species of *Aerophilus* (as *Lytopylus*). Sharkey et al. (2011) revised the 10 species reared in Costa Rica, as *Lytopylus*. One species has been recorded from Australia (Stevens et al., 2010). *Aerophilus* is diverse in Africa (where it has never been revised) and throughout the New World. The genus is not species-rich in Eurasia or in the Australian and Oriental regions, and it is unknown in Pacifica. For a world distribution of the *Aerophilus* specimens we have included in our Symbiota database, see our map online (<http://bit.ly/1M9DhqM>).



Figure 2 *Lytopylus azygos*: A. dorsal metasoma, B. anterior head.

METHODS

Morphological terms are from Sharkey and Wharton (1997) and are matched to the Hymenoptera Anatomy Ontology (HAO; <http://glossary.hymao.org>; Yoder et al., 2010). Anatomical concepts in HAO are provided to enable readers to confirm their understanding of the anatomical structures being referenced. To find out more about a given structure, including images, references, and other metadata, simply search for the anatomical structure at hand and select the best match from the list that appears (e.g., typing “frons” returns a list of 11 possible matches). In electronic versions of this paper, terms are hyperlinked to the ontology the first time they appear, either in the text, key, or subsequent species descriptions.

Museum acronyms found in the “Specimens Examined” sections of this paper are taken from “Abbreviations for Insect and Spider Collections of the World” (Evenhuis, 2014). Host records for each species were taken from Taxapad (Yu et al., 2015). All species are treated with a diagnosis and distributional data. For previously published species, the states and provinces from which they are recorded are listed; however, due to the degree of misidentifications that are present in collections, only those specimens determined by M.J.S. are included in the linked distribution maps. These records are stored in the Symbiota database (Gries et al., 2014) under the Hymenoptera Institute Collection (HIC). The maps were generated by conducting a map search for each species on the SCAN portal (Symbiota Collections of Arthropods Network; <http://symbiota4.acis.ufl.edu/scan/portal/>), querying only specimens in the HIC. This generates a map URL that contains a search query for the taxon at hand in the HIC database. Mouse over any data point on the maps to access the details of each record (including images if present). These are not static maps; therefore, as georeferenced specimens are added to the HIC Symbiota database, they will automatically be added to the map in real time. Also, because these data are public, anyone can generate a map search for any taxon in our Symbiota database: From the Symbiota link above, under the *Search* menu, select *Map Search*. This will open a new tab with a map that has an *Open* icon at the top left, which opens a dialog box with many options for searching any or all of the databases in the Symbiota network. If one wishes only to search within the HIC database, select only *HIC* under the *Collections* tab.

All species are illustrated with color photos using a JVC digital camera mounted on a Leica MZ16 microscope and Auto-Montage® stacking software. Species descriptions are of the holotype, and variation is given in parentheses.

DNA EXTRACTION, PCR, AND SEQUENCING

DNA was extracted from individual legs with the Qiagen DNeasy Blood and Tissue Kit using the animal tissue protocol (Qiagen Inc., Chatsworth, California, USA). The mitochondrial cytochrome *c* oxidase subunit I (COI) gene was amplified with the COI primer pairs LepF1 and LepR1 (~655 bp between the primers; Hebert et al., 2004), and when this fragment did not amplify, we employed LepF1 and Crem155R (Tucker et al., 2015) to amplify a smaller fragment (~135 bp). We also sequenced the D2–D3 regions of 28S using the primer pairs 28SD2F (Belshaw and Quicke, 1997) and D3R (Harry et al., 1996). PCR was conducted using Takara reagents for COI, with each reaction consisting of 1X buffer, 0.3 mM nucleotides, 0.4 μM of each primer, 0.625 U Takara *Ex Taq*, ddH₂O, and 1–3 μL template DNA in a total reaction volume of 25 μL. The thermal cycling protocol had an initial denaturation period at 95 °C for 2.5 min, followed by 40 cycling steps which denatured at 95 °C for 30 s, annealed at 44 °C for 30 s and extended at 68 °C for 45 s, with a final extension step

of 72 °C for 7 min. For 28S, PCR reactions consisted of Qiagen 1X buffer, 4 mM MgSO₄, 0.3 mM dNTP, 0.4 μM of each primer, 0.625 U Qiagen *Taq*, ddH₂O, and 1–3 μL template DNA with a total reaction volume of 25 μL. Thermal cycling was as above except annealing at 53 °C, extending for 70 s, and a total of 35 cycles. PCR products were outsourced for Sanger sequencing either by the Advanced Genetic Technologies Center (University of Kentucky, Lexington, Kentucky, USA) or Beckman Coulter Genomics (Danvers, Massachusetts, USA) using labeled dideoxynucleotides with ABI 3730 BigDye Terminator mix v. 3.0 or with ABI PRISM 3730xl, BigDye Terminator mix v. 3.1 (Applied Biosystems, Foster City, California, USA).

DNA ASSEMBLY AND PHYLOGENETIC ANALYSIS

Bidirectional sequences were aligned and edited using Geneious Pro (v. 6.1.5; Drummond et al., 2009) and multiple alignments were assembled using the default settings on the MAFFT server (<http://www.ebi.ac.uk/Tools/msa/mafft/>; v. 7; Katoh et al., 2006). We conducted maximum likelihood (ML) analyses on two data sets: COI (655 nt, 110 operational taxonomic units [OTU]) and a concatenated (using MacClade v. 4.08; Maddison and Maddison, 2005) COI+28S (1,161 nt, 127 OTU) data set using Garli (v. 2.01; Zwickl, 2006). The data were partitioned by gene region and codon position for 28S+COI (total of four partitions) and by codon position for COI (three partitions). We applied the most complex model available (GTR+I+G; Rodriguez et al., 1990) to each partition as per recommendations of Huelsenbeck and Rannala (2004) for likelihood-based analyses. Garli applies separate parameter estimates to each partition. For both data sets, a 200-replicate ML analysis was conducted using the default settings. Nodal support was assessed by conducting a 500-replicate ML bootstrap analysis (Felsenstein, 1985) on each data set using the default settings, with three independent search replicates per bootstrap replicate. The COI analyses (Supp. Figs. 1 and 2; summarized in Fig. 3) was used to help make decisions regarding species delimitation, as 28S is not variable enough to reliably separate closely related lineages, whereas the analyses of the COI+28S data set (Supp. Figs. 3 and 4; summarized in Fig. 4) was conducted to find the best estimate of phylogeny.

A Bayesian inference (BI) phylogenetic analysis was also conducted on the COI+28S data set with MrBayes (v. 3.1.2; Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). As in the Garli analyses, the data were partitioned by gene region and codon position. To allow each partition to have its own set of parameter estimates, *reumat*, *tratio*, *statefreq*, *shape*, and *pinvar* were all unlinked during the analyses. To obtain the most accurate branch length estimates possible, the option *prset ratepr = variable* (which assigns a separate branch length parameter for each partition) was employed as per the recommendations of Marshall et al. (2006). Two independent, simultaneous BI searches were run for 100 million generations, saving a tree every 1,000 generations, with four search chains each. The average standard deviation of split frequencies fell below 0.02 just before 80 million generations. The 20,000 post-burn-in trees from each run (40,000 total), determined by examination of the log probability of observing the data by generation plot with Tracer (v. 1.5; Rambaut and Drummond, 2009), were used to calculate the majority rule consensus tree using PAUP* (v. 4.0β10; Swofford, 2003). The tree of highest posterior probability from the Bayesian analysis is shown in Supplemental Figure 5, and the majority rule consensus tree is shown in Supplemental Figure 6. The data sets analyzed herein are available from the authors upon request.

RESULTS

NOMENCLATORIAL CONSIDERATIONS

The senior author (M.J.S.) recently had the opportunity to view the type of *Lytopylus* Förster, 1862, *Lytopylus azygos* Viereck, 1905. Förster (1862) did not include any species under *Lytopylus*, therefore the type species by monotypy became the first included species, in this case *L. azygos*. Unfortunately this species does not conform to the generic concept that has been applied to it in recent years (Sharkey et al., 2009, 2011; van Achterberg, 2011). Rather, it fits the concept of *Austroearinus* (Figs. 1 and 2) proposed by Sharkey et al. (2006). This necessitates the synonymy of *Austroearinus* under *Lytopylus* n. syn. Furthermore, two other nominal genera fit my (M.J.S.) concept of *Austroearinus* that must be synonymized under *Lytopylus*, namely, *Ditropia* Enderlein, 1920, n. syn. and *Agathellina* Enderlein, 1920, n. syn. Figure 1 is a plate of the type species of *Lytopylus*. The type is missing both the head and metasoma; therefore, Figure 2 is included to show these body parts in what I (M.J.S.) believe to be a conspecific specimen. Characters consistent with the concept of *Austroearinus* are: sessile second submarginal cell, that is, lacking a petiole (Fig. 1C); notauli not impressed (Fig. 1D); propodeum with sculpture confined to the midline posteriorly (Fig. 1F); terga of metasoma smooth except for pair of longitudinal carinae on first median tergite (Fig. 2A); interantennal space with a weak medial depression (Fig. 2B); sclerite between metasomal and coxal foramina narrow.

The oldest name that applies to the old (misinformed) concept of *Lytopylus* is *Aerophilus* Szépligeti, 1902. All species recently described under *Lytopylus* are transferred to *Aerophilus*. The new combinations for both *Aerophilus* and *Lytopylus* are presented below.

Aerophilus Szépligeti, 1902

TYPE SPECIES. *Aerophilus brullei* Szépligeti, 1902 (by monotypy).

Aerophilina Enderlein, 1920, **syn. n.** Type species: *Aerophilina bicristata* Enderlein, 1920.

Aerophilopsis Viereck, 1913, **syn. n.** Type species: *Bassus erythrogaster* Viereck, 1913.

Facilagathis van Achterberg and Chen, 2004, **syn. n.** Type species: *Facilagathis spinulata* van Achterberg and Chen, 2004.

Hormagathis Brues, 1926, **syn. n.** Type species: *Hormagathis mellea* Brues, 1926.

Ioxia Enderlein, 1920, **syn. n.** Type species: *Ioxia faceta* Enderlein, 1920.

Neomicrodus Szépligeti, 1908, **syn. n.** Type species: *Neomicrodus boliviensis* Szépligeti, 1908.

Obesomicrodus Papp, 1971, **syn. n.** Type species: *Obesomicrodus niger* Papp, 1971.

NEW COMBINATIONS (alphabetized by epithet)

Microdus astioles Nixon, 1950, to *Aerophilus astioles*

Bassus barbieri Simbolotti and van Achterberg, 1992, to *Aerophilus barbieri*

Metriosoma bicarinatum Enderlein, 1920, to *Aerophilus bicarinatum*

Aerophilina bicristata Enderlein, 1920, to *Aerophilus bicristatus*

Neomicrodus boliviensis Szépligeti, 1908, to *Aerophilus boliviensis*

Lytopylus bradzlotnicki Sharkey, 2011, to *Aerophilus bradzlotnicki*

Metriosoma brasiliense Enderlein, 1920, to *Aerophilus brasiliense*

Lytopylus brevitarsus van Achterberg, 2011, to *Aerophilus brevitarsus*

Lytopylus colleenhitchcockae Sharkey, 2011, to *Aerophilus colleenhitchcockae*

Agathis ebula Nixon, 1950, to *Aerophilus ebulus*

Agathis burmensis Bhat and Gupta, 1977, to *Aerophilus burmensis* (junior synonym of *Agathis ebula*)

Ioxia faceta Enderlein, 1920, to *Aerophilus facetus*

Microdus femoratus Cameron, 1887, to *Aerophilus femoratus*

Metriosoma flavicalcar Enderlein, 1920, to *Aerophilus flavicalcar*

Microdus fortipes Reinhard, 1867, to *Aerophilus fortipes*

Lytopylus gregburtoni Sharkey, 2011, to *Aerophilus gregburtoni*

Microdus infumatus Granger, 1949, to *Aerophilus infumatus*

Lytopylus jessicadimauroae Sharkey, 2011, to *Aerophilus jessicadimauroae*

Lytopylus jessiehillae Sharkey, 2011, to *Aerophilus jessiehillae*

Microdus leucotretae Nixon, 1941, to *Aerophilus leucotretae*

Bassus macadamiae Briceño and Sharkey, 2000, to *Aerophilus macadamiae*

Microdus melanocephalus Cameron, 1887, to *Aerophilus melanocephalus*

Hormagathis mellea Brues, 1926, to *Aerophilus melleus*

Lytopylus mingfangi Sharkey, 2011, to *Aerophilus mingfangi*

Obesomicrodus niger Papp, 1971, to *Aerophilus niger*

Cremnops nigrobalteatus Cameron, 1911, to *Aerophilus nigrobalteatus*

Bassus pastranai Blanchard, 1952, to *Aerophilus pastranai*

Lytopylus persicus Farahani and Talebi, 2014, to *Aerophilus persicus*

Agathis philippinensis Bhat and Gupta, 1977, to *Aerophilus philippinensis*

Microdus pilosus Tobias, 1976, to *Aerophilus pilosus* (this species fits well with the concept of *Aerophilus*, with the exception of a shorter distance between the hind coxal cavities and the metasomal foramen.)

Microdus rugulosus Nees, 1834, to *Aerophilus rugulosus*

Lytopylus rebeccashapleyae Sharkey, 2011, to *Aerophilus rebeccashapleyae*

Lytopylus robpringlei Sharkey, 2011, to *Aerophilus robpringlei*

Microdus romani Shestakov, 1940, to *Aerophilus romani*

Bassus ater Chou and Sharkey, 1989, to *Aerophilus ater* (junior synonym of *Microdus romani*)

Microdus rufipes Nees, 1812, to *Aerophilus rufipes*

Microdus amurensis Shestakov, 1940, to *Aerophilus amurensis* (junior synonym of *Microdus rufipes*)

Bassus diversus Muesebeck, 1933, to *Aerophilus diversus* (junior synonym of *Microdus rufipes*)

Braunsia germanica Enderlein, 1904, to *Aerophilus germanicus* (junior synonym of *Microdus rufipes*)

Lytopylus sandraberriosae Sharkey, 2011, to *Aerophilus sandraberriosae*

Microdus sculptilis Tobias, 1986, to *Aerophilus sculptilis*

Facilagathis spinulata van Achterberg and Chen, 2004, to *Aerophilus spinulatus*

Bassus tayrona Campos, 2007, to *Aerophilus tayrona*

Lytopylus vaughntani Sharkey, 2011, to *Aerophilus vaughntani*

REINSTATED ORIGINAL COMBINATIONS

Aerophilus brullei Szépligeti, 1902 (from *Bassus*)

Aerophilus lamelliger Granger, 1949 (from *Bassus*)

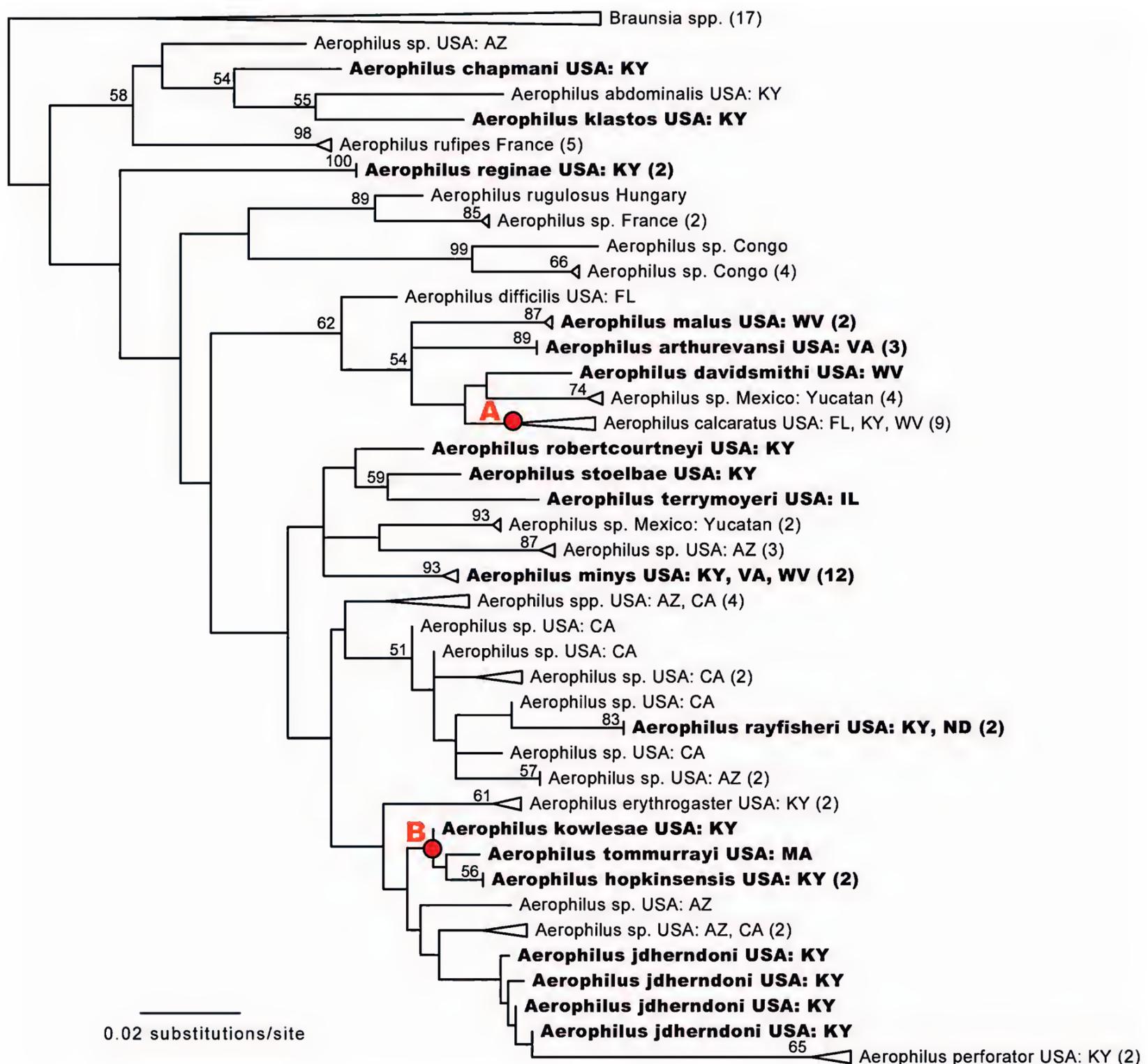


Figure 3 Tree of highest log-likelihood from 200 ML search reps of the COI data set. Terminals in bold-faced type indicate species described herein. ML bootstrap values appear above the branches. Triangles represent collapsed clades; their widths represent distances from the node to the tip of the longest branch. The number of specimens each triangle represents is given in parentheses following the species name and locality information. Nodes labeled with red letters are those discussed in the text.

Aerophilus sulcatus Granger, 1949 (from *Bassus*)
Aerophilus lucidus Granger, 1949 (from *Bassus*)
Aerophilus rufus Granger, 1949 (from *Bassus*)
Aerophilus speciosicornis Granger, 1949 (from *Bassus*)
Aerophilus sulcatus Granger, 1949 (from *Bassus*)

Lytopylus Föster, 1862

TYPE SPECIES. *Lytopylus azygos* Viereck, 1905, by monotypy, first included species.

Agathellina Enderlein, 1920, **syn. n.** Type species: *Agathellina columbiana* Enderlein, 1920.

Ditropia Enderlein, 1920 **syn. n.** Type species: *Ditropia strigata* Enderlein, 1920.

Austroearinus Sharkey, 2006, **syn. n.** Type species: *Bassus rufofemoratus* Muesebeck, 1927.

Austroearinus chrysokeras Sharkey, 2006, to *Lytopylus chrysokeras*

Agathellina columbiana Enderlein, 1920, to *Lytopylus columbianus*

Austroearinus melanopodes Sharkey, 2006, to *Lytopylus melanopodes*

Bassus rufofemoratus Muesebeck, 1927, to *Lytopylus rufofemoratus*

Ditropia strigata Enderlein, 1920, to *Lytopylus strigata*

Orgilus unicolor Schrottky, 1902, to *Lytopylus unicolor*. Note: *Orgilus unicolor* was renamed *Agathis unicoloratus* when it was transferred to *Agathis* by Shenefelt (1970) due to preoccupation of *unicolor* in the genus *Agathis* by Cameron (1908).

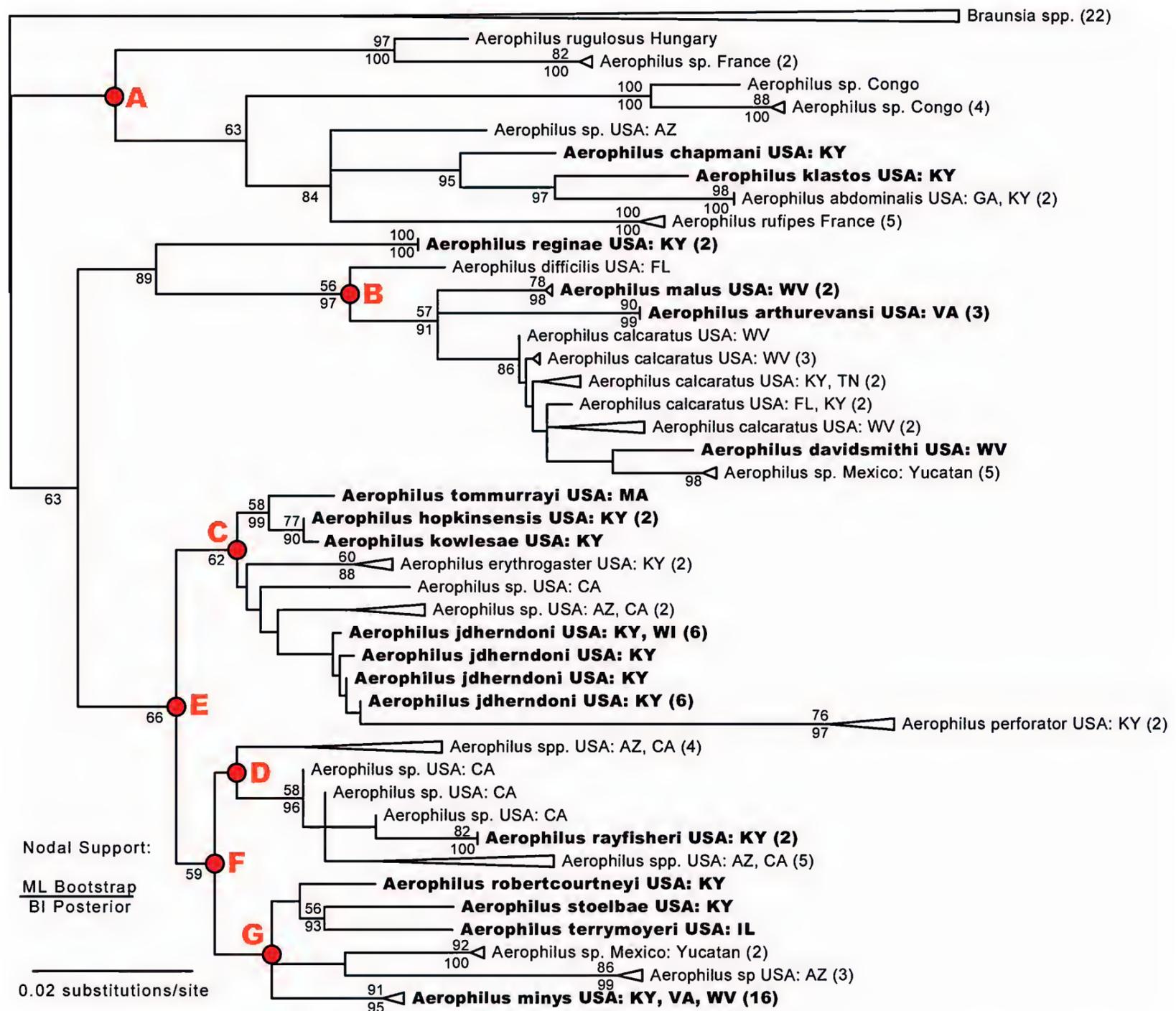


Figure 4 Tree of highest log-likelihood from 200 ML search reps of the combined COI+28S data set. Terminals in boldface type indicate species described herein. Triangles represent collapsed clades; their widths (horizontal) represent distances from the basal node to the tip of the longest branch. The number of specimens each triangle represents is given in parentheses following the species name and locality information. Nodes labeled with red letters are those discussed in the text.

Species Delimitation

The ML tree in Figure 3 is based solely on COI and was generated to assist in the delimitation of species and not to represent a phylogenetic hypothesis. We used ML instead of neighbor joining because with ML, mutations are more accurately modeled, with rare mutations contributing more to branch lengths than common ones. We did not employ any particular branch length to determine species status. Rather, we preferred a total-evidence approach using both morphology and COI differences to come to species decisions.

My (M.J.S.) first pass at delimiting species was strictly morphological, and I then tested these concepts with molecular, primarily COI, data. Although many morphospecies concepts were corroborated (e.g., *A. perforator*) with these data, others were falsified with both lumping and splitting errors. The cladogram in Figure 3 shows the ML distance generated from COI data. Clade A represents specimens of what I determined to be *A. calcaratus*. The triangle in clade A represents nine specimens, and the length of the triangle is

related to the COI differences among the specimens. For more exact detail of distances between specimens, refer to Supplemental Figure 1, the tree of highest log-likelihood from 200 ML replicates, which includes all terminals with COI data. There is considerable molecular variation within this concept of *A. calcaratus*, for example, more variation than there is across all three species in clade B of Figure 3. The specimens within *A. calcaratus* are morphologically homogeneous, and there are no large differences in COI when all specimens are considered, i.e., no gaps that might indicate separate species. Conversely, specimens of *A. jdherndoni* vary considerably morphologically yet there is a continuum in this variability and few sequence differences. In this case it would have been very difficult to decide on species limits without the addition of COI data.

Phylogenetic Considerations

Figure 4 is the best ML tree based on COI and 28S sequence data in which redundant terminals have been compressed. In

supplemental documentation we have included uncompressed trees from three analyses: Supplemental Figure 3, 200 replicate ML search for the tree of highest log-likelihood; Supplemental Figure 4, ML bootstrap tree from 500 replicates; Supplemental Figure 5, Bayesian tree of highest posterior probability; Supplemental Figure 6, Bayesian majority rule consensus tree. We selected a suite of species of *Braunsia* as the outgroup because the genus has been shown to be the sister group of *Aerophilus* (Sharkey et al., 2006; Sharkey and Chapman, 2015).

Clade A of Figure 4 is the only branch containing Old World (Africa and Europe) species; it also contains some Nearctic species. Although lacking strong support values, all but one of the nine species have the relatively rare condition of metasomal median tergites 1–3 with completely striate sculpture. The exception is specimen H2201 from The Republic of Congo (Supp. Fig. 3), which has these tergites unusually smooth. The six species comprising clade B (Fig. 4) are quite uniform, in that none have elongate genae; all are bicolored with the abdomen (including propodeum) reddish and the head and thorax black; all have obvious notauli; none have heavily striate metasomal terga; and all but one have the propodeum evenly areolate, as in Figure 24D. There are no obvious morphological synapomorphies for this group, as all of the aforementioned character states are common throughout the genus.

Clade C is not well supported, and there is an heterogeneous mix of morphological character states in the group. Of particular interest is the presence of *A. perforator* in this clade. *A. perforator* and its probable sister species, *A. pookae*, for which

we do not have molecular data, are unique in that they are small, have heavily striate metasomal terga 1–3, and very elongate genae (Fig. 30). The long branch leading to *A. perforator* coupled with low support at node C suggests that it may be misplaced in the phylogeny. Running the analysis without *A. perforator* increases the ML bootstrap value of node E from 53 to 72.

Clade D (Fig. 4), although not highly supported by molecular data, is supported by one morphological character state (i.e., the genae and mouthparts of all members are very elongate). With reference to the mouthparts, the most easily measured character state is the length of the penultimate labial palpomere, which unlike most members of the genus, is more than half the length of the apical palpomere in this clade. This group is largely confined to the western USA and northwestern Mexico, although some species are found in the east, for example, *A. rayfisheri*. The long mouthparts are thought to be adaptations associated with deep nectaries, which are common in dry habits where shallow nectaries are more at risk of desiccation (Jervis, 1998). Long genae and associated long mouthparts are a reoccurring theme in the evolution of the Agathidinae. This character state is almost universal in *Agathis*, *Disophrys*, and *Cremnops* and rare or absent in other genera. Within *Aerophilus* these character states are found only in Nearctic species.

There are no obvious morphological synapomorphies for clades E, D, and F. Members of clade G are quite variable in most characteristics, but none has an elongate gena and mouthparts, and the notauli are weak or absent in all.

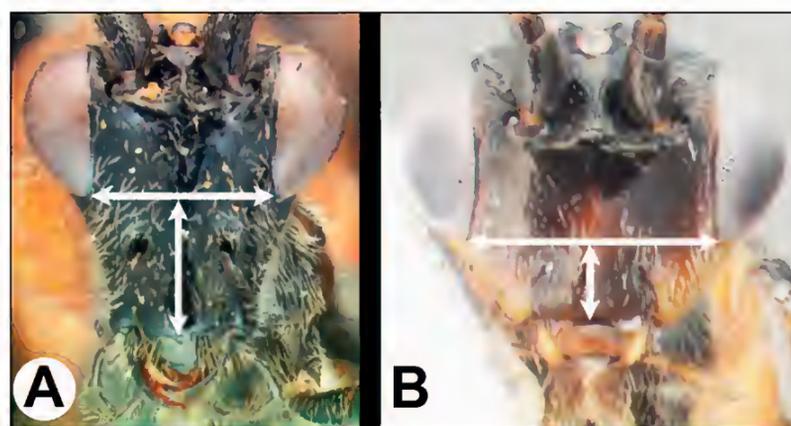
KEY TO THE SPECIES OF AEROPHILUS OF THE USA AND CANADA WITH AN EMPHASIS ON EASTERN FAUNA

- 1 A. Hind coxa in lateral view entirely melanic..... 2
- B. Hind coxa in lateral view entirely pale..... 11
- C. Hind coxa in lateral view bicolored, melanic and pale 35



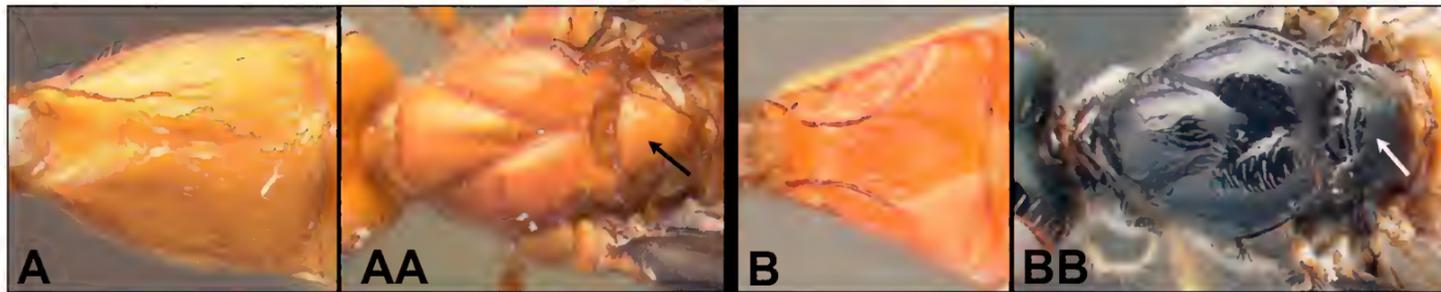
Couplet 1

- 2(1) A. Gena elongate, distance between eyes twice the distance from eyes to apex of clypeus or less, measured along the midline of the face..... 6
- B. Gena not elongate, distance between eyes more than 2.5 times distance from eyes to apex of clypeus, measured along the midline of the face 3



Couplet 2

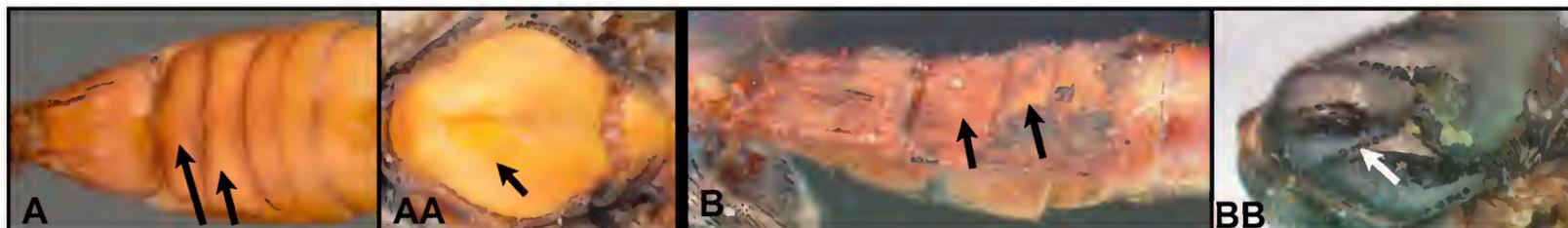
- 3(2) A. First metasomal median tergite usually mostly covered with longitudinal striae, rarely striae restricted to area between pair of longitudinal carinae. AA. Mesoscutellum usually, partly or entirely pale (yellow to orange); if entirely melanic, then hind femur mostly or entirely melanic..... 4
- B. First metasomal median tergite mostly smooth or otherwise sculptured, longitudinal striae, if present, weak and irregular. BB. Mesoscutellum entirely melanic; hind femur pale (yellow to orange)..... 5



Couplet 3

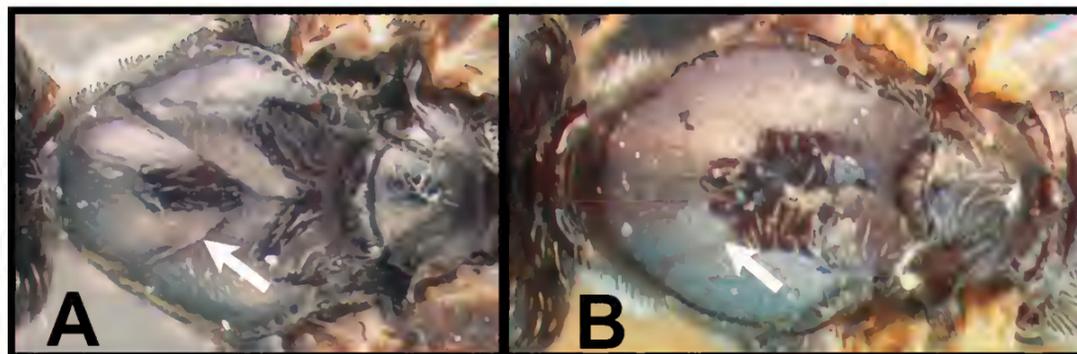
- 4(3) A. Raised areas of median metasomal tergite 2 smooth; striae, if present, restricted to troughs of transverse depressions. BB. Notauli smooth without crenulae, or with one or two crenulae restricted to extreme anterior at border of mesoscutum *A. minys* n. sp. (in part)
- B. Raised areas of median metasomal tergite 2 mostly longitudinally striate or granulate, except sometimes for posterior margin. AA. Notauli with crenulae extending well along its length, present at least in anterior 1/3 (Texas) *A. aciculatus* (Ashmead)

Note: *A. rufipes*, a European species, will key here. It has been introduced into the western USA to control the codling moth (Mills, 2005) but does not seem to have become established. It can be distinguished from all Nearctic species by its predominantly black color.



