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INTRODUCCIÓN

Las interacciones biológicas intra- e inter-específicas son de los procesos ecológicos y evolutivos que determinan la estructura de las comunidades y los patrones espacio-temporales de diversidad de especies (Hartley, 2000; Rico-Gray, 2001; Thompson, 2003). Particularmente, la competencia entre especies por recursos resulta en una gran variedad de interacciones y estrategias potencialmente adaptativas para la obtención de los mismos, así como para asegurar su permanencia en el medio.

La herbivoría por diferentes gremios de insectos es una interacción antagónica que a menudo resulta en una reducción significativa en el crecimiento y éxito reproductivo de las plantas hospederas. Los herbívoros ejercen presiones selectivas sobre sus plantas hospederas (Hartley, 2000; Schardl, 1999). Del mismo modo, las plantas han evolucionado diferentes tipos de defensa (e.g. mecánica, química) como respuesta a estas presiones selectivas, que a su vez resultan ser presiones sobre los herbívoros (Ehrlich y Raven, 1964). Se conoce que las plantas han desarrollado diferentes estrategias para defenderse de los herbívoros. La resistencia que presentan las plantas es un mecanismo de defensa que resulta de la inversión de recursos para producir metabolitos secundarios. La tolerancia se refiere al uso de la defensa química con la que ya cuenta la planta (i.e. constitutiva) y en donde las plantas pueden tolerar diferentes ataques por herbívoros sin inducir ningún nuevo compuesto químico de defensa (Coley y Barone, 1996; Hartley, 2000; Walton, 2001). Sin embargo, no solo las plantas han desarrollado mecanismos de defensa contra el ataque por herbívoros, sino que también los insectos han respondido a estas defensas vegetales en diferentes vías: (i) mitigando el impacto de las condiciones adversas al modificar el entorno local, por ejemplo excavando, construyendo refugios, agrupándose, eligiendo el sitio de alimentación y oviposición, (ii) desarrollando sistemas de desintoxicación contra compuestos secundarios e (iii) induciendo una respuesta en la planta como el caso de los insectos formadores de agallas (Danks, 2002). Particularmente, la formación de agallas representa para los insectos una fuente de recursos de alto valor, que combina alimento, protección física y potencialmente protección química, bajo el supuesto de que los compuestos fenólicos producidos por la planta ante la presencia de insectos agalleros, pueden ser utilizados por éstos para defenderse de sus enemigos naturales (Abrahamson *et al.,* 1991; Danks, 2002; Pascual-Alvarado *et al.,* 2012).

I.2 insectos formadores de agallas

Las características mediadoras de la interacción planta-herbívoro están determinadas por la fenología, la fitoquímica y por procesos metabólicos complejos, tanto de la planta como del animal (Burdon, 1987; Orians, 2000; Yukawa, 2000). Un ejemplo de ello es la interacción entre plantas e insectos herbívoros endófagos formadores de agallas. Estos insectos endófagos se alimentan del tejido mesófilo de la hoja y al mismo tiempo alteran los patrones de crecimiento vegetal que resultan en la formación de estructuras denominadas agallas (Ananthakhrishnan, 1984).

Jones y colaboradores (1994) describen a los insectos formadores de agallas como ingenieros de ecosistemas debido a que son organismos que directa o indirectamente controlan la disponibilidad de recursos de la planta afectando a organismos de diferentes niveles tróficos y causando cambios ecológicos en las interacciones bióticas. La función primaria de las agallas es garantizar la disponibilidad de alimento del insecto agallero. Las larvas de los insectos de las agallas de cinípidos (Hymenoptera) y de cecidómidos (Diptera) se alimentan de una capa especial de células nutritivas (Shorthouse y Rohfitsch, 1992; Wool *et al*., 1999). Las agallas se pueden definir como estructuras anormales de partes de tejidos u órganos de las plantas que se desarrollan por la reacción química como resultado de la presencia o actividad de sustancias análogas a las auxinas secretadas en la saliva por el insecto en el momento de la oviposición o durante la alimentación de las larvas y que incluye, sin excepción, fenómenos de hipertrofia (i.e. crecimiento anormal de las células) e hiperplaxia (i.e. multiplicación anormal de las células) (Nieves, 1998; Hernández-Soto, 2015), lo que permite el desarrollo *in situ* de huevos y larvas (Meyer, 1987; Shorthouse y Rohfritsch, 1992; Nieves, 1998). Como resultado de esta oviposición y alimentación se lleva a cabo una reacción química de la planta alterando los patrones de crecimiento y desarrollo en células, tejidos u órganos, desviando los recursos asignados al crecimiento vegetal para la formación de agallas (Ananthakrishan, 1984; Hernández-Soto, 2015). Por lo tanto, los insectos formadores de agallas alteran el estado fisiológico del tejido de la planta, particularmente el de las células más cercanas al huevo o a la larva.

La formación de agallas o cecidogénesis, involucra la interacción química entre el estímulo del insecto y la reacción de la planta liberando sustancias químicas análogas a las auxinas (i.e. fito-hormonas de crecimiento), lo que resulta en la formación de la agalla, la cual permite el desarrollo adecuado de los insectos aunque también se puede considerar como una respuesta ofensiva de las plantas hospederas (Ananthakrishan, 1984). El fenómeno de la formación de agallas es específico y complejo. El estímulo inicial de la formación de la agalla puede presentarse en el momento de la oviposición, cuando el insecto inyecta el material estimulante junto con el huevo, el estímulo debe ser continuo para que se desarrolle completamente la agalla. El huevo es depositado sobre la planta o en los tejidos de la misma; en el último caso, al romperse el huevo, la larva va hacia el cambium o en alguna porción de la planta capacitada para crecer. Por lo regular, el crecimiento anormal en las plantas no se da sino hasta que eclosiona el insecto, entonces, la agalla crece junto con el insecto, el cual se alimenta de las sustancias nutritivas producidas por la planta. Dependiendo de la especie, los insectos pueden tener partes bucales masticadoras, que destruyen las células, o bien pueden tener un aparato succionador y chupar los contenidos celulares, alimentándose dentro de la agalla.

Los insectos formadores de agallas pertenecen a los herbívoros más especializados. Desde el punto de vista evolutivo, las agallas parecen ser adaptaciones que permiten a algunos taxa de insectos alimentarse sobre tejidos de alta calidad nutricional, protegerse contra enemigos naturales y estrés ambiental (Hartley y Lawton, 1992; Hartley, 1998). La alta especialización de los insectos formadores de agallas sobre sus plantas hospederas pudo originarse como resultado de mecanismos de defensa de las plantas, restringiendo a los insectos a desarrollarse dentro de la agalla. La última defensa de la planta contra el insecto formador de agallas es no activarse