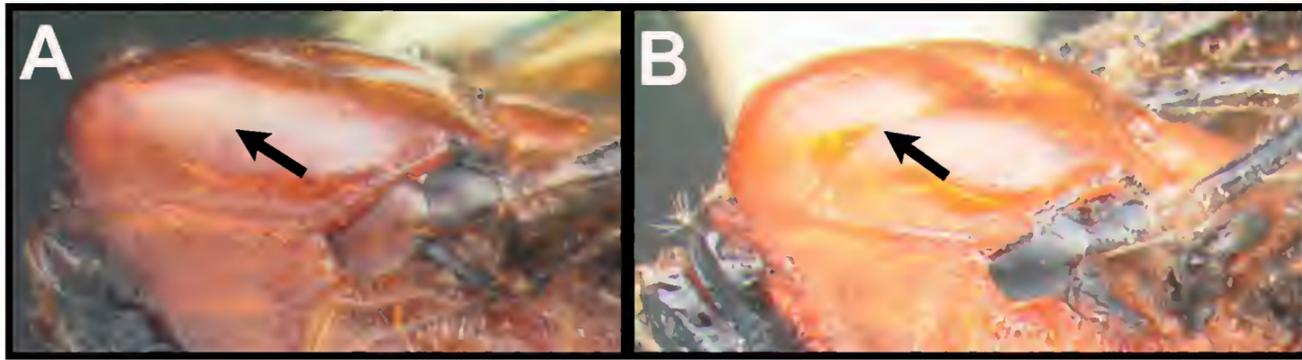
Couplet 4

- 5(3) A. Notauli well impressed. Hind trochanter mostly or entirely melanic *A. davidsmithi* n. sp.
- B. Notauli barely perceptible or weakly impressed. Hind trochanter mostly or entirely pale *A. binominatus* (Muesebeck)



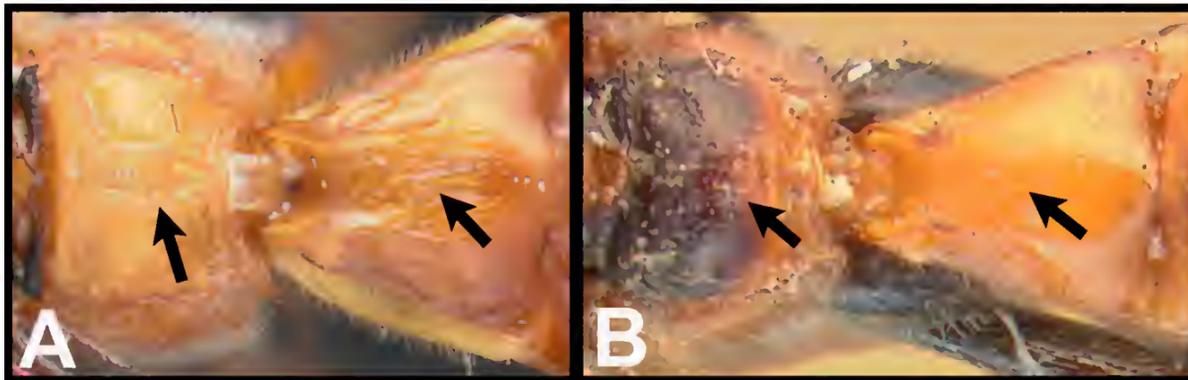
Couplet 5

- 6(2) A. Notauli barely perceptible or entirely absent..... 7
- B. Notauli impressed 9



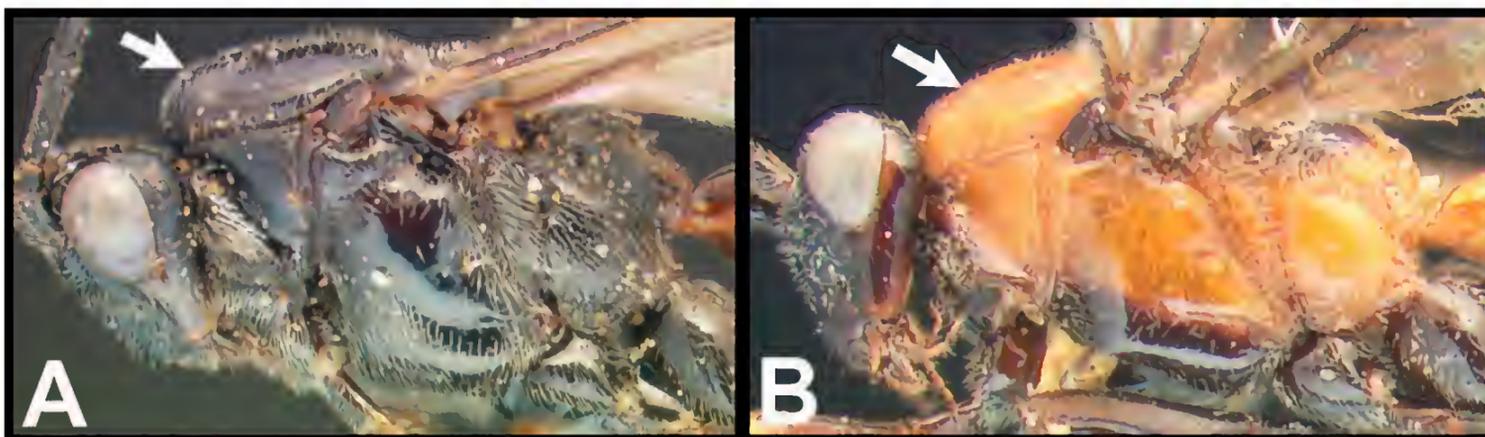
Couplet 6

- 7(6) A. Propodeum with a well-defined median areola, and extensively sculptured; first metasomal median tergite wider, slightly wider than long, and with more sculpture *A. rayfisheri* n. sp.
- B. Propodeum lacking a well-defined median areola and with less sculpture; first metasomal median tergite narrower, slightly longer than wide, and with less sculpture 8



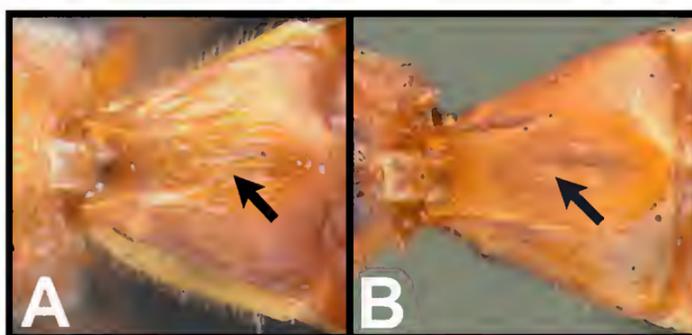
Couplet 7

- 8(7) The images below are of the holotypes of the respective species
- A. Mesoscutum black (Colorado) *A. bakeri* (Muesebeck)
- B. Mesoscutum pale (Wyoming) *A. wyomingensis* (Viereck)



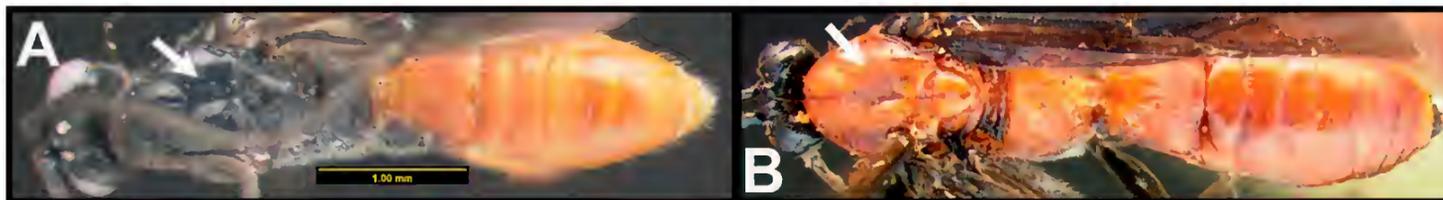
Couplet 8

- 9(6) A. First metasomal median tergite usually mostly covered with longitudinal striae 10
- B. First metasomal median tergite mostly smooth or otherwise sculptured, longitudinal striae, if present, weak and irregular (western species) *A. nigripes* (Cresson)



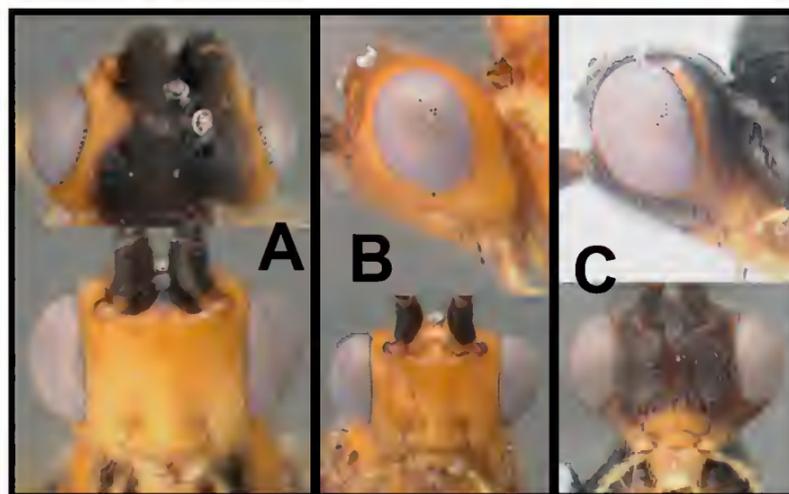
Couplet 9

- 10(9) A. Mesoscutum entirely melanic *A. tommurrayi* n. sp.
 B. Mesoscutum entirely pale *A. crassicornis* (Muesebeck)



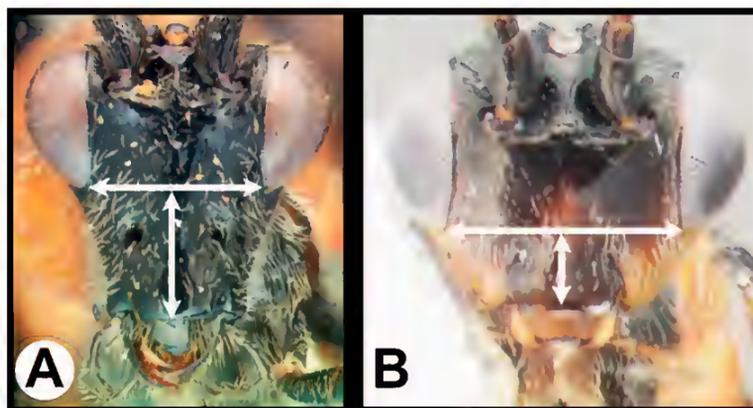
Couplet 10

- 11(1) A. Head color mostly pale, black dorsally 12
 B. Head color entirely pale, orange to yellow 16
 C. Head color mostly or entirely black, usually with some pale color on eye orbits, gena and clypeus 21



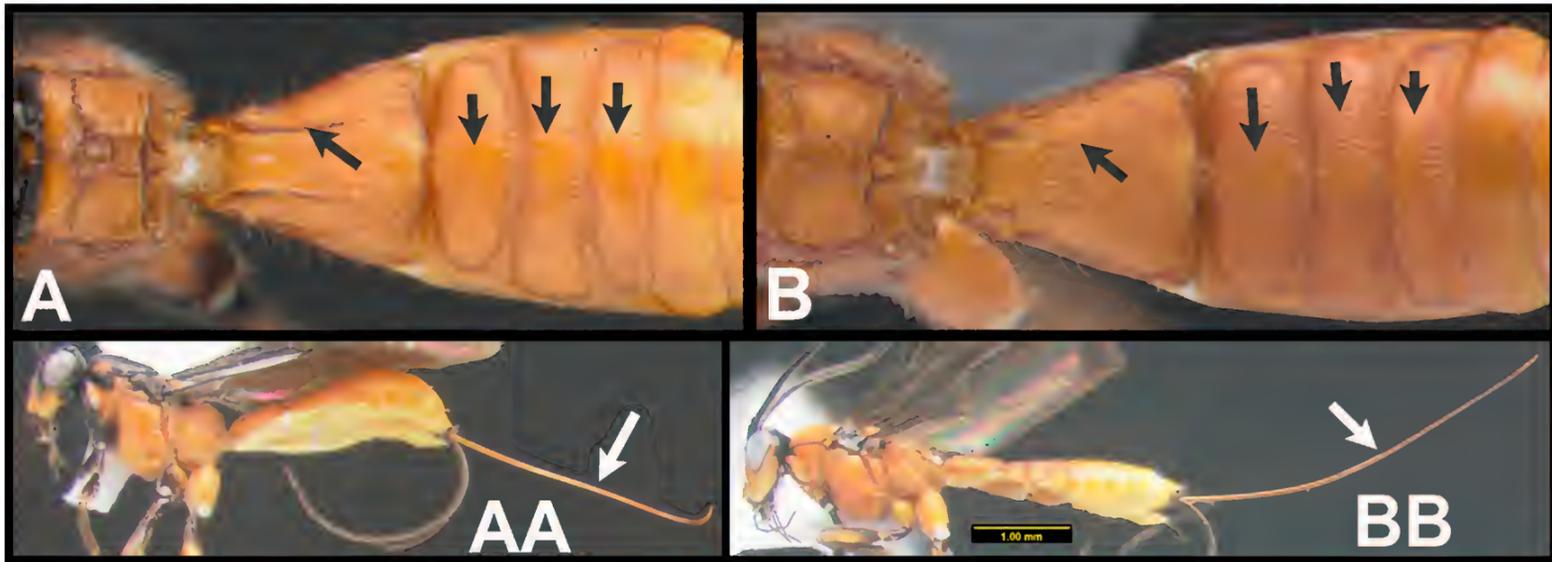
Couplet 11

- 12(11) A. Gena elongate, distance between eyes twice the distance from eyes to apex of clypeus or less, measured along the midline of the face 13
 B. Gena not elongate, distance between eyes more than 2.5 times distance from eyes to apex of clypeus, measured along the midline of the face 14



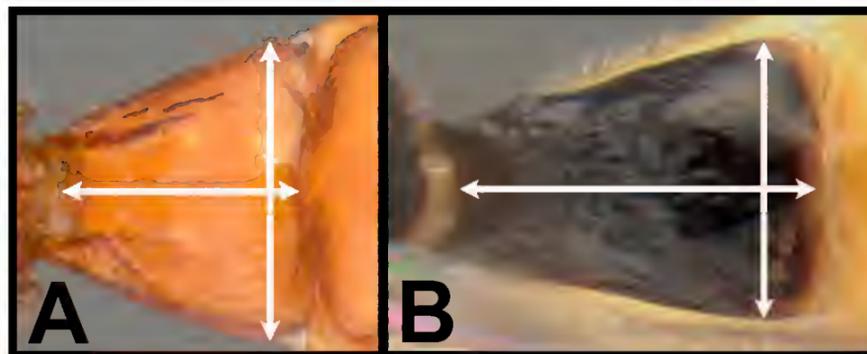
Couplet 12

- 13(12) A. Pair of carinae on first median tergite long and strong, extending past midpoint of tergite. Anterior three raised areas of syntergite 2+3 partly smooth or weakly striate. AA. Ovipositor shorter *A. perforator* (Provancher) (in part)
 B. Pair of carinae on first median tergite short and weak, extending to midpoint of tergite. Anterior three raised areas of syntergite 2+3 entirely striate. BB. Ovipositor longer *A. pookae* n. sp.



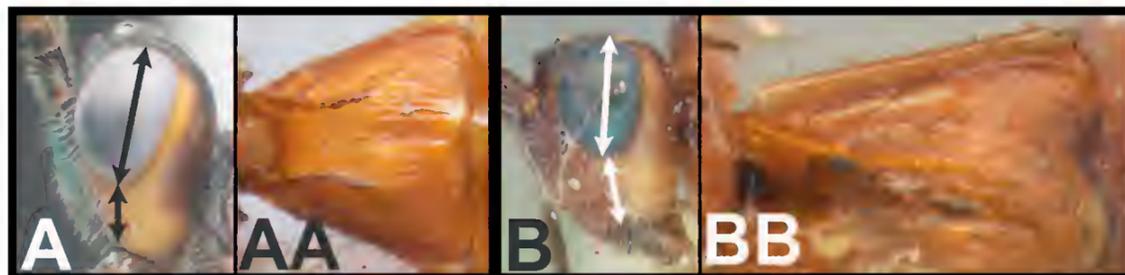
Couplet 13

- 14(13) A. First metasomal median tergite about as long as posterior width..... 15
- B. First metasomal median tergite clearly longer than posterior width..... *A. reginae* n. sp. (in part)



Couple 14

- 15(13) A. Ratio of malar space to eye height smaller (0.3–0.4). AA. First median tergite mostly covered with fine striae..... *A. minys* n. sp. (in part)
- B. Ratio of malar space to eye height greater (0.5–0.6). BB. First median tergite mostly smooth with several weak, smooth, wide striae..... *A. buttricki* (Viereck) (in part)



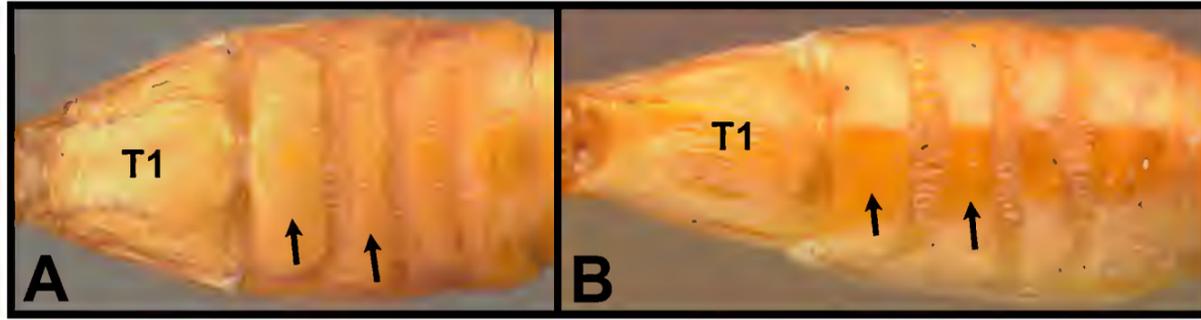
Couplet 15

- 16(11) A. Notauli absent or barely perceptible and always lacking sculpture..... 17
- B. Notauli impressed, with or without sculpture 19



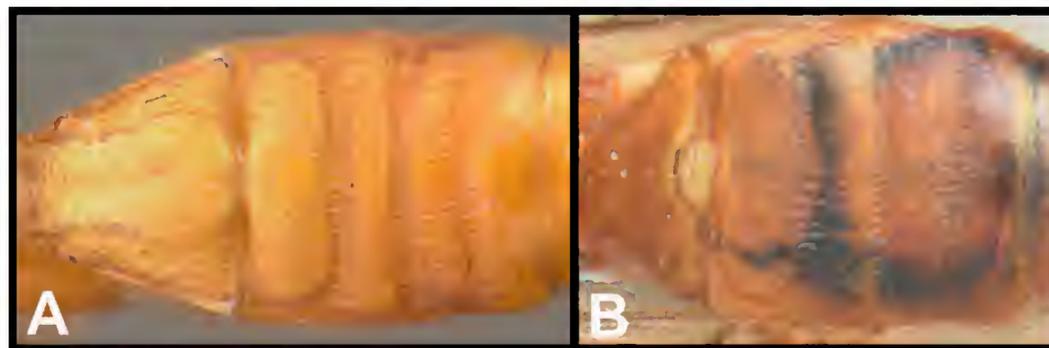
Couplet 16

- 17(16) A. Second median tergite sculptured in raised areas; first median tergite about as wide as long..... 18
 B. Second median tergite smooth in raised areas; first median tergite longer than wide (Arizona).....
 *A. tenuiceps* (Muesebeck)



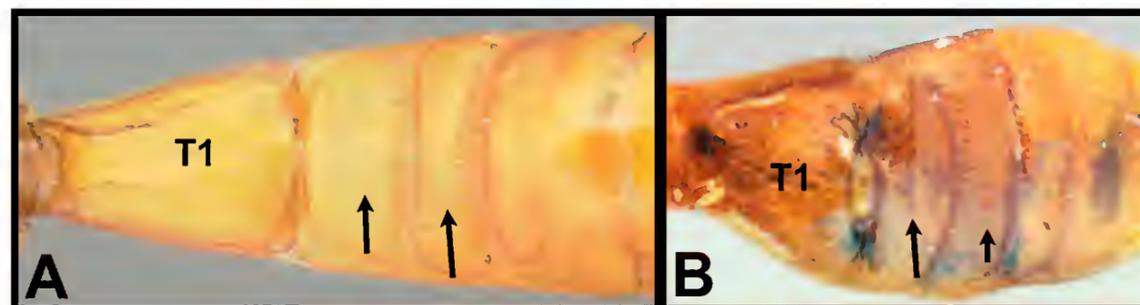
Couplet 17

- 18(17) A. Second + third syntergite smoothly and uniformly striate.....*A. robertcourtneyi* n. sp.
 B. Second + third syntergite finely striogranulate with striae more apparent in and near transverse depressions
 *A. reticulatus* (Muesebeck)



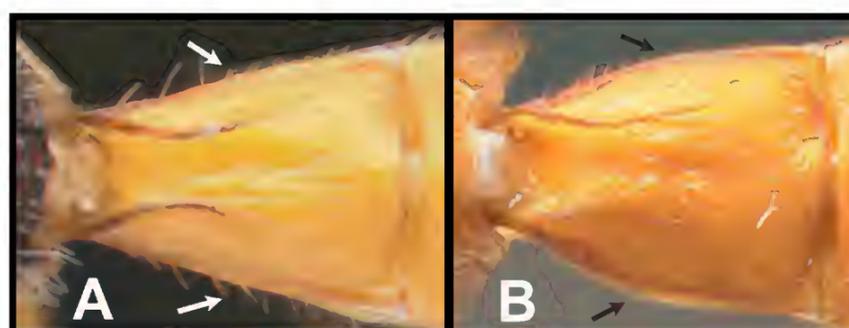
Couplet 18

- 19(16) A. Second median tergite striate in raised areas; first median tergite clearly longer than posterior width..... 20
 B. Second median tergite smooth in raised areas; first median tergite about as long as posterior width. (image is of holotype)*A. buttricki* (Viereck) (in part)



Couplet 19

- 20(19) A. First median tergite relatively finely striate and straight laterally *A. abdominalis* (Muesebeck)
 B. First median tergite relatively coarsely striate and angled laterally *A. klastos* n. sp.



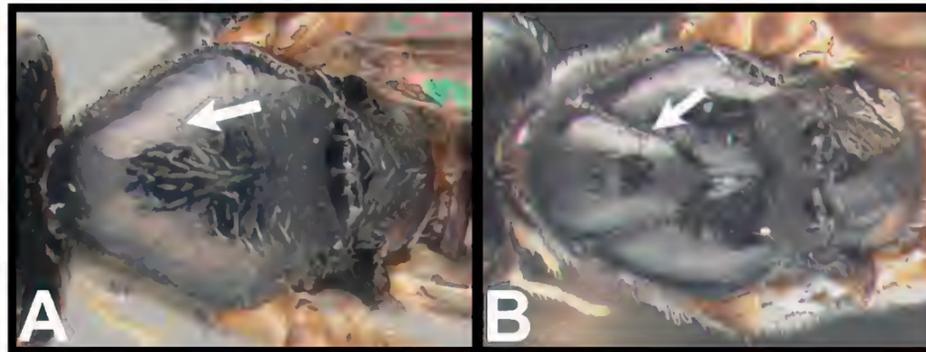
Couplet 20

- 21(11) A. Mesoscutellum entirely melanic..... 22
 B. Mesoscutellum partly or entirely pale (yellow to brownish orange) 33



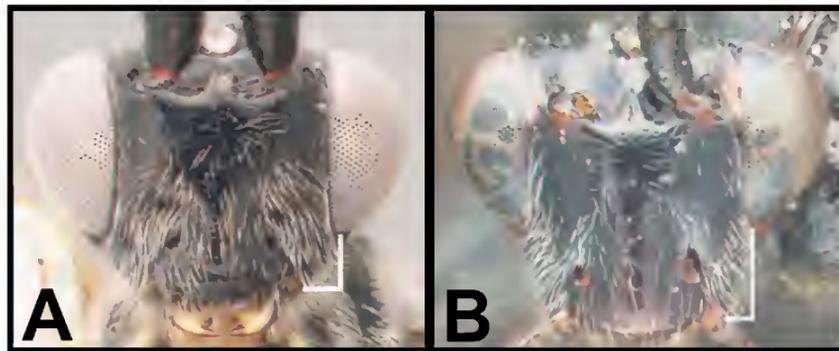
Couplet 21

- 22(21) A. Notauli barely perceptible or weakly impressed (at least indiscernible in posterior half) 23
 B. Notauli well impressed 25



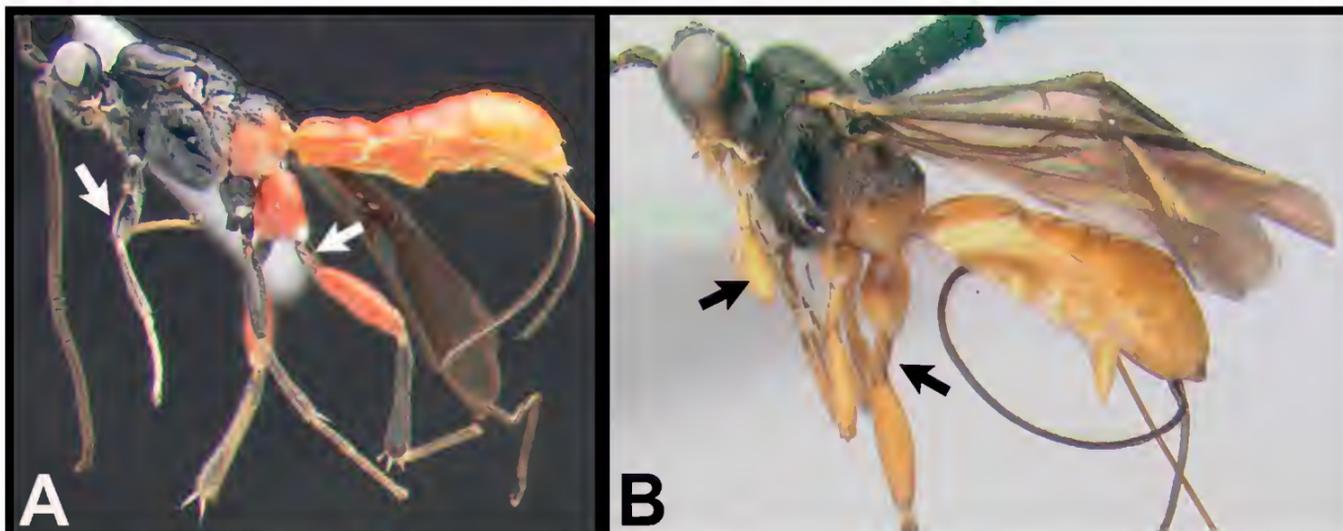
Couplet 22

- 23(22) A. Gena shorter and tapering sharply toward mandibles 24
 B. Gena longer and not tapering as sharply toward mandibles *A. rugareolatus* (Viereck)



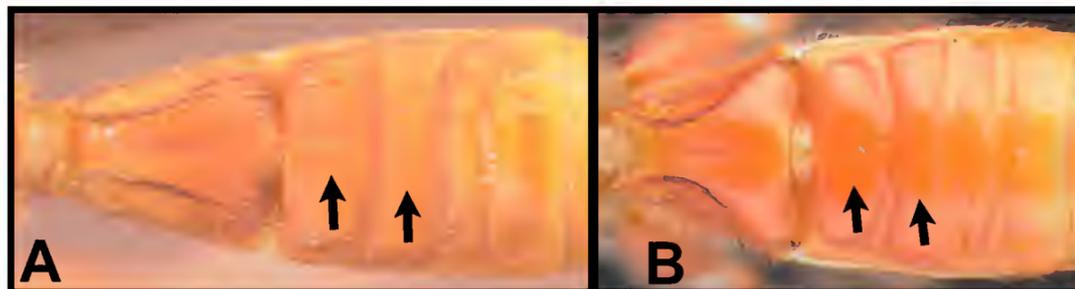
Couplet 23

- 24(23) A. Hind trochanter mostly or entirely melanic; forefemur almost entirely melanic with a pale (yellow to orange) patch apicomediaally *A. erythrogaster* (Viereck) (in part)
 B. Hind trochanter mostly or entirely pale; forefemur entirely pale *A. stoelbae* n. sp. (in part)



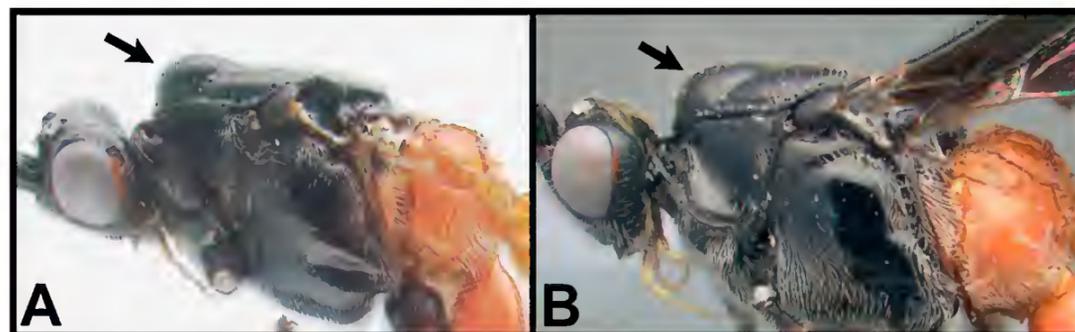
Couplet 24

- 25(22) A. Second median tergite completely striate in raised areas *A. chapmani* n. sp.
 B. Second median tergite partly or entirely smooth in raised areas 26



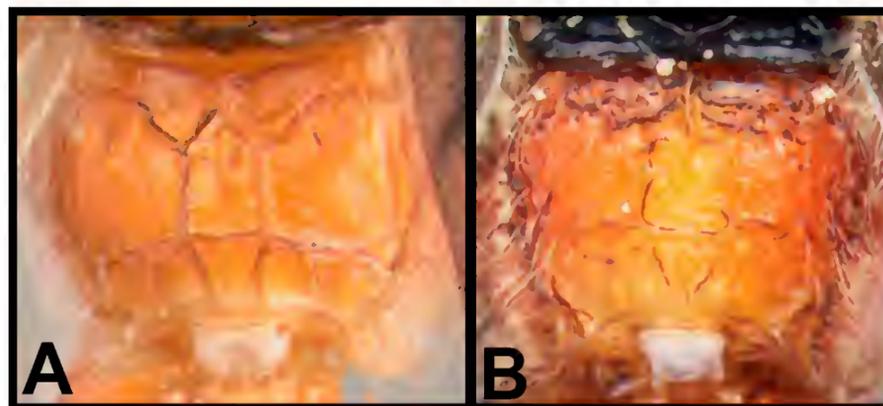
Couplet 25

- 26(25) A. Middle lobe of mesoscutum bulging and elevated above lateral lobes *A. difficilis* (Muesebeck)
 B. Middle lobe of mesoscutum not bulging and not elevated above lateral lobes 27



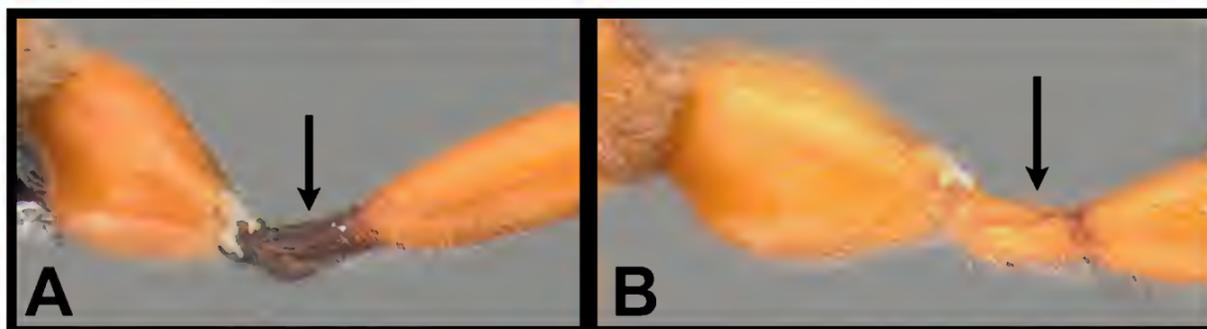
Couplet 26

- 27(26) A. Propodeum with distinct areolae; antenna with more than 30 flagellomeres 29
 B. Propodeum without distinct areolae, with more rugose sculpture; antenna with less than 30 flagellomeres 28



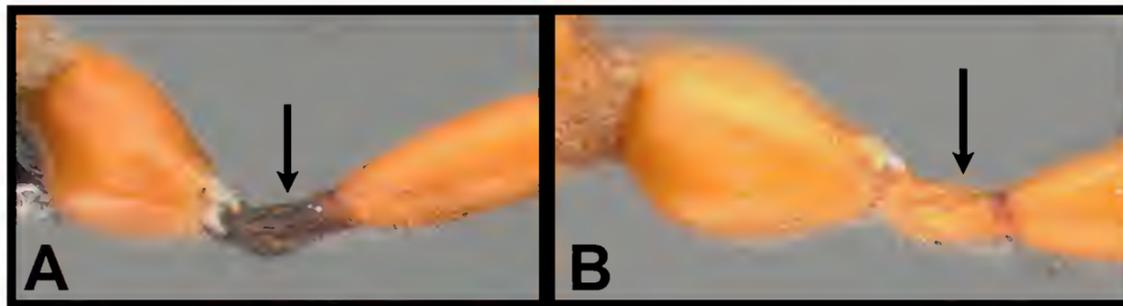
Couplet 27

- 28(27) A. Hind trochanter mostly or entirely melanic *A. erythrogaster* (Viereck) (in part)
 B. Hind trochanter mostly or entirely pale *A. jdherndoni* n. sp.



Couplet 28

- 29(27) A. Hind trochanter mostly or entirely melanic 30
- B. Hind trochanter mostly or entirely pale 31

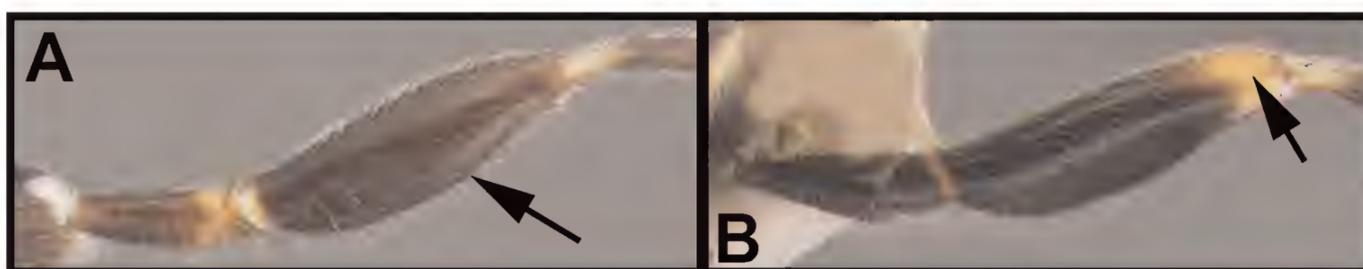


Couplet 29

- 30(29) A. Antenna with 36 or more flagellomeres *A. malus* n. sp. (in part)
- B. Antenna with 35 or fewer flagellomeres *A. calcaratus* (Cresson)

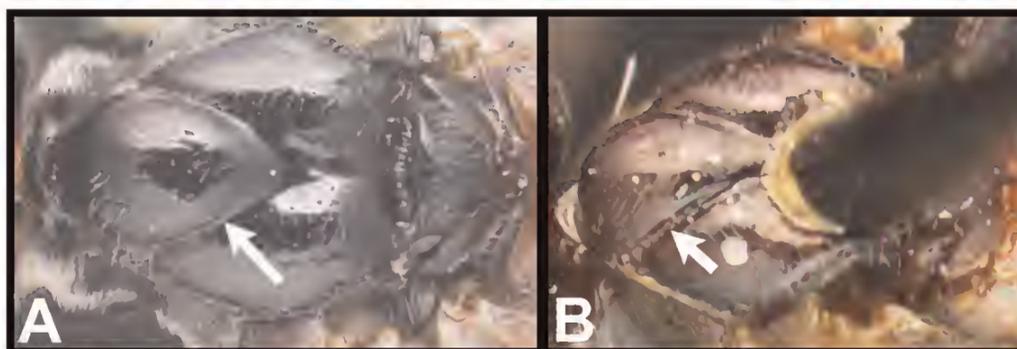
Note: these two species are very similar morphologically and this couplet may not be sufficient to distinguish them.

- 31(29) A. Forefemur entirely melanic..... *A. malus* n. sp. (in part)
- B. Forefemur melanic basally, pale (yellow to orange) apically, often with more pale color than shown below 32



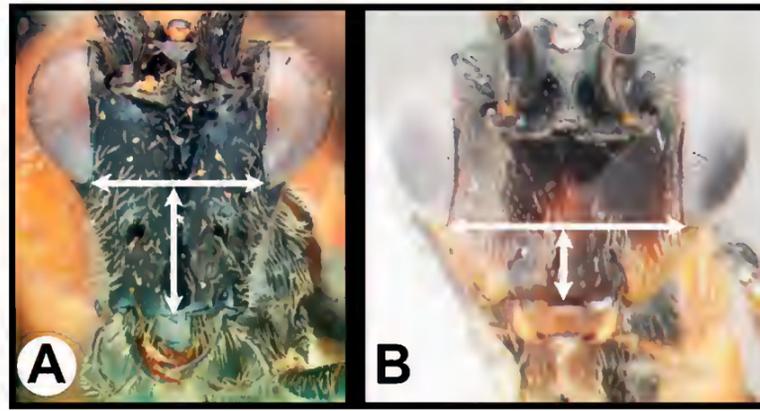
Couplet 31

- 32(31) A. Notauli smooth without crenulae or with one or two crenulae restricted to extreme anterior at border of mesoscutum *A. arthurevansi* n. sp.
- B. Notauli with crenulae extending well along its length, present at least in anterior 1/3 *A. usitatus* (Gahan)



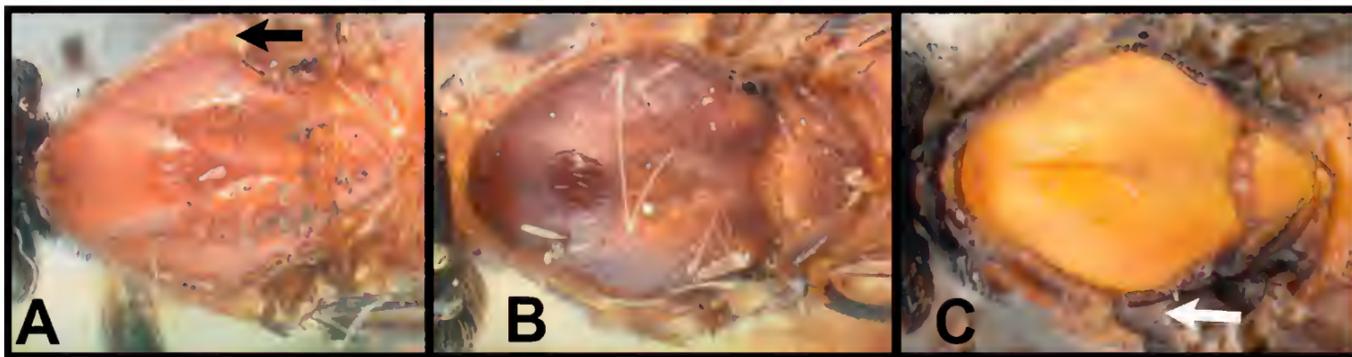
Couplet 32

- 33(21) A. Gena elongate, distance between eyes twice the distance from eyes to apex of clypeus or less, measured along the midline of the face *A. perforator* (Provancher) (in part)
- B. Gena not elongate, distance between eyes more than 2.5 times distance from eyes to apex of clypeus, measured along the midline of the face 34



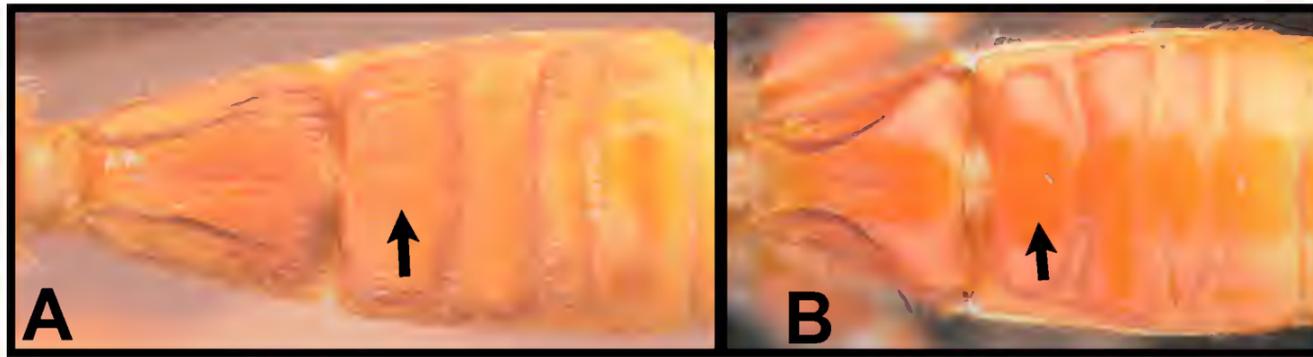
Couplet 33

- 34(33) A. Mesonotum and tegula entirely pale, reddish brown (California) *A. nucicola* (Muesebeck)
- B. Mesonotum dark brownish orange, tegula variable but not black (Texas) *A. acrobasis* (Cushman)
- C. Mesonotum mostly pale (yellow to orange); tegula black..... *A. minys* n. sp. (in part)



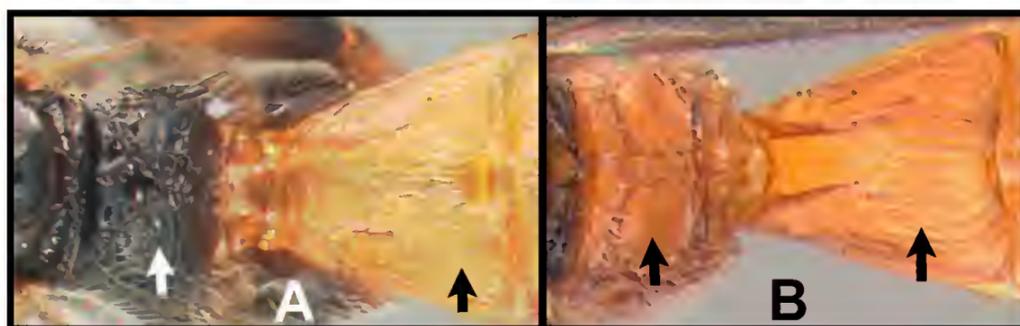
Couplet 34

- 35(1) A. Anterior lobe of median tergite 2 completely striate in raised areas 36
- B. Anterior lobe of median tergite 2 partly or entirely smooth in raised areas..... 37



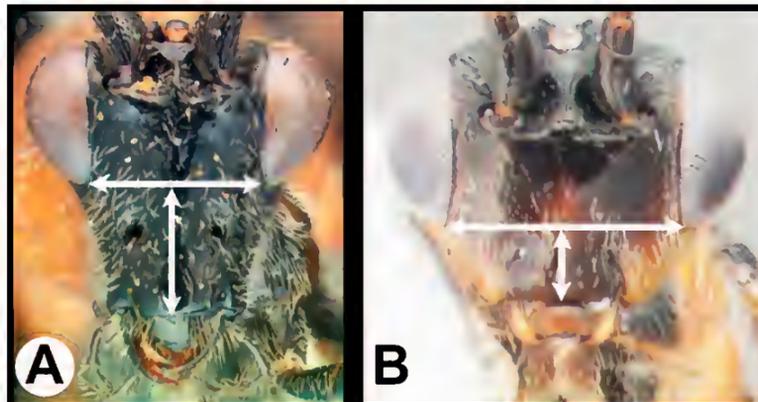
Couplet 35

- 36(35) A. Propodeum melanic, first median tergite with finer striae *A. stoelbae* n. sp. (in part)
- B. Propodeum pale, first median tergite with coarser striae *A. terrymoyeri* n. sp.



Couplet 36

- 37(35) A. Gena elongate, distance between eyes twice the distance from eyes to apex of clypeus or less, measured along the midline of the face *A. perforator* (Provancher) (in part)
- B. Gena not elongate, distance between eyes more than 2.5 times distance from eyes to apex of clypeus, measured along the midline of the face 38



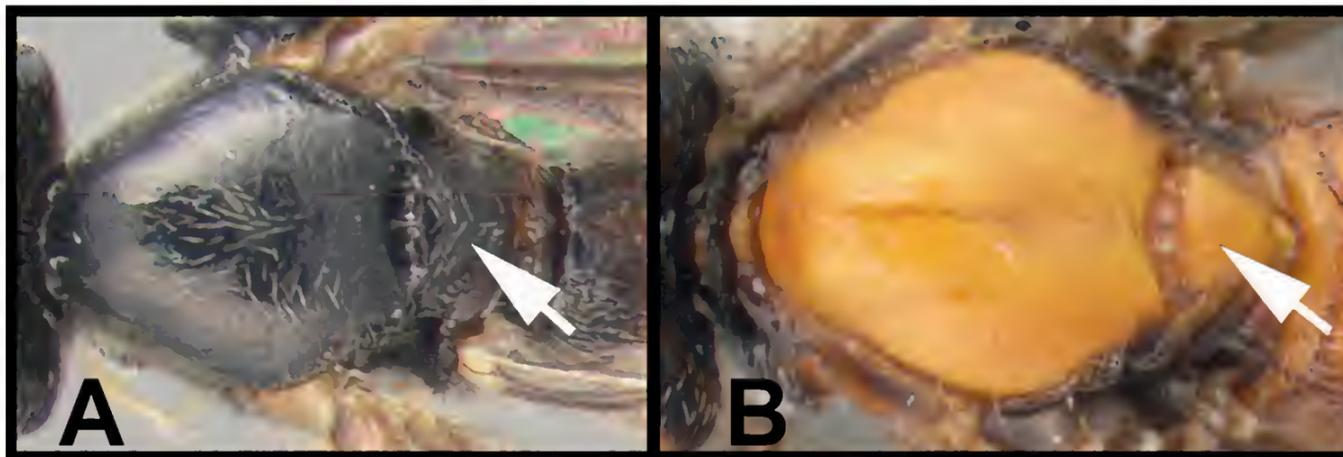
Couplet 37

- 38(37) A. Metasomal terga black and pale *A. reginae* n. sp. (in part)
- B. Metasomal terga all pale..... 39



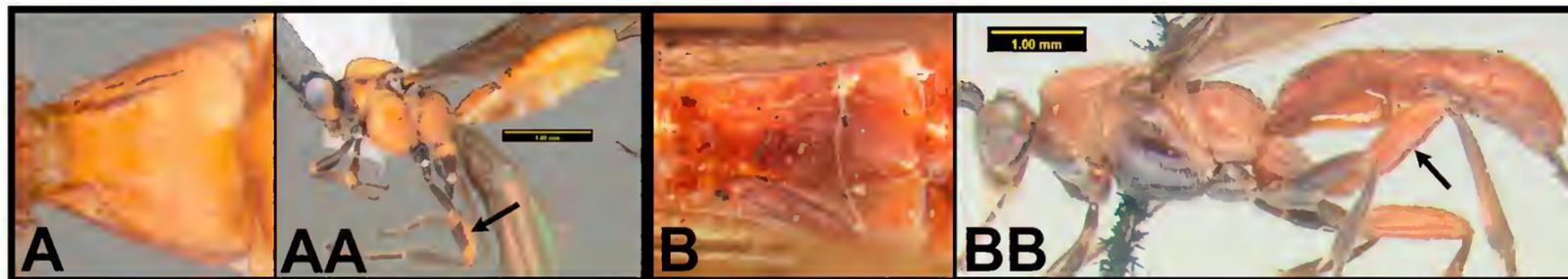
Couplet 38

- 39(38) A. Mesoscutellum entirely melanic; hind femur pale (yellow to orange)..... *A. kowlesae* n. sp.
- B. Mesoscutellum often partly or entirely pale (yellow to orange); if entirely melanic then hind femur mostly or entirely melanic 40



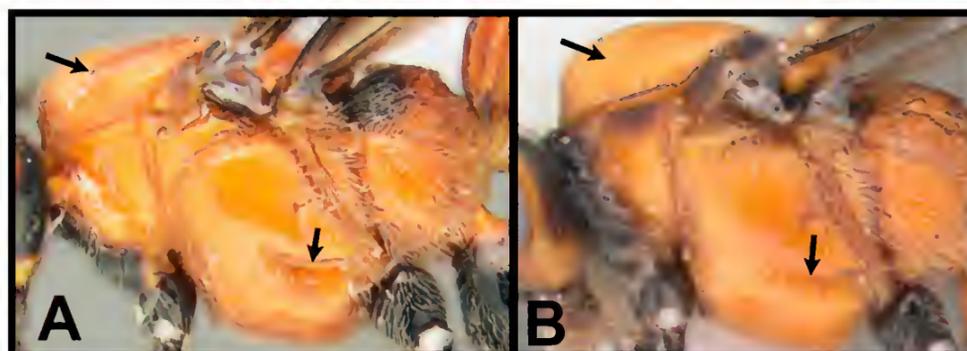
Couplet 39

- 40(39) A. First metasomal median tergite wider than long. AA. Hind femur with extensive melanic color 41
 B. First metasomal median tergite longer than posterior width. BB. Hind femur entirely pale (Arizona, California) (image of holotype)..... *A. ninanae* (Muesebeck)



Couplet 40

- 41(40) A. Notauli well impressed; sternaulus deep with some fovea; antenna with more than 30 flagellomeres
 *A. hopkinsensis* n. sp.
 B. Notauli relatively weak and shallow; sternaulus shallow and smooth; antenna with fewer than 28 flagellomeres
 *A. minys* n. sp. (in part)



Couplet 41

SYSTEMATICS

Descriptions are of the holotype with variation given in parentheses.

Aerophilus abdominalis (Muesebeck, 1927) n. comb.

Figure 5

Bassus abdominalis Muesebeck, 1927:35–36. Other combinations: *Agathis*.

DIAGNOSIS. Face not elongate; notauli impressed and sculptured; first metasomal median tergite longitudinally rugosostriate; body almost entirely yellow except for small areas of the mesosoma, the flagellum, and extremities of some legs; very similar to *A. klastos* but distinguished by characters given in the key and wings less infuscate in *A. abdominalis*.

DESCRIPTION. Length 5.0 mm. Ovipositor length 3.9 mm. Flagellomere number 32 (31–32). Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.5. Notauli well impressed and completely pitted. Propodeum entirely rugose and lacking cells. Forewing hyaline. First metasomal median tergite clearly longer than posterior width. First median tergite entirely striogranulate; pair of carinae extending to midlength.

Median syntergite 2+3 longitudinally striate, except posterior half of tergite 3 smooth.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Louisiana, C.F. Baker (USNM type 28681). Other material examined: southeast Texas (FSCA), Oklahoma (FSCA), Georgia (HIC), Louisiana (HIC), Kentucky (HIC). Published state records: Arizona, Florida, Louisiana, Michigan, Missouri, South Dakota, Texas. For a map of the examined material see <http://bit.ly/1PSUefd>.

Aerophilus aciculatus (Ashmead, 1889) n. comb.

Figure 6

Microdus aciculatus Ashmead, 1889:639. Other combinations: *Agathis*, *Bassus*.

DIAGNOSIS. Second median tergite completely striate in raised areas; hind coxa in lateral view entirely melanic; notauli with crenulae extending over entire length or almost so; face not elongate.

DESCRIPTION. Length 5.3 mm. Ovipositor length 4.3 mm. Flagellomere number undetermined (broken on holotype and not recorded in the original description). Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.5. Notauli

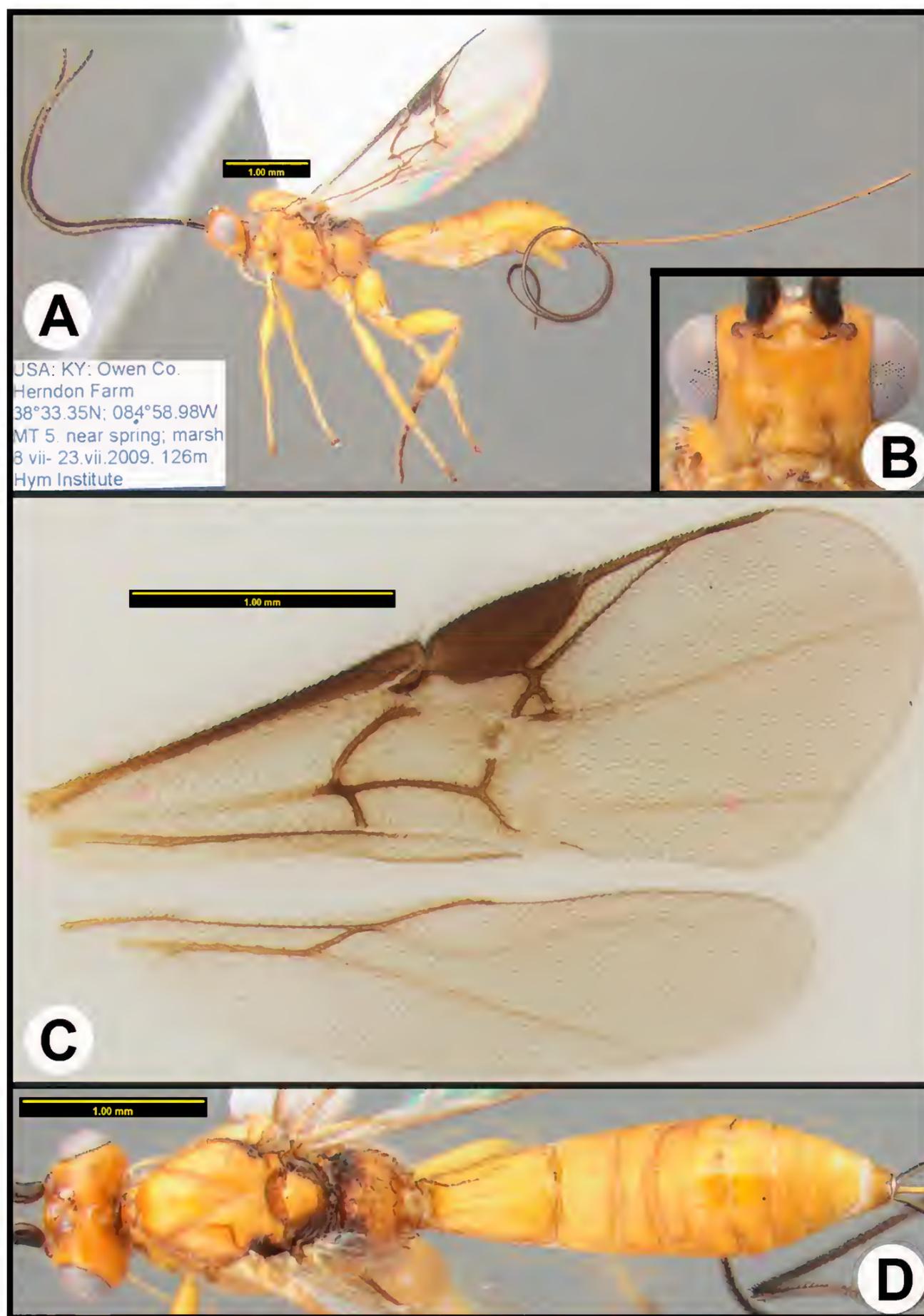


Figure 5 *Aerophilus abdominalis*: A. lateral habitus, B. anterior head, C. wings. D. dorsal habitus.

well impressed and completely pitted. Propodeum rugose medially, smooth laterally, with poorly defined cells. Forewing infuscate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite entirely striate; pair of carinae extending to midlength. Median syntergite 2+3 longitudinally striate, except posterior third of tergite 3 smooth.

MATERIAL EXAMINED AND DISTRIBUTION. Lectotype female: Texas, coll. Belfrage (USNM type 2956). Other

material examined: Texas (FSCA). Published state records: Arizona, Texas. For a map of the examined material see <http://bit.ly/1MWOACC>.

Aerophilus acrobasidis (Cushman, 1920) n. comb.

Figure 7

Bassus acrobasidis Cushman, 1920:289. Other combinations: *Agathis*.

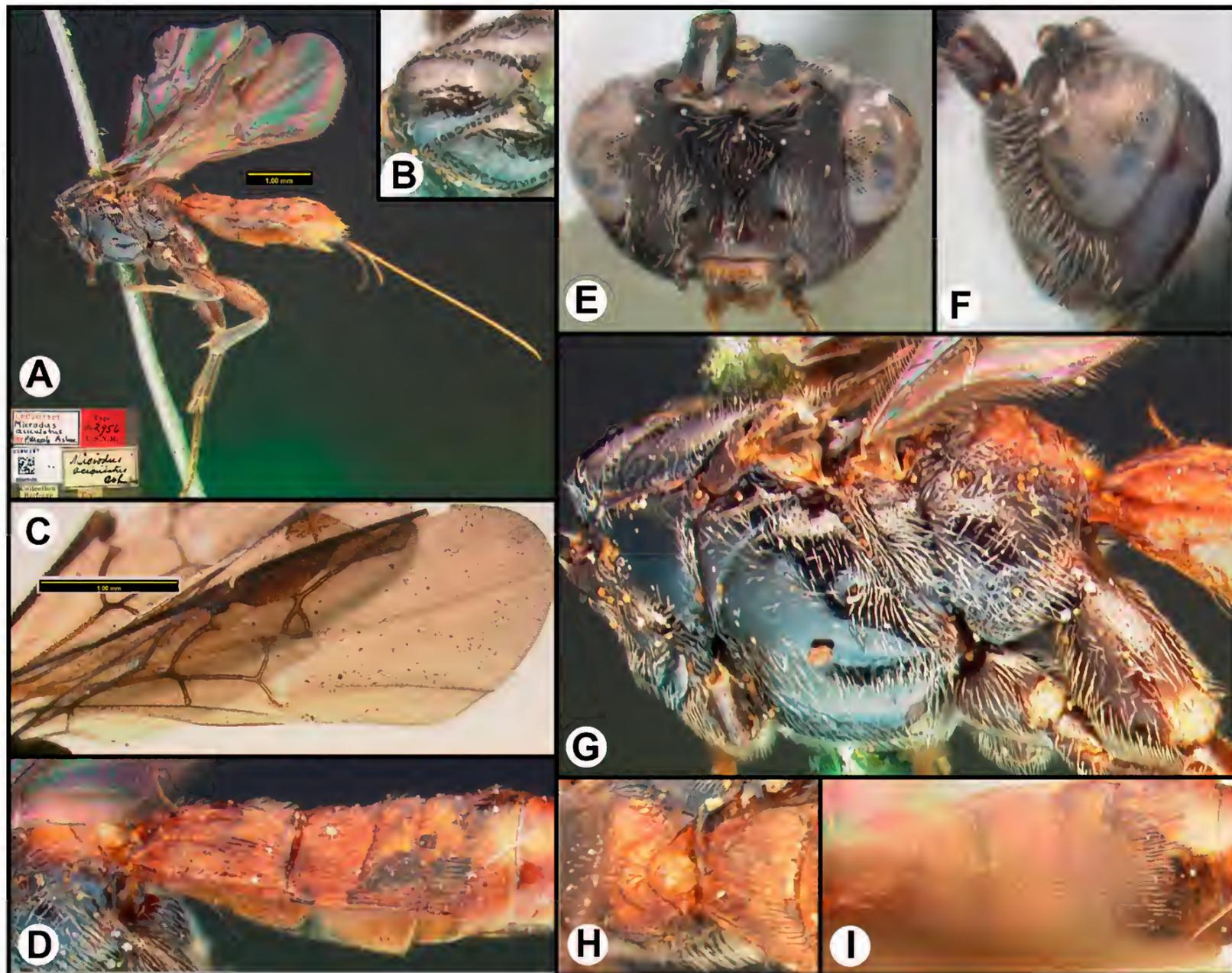


Figure 6 *Aerophilus aciculatus*, holotype: A. lateral habitus; B. dorsal mesoscutum showing pitted notauli; C. forewing; D. dorsolateral metasoma; E. anterior head; F. lateral head; G. lateral mesosoma; H. propodeum and angled view of median tergite 1; I. median tergites 1–3, partially obscured by wing (the latter is out of focus).

DIAGNOSIS. Notauli weakly impressed, barely perceptible; hind femur entirely pale; antenna with more than 30 flagellomeres; face not elongate; hind trochanter mostly or entirely pale concolorous with coxa and femur.

DESCRIPTION. Length 5.0 mm. Ovipositor length 4.3 mm. Flagellomere number 34. Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.4. Notauli barely perceptible and lacking pits. Propodeum mostly smooth with weak smooth rugae, cells not present. Forewing infuscate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite mostly smooth with weak smooth striae; pair of carinae extending past midlength of tergite. Median syntergite 2+3 mostly smooth with longitudinal striae in the three transverse depressions.

HOSTS. *Batrachedridae*: *Batrachedra curvilineella*, *Acrobasis caryae*, *Acrobasis caryae* (*Carya illinoensis*), *Acrobasis caryivorella*, *Acrobasis caryivorella* (*Carya illinoensis*), *Acrobasis evanescentella*, *Acrobasis exsulella*, *Acrobasis juglandis*, *Acrobasis nuxvorella* (*Carya illinoensis*), *Acrobasis stigmella*. *Tortricidae*: *Choristoneura fumiferana*, *Choristoneura occidentalis*, *Cudonigera houstonana*, *Cydia ingens*, *Rhyacionia frustrana*, *Rhyacionia frustrana* (*Pinus taeda*), *Rhyacionia rigidana*. This species has been used in the biocontrol of *Acrobasis*

nuxvorella (the pecan nut casebearer) and *Cydia caryana* (the hickory shuckworm) (Ellington et al., 1995; Romero et al., 2001).

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Texas, Brownwood, 2.vii.1918, A.I. Fabis, Quaintance 16787, parasite of *Acrobasis* SR, 4-vii-1918 (USNM type 22867). Published state records: Canada: Ontario. USA: Arkansas, Colorado, Florida, Georgia, Kansas, Maryland, Mississippi, New Mexico, North Carolina, Oregon, South Carolina, Texas, Virginia. For a map of the examined material see <http://bit.ly/1M3tJBb>.

Aerophilus arthurevansi Sharkey n. sp.

Figure 8

DIAGNOSIS. Mesoscutellum entirely melanic; propodeum with well-defined cells; hind femur pale (yellow to orange); first metasomal median tergite mostly smooth; forefemur almost entirely melanic with a pale (yellow to orange) patch apically; hind coxa in lateral view entirely pale; hind trochanter mostly or entirely pale, concolorous with femur; notauli smooth without crenulae, or with one or two crenulae anteriorly.

DESCRIPTION. Length 6.4 mm. Ovipositor length 5.0 mm. Flagellomere number 35 (34–37). Gena not elongate; ratio of

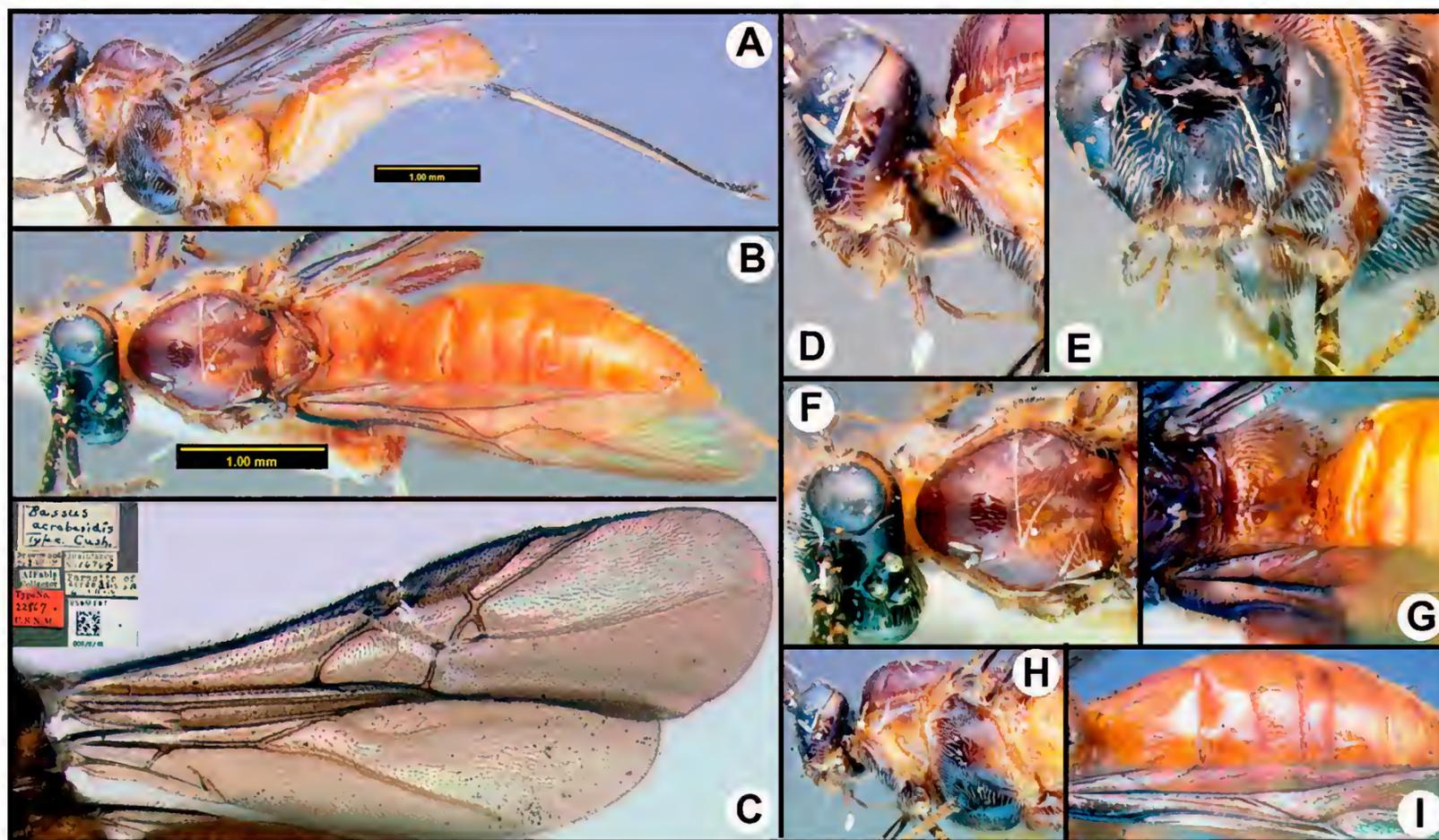


Figure 7 *Aerophilus acrobasisidus*, holotype: A. lateral habitus, B. dorsal habitus, C. wings, D. lateral head, E. anterior head, F. dorsal head and mesoscutum, G. propodeum, H. lateral head and mesosoma, I. dorsal metasoma.

length of malar space to eye height, viewed laterally, 0.4. Notauli well impressed without pits (or with pits extending up to 1/2 length). Propodeum smooth except for well-defined cells. Forewing infuscate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite entirely smooth; pair of carinae extending well past midpoint of tergite. Median syntergite 2+3 smooth with a few striae in second transverse groove.

ETYMOLOGY. Named in honor of one of the collectors of the type series, Arthur Evans.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Virginia, Isle of Wight Co., Backwater Ecological Preserve, 36.82328°N, 76.85229°W, pine/oak sand hills 3.vi.2010, Mal. trap, A.V. Evans and D.E. Loomis (HIC, specimen H8554). Paratypes. 3 females, Virginia, 36.751°N, 77.49°W, 25.v–28.vi.2011 (HIC). For a map of the examined material see <http://bit.ly/1LZTgYr>.

Aerophilus bakeri (Muesebeck, 1927) n. comb.

Figure 9

Bassus bakeri Muesebeck, 1927:42. Other combinations: *Agathis*.

DIAGNOSIS. This is the only species with an elongate face with the body of the mesosoma and the hind legs entirely melanic.

DESCRIPTION. Length 5.4 mm. Ovipositor length 5.4 mm. Flagellomere number 22. Gena slightly elongate; ratio of length of malar space to eye height, viewed laterally, 0.6. Notauli weakly impressed and lacking pits. Propodeum mostly smooth posteriorly and laterally, rugose anteriorly with anterior margins of irregular weak median cell indicated. Forewing hyaline. First metasomal median tergite slightly longer than posterior width. First median tergite smooth with pair of longitudinal carinae

extending past midlength. Median syntergite 2+3 smooth with weak striae in second transverse depression medially.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Colorado, C.F. Baker (USNM type 28684). Distribution. Colorado. Published state records: Alaska, California, Colorado, Michigan, Minnesota, Washington. For a map of the examined material see <http://bit.ly/1LZTmiE>.

Aerophilus binominatus (Muesebeck, 1958) n. comb.

Figure 10

Agathis binominata Muesebeck, 1958:26. Originally described as *Microdus bicolor* Provancher, 1880:179, which was preoccupied by *Microdus bicolor* Brullé, 1846:483. Due to this homonymy, Muesebeck (1958) changed the name to *binominata*. Other combinations: *Bassus*.

DIAGNOSIS. First metasomal tergite mostly melanic, remaining tergites pale; face not elongate; raised areas of median tergite 2 smooth, lacking striae.

DESCRIPTION. Length 3.6 mm. Ovipositor length 3.0 mm. Flagellomere number 29. Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.5. Notauli barely perceptible and lacking pits. Propodeum smooth laterally, rugose medially, median cell not defined, posterior transverse carina well defined. Forewing hyaline. First metasomal median tergite slightly longer than posterior width. First median tergite mostly smooth with a few weak striae medially; pair of carinae extending past midlength of tergite. Median syntergite 2+3 mostly smooth with longitudinal striae in the three transverse depressions, striae more pronounced medially.

HOSTS. Tortricidae: *Aethes rutilana*, *Choristoneura fumiferana*, *Endothenia albolineana*, *Epiblema desertana*, *Epinotia nanana*, *Petrova comstockiana*, *Rhyacionia buoliana*. Coleophoridae: *Coleophora laricella*. Gelechiidae: *Coleotechnites* sp.,

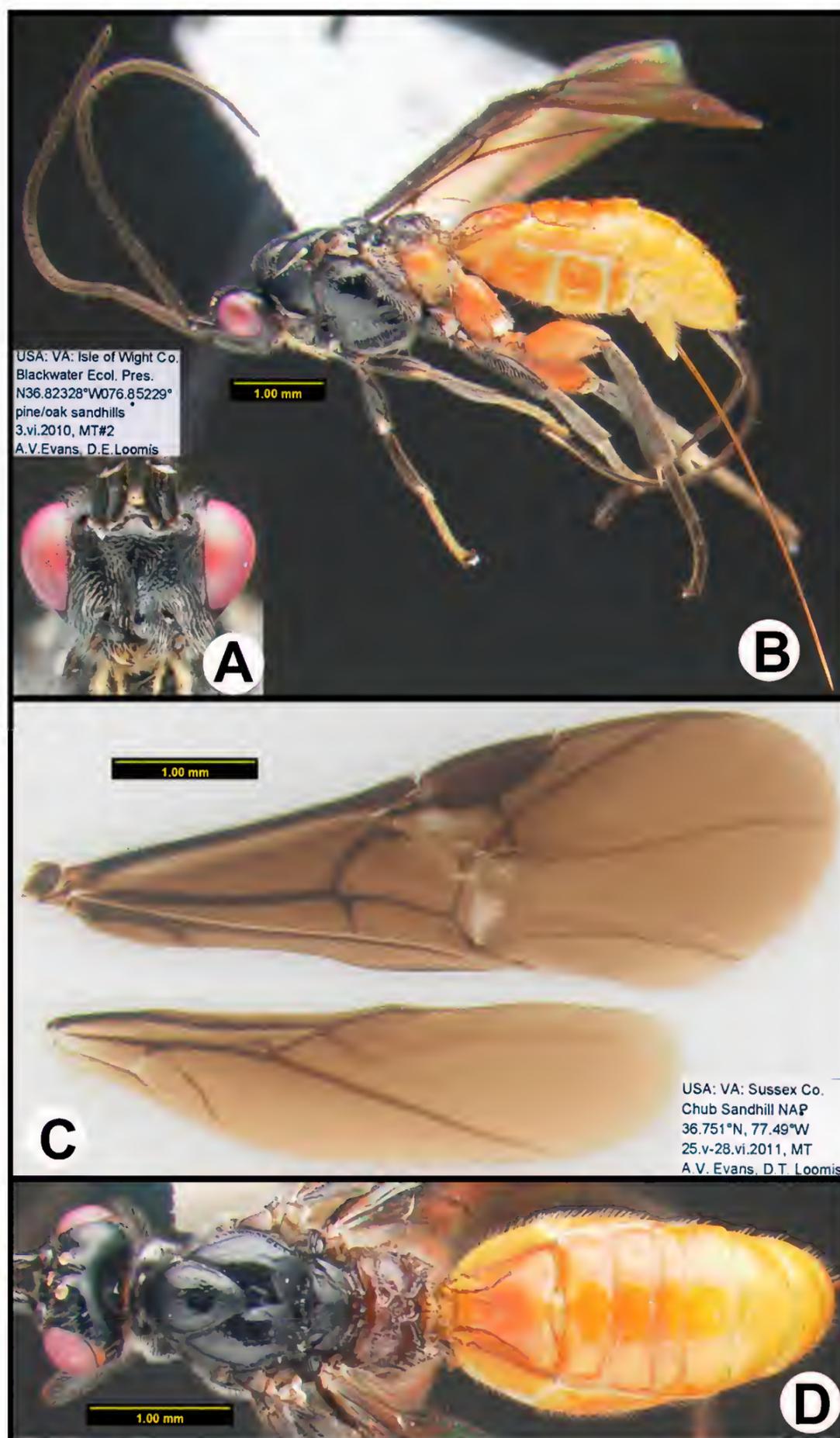


Figure 8 *Aerophilus arthurevansi*: A. anterior head, B. lateral habitus, C. wings, D. dorsal habitus.

Coleotechnites coniferella; *Coleotechnites piceaella*. Pyralidae:
Dioryctria banksiella.

MATERIAL EXAMINED AND DISTRIBUTION. Lectotype female. Not examined: Canada, (probably southern Quebec) (ULQC). Other material examined: Maine (HIC). Published state records: Canada: New Brunswick, Ontario, Quebec, Saskatchewan. USA: Maine, Massachusetts, New Hampshire, New York, Pennsylvania, Virginia. For a map of the examined material see <http://bit.ly/2dFF40V>.

Aerophilus buttricki (Viereck, 1917)

Figure 11

Bassus (Lytopylus) buttricki Viereck, 1917. Other combinations:
Agathis.

DIAGNOSIS. Similar to *A. minys* but distinguished by characters in the key; hind coxa in lateral view entirely pale; first metasomal median tergite about as wide as long and mostly

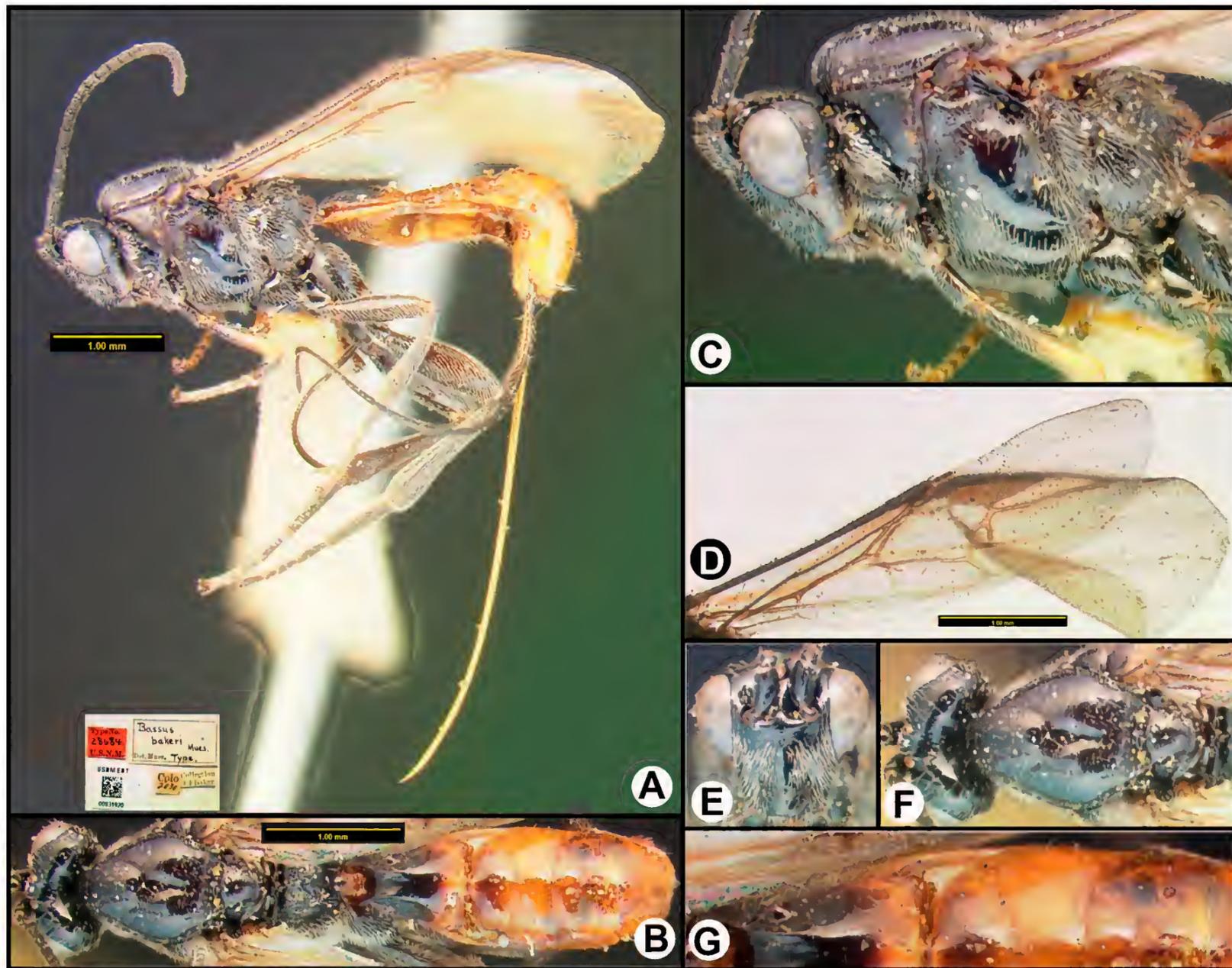


Figure 9 *Aerophilus bakeri*, holotype: A. lateral habitus, B. dorsal habitus, C. lateral head and mesosoma, D. wings, E. anterior head, F. dorsal head and thorax, G. dorsal view of right half of tergites 1-3.

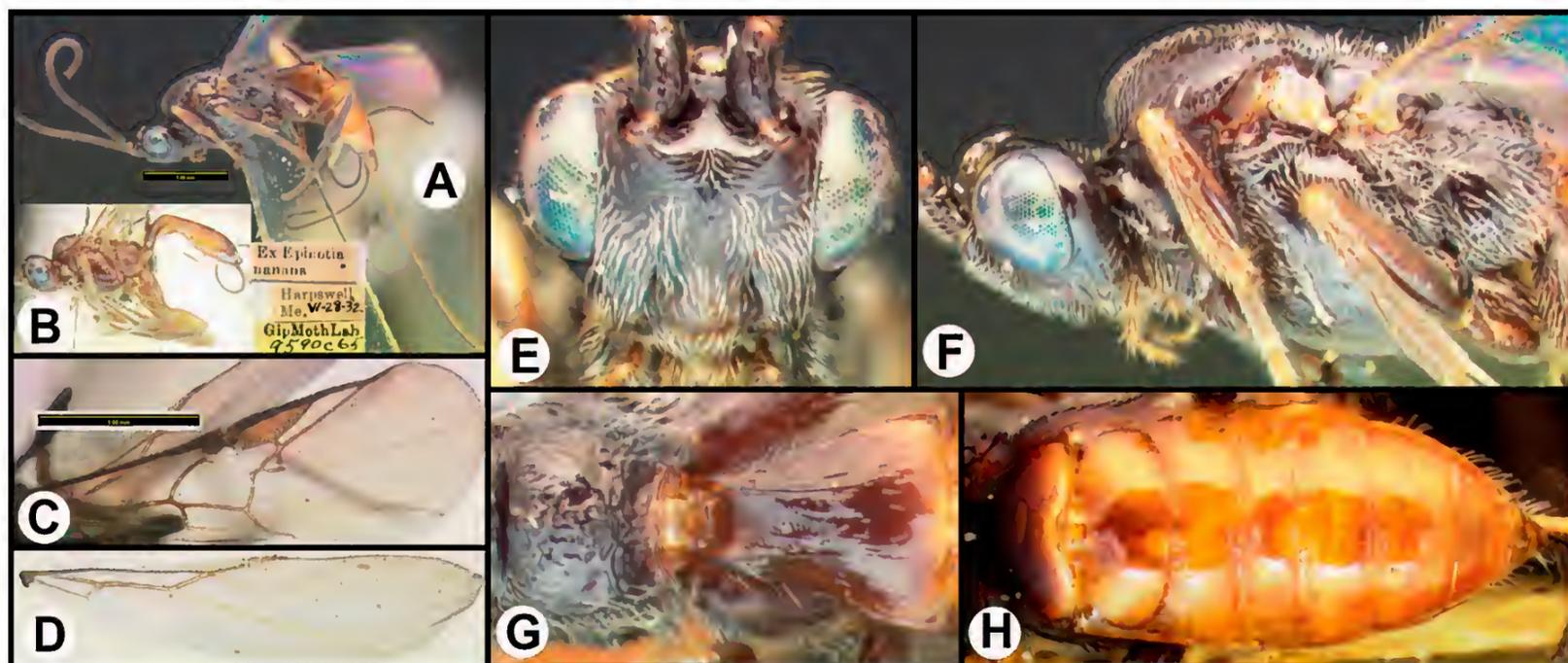


Figure 10 *Aerophilus binominatus*, specimens identified by Muesebeck (USNM): A. lateral habitus showing most common coloration, B. lateral habitus showing color variation, C. forewing, D. hindwing, E. anterior head, F. lateral head and mesosoma, G. dorsal propodeum and tergite 1, H. dorsal metasoma.

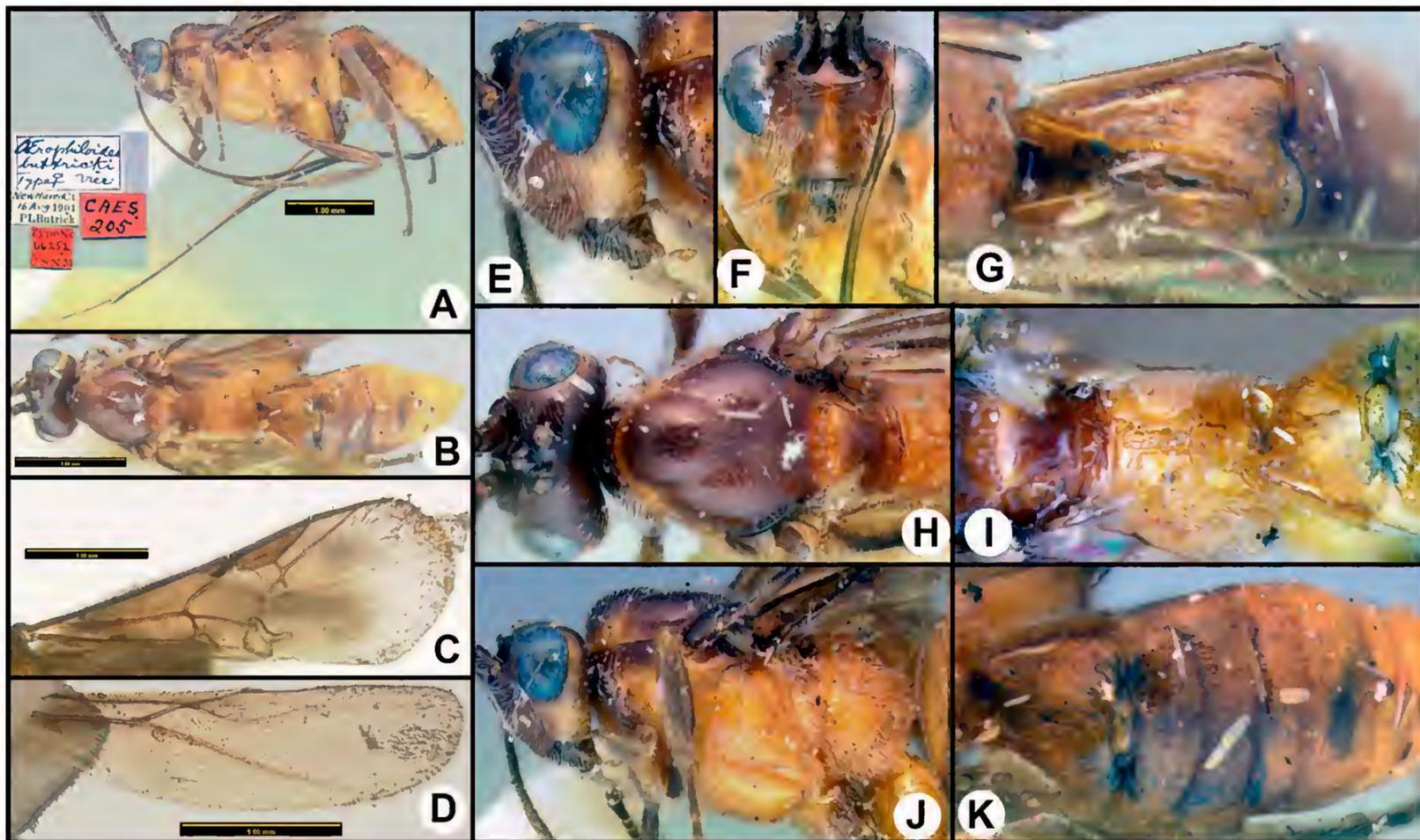


Figure 11 *Aerophilus buttricki*, holotype: A. lateral habitus, B. dorsal habitus, C. forewing, D. hindwing, E. lateral head, F. anterior head, G. tergite 1, H. dorsal head and thorax, I. propodeum, J. lateral head and mesosoma, K. dorsal metasoma.

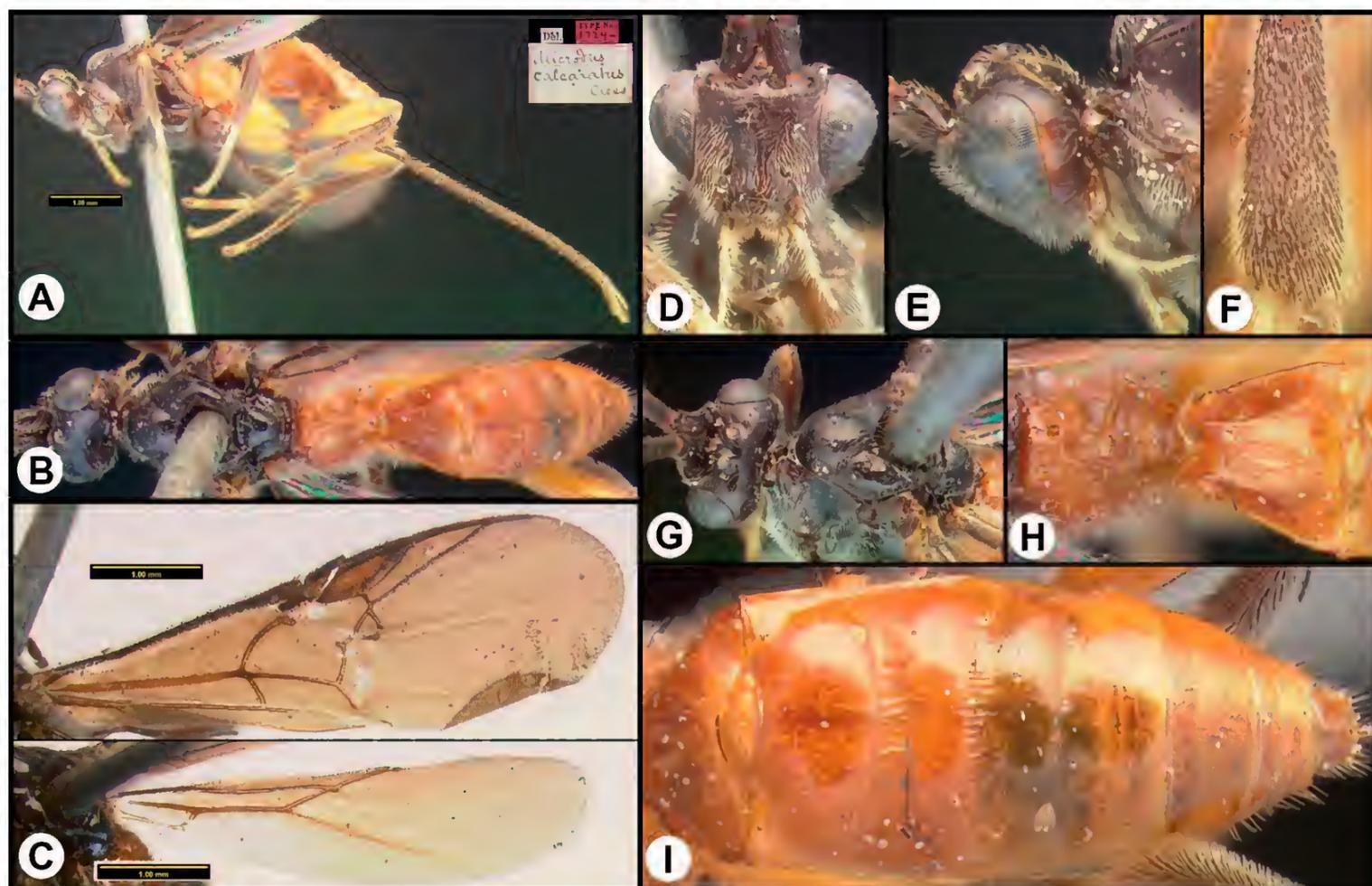


Figure 12 *Aerophilus calcaratus*, holotype: A. lateral habitus, B. dorsal habitus, C. wings, D. anterior head, E. lateral head, F. apex of hind tibia, G. dorsal head and thorax, H. propodeum and tergite 1, I. dorsal metasoma.

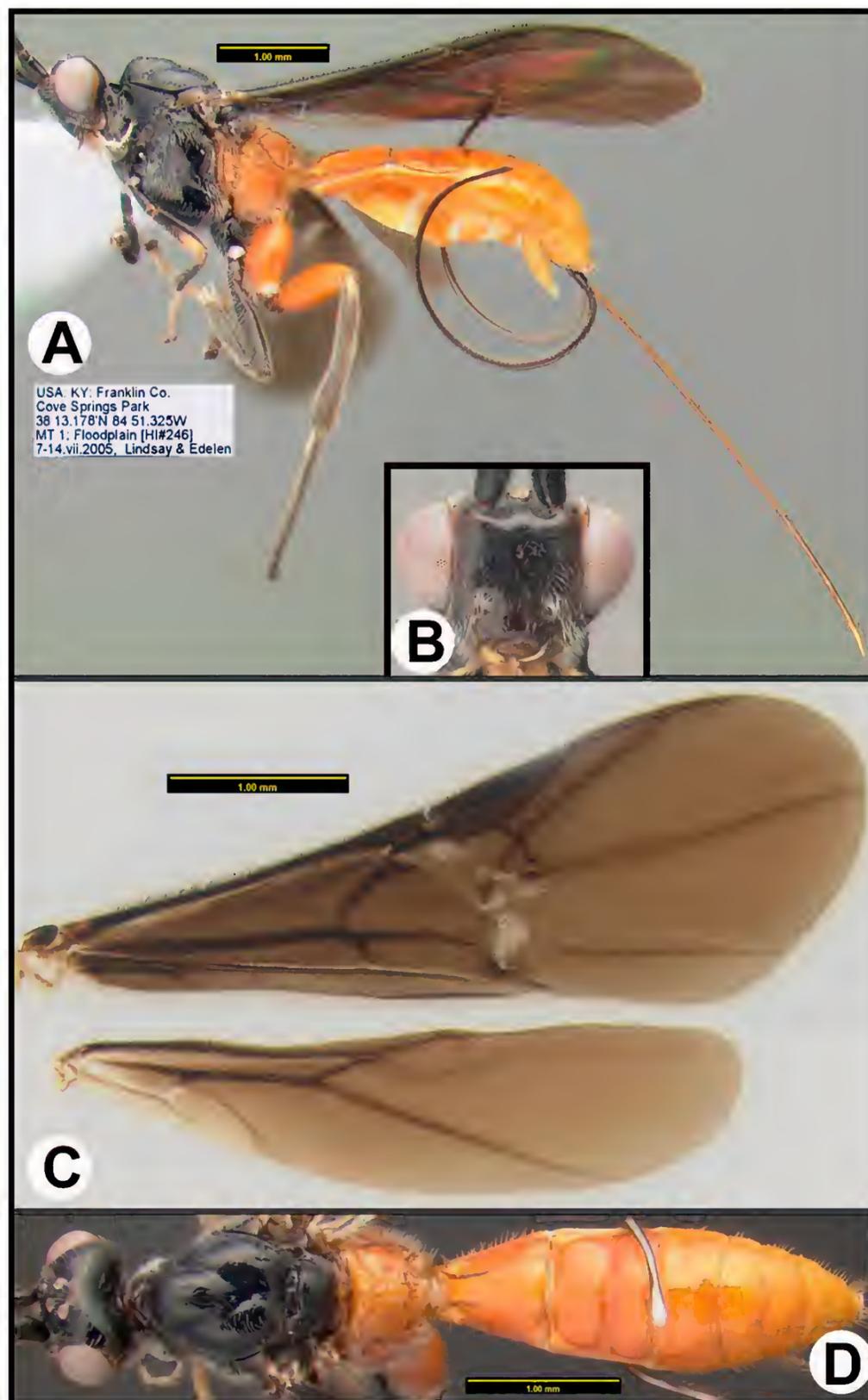


Figure 13 *Aerophilus calcaratus*: A. lateral habitus, B. anterior head, C. wings, D. dorsal habitus.

smooth, except for the two longitudinal carinae; face not elongate.

DESCRIPTION. Length 4.4 mm. Ovipositor length 5.0 mm. Flagellomere number 23–27 (according to Muesebeck, 1927), broken on holotype. Gena slightly elongate; ratio of length of malar space to eye height, viewed laterally, 0.6. Notauli well impressed and lacking pits. Propodeum smooth with well-defined cells, some rugae in median cell and elsewhere. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite mostly smooth with a few thick smooth striae; pair of carinae extending well past midlength of tergite. Median syntergite 2+3 mostly smooth with longitudinal striae in the three transverse depressions, striae weak and only present medially in posterior-most transverse depression.

HOSTS. Gelechiidae: *Isophrictis*, *Isophrictis*, *Acrobasis rubrifasciella*. Pyralidae: *Homoeosoma electellum*. Tortricidae: *Aethes rutilana*, *Phtheochroa straminoides*, *Phtheochroa voxcana*, *Sulleima helianthana*.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Connecticut, New Haven, 6.viii.1904, P.L. Buttrick (USNM type 66252). Published state records: Canada: Alberta. USA: Colorado, Connecticut, Florida, Georgia, Louisiana, Maine, Maryland, Massachusetts, Missouri, South Dakota, Texas, West Virginia. For a map of the examined material see <http://bit.ly/1SbNFCO>.

Aerophilus calcaratus (Cresson, 1873) n. comb.

Figures 12, 13

Microdus calcaratus Cresson, 1873:45. Other combinations: *Agathis*, *Bassus*, *Therophilus*.

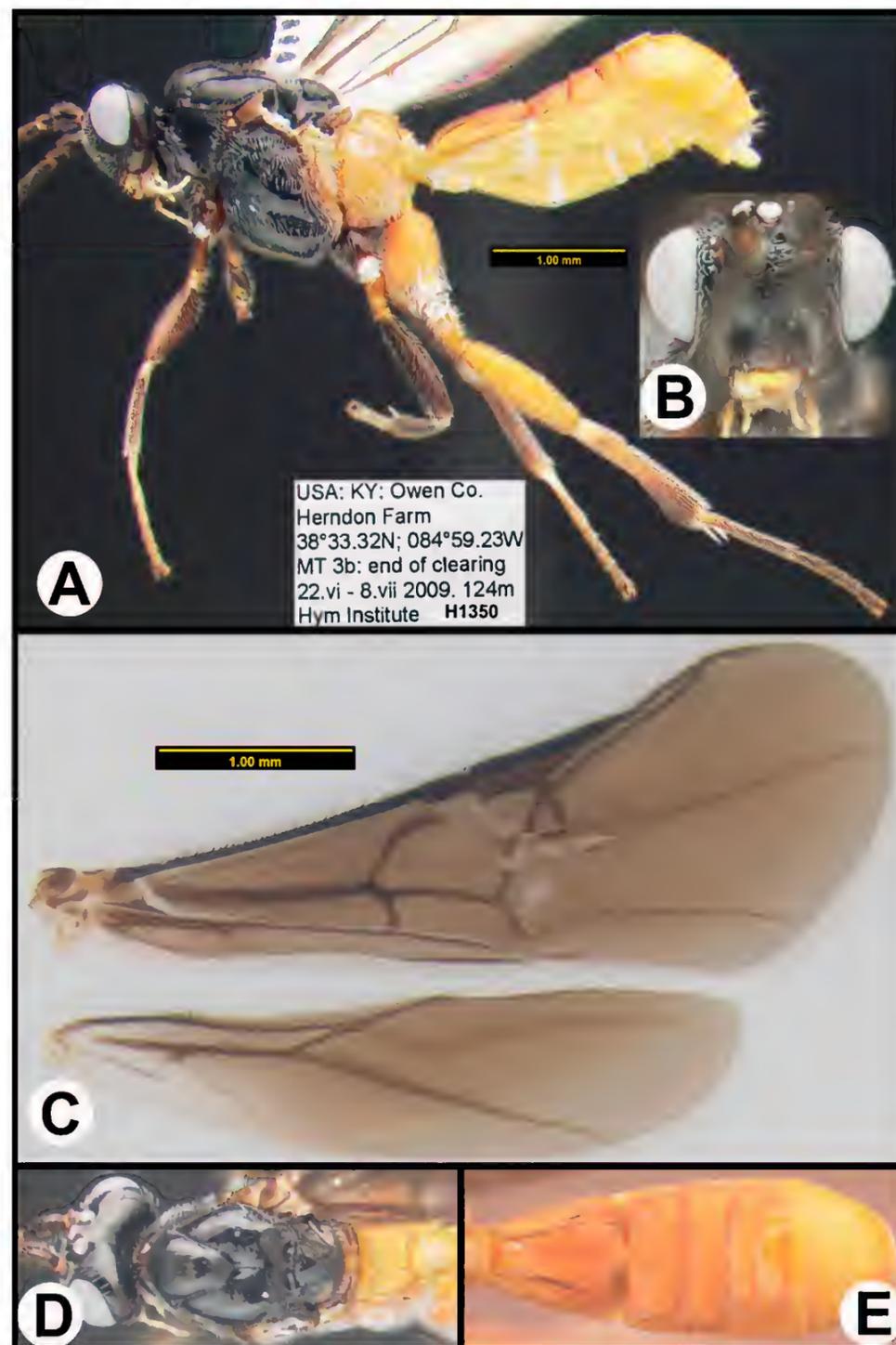


Figure 14 *Aerophilus chapmani*, holotype: A. lateral habitus, B. anterior head, C. wings, D. dorsal head and mesosoma, E. dorsal metasoma.

DIAGNOSIS. Cells of propodeum well-defined; median syntergite 2+3 mostly smooth with striae in some transverse depressions; middle lobe of mesoscutum not bulging and not elevated above lateral lobes (contrasting with *A. difficilis*); antenna with 35 or fewer flagellomeres; mesoscutellum entirely melanic; hind femur pale (yellow to orange); hind trochanter mostly or entirely melanic; first metasomal median tergite mostly smooth.

DESCRIPTION. Length 6.1 mm. Ovipositor length 5.0 mm. Flagellomere number 31–35 (32–38, according to Muesebeck, 1927). Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.4. Notauli well impressed with pits in anterior 1/3. Propodeum smooth with well-defined cells. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite smooth with a hint of irregularities medially at midlength; pair of carinae extending past midlength of tergite. Median syntergite 2+3 mostly smooth with longitudinal striae in the three transverse depressions, striae weak and only present medially in posterior two transverse depressions.

HOSTS. **Depressariidae:** *Psilocorsis cryptolechiella*, *Psilocorsis quercicella*; *Psilocorsis reflexella*. **Gelechiidae:** *Aroga trialbamaculella*, *Chionodes fuscomaculella*. **Gracillariidae:** *Acrocercops*; *Caloptilia*. **Pyralidae:** *Acrobasis betulella*, *Acrobasis caryalbella*, *Acrobasis caryivorella*, *Acrobasis comptoniella*, *Acrobasis indigenella*, *Acrobasis minimella*, *Acrobasis rubrifasciella*, *Acrobasis stigmella*. **Tortricidae:** *Croesia albicomana*, *Episimus argutanus*, *Olethreutes permundana*, *Olethreutes sericorana*, *Sparganothis pettitana*, *Sparganothis sulfureana*.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female, Delaware (ANSP type 1724). Other material examined: Arkansas (HIC), Kentucky (HIC), Maryland (HIC), Tennessee (HIC), West Virginia (HIC), Virginia (HIC), Florida (FSCA), Georgia (FSCA). A specimen from Savannah, Georgia, and deposited in the FSCA (H12026) was collected from gall on *Celtis* sp. (hackberry) 22.iii.1958. Specimens were collected throughout the year, with the earliest records from January in Florida. In Kentucky, Virginia, and West Virginia where Malaise traps have been run from April to November for many years in multiple localities, the temporal data suggest two generations,

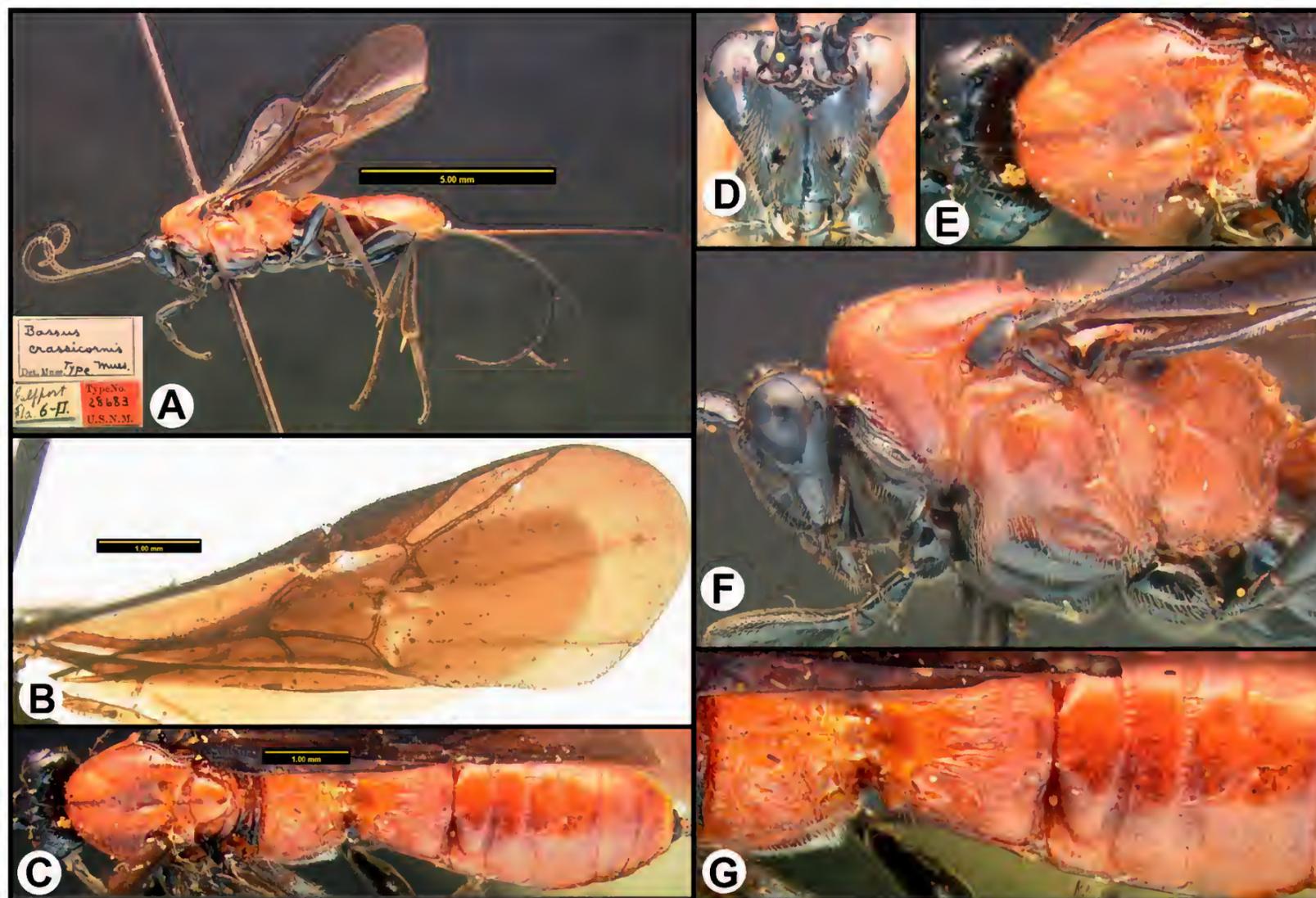


Figure 15 *Aerophilus crassicornis*, holotype: A. lateral habitus, B. wings, C. dorsal habitus, D. anterior head, E. dorsal head and mesonotum, F. lateral head and mesosoma, G. propodeum and tergites 1–3.

with the first peaking in May–June and the second in August–September. However, specimens are found in all months from May to October in these three states. Published state records: Canada: Ontario. USA: widespread throughout the Eastern States, from Maine to Florida and west to Texas, with one record from Arizona. Most records are somewhat suspect, due to the many species similar to *A. calcaratus*. For a map of the examined material see <http://bit.ly/1M3v7nn>.

Aerophilus chapmani Sharkey n. sp.

Figure 14

DIAGNOSIS. Second median tergite completely striate in raised areas; mesoscutum melanic, face not elongate; forefemur entirely melanic; hind coxa in lateral view entirely pale.

DESCRIPTION. Length 5.4 mm. Ovipositor length unknown, the sole known specimen is the holotype male. Flagellomere number 32. Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.3. Notauli well impressed with pits extending over 3/4 of length. Propodeum sculptured with irregular carinae but lacking distinct cells. Forewing infusate. First metasomal median tergite slightly longer than posterior width. First median tergite entirely striate; pair of carinae extending past midlength of tergite. Median syntergite 2+3 longitudinally striate except posterior half of tergite 3 smooth.

ETYMOLOGY. Named in honor of Dr. Eric Chapman, research associate in the Department of Entomology at the University of Kentucky, for his many years of assistance and advice.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype male: Kentucky, Owen Co., Herndon Farm, 38.55889°N, 84.98972°W, 22.vi–8.vii.209, 124 m. (HIC, specimen H1350). For a map see <http://bit.ly/1HecZ4H>.

Aerophilus crassicornis (Muesebeck, 1927) n. comb.

Figure 15

Bassus crassicornis Muesebeck, 1927:43. Other combinations: *Agathis*.

DIAGNOSIS. Very similar to *A. rayfisheri* but differing in that the notauli are completely absent in *A. rayfisheri*. *Aerophilus crassicornis* is the only species with an elongate face in combination with the first metasomal median tergite predominantly striate (the latter also shared by some *A. rayfisheri*) and distinctly impressed notauli.

DESCRIPTION. Length 8.0 mm. Ovipositor length 8.4 mm. Flagellomere number 27. Gena elongate; ratio of length of malar space to eye height, viewed laterally, 0.8. Notauli well impressed and lacking pits. Propodeal cells complete but irregular and with internal rugae. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite irregularly striate in posterior 2/3, smooth anteromedially; pair of longitudinal carinae weak and reaching midlength of tergite. Median syntergite 2+3 mostly smooth with striae in anterior two transverse depressions.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Florida, Gulfport, 6.ii.(year?) (USNM type 28683).

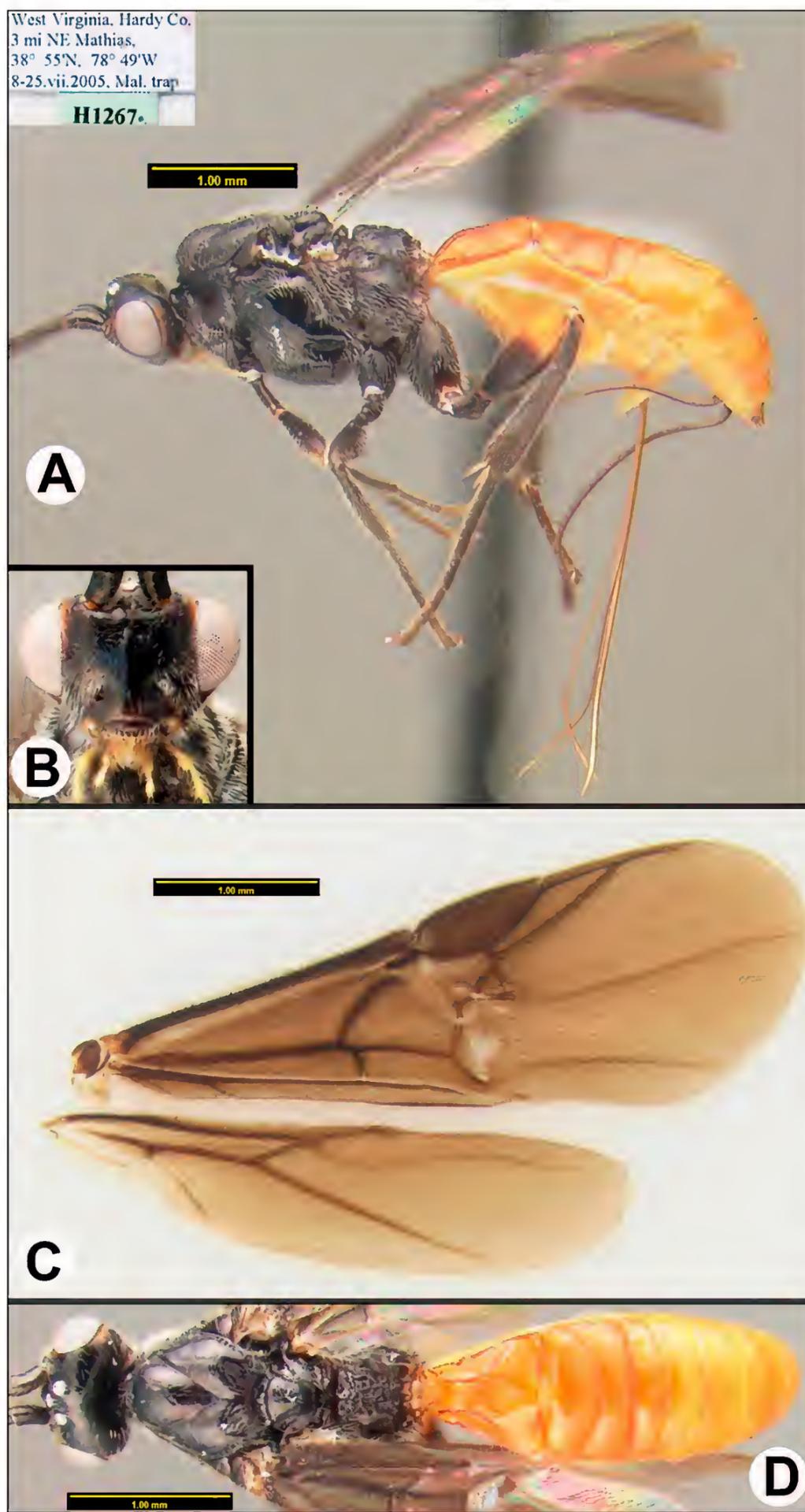


Figure 16 *Aerophilus davidsmithi*, holotype: A. lateral habitus, B. anterior head, C. wings, D. dorsal habitus.

Published state records: Florida, Missouri, Iowa. For a map of the examined material see <http://bit.ly/1Oah7dJ>.

Aerophilus davidsmithi Sharkey n. sp.

Figure 16

DIAGNOSIS. Hind coxa in lateral view entirely melanic; mesoscutellum entirely melanic; hind femur pale (yellow to orange); face not elongate.

DESCRIPTION. Length 4.9 mm. Ovipositor length 3.2 mm. Flagellomere number 31. Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.4. Notauli well impressed with a few weak pits anteriorly. Propodeum rugose medially smooth laterally with poorly defined cells. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite entirely smooth with hint of some irregularities at midlength; pair of

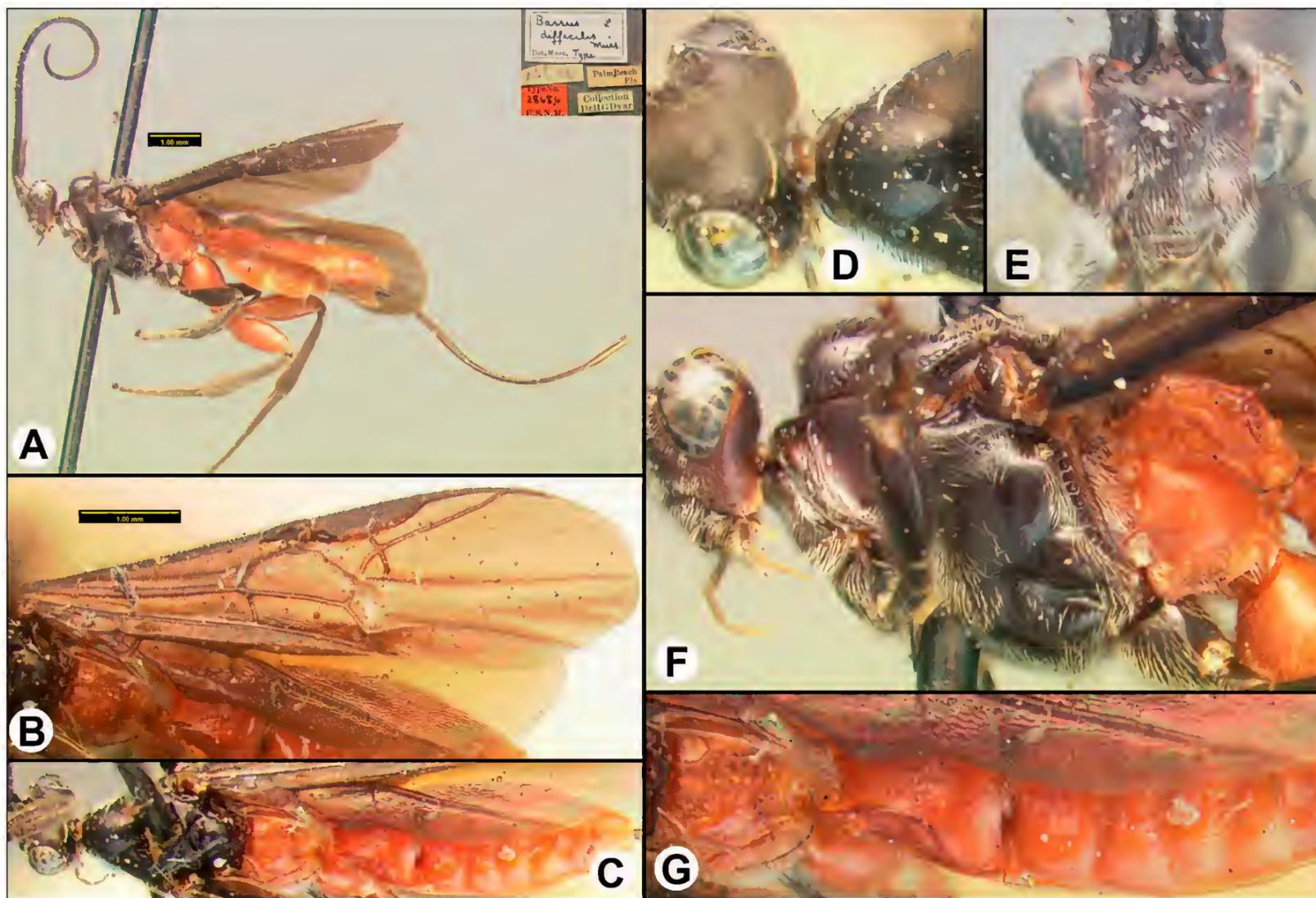


Figure 17 *Aerophilus difficilis*, holotype: A. lateral habitus, B. wings, C. dorsal habitus, D. dorsal head and anterior mesoscutum, E. anterior head, F. lateral head and mesosoma, G. propodeum and tergites 1–3.

carinae extending past midlength. Median syntergite 2+3 entirely smooth, with hint of longitudinal striae in second transverse depression.

ETYMOLOGY. Named in honor of Dr. David Smith who has been exchanging Malaise trap specimens with M.J.S. for many years, including the unique specimen of this species.

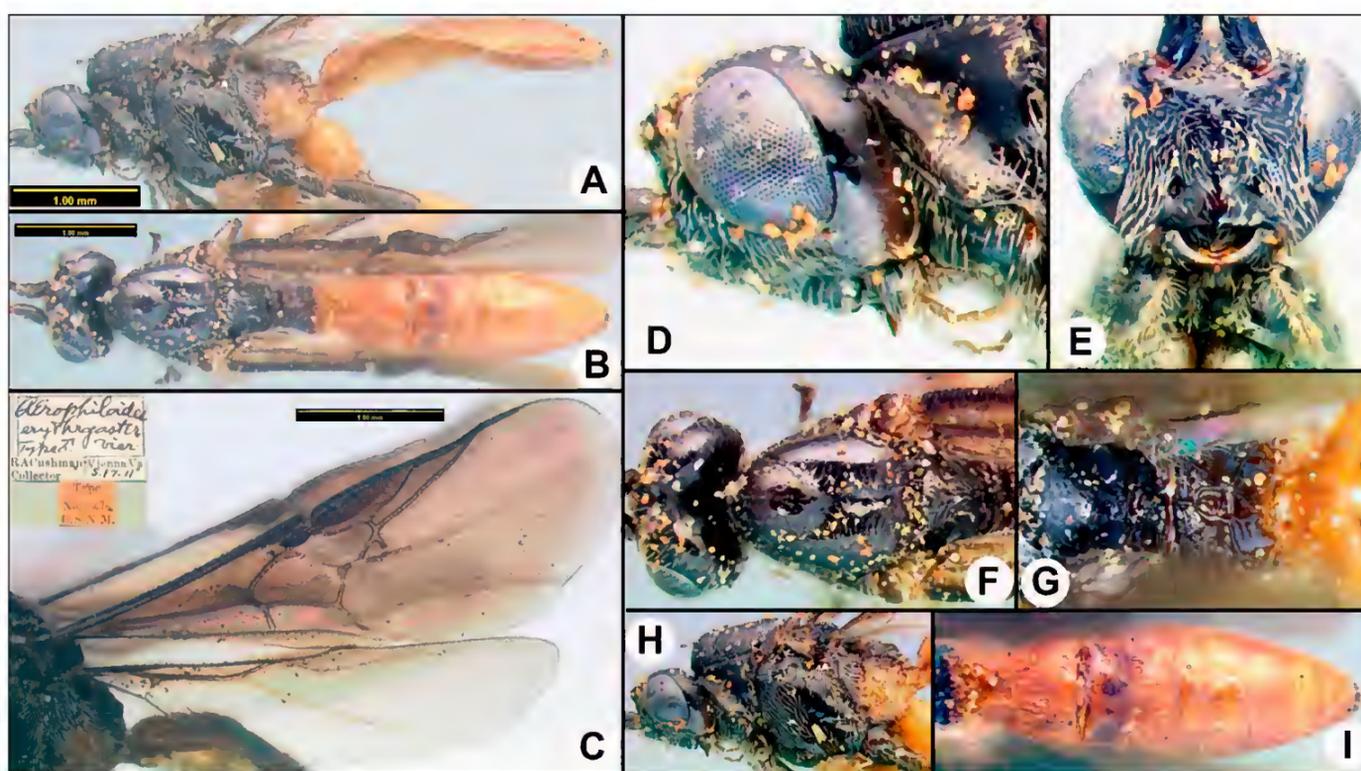


Figure 18 *Aerophilus erythrogaster*, holotype: A. lateral habitus, B. dorsal habitus, C. wings, D. lateral head, E. anterior head, F. dorsal head and thorax, G. scutellum and propodeum, H. lateral head and mesosoma, I. dorsal metasoma.

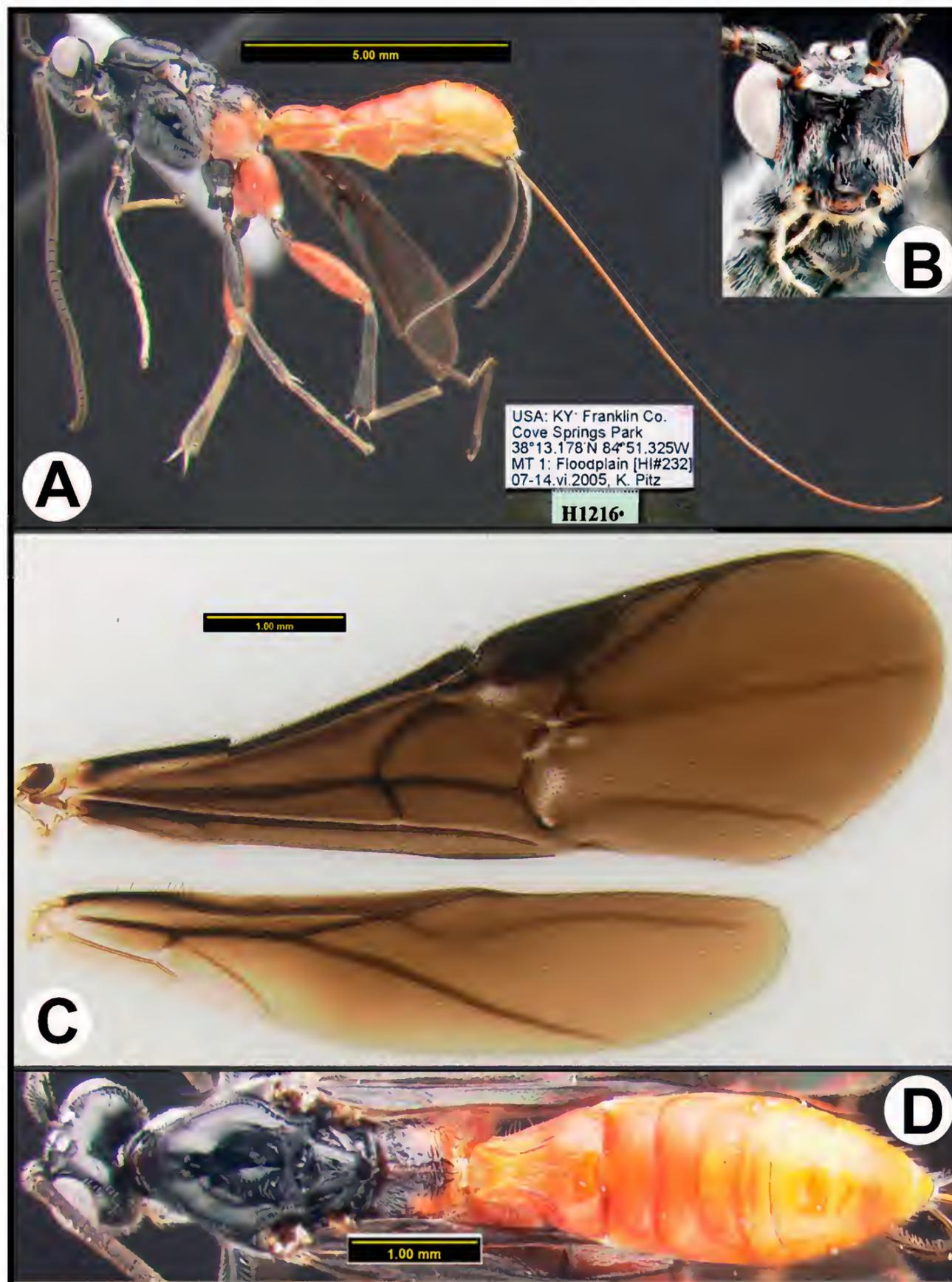


Figure 19 *Aerophilus erythrogaster*, fresh specimen: A. lateral habitus, B. anterior head, C. wings, D. dorsal habitus.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: West Virginia, Hardy Co., 3 mi N.E. Mathias, 38.9167°N, 78.8167°W, 8–25.vii.2005, Mal. trap, D.R. Smith (HIC, specimen H1267). For a map of the examined material see <http://bit.ly/1LZVuqB>.

Aerophilus difficilis (Muesebeck, 1927) n. comb.

Figure 17

Bassus difficilis Muesebeck, 1927:46. Other combinations: *Agathis*.

DIAGNOSIS. Cells of propodeum well defined; median syntergite 2+3 mostly smooth with striae in some transverse

depressions; middle lobe of mesoscutum bulging and elevated above lateral lobes (unlike *A. calcaratus*); antenna with more than 35 flagellomeres; mesoscutellum entirely melanic; hind femur pale (yellow to orange); hind trochanter mostly or entirely melanic; first metasomal median tergite mostly smooth.

DESCRIPTION. Length 7.7 mm. Ovipositor length 7.1 mm. Flagellomere number 38. Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.4. Notauli very well impressed with pits in anterior 1/3. Propodeum smooth with well-defined cells, some rugae in median cell and elsewhere. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite mostly smooth with weak rugose sculpture medially at mid-

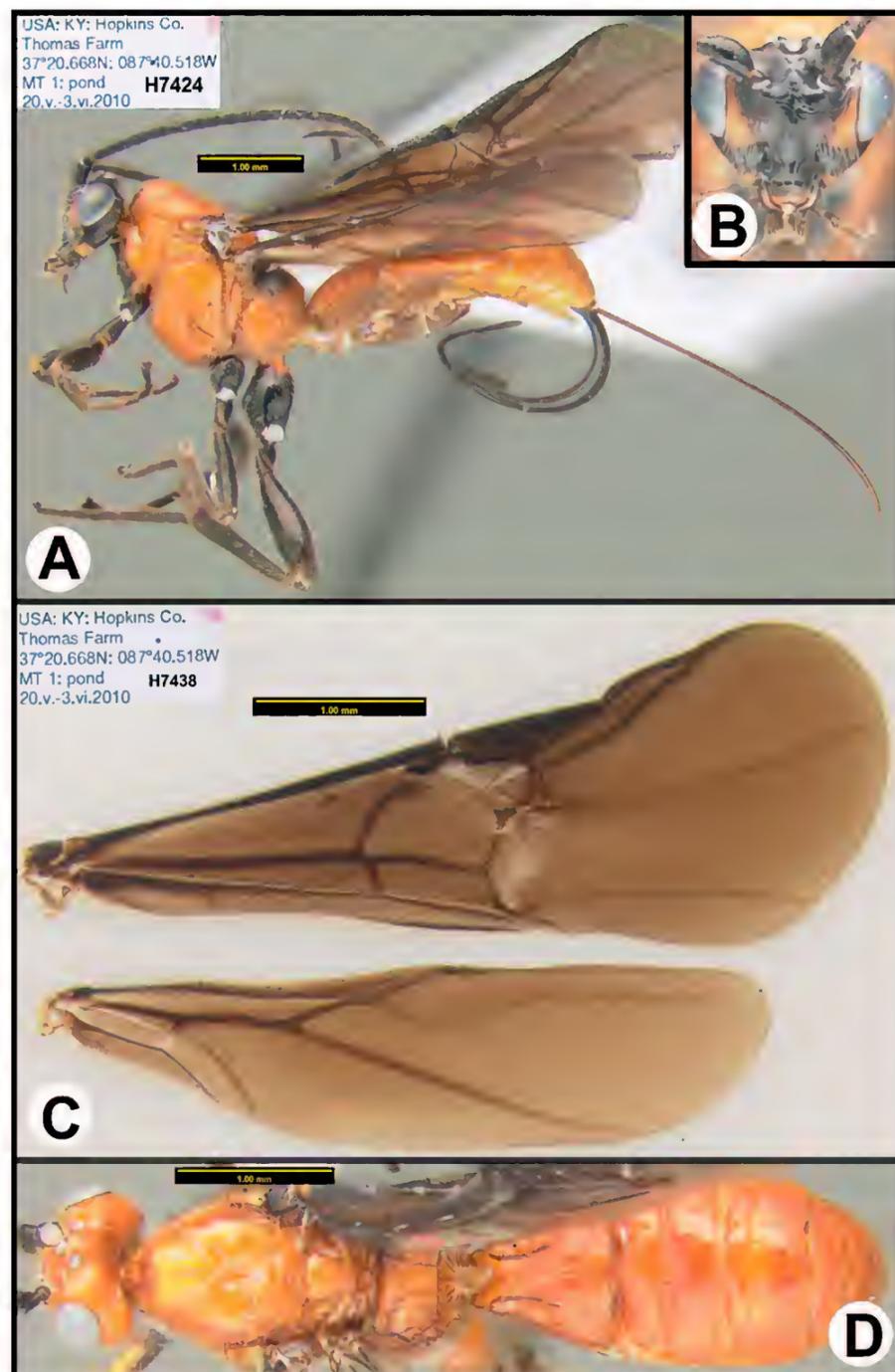


Figure 20 *Aerophilus hopkinsensis*, holotype: A. lateral habitus, B. anterior head, C. wings, D. dorsal habitus.

length; pair of carinae extending past midlength of tergite. Median syntergite 2+3 mostly smooth with striae in the three transverse depressions.

HOSTS. Blastobasidae: *Blastobasis repartella*. Coleophoridae: *Homaledra sabalella*. Pyralidae: *Acrobasis indigenella*, *Nephopterix crassifasciella*, *Nephopterix subcaesiella*, *Nephopterix uinella*.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Florida Palm Beach (USNM type 28686). Other material examined: Florida (HIC). Published state records: Arkansas, Florida, Georgia, Louisiana, North Carolina, South Dakota, Texas. Records, besides those from Florida, need confirmation. For a map of the examined material see <http://bit.ly/1Nb11z5>.

Aerophilus erythrogaster Viereck, 1913

Figures 18, 19

Bassus (*Aerophilopsis*) *erythrogaster* Viereck, 1913:555. Other combinations: *Agathis*, *Bassus* (*Lytopylus*).

SYNONYMS. *Bassus pini* Muesebeck, 1940:92. New Synonym.

DIAGNOSIS. Mesoscutellum entirely melanic; hind femur pale (yellow to orange); notauli weakly impressed; hind coxa in lateral view entirely pale; hind trochanter mostly or entirely melanic contrasting with pale coxa and femur; propodeal cells well defined.

DESCRIPTION. Length of male holotype 4.8 mm. Length of female (Fig. 17) 9.2 mm. Ovipositor length 11.8 mm. Flagellomere number (broken on holotype), 34 in female (Fig. 17). Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.3. Notauli well defined with pits in anterior 1/3. Propodeum smooth with well-defined cells, some rugae in median cell and elsewhere. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite mostly weakly striate; pair of carinae extending past midlength of tergite. Median syntergite 2+3 mostly smooth with striae in the three transverse depressions, striae prominent in first depression and weak in posterior two.

HOSTS. Tortricidae: *Epiblema strenuana*, *Rhyacionis comstockiana*.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Virginia, Vienna, 17.05.1911, R.A. Cushman (USNM type 15276). Holotype of *Bassus pini* Muesebeck, female: "Bred, July 10, 1937, Bar Harbor, Maine, Pars *Rhyacionis comstockiana*" (USNM type 54124). Other material examined: Kentucky (HIC). Distribution. Widespread in the eastern USA, from Maine south to Louisiana and west to Kansas. For a map of the examined material see <http://bit.ly/1OavgaP>.

Aerophilus hopkinsensis Sharkey n. sp.

Figure 20

DIAGNOSIS. Hind coxa in lateral view bicolored, melanic and pale; notauli well impressed; mesonotum entirely pale (orange); first metasomal median tergite about as long as posterior width.

DESCRIPTION. Length 5.9 mm. Ovipositor length 4.6 mm. Flagellomere number 31. Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.5. Notauli well impressed and lacking pits. Propodeum with a large median cell and irregular peripheral cells with irregular carinae. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite smooth with relatively widely spaced smooth longitudinal striae over 1/2 to 2/3 of surface; pair of carinae well developed and reaching slightly beyond midlength of tergite. Median syntergite 2+3 mostly smooth with longitudinal striae in the two anterior transverse depressions with a hint of striae in the third.

ETYMOLOGY. Named after the Kentucky county where the two known females were collected.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Kentucky, Hopkins Co., Thomas Farm, 37.34447°N, 87.6753°W, Malaise trap 1 near pond, 20.v-3.vi.2010 (HIC, specimen H7438). Paratype female, same data as holotype (specimen H7424). For a map of the examined material see <http://bit.ly/20dH8N2>.

Aerophilus jdherndoni Sharkey n. sp.

Figure 21

DIAGNOSIS. This species is quite variable in color. Face not elongate; propodeum sculptured but lacking distinct cells; notauli well impressed; first metasomal median tergite mostly striate; mesoscutellum entirely melanic; hind femur pale (yellow to orange).

DESCRIPTION. Length 3.7 mm. Ovipositor length 3.4 mm. Flagellomere number 26 (25-30). Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.5. Notauli

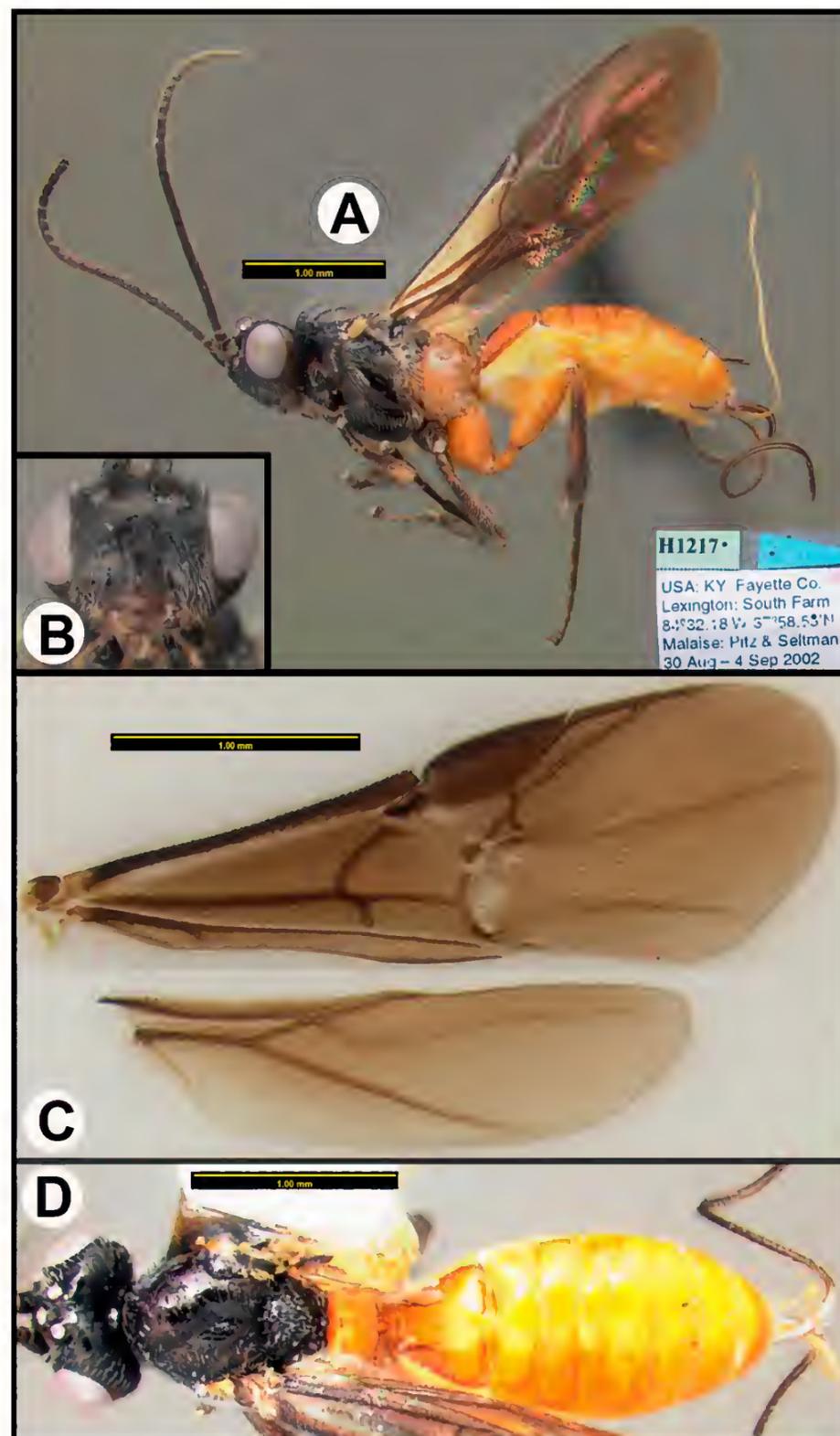


Figure 21 *Aerophilus jdherndoni*, holotype: A. lateral habitus, B. anterior head, C. wings, D. dorsal habitus.

well impressed without pits (or with up to three pits anteriorly). Propodeum with irregular cells broken with irregular carinae and rugae, smoother laterally. Forewing infuscate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite mostly smooth with several weak smooth striae at midlength, with pair of carinae extending to midlength. Median syntergite 2+3 mostly smooth except for all three transverse depressions with striae, weaker in posterior two depressions (sometimes striate anteromedially anterior to first transverse depression).

ETYMOLOGY. Named in honor of James (J.D.) Herndon, former undergraduate student in my (M.J.S.) insect taxonomy class and at whose farm most specimens of this species were captured.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Kentucky, Fayette Co., South Farm, 37.97217°N, 84.53633°W, 30.viii–4.ix.2002, Pitz and Seltmann, (HIC, specimen H1217). Paratypes. 42 females (no males.), Kentucky (39 females): Fayette, Jefferson, Owen, Hopkins, Harrison, and

Breathitt counties. Virginia (3 females): Fairfax and William counties. Paratypes from both states were mostly captured between August and October. Exceptions are two specimens from KY captured between late March and early May and one specimen from Virginia captured between April and May. Since Malaise traps were run from May to late October in these localities it seems likely that there are two generations or that the adults overwinter. The later hypothesis seems unlikely since this is not known for any other temperate species of *Aerophilus*. Specimens are deposited in HIC and UKIC. For a map of the type material see <http://bit.ly/1M00E6a>.

Aerophilus klastos Sharkey n. sp.

Figure 22

DIAGNOSIS. Face not elongate; notauli impressed and sculptured; first metasomal median tergite longer than wide

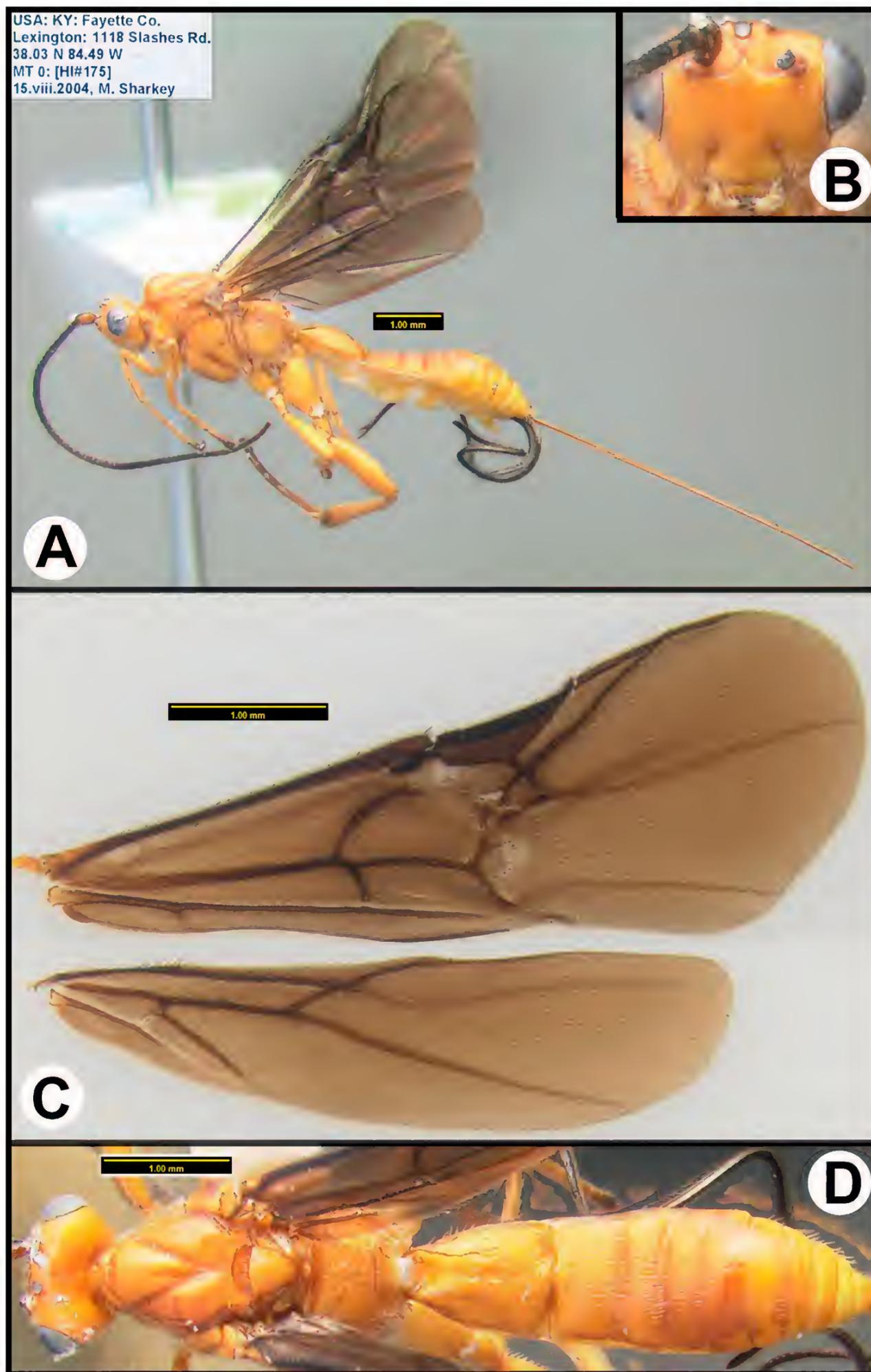


Figure 22 *Aerophilus klastos*, holotype: A. lateral habitus, B. anterior head, C. wings, D. dorsal habitus.

(posteriorly) and longitudinally rugosostriate; body almost entirely yellow except for flagellum and extremities of some legs; very similar to *A. abdominalis* but distinguished by characters given in the key and wings more infusate.

DESCRIPTION. Length 7.0 mm. Ovipositor length 6.5 mm. Flagellomere number undetermined (broken after 32 in the sole

specimen). Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.5. Notauli very deeply impressed and entirely pitted. Propodeum entirely rugose and lacking distinct cells. Forewing infusate. First metasomal median tergite clearly longer than posterior width. First median tergite entirely striate with some granulate microsculpture laterally; pair of

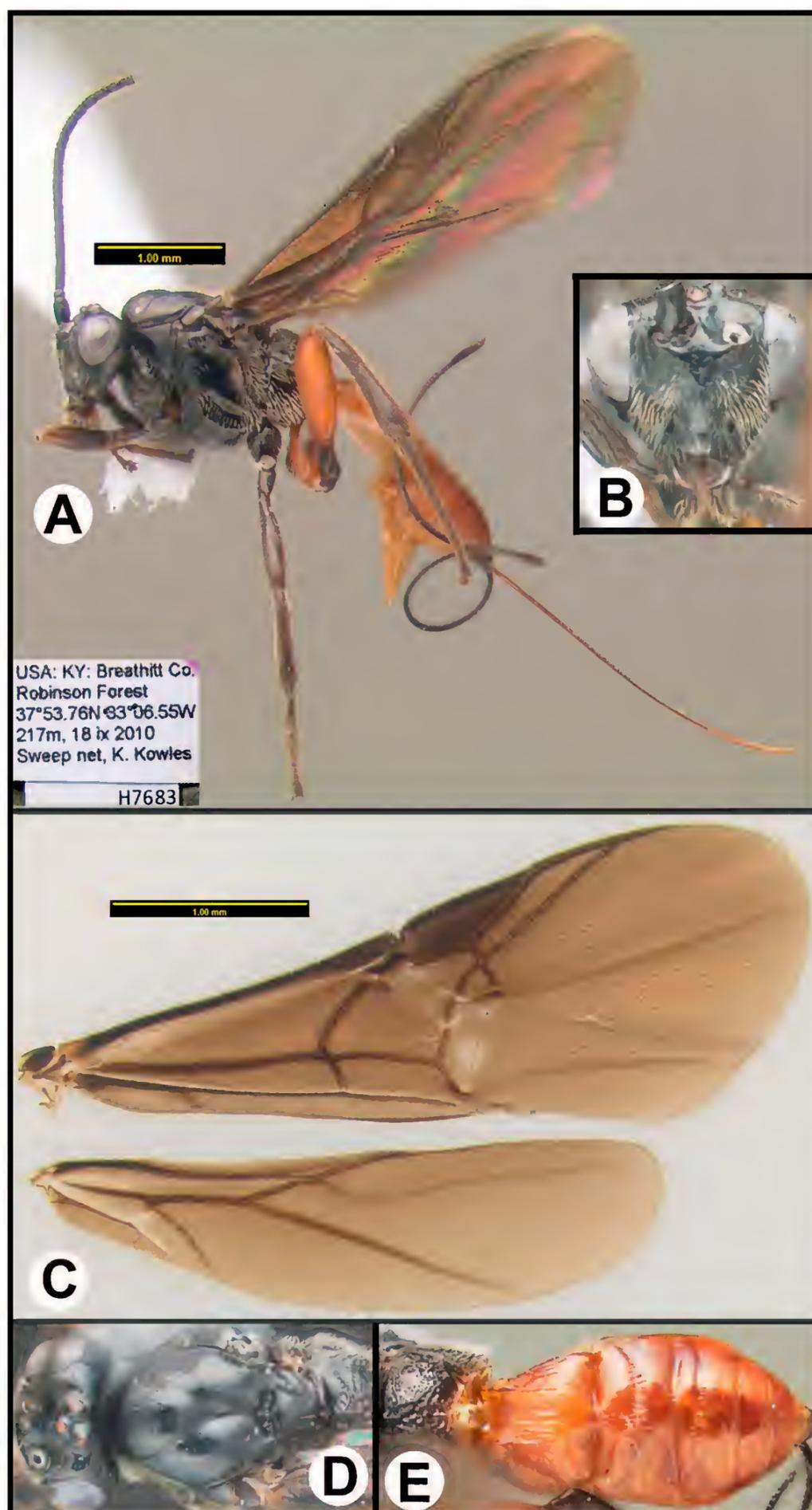


Figure 23 *Aerophilus kowlesae*, holotype: A. lateral habitus, B. anterior head, C. wings, D. dorsal head and thorax, E. dorsal propodeum and metasoma.

carinae reaching midlength of tergite. Median syntergite 2+3 longitudinally striate with some granulate microsculpture.

ETYMOLOGY. From the Greek word for “broken in pieces,” a reference to the condition of the holotype.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Kentucky, Fayette Co., Lexington, 38.05°N, 84.82°W, 15.viii.2004, [H#175] M. Sharkey (HIC, specimen H0205). For a map see <http://bit.ly/1P888YZ>.

Aerophilus kowlesae Sharkey n. sp.

Figure 23

DIAGNOSIS. Face slightly elongate; body of mesosoma and middle leg predominantly melanic; first median tergite predominantly striate.

DESCRIPTION. Length 4.1 mm. Ovipositor length 3.8 mm. Flagellomere number undetermined (broken on the only known

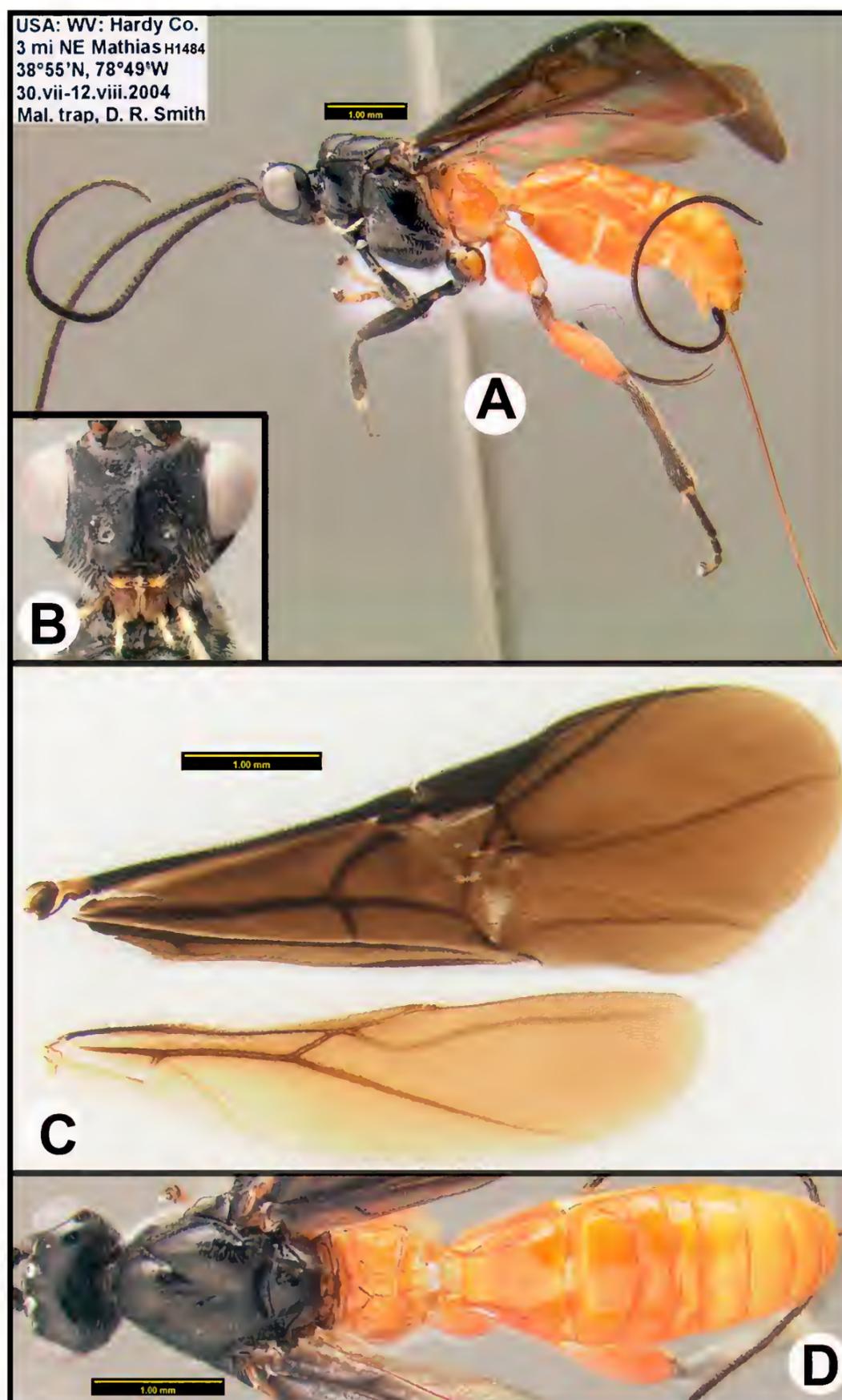


Figure 24 *Aerophilus malus*, holotype: A. lateral habitus, B. anterior head, C. wings, D. dorsal habitus.

specimen). Gena slightly elongate; ratio of length of malar space to eye height, viewed laterally, 0.6. Notauli absent anteriorly and posteriorly, or barely indicated there, well impressed at mid-length. Propodeum with irregular crenulae, smoother with punctures laterally, cells irregular and weakly indicated. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite mostly striate except posterior margin and anteromedial area, with pair of carinae extending past midlength. Median syntergite 2+3 smooth except transverse grooves striate.

ETYMOLOGY. Named in honor of Katelyn Kowles, former graduate student in the Department of Entomology at the University of Kentucky and collector of the type specimen.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Kentucky, Breathitt Co., 37.896°N, 83.10917°W, 217 m, 18.ix.2010, sweep net, K. Kowles (HIC, specimen H7683). For a map see <http://bit.ly/1imUtAw>.

Aerophilus malus Sharkey n. sp.

Figure 24

DIAGNOSIS. Very similar to *A. calcaratus*; the only character that may separate them is the number of flagellomeres; antenna with more than 35 flagellomeres; propodeum with distinct areolae; forefemur entirely melanic; mesoscutellum entirely

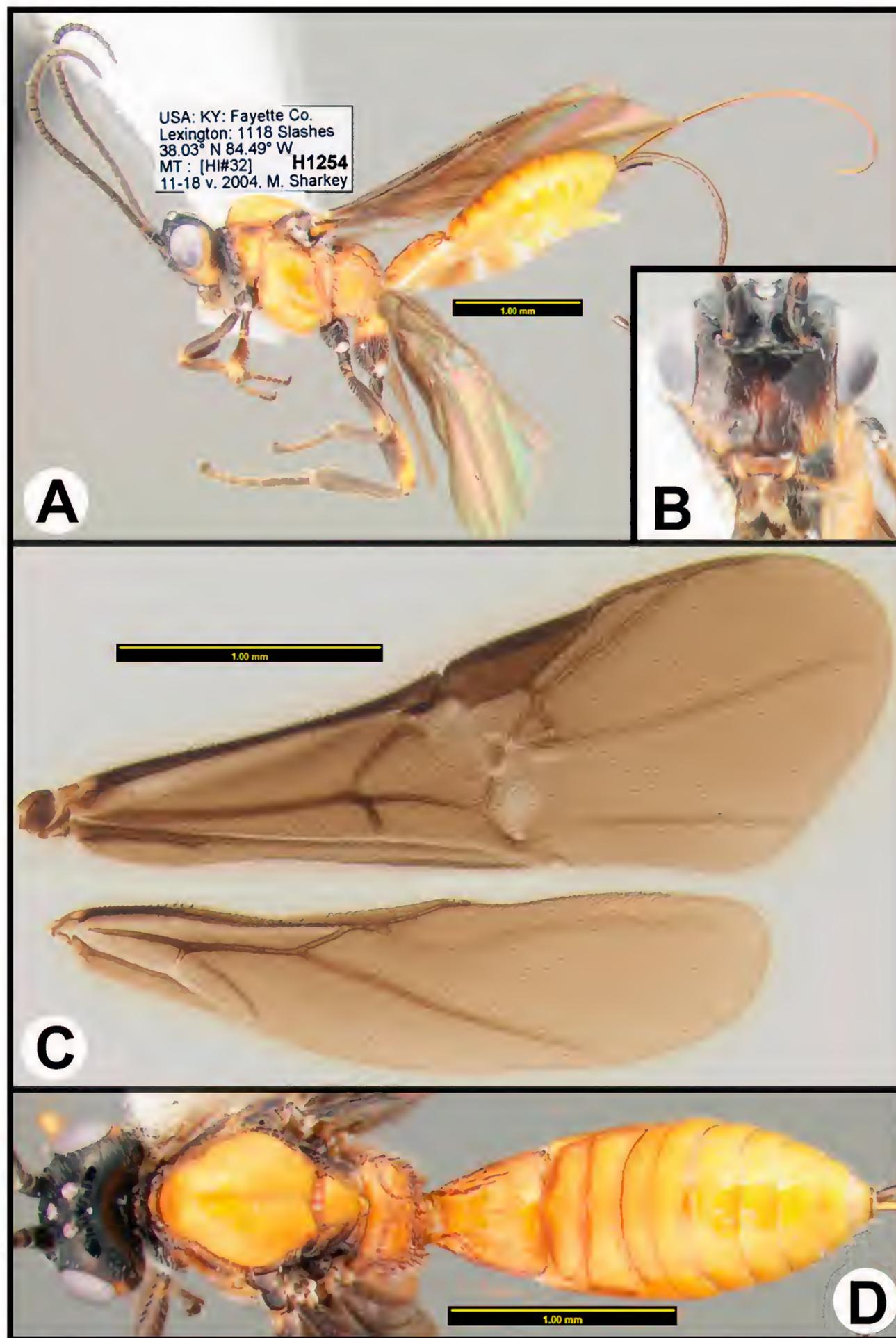


Figure 25 *Aerophilus minys*, holotype: A. lateral habitus, B. anterior head, C. wings, D. dorsal habitus.

melanic; hind femur pale; propodeum with distinct cells; middle lobe of mesoscutum not bulging and not elevated above lateral lobes.

DESCRIPTION. Length 6.5 mm. Ovipositor length 5.4 mm. Flagellomere number 36. Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.4. Notauli well impressed with pits in anterior 1/3. Propodeum smooth except for well-defined cells. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width.

First median tergite mostly smooth with weak longitudinal striae across midlength and laterally, pair of carinae extending past midlength of tergite and diverging posteriorly. Median syntergite 2+3 mostly smooth except for all three transverse depressions with striae, striae weaker in posterior two depressions.

ETYMOLOGY. From the Greek *malon*, meaning more. In this case a reference to the extra flagellomeres that (may) distinguish this species from the more common *A. calcaratus*.

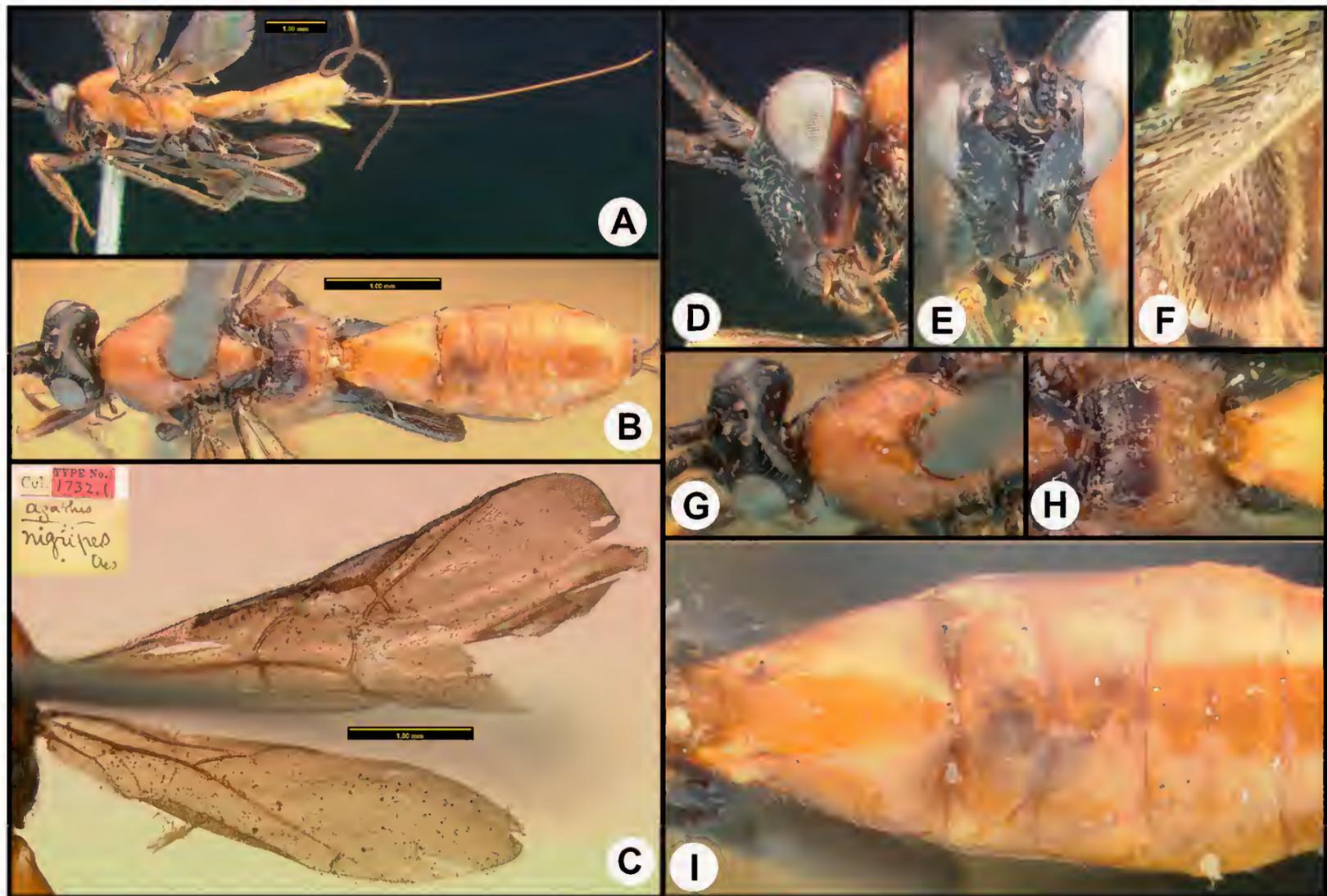


Figure 26 *Aerophilus nigripes*, holotype: A. lateral habitus, B. dorsal habitus, C. wings, D. lateral head. E. anterior head, F. apex of hind tibia, G. dorsal head and mesoscutum, H. propodeum, I. metasomal tergites 1–3.

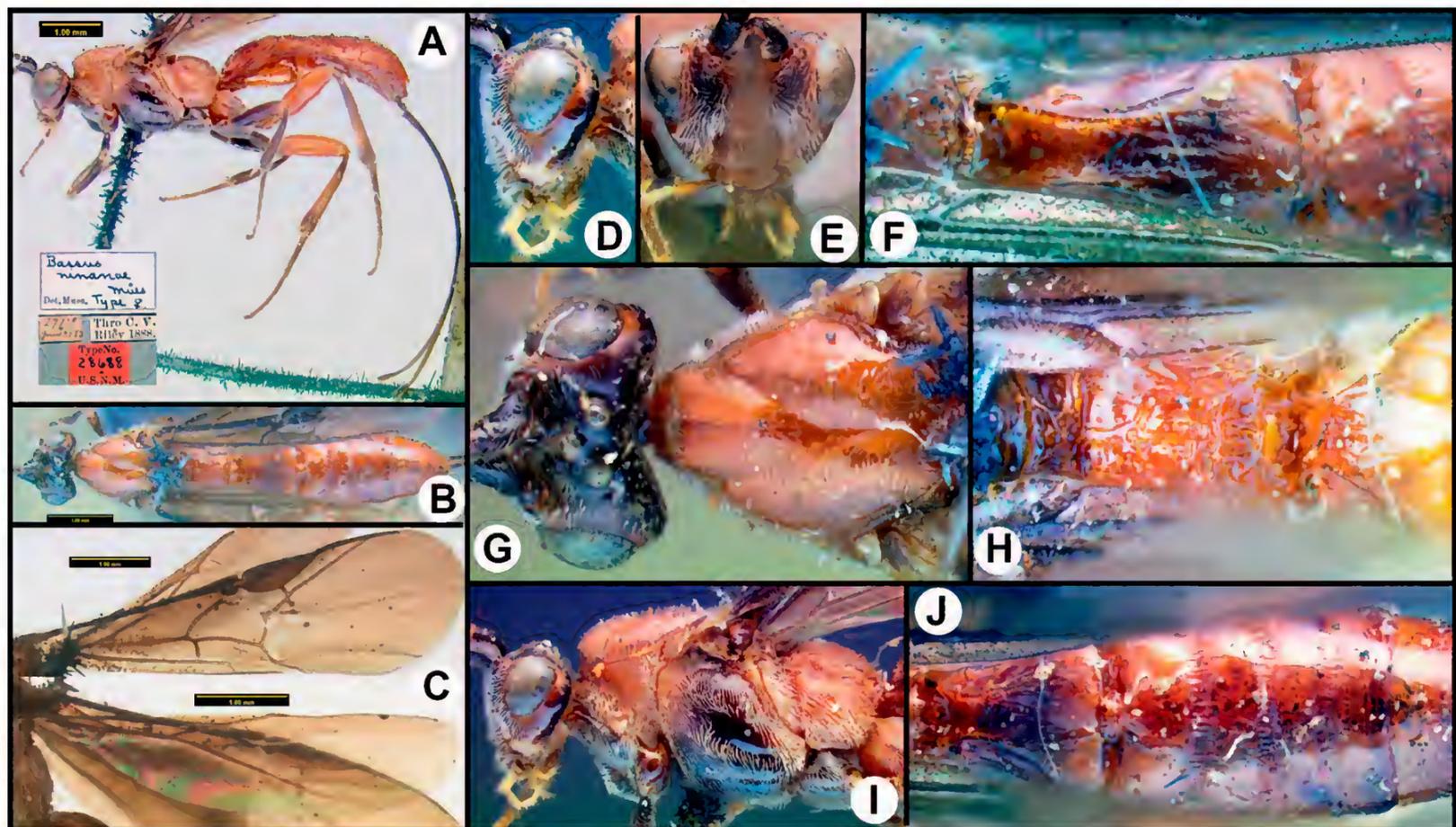


Figure 27 *Aerophilus ninanae*, holotype: A. lateral habitus, B. dorsal habitus, C. wings, D. lateral head, E. anterior head, F. tergites 1–2, G. dorsal head and mesoscutum, H. propodeum, I. lateral head and mesosoma, J. tergites 1–3.

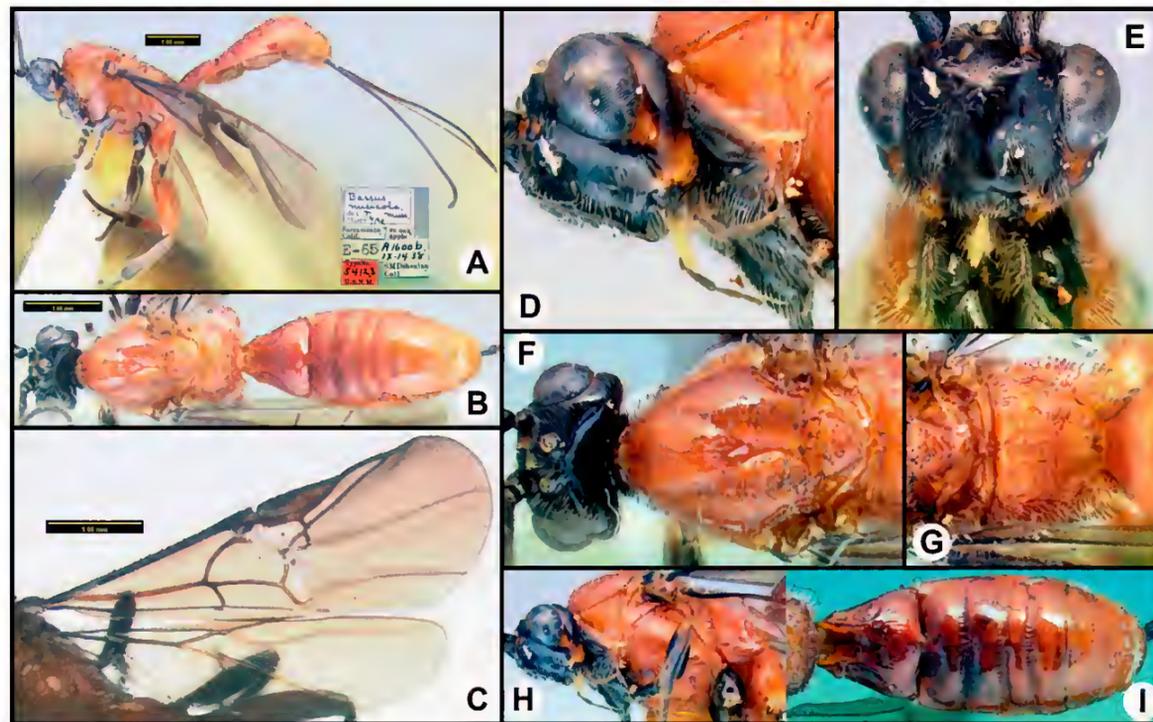


Figure 28 *Aerophilus nucicola*, holotype: A. lateral habitus, B. dorsal habitus, C. wings, D. lateral head, E. anterior head, F. dorsal head and thorax, G. propodeum, H. lateral head and mesosoma, I. dorsal metasoma.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: West Virginia, Hardy Co., 3 mi. N.E. Mathias, 38.9167°N, 78.8167°W, 30.vii–12.viii.2004, Mal. trap, D.R. Smith (HIC, specimen H1484). Paratype female. Same data as holotype except 26.vii–11.viii.2005 (HIC H1248). For a map of the examined material see <http://bit.ly/1LEFah5>.

Aerophilus minys Sharkey n. sp.

Figure 25

DIAGNOSIS. Similar to *A. buttricki* but distinguished by characters in the key; first metasomal median tergite mostly covered with longitudinal striae; mesoscutellum color mostly or entirely pale; mesonotum partly melanic, minimally melanic near wing sockets.

DESCRIPTION. Length 4.0 mm. Ovipositor length 3.7 mm. Flagellomere number 23 (22–26). Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.4. Notauli barely perceptible and lacking pits. Propodeum with carinae forming moderately regular cells, median cell with weak carinae. Forewing infuscate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite mostly striate with smooth widely spaced, shallow striae, smooth anteromedially and posteromedially; pair of carinae extending to midlength of tergite. Median syntergite 2+3 mostly smooth with longitudinal striae in the three transverse depressions and striate anteromedially, antiad first transverse depression.

ETYMOLOGY. From the Greek meaning small or short and referring to the size of specimens of this species.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Kentucky, Fayette Co., Lexington, 38.0667°N, 84.8167°W, 11–18.v.2004, M. Sharkey (HIC H1254). Paratypes: 39 specimens, 37 females, and 2 males. Kentucky, North Carolina, Tennessee, Virginia, West Virginia, May–August, all specimens deposited in HIC. For a map of the examined material see <http://bit.ly/1LEFegQ>.

Aerophilus nigripes (Cresson, 1865) n. comb.

Figure 26

Agathis nigripes Cresson, 1865:297. Other combinations: *Bassus*.

SYNONYMS. *Agathis nigriceps* Provancher, 1895:96 was synonymized by Muesebeck (1927) and is also recognized as a synonym here. *Agathis atripes* Cresson, 1865:296 n. syn.

DIAGNOSIS. Western species. Similar to *A. wyomingensis*, both of which have elongate faces. Unlike *A. wyomingensis*, *A. nigripes* has impressed notauli and has longer antenna with 32–34 flagellomeres, rather than the approximately 24 flagellomeres typical of *A. wyomingensis*. A number of undescribed western species further complicate the identity of both *A. nigripes* and *A. wyomingensis*.

DESCRIPTION. Length 5.3 mm. (5.0–7.2). Ovipositor length 6.9 mm. Flagellomere number undetermined (broken on type [32–33]). Gena elongate; ratio of length of malar space to eye height, viewed laterally, 0.7 (0.7–0.9). Notauli weakly impressed but distinct and lacking pits. Propodeum smooth posterolaterally, weakly rugose medially with weak smooth pits anteriorly, irregular median cell indicated (varying to almost entirely smooth with a narrow spindle-shaped median longitudinal cell). Forewing infuscate. First metasomal median tergite slightly longer than posterior width. First median tergite smooth with pair of carinae extending to midlength of tergite (or slightly past). Median syntergite 2+3 smooth, lacking microsculpture in transverse depressions (varying to mostly sculptured in transverse depressions).

HOSTS. Pyralidae: *Homoeosoma electellum*. Tortricidae: *Phaneta bucephaloides*.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Colorado (ANSP type 1732.1). Synonyms: *Agathis atripes* Cresson, holotype male, Colorado (ANSP type 1731). *Agathis nigriceps* Provancher lectotype female: Los Angeles, California, Coquillett [The collector, Coquillett, may have had a very broad concept of Los Angeles] (ULQC). Published state records: Since the identification of this species and its synonym *A. atripes* are problematic, the published distribution means little; however, the name is recorded from a wide area in the western USA with a smattering of records in the central and eastern USA and two from western Canada, Alberta and Manitoba. For a map of the examined material see <http://bit.ly/1RCRXID>.

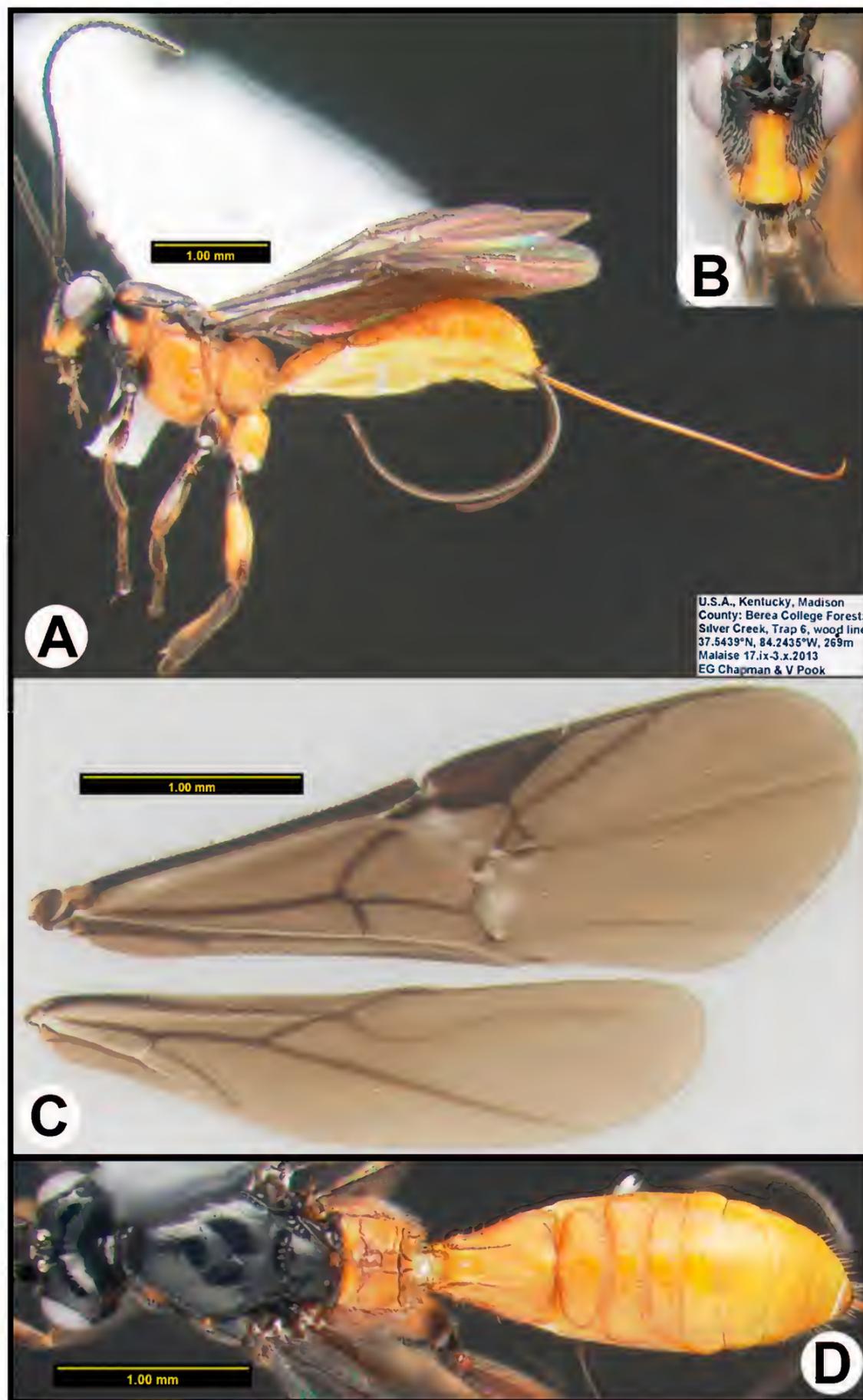


Figure 29 *Aerophilus perforator*: A. lateral habitus, B. anterior head, C. wings, D. dorsal habitus.

Aerophilus ninanae (Muesebeck, 1927) n. comb.

Figure 27

Bassus ninanae Muesebeck, 1927:48. Other combinations:
Agathis.

DIAGNOSIS. Mesoscutellum pale; hind coxa in lateral view bicolored, melanic and pale; notauli well impressed; face not elongate.

DESCRIPTION. Length 6.8 mm. Ovipositor length 6.5 mm. Flagellomere number 36. Gena not elongate; ratio of length of

malar space to eye height, viewed laterally, 0.5. Notauli well impressed and lacking pits. Propodeal cells complete but irregular and with internal rugae. Forewing infusate. First metasomal median tergite clearly longer than posterior width. First median tergite mostly weakly striate; pair of carinae extending past midlength of tergite. Median syntergite 2+3 mostly smooth with longitudinal striae in the three transverse depressions.

HOSTS. Tortricidae: *Cydia ninana*.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Arizona, Huachuca, 27.06.1983 (USNM type 28688).

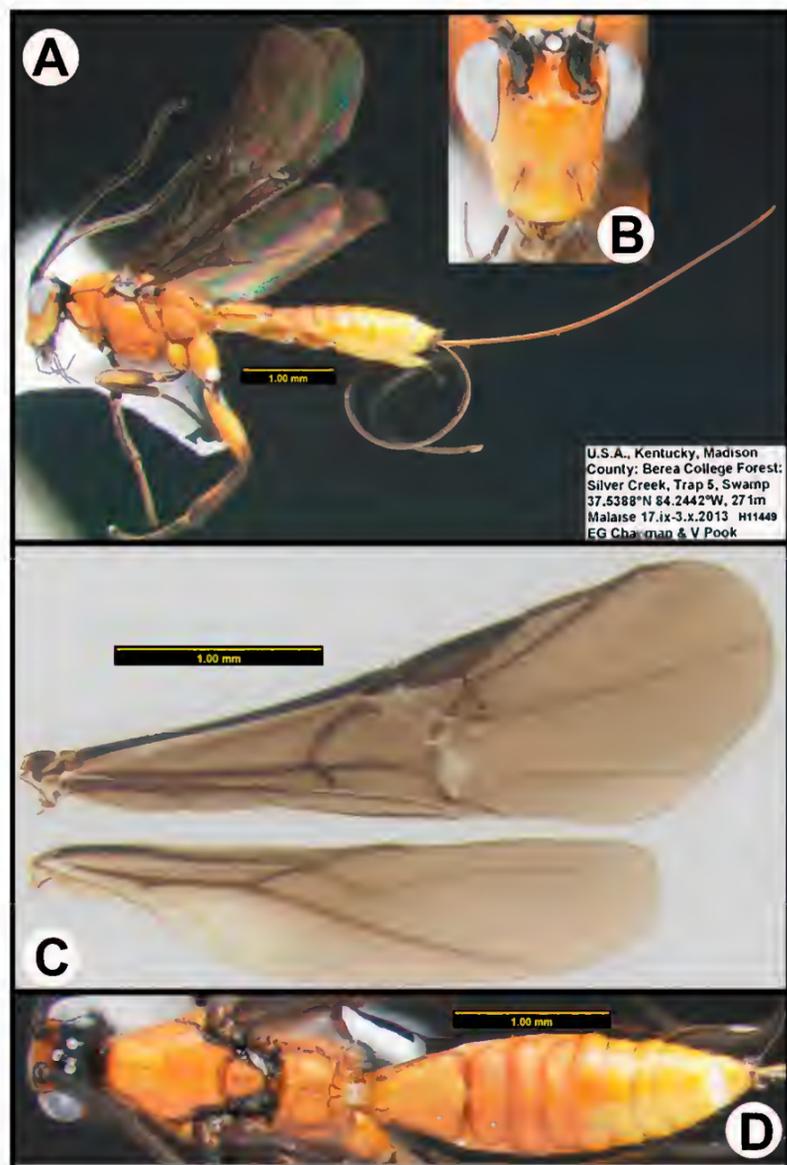


Figure 30 *Aerophilus pookae*, holotype: A. lateral habitus, B. anterior head, C. wings, D. dorsal habitus.

Published state records: Arizona, California. For a map of the examined material see <http://bit.ly/1WkbePz>.

Aerophilus nucicola (Muesebeck, 1940) n. comb.

Figure 28

Bassus nucicola Muesebeck, 1940:91. Other combinations: *Agathis*.

DIAGNOSIS. Notauli well impressed; mesoscutellum pale; hind coxa in lateral view entirely pale; head color mostly or entirely black, usually with some pale color on eye orbits or on gena; face not elongate.

DESCRIPTION. Length 6.3 mm. Ovipositor length 4.5 mm. Flagellomere number 33. Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.5. Notauli well impressed and lacking pits. Propodeal cells complete but irregular and with internal rugae. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite mostly smooth with a few striae posteriorly and laterally; pair of carinae extending past midlength of tergite. Median syntergite 2+3 mostly smooth with longitudinal striae in the three transverse depressions.

HOSTS. Tortricidae: *Cydia latiferreana* (from oak apple gall on *Quercus lobate*).

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: California, Sacramento, ex. oak apple, 14.ix.1938, S.M.

Dohanian (USNM type 54123). Published state records: California. For a map of the examined material see <http://bit.ly/1OawtyW>.

Aerophilus perforator (Provancher, 1880) n. comb.

Figure 29

Microdus perforator Provancher, 1880:177. Other combinations: *Agathis*, *Bassus*, *Therophilus*.

SYNONYMS. *Bracon* (*Agathis*) *femorator* Provancher, 1880:177. *Bracon* (*Agathis*) *branfordensis* Viereck, 1917:230. *Bracon* (*Agathis*) *sassicus* Viereck, 1917:230.

DIAGNOSIS. The smallest of those species with elongate faces, much smaller than the other species (*A. wyomingensis*, *A. nigripes*, *A. bakeri*, and *A. crassicornis*), a maximum of 4.1 mm versus a minimum of 5 mm. This is the most common and widespread eastern species.

DESCRIPTION. Length 4.1 mm. Ovipositor length 3.2 mm. Flagellomere number 25–29 (holotype not available). Gena elongate; ratio of length of malar space to eye height, viewed laterally, 0.7. Notauli barely perceptible or weakly impressed. Propodeum with distinct cells, median cell narrow, some rugae in median cell and elsewhere. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite finely striate except extreme base; pair of longitudinal carinae extending past midlength of tergite. Median syntergite 2+3 mostly finely striate except posterior half of tergite 3 smooth.

MATERIAL EXAMINED AND DISTRIBUTION. Lectotype female not examined: Canada, (probably southern Quebec) (ULQC). Synonyms: *Agathis femorator* Provancher, lectotype female, not examined: Canada, (probably southern Quebec) (ULQC). *Bracon* (*Agathis*) *branfordensis* Viereck, holotype male, Branford, Connecticut, 16.09.1904, H.W. Winkley (USNM type 66248). *Bracon* (*Agathis*) *sassicus* Viereck, holotype female, Stafford, Connecticut, 24.viii.1905, W.E. Britton (USNM type 66247). Other material examined: Kentucky (HIC). Published state records: Widespread in the eastern USA and Canada, west to South Dakota and Alberta. For a map of the examined material see <http://bit.ly/20dIII2>.

Aerophilus pookae Sharkey n. sp.

Figure 30

DIAGNOSIS. Face elongate; second median tergite completely striate in raised areas; head color mostly pale, black dorsally.

DESCRIPTION. Length 4.5 mm. Ovipositor length 4.8 mm. Flagellomere number 24. Gena elongate; ratio of length of malar space to eye height, viewed laterally, 0.7. Notauli barely perceptible and lacking pits. Propodeum rather neatly divided into cells with a few rugosities and some weak granulate microsculpture. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite entirely rugosostriate with weak short pair of carinae not extending past midlength of tergite. Median syntergite 2+3 rugosostriate except for posterior-most elevated area.

ETYMOLOGY. Named in honor of Victoria Pook, former student in the Department of Entomology, University of Kentucky.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Kentucky, Madison Co., Berea College Forest, Silver Creek, swamp, 37.5388°N, 84.2442°W, 17.ix–3.x.2013, E.G. Chapman and V. Pook (HIC, specimen H11449). For a map see <http://bit.ly/1NbcoXI>.

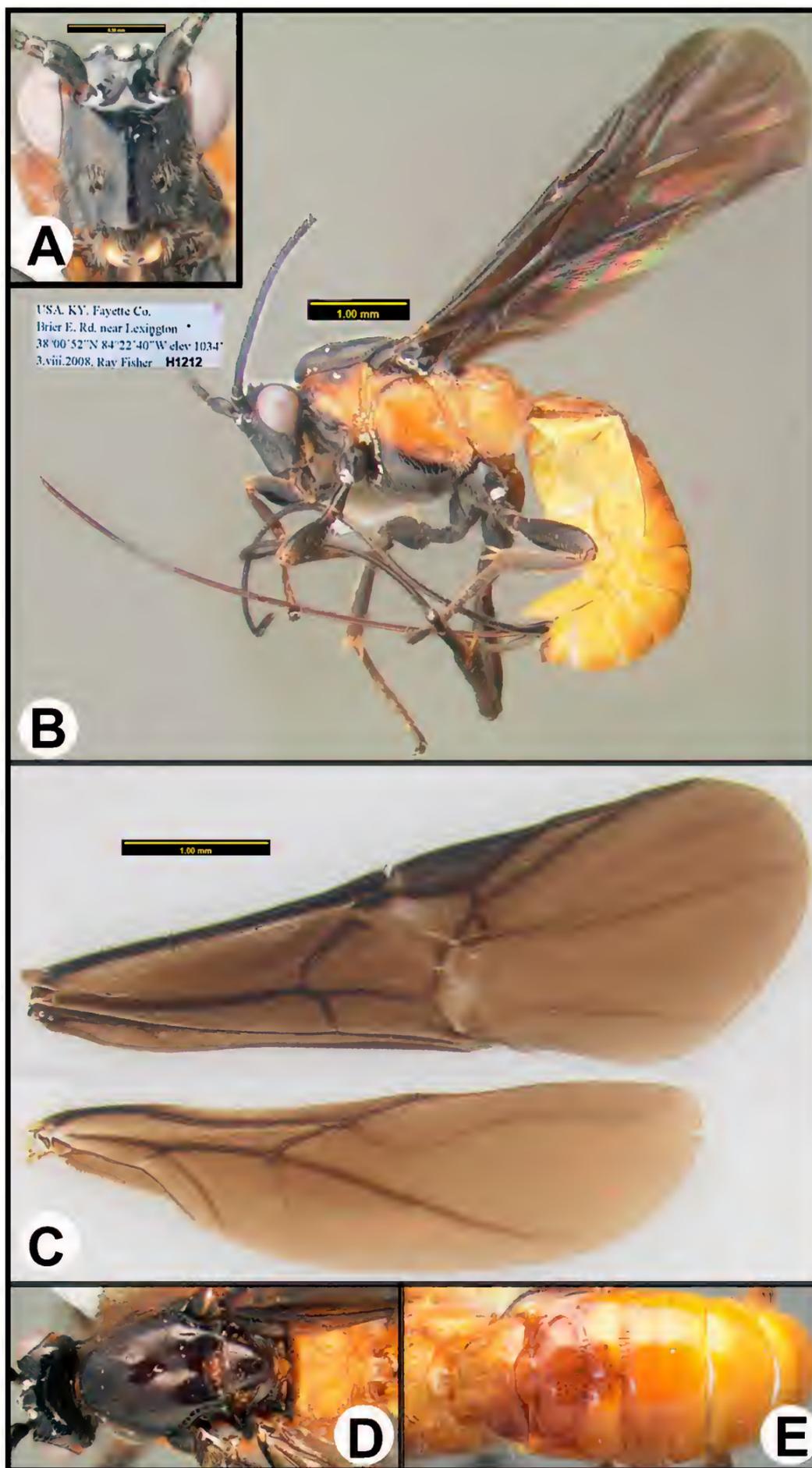


Figure 31 *Aerophilus rayfisheri*, holotype: A. anterior head, B. lateral habitus, C. wings, D. dorsal head and mesosoma, E. dorsal metasoma.

Aerophilus rayfisheri Sharkey n. sp.

Figure 31

DIAGNOSIS. Face elongate; propodeum areolated; notauli barely perceptible; similar to *A. wyomingensis* and *A. nigripes* but propodeum more sculptured, gena not as elongate, first metasomal median tergite wider.

DESCRIPTION. Length 6.7 mm. Ovipositor length 6.9 mm. Flagellomere number undetermined (both the holotype and sole

paratype have incomplete antennae). Gena elongate; ratio of length of malar space to eye height, viewed laterally, 0.7. Notauli barely perceptible and lacking pits. Propodeum mostly roughly sculptured with irregular cells, median cell well defined. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite entirely smooth with pair of carinae very pronounced and extending past midlength of tergite. Median syntergite 2+3 mostly smooth with some striae medially in anterior two transverse depressions.



Figure 32 *Aerophilus reginae*, holotype: A. lateral habitus, B. anterior head, C. wings, D. dorsal habitus.

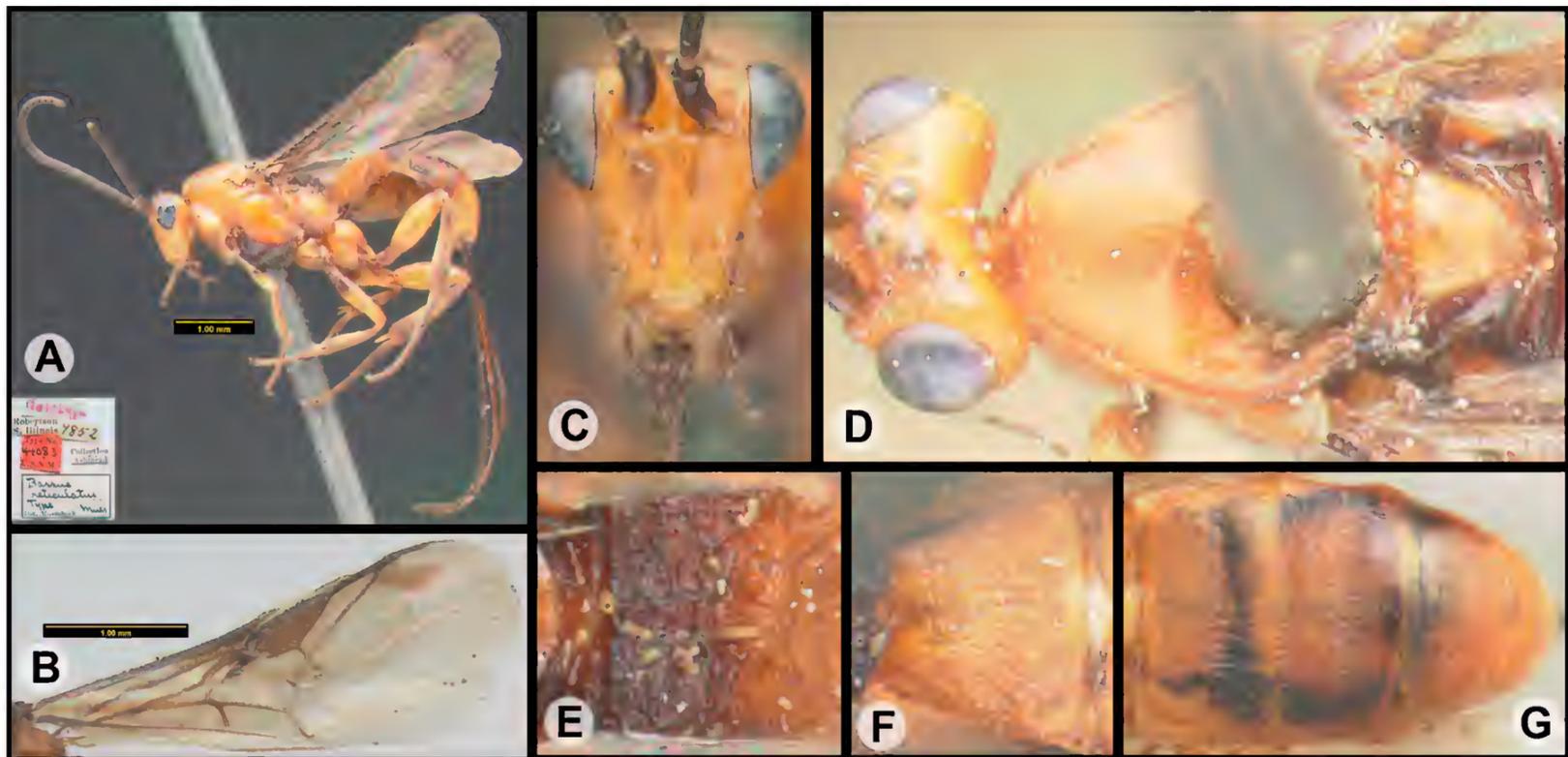
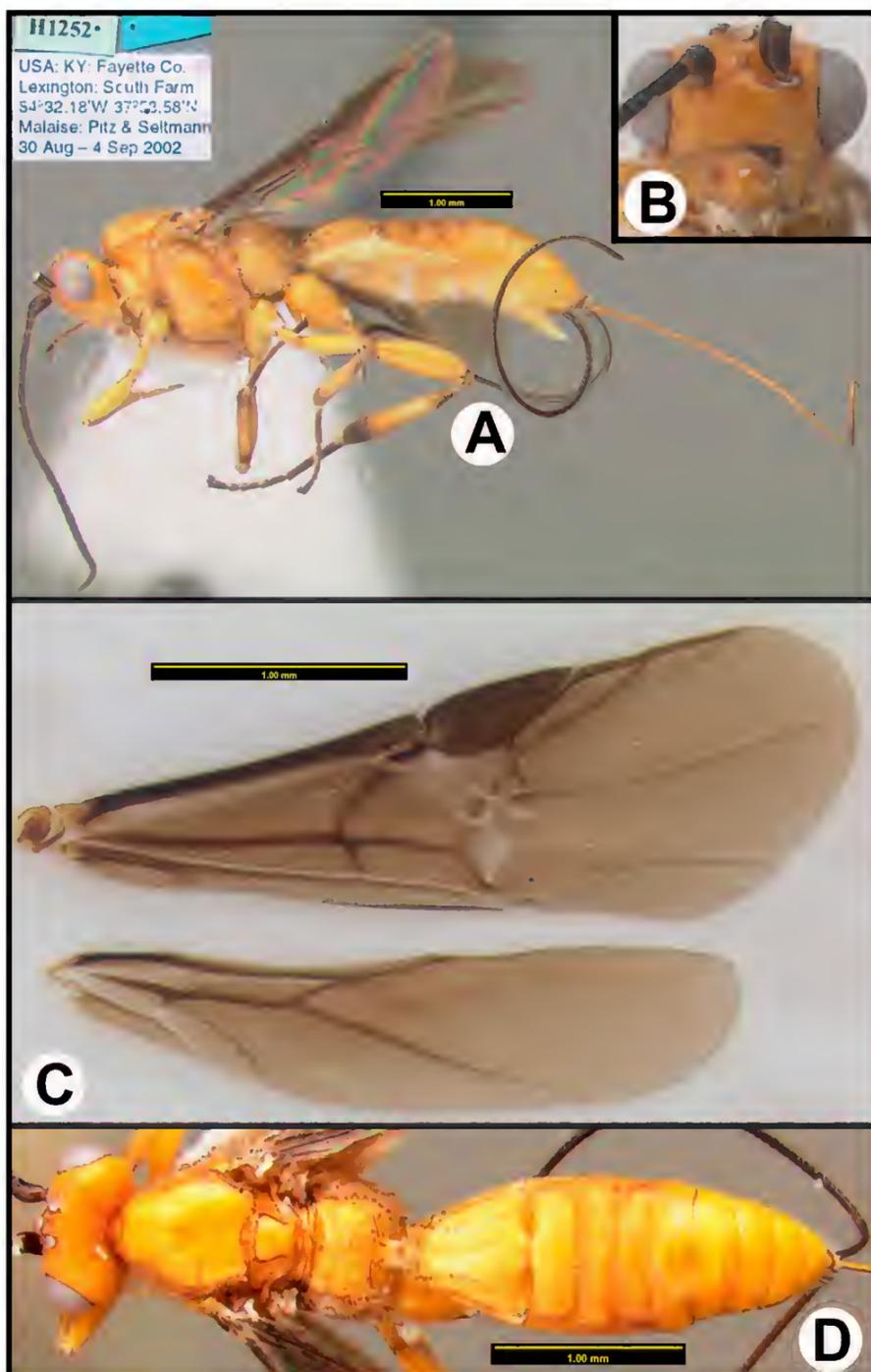


Figure 33 *Aerophilus reticulatus*, holotype: A. lateral habitus, B. wings, C. anterior head, D. dorsal head and thorax, E. propodeum, F. tergite 1, G. posterior tergites, tergites 2–7.



ETYMOLOGY. Named in honor of Ray Fisher, former graduate student of M.J.S. and collector of the type specimen.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Kentucky, Fayette Co., Lexington, Brier E Rd., 38.00867°N, 84.38778°W, 3.viii.2008, Ray Fisher, (HIC H1212). Paratype female: North Dakota, Ransom Co., 7 mi SE Sheldon, 23.vii.1995, J.R. Powers (CISC, specimen H4922). For a map of the examined material see <http://bit.ly/1kWe7Fj>.

Aerophilus reginae Sharkey n. sp.

Figure 32

DIAGNOSIS. Face not elongate; wings hyaline; face yellow, occiput mostly melanic; first metasomal median tergite predominantly melanic; syntergite 2+3 partly to entirely yellow or tan colored with some more posterior terga partly or entirely melanic.

DESCRIPTION. Length 4.4 mm. Ovipositor length 5.5 mm. Flagellomere number 29 (28–29). Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.3. Notauli barely perceptible. Propodeum with distinct cells, median cell narrow, some rugae in median cell and elsewhere. Forewing hyaline. First metasomal median tergite clearly longer than posterior width. First median tergite weakly rugosostriate over much of surface, smooth posterolaterally; pair of longitudinal carinae weak and extending to midlength of tergite. Median syntergite 2+3 mostly smooth with longitudinal striae in the three transverse depressions.

HOSTS. Gelechiidae: *Coleotechnites apictripunctella*, *Coleotechnites gibsonella*.

ETYMOLOGY. Named in honor of the junior author's (G.I.d.C.) mother, Regina.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Kentucky, Harlan Co., Blanton Forest N.P., 36.86370°N,

←

Figure 34 *Aerophilus robertcourtneyi*, holotype: A. lateral habitus, B. anterior head, C. wings, D. dorsal habitus.

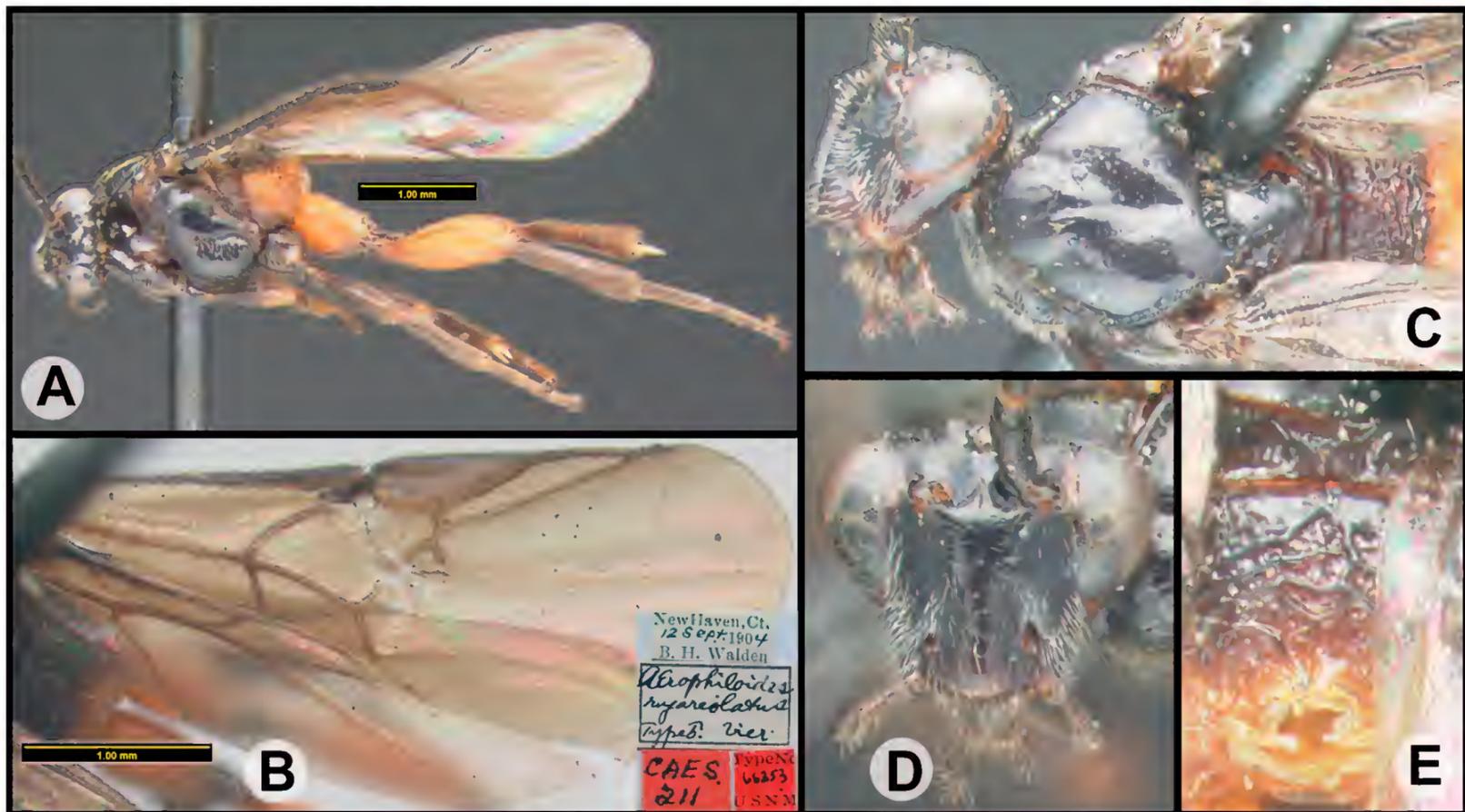


Figure 35 *Aerophilus rugareolatus*, holotype: A. lateral habitus, B. wings, C. lateral head and dorsal mesosoma, D. anterior head, E. propodeum.

83.36998°W, 25.iv–5.vii.2007, 1,476 ft. [450 m.], (HIC H1280). Paratypes: 58 specimens, 36 females, 22 males. Canada: Ontario, Quebec, New Brunswick. USA: New York, Kentucky, North Carolina, Florida. Late April to late August. All paratypes except one from Kentucky are deposited in the CNC. For a map of the examined material see <http://bit.ly/1NDUvnJ>.

Aerophilus reticulatus (Muesebeck, 1932) n. comb.

Figure 33

Bassus reticulatus Muesebeck, 1932:332. Other combinations: *Agathis*.

DIAGNOSIS. Forefemur pale in apical 2/3, melanic in basal 1/3; raised areas of metasomal median syntergite 2+3 longitudinally striogranulate or granulate; propodeum areolate rugose with some granulae.

DESCRIPTION. Length 4.7 mm. Ovipositor length 5.1 mm. Flagellomere number 20, contrary to the Muesebeck's (1932) description, which states 21 segments, indicating 19 flagellomeres (two female paratypes with 18 flagellomeres). Gena elongate; ratio of length of malar space to eye height, viewed laterally, 1.1. Notauli absent and lacking pits. Propodeum entirely rugosoreticulate with a deep irregular median longitudinal cell/depression. Forewing infuscate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite almost entirely rugosogranulate with a hint of irregular longitudinal striation; pair of carinae short and blunt. Median syntergite 2+3 entirely sculptured except for smooth posterior margin; sculptured mostly with granulate microstriae, striae deeper and more pronounced in transverse depressions.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female, Illinois (southern), C. Robertson (USNM type 44083). Published state records: Illinois, Kansas, Missouri. For a map see <http://bit.ly/1M01boK>.

Aerophilus robertcourtneyi Sharkey n. sp.

Figure 34

DIAGNOSIS. Face slightly elongate; head color entirely pale, orange to yellow; hind femur entirely pale; similar to *A. abdominalis* and *A. klastos* but differs from those species in the smooth, barely perceptible notauli.

DESCRIPTION. Length 4.4 mm. Ovipositor length 4.0 mm. Flagellomere number 26 (26–27). Gena slightly elongate; ratio of length of malar space to eye height, viewed laterally, 0.6. Notauli barely perceptible and lacking pits. Propodeum with distinct cells, cells are filled with smooth rugae. Forewing infuscate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite entirely striate; pair of carinae weak and almost reaching midlength of tergite. Median syntergite 2+3 longitudinally striate except extreme apex smooth.

ETYMOLOGY. Named in honor of Mr. Robert Courtney, owner of the horse farm where the paratype was collected.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Kentucky, Fayette Co., South Farm, 37.9755°N, 84.53633°W, 30.viii–4.ix.2002, Pitz and Seltmann, (HIC, specimen H1252). Paratype female, Kentucky, Fayette Co., Stonebridge Horse Farm, 38.00467°N, 84.36817°W, 21.ix–8.x.2012 (HIC, specimen H10026). For a map of the examined material see <http://bit.ly/1jUQsFa>.

Aerophilus rugareolatus (Viereck, 1917) n. comb.

Figure 35

Bassus (*Lytopylus*) *rugareolatus* Viereck, 1917:228. Other combinations: *Agathis*.

DIAGNOSIS. Gena intermediate in length; hind femur entirely pale; head color mostly or entirely black, with some pale color on eye orbits or on gena; propodeum areolate rugose; metasoma entirely pale (according to Viereck, 1917).

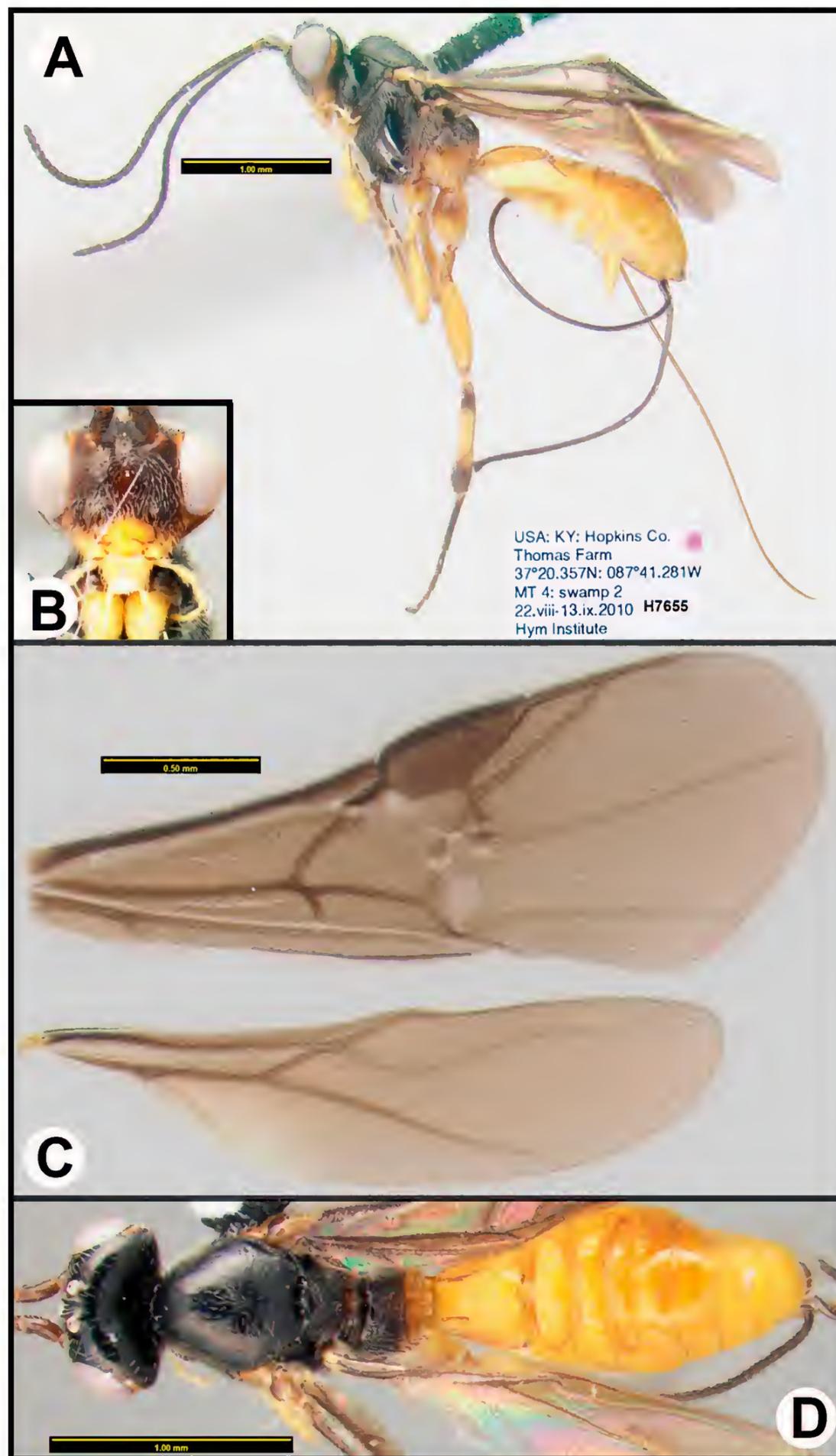


Figure 36 *Aerophilus stoelbae*, holotype: A. lateral habitus, B. anterior head, C. wings, D. dorsal habitus.

DESCRIPTION. Length 4.8 mm. Ovipositor length unknown, the sole known specimen is the holotype male. Flagellomere number unknown. Gena slightly elongate; ratio of length of malar space to eye height, viewed laterally, 0.6. Notauli very weakly impressed and lacking pits. Propodeum entirely rugoso-reticulate with an irregular median cell. Forewing infusate. Metasoma missing from holotype.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype male, Connecticut, New Haven, 12.09.1904, B.H. Walden

(USNM type 66253). Published state records: Connecticut. For a map of the examined material see <http://bit.ly/1imWNHB>.

Aerophilus stoelbae Sharkey n. sp.

Figure 36

DIAGNOSIS. Small specimens 3.2–3.4 mm.; antenna with 22–24 flagellomeres; notauli barely impressed; metasomal median tergites 1–3 often mostly striate.

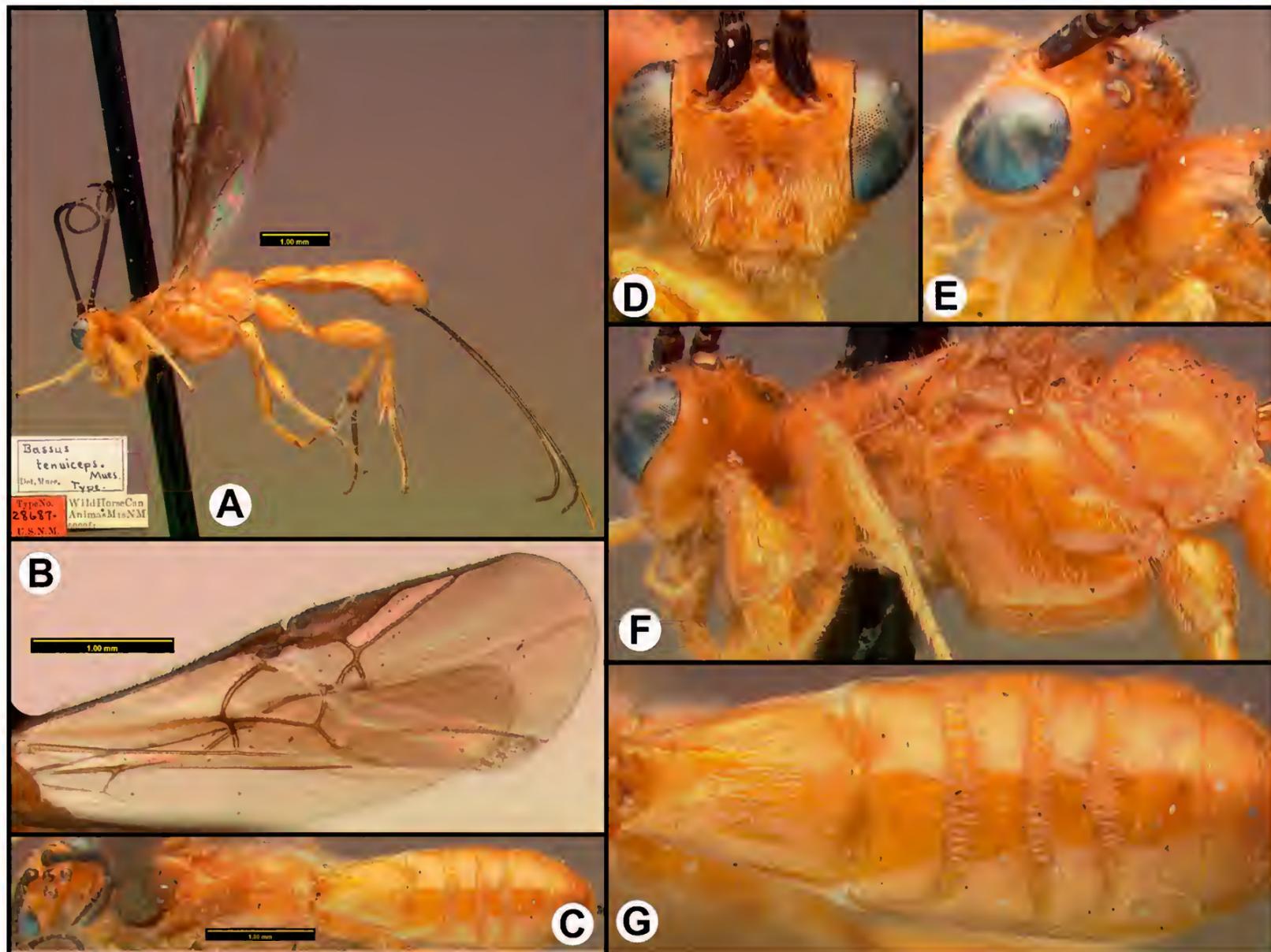


Figure 37 *Aerophilus tenuiceps*, holotype: A. lateral habitus, B. wings, C. dorsal habitus, D. anterior head, E. dorsolateral head, F. lateral head and mesosoma, G. dorsal metasoma.

DESCRIPTION. Length 3.2 mm (3.2–3.4). Ovipositor length 3.0 mm (3.0–3.2). Flagellomere number 22 (22–24). Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.5 (0.4–0.5). Notauli barely perceptible and lacking pits. Propodeum with carinae forming moderately regular cells, median cell with weak carinae. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite with weak shallow striae over half of surface (varying to entirely striate), smoother antero- and posteromedially; pair of longitudinal carinae extending to midlength of tergite (or slightly past). Median syntergite 2+3 mostly smooth with longitudinal striae in the three transverse depressions and with weak smooth striae in anterior lobe of median tergite 2; sometimes striate anteromedially, antierad first transverse depression and on first raised area (varying to entirely striate except posterior lobe of median tergite 3).

ETYMOLOGY. Named in honor of Stephanie Stoelb, former technician extraordinaire in the Department of Entomology, University of Kentucky.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Kentucky, Hopkins Co., Thomas Farm, 37.33928°N, 87.68802°W, 22.viii–13.ix.2010, MT 4: swamp 2 (HIC H7655). Paratypes: 4 females, Kentucky, Breathitt Co., Robertson forest, 17–18.ix.2010, 37.7883°N, 83.23833°W, (HIC 11799, 6502, 6695). For a map of the examined material see <http://bit.ly/1P89enA>.

Aerophilus tenuiceps (Muesebeck, 1927) n. comb.

Figure 37

Bassus tenuiceps Muesebeck, 1927:47. Other combinations: *Agathis*.

DIAGNOSIS. Head, metasoma, and body of mesosoma entirely pale; notauli weakly impressed, barely perceptible; second median tergite smooth in raised areas.

DESCRIPTION. Length 5.7 mm. Ovipositor length 4.9 mm. Flagellomere number 32. Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.4. Notauli barely perceptible or weakly impressed. Propodeum with irregular cells, smooth weak rugae in cells. Forewing hyaline. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite weakly striate over much of surface, smooth posterolaterally; pair of carinae weak and extending to midlength of tergite. Median syntergite 2+3 mostly smooth with longitudinal striae in the three transverse depressions.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: New Mexico, Wild Horse Canyon, Animas Mts. 5,000 ft. [1524 m] (USNM type 28687). Published state records: Arizona, New Mexico. For a map of the examined material see <http://bit.ly/1XCkImp>.

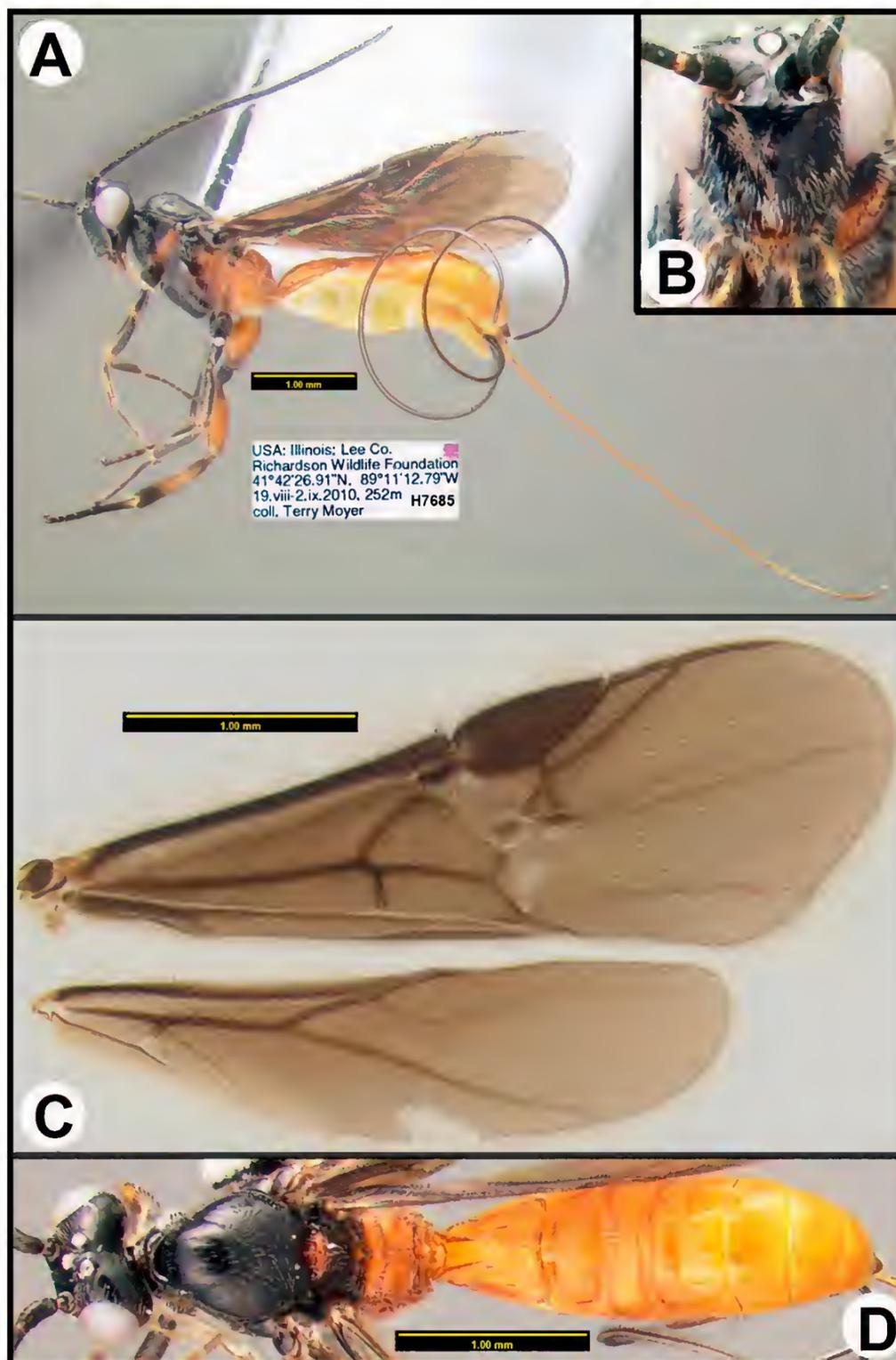


Figure 38 *Aerophilus terrymoyeri*, holotype: A. lateral habitus, B. anterior head, C. wings, D. dorsal habitus.

Aerophilus terrymoyeri Sharkey n. sp.

Figure 38

DIAGNOSIS. Second median tergite completely striate in raised areas; gena slightly elongate.

DESCRIPTION. Length 4.6 mm. Ovipositor length 5.5 mm. Flagellomere number 30 (28–30). Gena slightly elongate; ratio of length of malar space to eye height, viewed laterally, 0.6. Notauli weakly impressed and lacking pits. Propodeum mostly smooth with well-defined cells, median cell with some rugae. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite entirely striate except anteromedially between longitudinal carinae; pair of longitudinal carinae extending to midlength of tergite. Median syntergite 2+3 longitudinally striate except posterior half of tergite 3 smooth.

ETYMOLOGY. Named in honor of Terry Moyer, manager of The Richardson Wildlife Foundation Reserve.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Illinois, Lee Co., Richardson Wildlife Foundation, 41.70748°N, 89.18689°W, 19.viii–2.ix.2010, 252 m, coll. Terry Moyer (HIC, specimen H7685). Paratype female, same data as holotype except 2–15.ix.2010 (HIC, specimen H7550). For a map of the examined material see <http://bit.ly/1Ml2oWL>.

Aerophilus tommurrayi Sharkey n. sp.

Figure 39

DIAGNOSIS. Face moderately elongate; head, body of mesosoma, and all coxae melanic; first metasomal median tergite entirely striate.

DESCRIPTION. Length 4.4 mm. Ovipositor length unknown, the sole known specimen is the holotype male. Flagellomere number 28. Gena elongate; ratio of length of malar space to eye height, viewed laterally, 0.7. Notauli well impressed with pits in anterior 1/3. Propodeum with irregular cells broken by irregular carinae and rugae. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width.

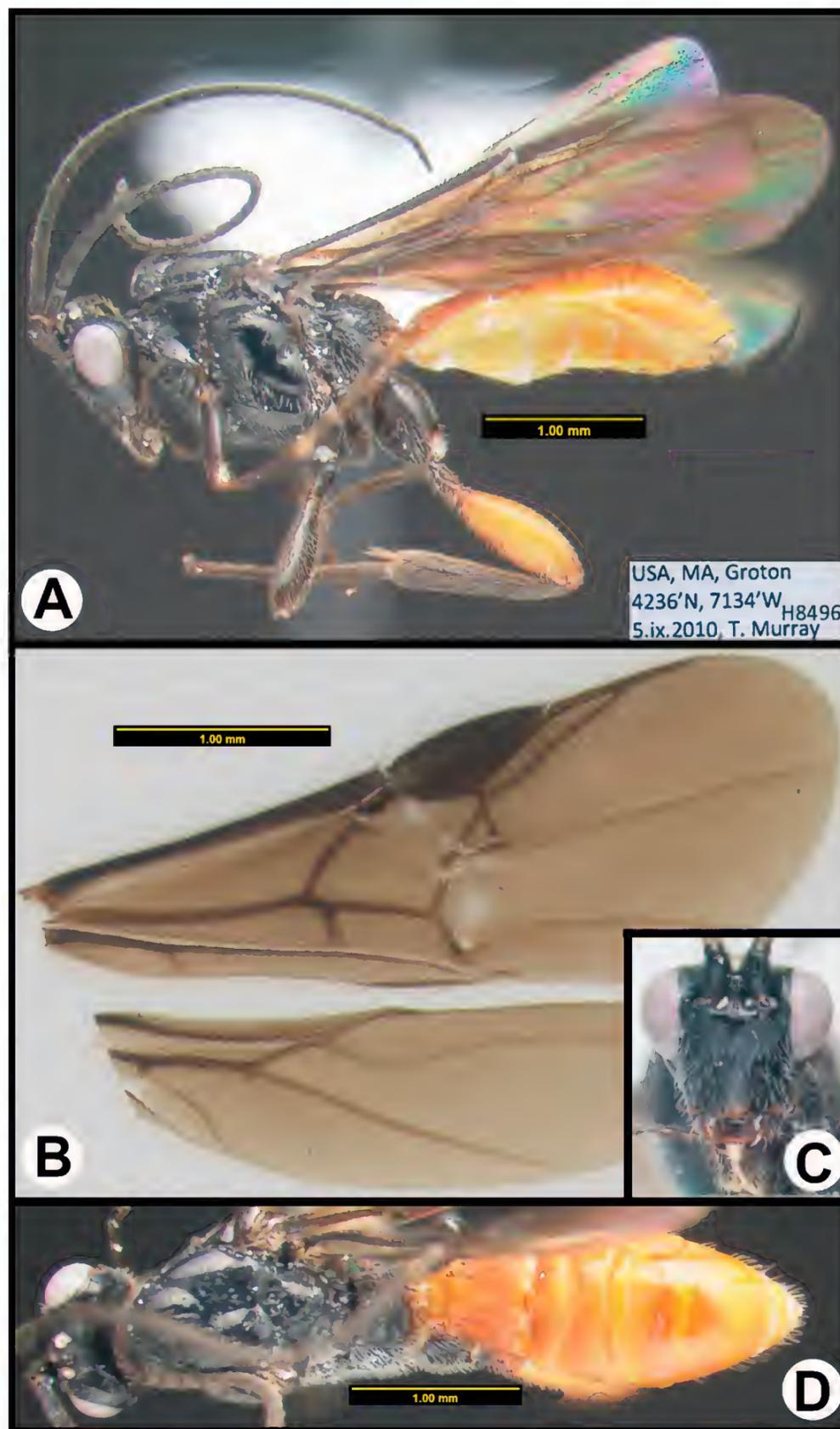


Figure 39 *Aerophilus tommurrayi*, holotype: A. lateral habitus, B. wings, C. anterior head, D. dorsal habitus.

First median tergite entirely striate with pair of weak carinae not extending past midlength of tergite. Median syntergite 2+3 with all transverse depressions and anterior-most elevated area striate.

ETYMOLOGY. Named in honor of the collector of the type specimen.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Massachusetts, Groton, 42.60°N, 71.5667°W, 5.ix.2010, T. Murray (HIC, specimen H8496). For a map see <http://bit.ly/1imXnFs>.

Aerophilus usitatus (Gahan, 1919) n. comb.

Figure 40

Bassus tenuiceps Gahan, 1919:119. Other combinations:
Agathis.

DIAGNOSIS. Propodeum entirely pale; transverse grooves of syntergite 2+3 all smooth; notauli with crenulae/pits in anterior 1/2 or more; first metasomal median tergite smooth except for pair of carinae; forefemur almost entirely melanic with a pale patch apically.

DESCRIPTION. Length 4.7 mm. Ovipositor length 3.5 mm. Flagellomere number undetermined (broken after flagellomere 14). Gena not elongate; ratio of length of malar space to eye height, viewed laterally, 0.2. Notauli well impressed with pits in anterior 1/2. Propodeum smooth with well-defined cells. Forewing infuscate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite smooth; pair of carinae extending past

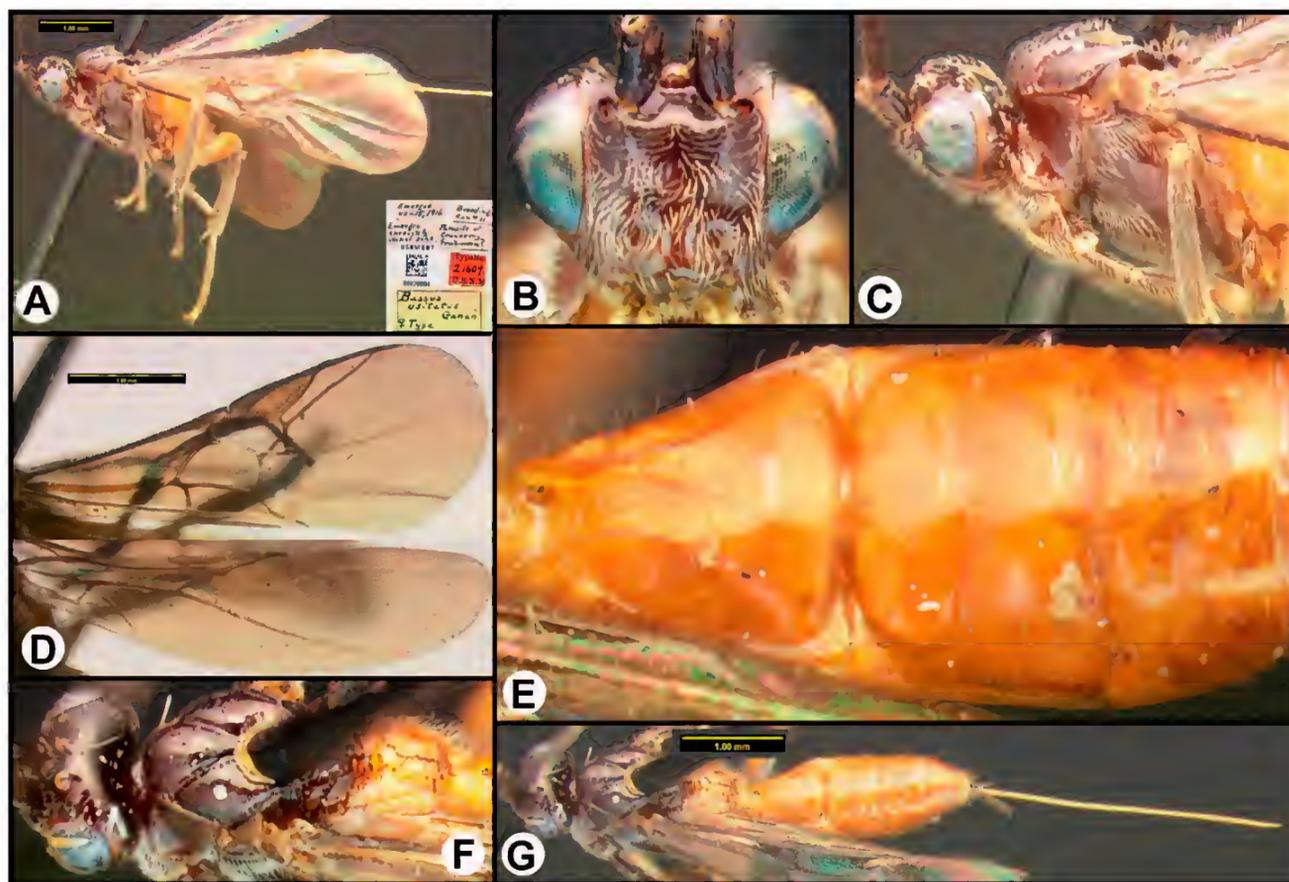


Figure 40 *Aerophilus usitatus*, holotype: A. lateral habitus, B. anterior head, C. lateral head and thorax, D. wings, E. tergites 1–3, F. dorsal head and mesosoma, G. dorsal habitus.

midlength of tergite. Median syntergite 2+3 smooth, transverse depressions lacking striae.

HOSTS. Pyralidae: *Acrobasis vaccinii*.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Massachusetts, East Wareham, 15.vii.1916, parasite of cranberry fruit-worm [sic] (USNM type 21609). Published state records: Massachusetts, Michigan. For a map of the examined material see <http://bit.ly/1Nbdfrn>.

Aerophilus wyomingensis (Viereck, 1905) n. comb.

Figure 41

Agathis wyomingensis Viereck, 1905:284. Other combinations: *Bassus*.

SYNONYMS. Synonymized under *Agathis nigripes* Cresson, 1865:297 by Muesebeck (1927) but reinstated here.

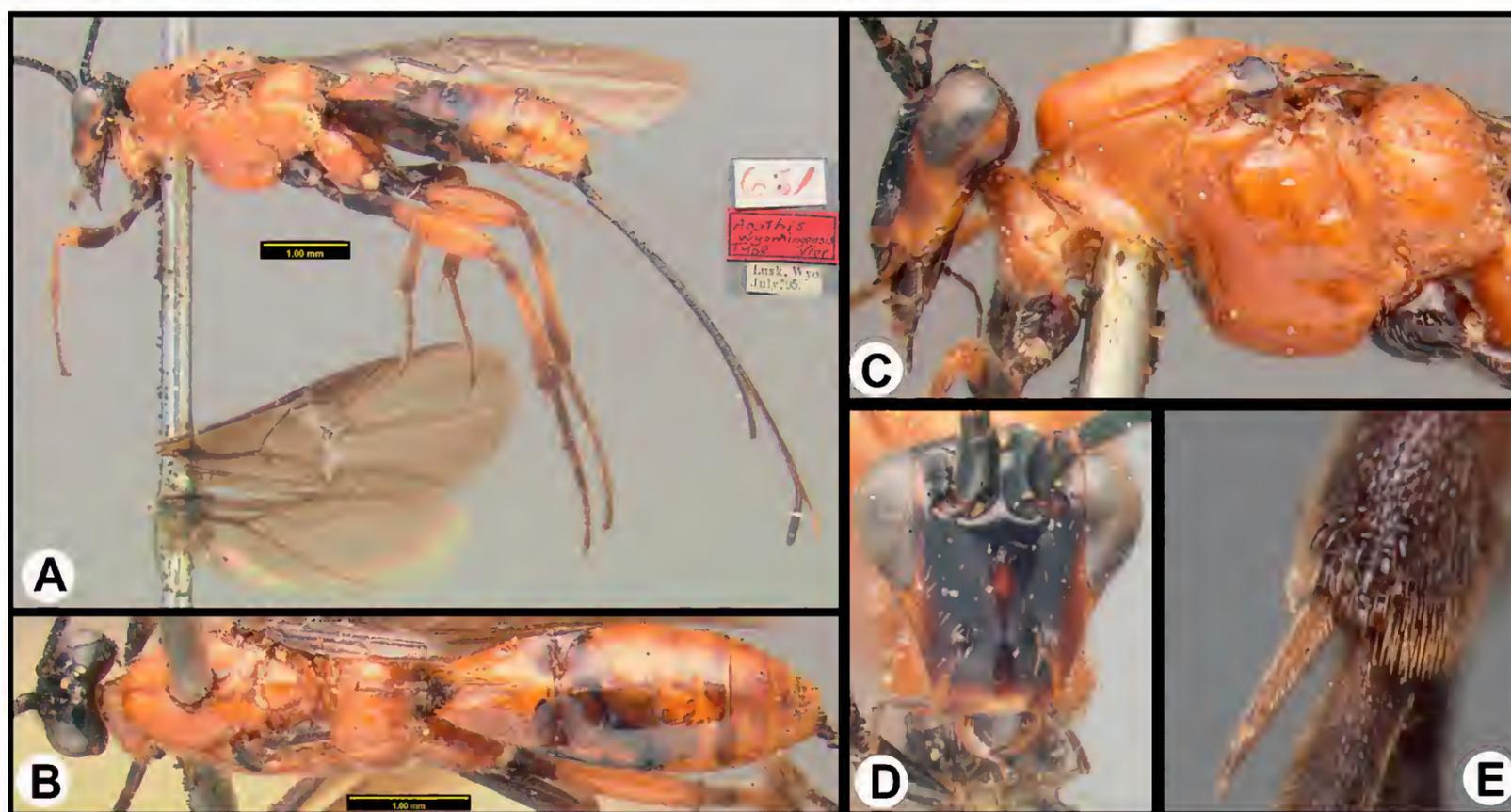


Figure 41 *Aerophilus wyomingensis*, holotype: A. lateral habitus and wings, B. dorsal habitus, C. lateral head and mesosoma, D. anterior head, E. apex of hind tibia.

DIAGNOSIS. Western species. Similar to *A. nigripes* both of which have elongate faces. Unlike *A. nigripes*, *A. wyomingensis* lacks notauli and has shorter antennae with an average of 24 flagellomeres, rather than the 32–34 flagellomeres typical of *A. nigripes*. A number of undescribed western species further complicate the identity of both *A. nigripes* and *A. wyomingensis*.

DESCRIPTION. Length 6.5 mm. Ovipositor length 6.0 mm. Flagellomere number (24–25) broken on holotype. Gena elongate; ratio of length of malar space to eye height, viewed laterally, 0.8. Notauli barely indicated (to completely absent) and lacking pits. Propodeum mostly smooth with a narrow spindle-shaped median longitudinal cell. Forewing infusate. First metasomal median tergite about as long as, or slightly longer than, posterior width. First median tergite smooth with carinae extending to midlength of tergite. Median syntergite 2+3 smooth, lacking microsculpture in transverse depressions.

HOSTS. Due to some historic confusion over the identity of this species the two hosts (*Homoeosoma electellum* and *Phaneta bucephaloides*) attributed to *A. nigripes* may rather be hosts of *A. wyomingensis*.

MATERIAL EXAMINED AND DISTRIBUTION. Holotype female: Wyoming, Lusk, vii.1895 (SEMC). Published state records: Wyoming. For a map of the examined material see <http://bit.ly/1jURNM0>.

ACKNOWLEDGMENTS

We thank the collectors of all of the specimens employed in this revision, especially David Smith, who has been sharing Malaise trap residues for many years. This project was made possible in part by the support of Southwest Collections of Arthropods Network (SCAN) NSF EF 1207371. Funding for this research was provided by Hatch projects KY008041 and KY008065 (to M.J.S.). The information reported in this paper (15-08-127) is part of a project of the Kentucky Agricultural Experiment Station and is published with the approval of the Director. We also thank Dominique Zimmermann for the translation of some German text; Dicky Yu for help with literature; Brian Brown, Paul Hanson, and an anonymous reviewer for comments on a draft; Doug Yanega for lessons on the Code of Zoological nomenclature; and Kees van Achterberg for advice.

LITERATURE CITED

- Allen, H.W., and W.P. Yetter. 1949. *Bassus diversus*, an oriental fruit moth parasite established in the United States. *Journal of Economic Entomology* 42(3):540.
- Ashmead, W.H. 1889. Descriptions of new Braconidae in the collection of the U.S. National Museum. *Proceedings of the United States National Museum* 11(1888):611–671.
- Belshaw, R., and D. Quicke. 1997. A molecular phylogeny of the Aphidiinae (Hymenoptera: Braconidae). *Molecular Phylogenetics and Evolution* 7(3):281–293.
- Brullé, M.A. 1846. Tome Quatrième. Des Hyménoptères. Les Ichneumonides. In: Lepeletier de Saint-Fargeau A. Histoire Naturelles des Insectes. Paris. 680 pp. pp. 56–521.
- Cresson, E.T. 1865. Catalogue of Hymenoptera in the collection of the Entomological Society of Philadelphia, from Colorado Territory. *Proceedings of the Entomological Society of Philadelphia* 4: 242–313.
- Cresson, E.T. 1873. Descriptions of North American Hymenoptera, No. 5. *Canadian Entomologist* 5:51–54.
- Cushman, R.A. 1920. North American Ichneumon-flies, new and described, with taxonomic and nomenclatorial notes. *Proceedings of the United States National Museum* 58:251–292.
- Drummond, A.J., B. Ashton, M. Cheung, J. Heled, M. Kearse, R. Moir, S. Stones-Havas, T. Thierer, and A. Wilson. 2009. Geneious version 6.1.5. Available from <http://www.geneious.com> (accessed 1 April 2015).

- Ellington, J.J., T.D. Carrillo, D. LaRock, D.B. Richman, B.E. Lewis, and A.H.A. El-Salam. 1995. Biological control of pecan insects in New Mexico. *Horticultural Technology* 5(3):230–233.
- Evenhuis, N.L. 2014. Abbreviations for insect and spider collections of the world. Available from <http://hbs.bishopmuseum.org/codens/codens-inst.html> (accessed 7 July 2015).
- Farahani, S., A. Asghar, E. Rakhshani, C. van Achterberg, and M.J. Sharkey. 2014. A contribution to the knowledge of Agathidinae (Hymenoptera: Braconidae) from Iran with description of a new species. *Biologia* 69(2):228–235.
- Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39:783–791.
- Gahan, A.B. 1919. New reared parasitic Hymenoptera, with some notes on synonymy. *Proceedings of the United States National Museum* 55(2261):113–128.
- Gries, C., E.E. Gilbert, and N.M. Franz. 2014. Symbiota—A virtual platform for creating voucher-based biodiversity information communities. *Biodiversity Data Journal*. doi: 10.3897/BDJ.2.e1114.
- Harry, M., M. Solignac, and D. Lachaise. 1996. Adaptive radiation in the Afrotropical region of the Paleotropical genus *Lissocephala* (Drosophilidae) on the pantropical genus *Ficus* (Moraceae). *Journal of Biogeography* 23:543–552.
- Hebert, P.D.N., E.H. Penton, J.M. Burns, D.H. Janzen, and W. Hallwachs. 2004. Ten species in one: DNA barcoding reveals cryptic species in the Neotropical skipper butterfly *Astraptes fulgerator*. *Proceedings of the National Academy of Sciences of the United States of America* 101:14812–14817.
- Huelsenbeck, J.P., and B. Rannala. 2004. Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. *Systematic Biology* 53:904–913.
- Huelsenbeck, J.P., and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17:754–755.
- Jervis, M. 1998. Functional and evolutionary aspects of mouthpart structure in parasitoid wasps. *Biological Journal of the Linnean Society* 63(4):461–493.
- Katoh, K., K. Kuma, H. Toh, and T. Miyata. 2006. MAFFT version 5: Improvement in accuracy of multiple sequence alignment. *Nucleic Acids Research* 33:511–518.
- Maddison, W.P., and D.R. Maddison. 2005. MacClade: Analysis of phylogeny and character evolution. Version 4.08a. Available from <http://www.macclade.org/> (accessed 1 April 2015).
- Marshall, D.C., C. Simon, and T.R. Buckley. 2006. Accurate branch length estimation in partitioned Bayesian analyses requires accommodation of among-partition rate variation and attention to branch length priors. *Systematic Biology* 55:992–1003.
- Mills, N. 2005. Selecting effective parasitoids for biological control introductions: Codling moth as a case study. *Biological Control* 34:274–282.
- Muesebeck, C.F.W. 1927. A revision of the parasitic wasps of the subfamily Braconinae occurring in America north of Mexico. *Proceedings of the United States National Museum* 69:1–73.
- Muesebeck, C.F.W. 1932. Four new North American species of *Bassus* Fabricius (Hymenoptera: Braconidae), with notes on the genotype. *Journal of the Washington Academy of Sciences* 22:329–333.
- Muesebeck, C.F.W. 1940. Two new reared species of *Bassus* (Hymenoptera: Braconidae). *Proceedings of the Entomological Society of Washington* 42(4):91–93.
- Muesebeck, C.F.W. 1958. Family Braconidae. In: Krombein K.V. (Ed.) Hymenoptera of America North of Mexico synoptic catalog (Agriculture Monograph No. 2), first supplement. United States Government Printing Office, Washington, D.C. U.S.A. 584 pp. pp. 18–36.
- Provancher, L. 1880. Faune canadienne. Les insectes - Hyménoptères. *Naturaliste Canadien* 12:161–180.
- Provancher, L. 1895. Les dernières descriptions de l'Abbé Provancher. *Naturaliste Canadien* 22:79–80, 95–97.
- Rambaut, A., and A.J. Drummond. 2009. Tracer v. 1.5. Available from <http://tree.bio.ed.ac.uk/software/tracer/> (accessed March 2015).
- Rodriguez, F., J.L. Oliver, A. Marin, and J.R. Medina. 1990. The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology* 142:485–501.
- Romero, J.C., J.J. Ellington, and D.B. Richman. 2001. Pecan nut casebearer, *Acrobasis nuxvorella* Neunzig parasites collected in

- Doña Ana County, NM, and El Paso County, TX. *Southwestern Entomologist* 26(3):269–270.
- Ronquist, F., and J.P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.
- Sharkey, M.J. 1996. The Agathidinae (Hymenoptera: Braconidae) of Japan. *Bulletin of the National Institute of Agro-Environmental Sciences* 13:1–100.
- Sharkey, M.J., and E.G. Chapman. 2015. The Nearctic genera of Agathidinae (Hymenoptera: Braconidae) with a phylogenetic analysis, illustrated generic key and the description of three new genera. *Zootaxa* 4000(1):49–72.
- Sharkey, M.J., S.A. Clutts Stoelb, E.M. Tucker, D. Janzen, W. Hallwachs, T. Dapkey, and M.A. Smith. 2011. *Lytopylus* Förster (Hymenoptera, Braconidae, Agathidinae) species from Costa Rica, with an emphasis on specimens reared from caterpillars in Area de Conservación Guanacaste. *Zookeys* 130:379–419.
- Sharkey, M.J., N.M. Laurenne, B.J. Sharanowski, D.L.J. Quicke, and D. Murray. 2006. Revision of the Agathidinae (Hymenoptera: Braconidae) with comparisons of static and dynamic alignments. *Cladistics* 22:546–567.
- Sharkey, M.J., and R.A. Wharton. 1997. Morphology and terminology. In *Manual of the New World genera of Braconidae (Hymenoptera)*, eds. R.A. Wharton, P.M. Marsh, and M.J. Sharkey. Special Publication of the International Society of Hymenopterists, vol. 1, 1–439.
- Sharkey, M.J., D.S. Yu, S. van Noort, K. Seltmann, and L. Penev. 2009. Revision of the Oriental genera of Agathidinae (Hymenoptera, Braconidae) with an emphasis on Thailand including interactive keys to genera published in three different formats. *Zookeys* 21:19–54.
- Simbolotti, G., and C. van Achterberg. 1992. Revision of the west Palaearctic species of the genus *Bassus* (Hymenoptera: Braconidae). *Zoologische Verhandlungen* 281:1–80.
- Stevens, N.B., A.D. Austin, and J.T. Jennings. 2010. Synopsis of Australian agathidine wasps (Hymenoptera: Braconidae: Agathidinae). *Zootaxa* 2480:1–26.
- Swofford, D.L. 2003. PAUP* Phylogenetic analysis using parsimony (*and other methods) Version 4. Sunderland, Massachusetts: Sinauer Associates.
- Tucker, E.M., E.G. Chapman, and M.J. Sharkey. 2015. A revision of the New World species of *Cremnops* Förster (Hymenoptera: Braconidae: Agathidinae). *Zootaxa* 3916(1):1–83.
- van Achterberg, C. 2011. Order Hymenoptera, family Braconidae. The subfamily Agathidinae from the United Arab Emirates, with a review of the fauna of the Arabian Peninsula. *Arthropod Fauna of the United Arab Emirates* 4:286–352.
- Viereck, H.L. 1905. Notes and descriptions of Hymenoptera from the western United States, in the collection of the University of Kansas. *Transactions of the Kansas Academy of Science* 19:264–326.
- Viereck, H.L. 1917. Guide to the insects of Connecticut. Part III. The Hymenoptera, or wasp-like insects of Connecticut. Ichneumonoidea. State of Connecticut. State Geological and Natural History Survey. Bulletin No. 22(1916). Hartford. 824 pp.
- Yoder, M.J., I. Mikó, K.C. Seltmann, M.A. Bertone, and A.R. Deans. 2010. A gross anatomy ontology for Hymenoptera. *PLoS ONE* 5(12):e15991.
- Yu, D.S.K., C. van Achterberg, and K. Horstmann. 2015. Taxapad. Database on flash-drive. Available from www.taxapad.com (accessed November 10, 2016).
- Zwickl, D.J. 2006. *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion*. Ph.D. dissertation. Austin, Texas: The University of Texas. Available from <https://repositories.lib.utexas.edu/handle/2152/2666> (accessed May 17, 2016).

Received 18 November 2015; accepted 4 June 2016.

Appendix Table Specimens used in the phylogenetic analyses, including specimen numbers, GenBank and BOLD (Barcode of Life Data) Systems accession numbers, and rough geographical information.

Taxon name	No.	Country: region	Type status	COI	28S
<i>Braunsia bilunata</i>	H1115	Sao Tome & Principe		—	KU058993
<i>Braunsia</i> sp.	H2374	Central African Republic		KU059043	—
<i>Braunsia</i> sp.	H1876	Congo: Pool		ATRMK331-11	KU058998
<i>Braunsia</i> sp.	H1891	Congo: Pool		ATRMK337-11	KP943695
<i>Braunsia</i> sp.	H2370	Congo: Pool		—	KU058997
<i>Braunsia</i> sp.	H2371	Congo: Poolsw		KU059045	—
<i>Braunsia</i> sp.	H2373	Congo: Pool		KU059046	—
<i>Braunsia</i> sp.	H2375	Congo: Pool		KU059050	—
<i>Braunsia</i> sp.	H2376	Congo: Pool		KU059044	—
<i>Braunsia</i> sp.	H2377	Congo: Pool		KU059047	—
<i>Braunsia</i> sp.	H2378	Congo: Pool		KU059051	—
<i>Braunsia</i> sp.	H2379	Congo: Pool		KU059048	—
<i>Braunsia</i> sp.	H2380	Congo: Pool		KU059049	—
<i>Braunsia</i> sp.	H2381	Congo: Pool		KU059052	—
<i>Braunsia</i> sp.	H1895	Equatorial Guinea		—	KU058995
<i>Braunsia</i> sp.	H1889	Kenya: Eastern		—	KU058991
<i>Braunsia</i> sp.	H1884	Kenya: Nyanza		ATRMK333-11	KU058996
<i>Braunsia</i> sp.	H1890	Kenya: Nyanza		—	KU058994
<i>Braunsia</i> sp.	H1892	Kenya: Nyanza		ATRMK338-11	KU058992
<i>Braunsia</i> sp.	H2384	Madagascar: Antsiranana		ATRMK543-11	—
<i>Braunsia</i> sp.	H1297	Madagascar: Toliara		ATRMK447-11	—
<i>Braunsia</i> sp.	H1893	Uganda		ATRMK435-11	KU058999
<i>Aerophilus abdominalis</i>	H1253	USA: GA		—	KU059000
<i>Aerophilus abdominalis</i>	H1313	USA: KY		ATRMK294-11	KP943685
<i>Aerophilus arthurevansi</i>	H5615	USA: VA	Paratype	KP943622	—
<i>Aerophilus arthurevansi</i>	H8554	USA: VA	Holotype	KP943628	—
<i>Aerophilus arthurevansi</i>	H8556	USA: VA	Paratype	KP943629	—
<i>Aerophilus calcaratus</i>	H209	USA: KY		KU059053	KU059001
<i>Aerophilus calcaratus</i>	H1220	USA: WV		ATRMK559-11	—
<i>Aerophilus calcaratus</i>	H1246	USA: WV		ATRMK566-11	—
<i>Aerophilus calcaratus</i>	H1247	USA: FL		ATRMK567-11	—
<i>Aerophilus calcaratus</i>	H1249	USA: WV		ATRMK280-11	KU059002
<i>Aerophilus calcaratus</i>	H1250	USA: TN		ATRMK569-11	—
<i>Aerophilus calcaratus</i>	H1457	USA: WV		ATRMK307-11	KP943692
<i>Aerophilus calcaratus</i>	H1461	USA: KY		—	KU059003
<i>Aerophilus calcaratus</i>	H1478	USA: WV		ATRMK308-11	KU059004
<i>Aerophilus calcaratus</i>	H1487	USA: WV		ATRMK310-11	KU059005
<i>Aerophilus chapmani</i>	H1350	USA: KY	Holotype	ATRMK302-11	KP943689
<i>Aerophilus davidsmithi</i>	H1267	USA: WV	Holotype	ATRMK289-11	KP943679
<i>Aerophilus difficilis</i>	H11965	USA: FL		KP943633	—
<i>Aerophilus erythrogaster</i>	H1216	USA: KY		KP943615	KU059006
<i>Aerophilus erythrogaster</i>	H8274	USA: KY		KP943626	—
<i>Aerophilus hopkinsensis</i>	H7424	USA: KY	Paratype	KP943623	KU059007
<i>Aerophilus hopkinsensis</i>	H7438	USA: KY	Holotype	KP943624	KU059008
<i>Aerophilus jdherndoni</i>	H1217	USA: KY	Holotype	KU059054	KU059009
<i>Aerophilus jdherndoni</i>	H1218	USA: KY	Paratype	ATRMK557-11	KP943676
<i>Aerophilus jdherndoni</i>	H1256	USA: KY	Paratype	ATRMK285-11	KU059010
<i>Aerophilus jdherndoni</i>	H1265	USA: KY	Paratype	KU059055	KU059011
<i>Aerophilus jdherndoni</i>	H1268	USA: KY	Paratype	—	KU059012
<i>Aerophilus jdherndoni</i>	H1307	USA: KY	Paratype	ATRMK293-11	KU059013
<i>Aerophilus jdherndoni</i>	H1311	USA: KY	Paratype	—	KU059014
<i>Aerophilus jdherndoni</i>	H1380	USA: KY	Paratype	—	KU059015
<i>Aerophilus jdherndoni</i>	H1400	USA: KY	Paratype	ATRMK306-11	KU059016
<i>Aerophilus jdherndoni</i>	H1486	USA: KY	Paratype	—	KU059017
<i>Aerophilus jdherndoni</i>	H6033	USA: WI	Paratype	KU059056	KU059018
<i>Aerophilus jdherndoni</i>	H7682	USA: KY	Paratype	—	KU059019
<i>Aerophilus jdherndoni</i>	H8848	USA: KY	Paratype	KU059057	—
<i>Aerophilus jdherndoni</i>	H10030	USA: KY	Paratype	KU059058	—
<i>Aerophilus klastos</i>	H205	USA: KY	Holotype	KP943612	KP943664
<i>Aerophilus kowlesae</i>	H7683	USA: KY	Holotype	KP943625	KU059020
<i>Aerophilus malus</i>	H1248	USA: WV	Paratype	ATRMK568-11	—
<i>Aerophilus malus</i>	H1484	USA: WV	Holotype	ATRMK309-11	KP943693
<i>Aerophilus minys</i>	H206	USA: KY	Paratype	KU059059	KU059021
<i>Aerophilus minys</i>	H966	USA: KY	Paratype	ATRMK267-11	KU059022
<i>Aerophilus minys</i>	H1215	USA: KY	Paratype	ATRMK279-11	KU059023
<i>Aerophilus minys</i>	H1219	USA: WV	Paratype	ATRMK558-11	KU059024
<i>Aerophilus minys</i>	H1222	USA: KY	Paratype	—	KU059025
<i>Aerophilus minys</i>	H1251	USA: KY	Paratype	ATRMK281-11	KU059026

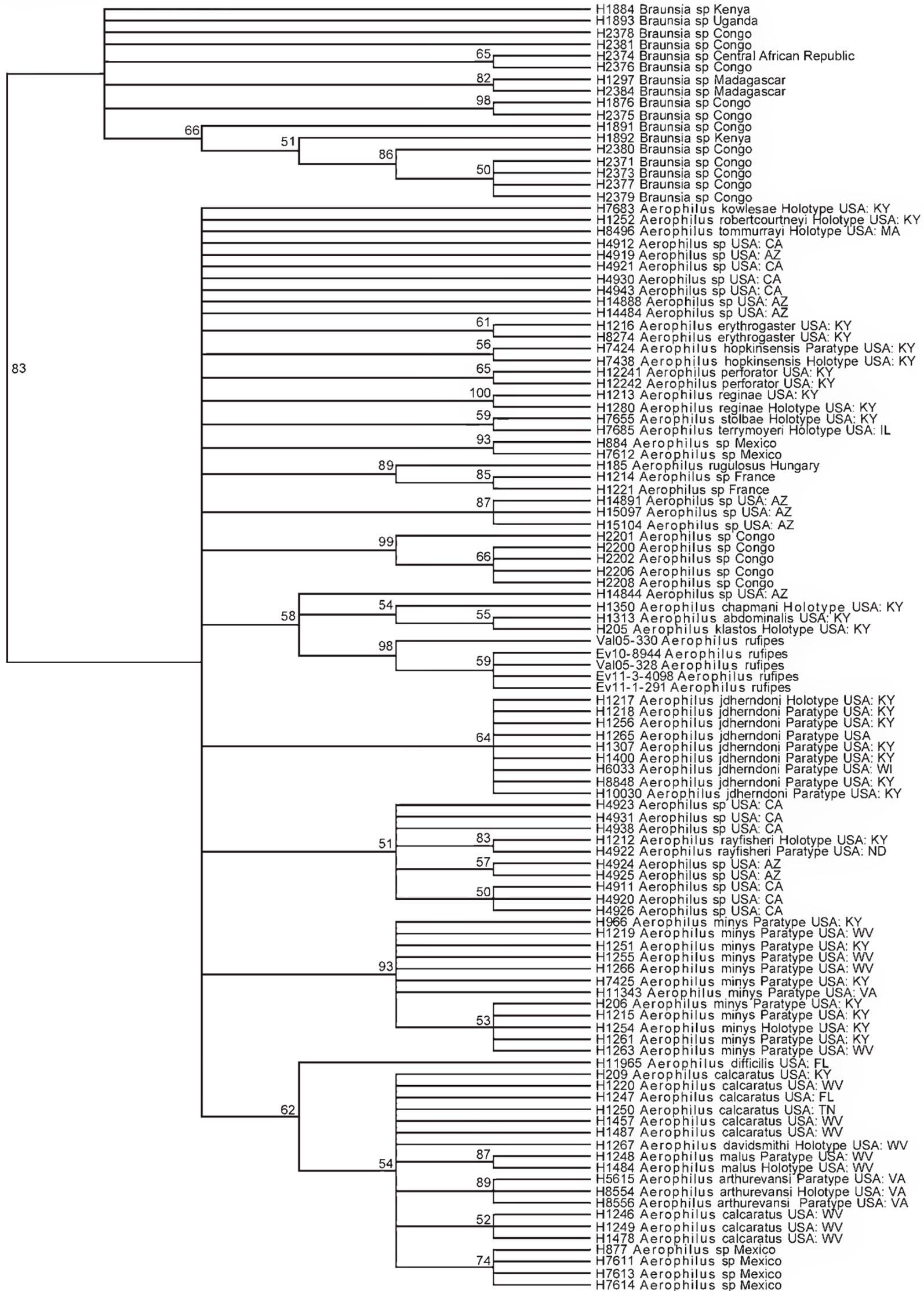
Appendix Table [Continued]

Taxon name	No.	Country: region	Type status	COI	28S
<i>Aerophilus minys</i>	H1254	USA: KY	Holotype	ATRMK283-11	KU059027
<i>Aerophilus minys</i>	H1255	USA: WV	Paratype	ATRMK284-11	KP943678
<i>Aerophilus minys</i>	H1257	USA: KY	Paratype	—	KU059028
<i>Aerophilus minys</i>	H1261	USA: KY	Paratype	ATRMK286-11	KU059029
<i>Aerophilus minys</i>	H1262	USA: KY	Paratype	—	KU059030
<i>Aerophilus minys</i>	H1263	USA: WV	Paratype	ATRMK287-11	KU059031
<i>Aerophilus minys</i>	H1266	USA: WV	Paratype	ATRMK288-11	KU059032
<i>Aerophilus minys</i>	H6029	USA: KY	Paratype	—	KU059033
<i>Aerophilus minys</i>	H7425	USA: KY	Paratype	ATRMK380-11	KU059034
<i>Aerophilus minys</i>	H11343	USA: VA	Paratype	KU059060	—
<i>Aerophilus perforator</i>	H12241	USA: KY		KP943634	—
<i>Aerophilus perforator</i>	H12242	USA: KY		KP943635	—
<i>Aerophilus rayfisheri</i>	H1212	USA: KY	Holotype	ATRMK278-11	KP943675
<i>Aerophilus rayfisheri</i>	H4922	USA: ND	Paratype	KU059061	—
<i>Aerophilus reginae</i>	H1213	USA: KY		KU059062	—
<i>Aerophilus reginae</i>	H1280	USA: KY	Holotype	KP943616	KP943681
<i>Aerophilus robertcourtneyi</i>	H1252	USA: KY	Holotype	ATRMK282-11	KP943677
<i>Aerophilus rufipes</i>	Ev10-8944	France		KP402064	—
<i>Aerophilus rufipes</i>	Ev11-1-291	France		KP402062	—
<i>Aerophilus rufipes</i>	Ev11-3-4098	France		KP402063	—
<i>Aerophilus rufipes</i>	Val05-328	France		KP402060	—
<i>Aerophilus rufipes</i>	Val05-330	France		KP402061	—
<i>Aerophilus stoelbae</i>	H7655	USA: KY	Holotype	ATRMK418-11	—
<i>Aerophilus terrymoyeri</i>	H7685	USA: IL	Holotype	ATRMK433-11	KU059035
<i>Aerophilus tommurrayi</i>	H8496	USA: MA	Holotype	KP943627	—
<i>Aerophilus</i> sp.	H877	Mexico: Yucatan		ATRMK249-11	KU059036
<i>Aerophilus</i> sp.	H884	Mexico: Yucatan		ATRMK252-11	KU059037
<i>Aerophilus</i> sp.	H2200	Congo: Pool		KU059063	KU059038
<i>Aerophilus</i> sp.	H2201	Congo: Pool		KU059067	KU059039
<i>Aerophilus</i> sp.	H2202	Congo: Pool		KU059064	—
<i>Aerophilus</i> sp.	H2206	Congo: Pool		KU059065	—
<i>Aerophilus</i> sp.	H2208	Congo: Pool		KU059066	—
<i>Aerophilus</i> sp.	H1214	France: Languedoc		ATRMK496-11	—
<i>Aerophilus</i> sp.	H1221	France: Languedoc		ATRMK560-11	—
<i>Aerophilus</i> sp.	H7611	Mexico: Yucatan		ATRMK398-11	KU059040
<i>Aerophilus</i> sp.	H7612	Mexico: Yucatan		ATRMK399-11	KP943707
<i>Aerophilus</i> sp.	H7613	Mexico: Yucatan		ATRMK400-11	KP943708
<i>Aerophilus</i> sp.	H7614	Mexico: Yucatan		ATRMK401-11	KU059041
<i>Aerophilus</i> sp.	H7615	Mexico: Yucatan		—	KU059042
<i>Aerophilus</i> sp.	H4919	USA: AZ		KU059070	—
<i>Aerophilus</i> sp.	H4924	USA: AZ		KU059074	—
<i>Aerophilus</i> sp.	H4925	USA: AZ		KU059075	—
<i>Aerophilus</i> sp.	H14484	USA: AZ		KP943639	—
<i>Aerophilus</i> sp.	H14844	USA: AZ		KP943640	—
<i>Aerophilus</i> sp.	H14888	USA: AZ		KP943642	—
<i>Aerophilus</i> sp.	H14891	USA: AZ		KP943641	—
<i>Aerophilus</i> sp.	H15097	USA: AZ		KP943645	—
<i>Aerophilus</i> sp.	H15104	USA: AZ		KU059081	—
<i>Aerophilus</i> sp.	H4911	USA: CA		KU059068	—
<i>Aerophilus</i> sp.	H4912	USA: CA		KU059069	—
<i>Aerophilus</i> sp.	H4920	USA: CA		KU059071	—
<i>Aerophilus</i> sp.	H4921	USA: CA		KU059072	—
<i>Aerophilus</i> sp.	H4923	USA: CA		KU059073	—
<i>Aerophilus</i> sp.	H4926	USA: CA		KU059076	—
<i>Aerophilus</i> sp.	H4930	USA: CA		KU059077	—
<i>Aerophilus</i> sp.	H4931	USA: CA		KU059078	—
<i>Aerophilus</i> sp.	H4938	USA: CA		KU059079	—
<i>Aerophilus</i> sp.	H4943	USA: CA		KU059080	—



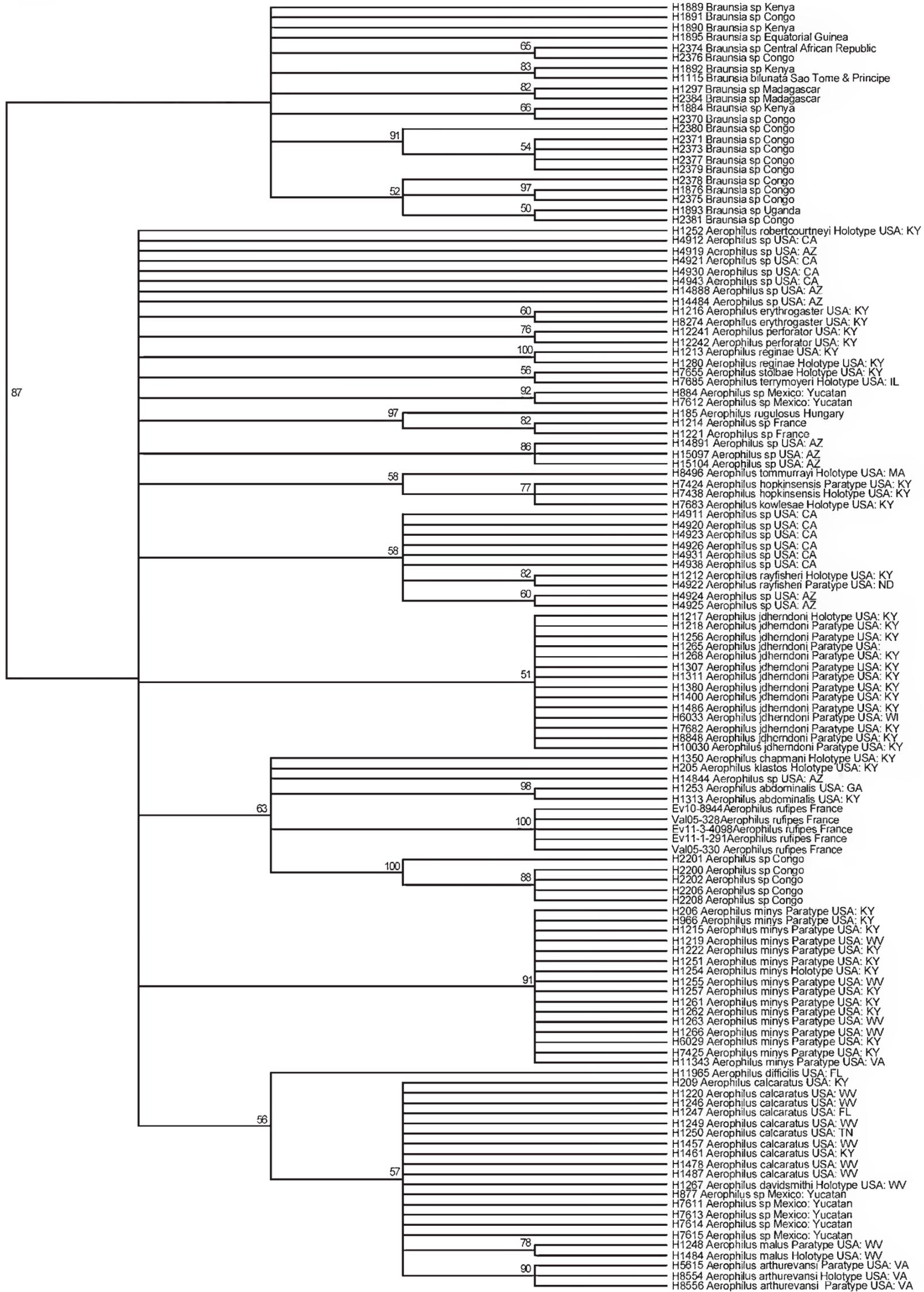
Supplemental Figure 1 Tree of highest log-likelihood from a 200-replicate ML analysis of the combined COI data set (summarized in Figure 3). ML bootstrap values are plotted above the branches (see Supplemental Figure 2).

Majority rule



Supplemental Figure 2 ML bootstrap analysis (500 replicates) of the COI data set.

Majority rule



Supplemental Figure 4 ML bootstrap analysis (500 replicates) of the combined COI+28S data set.

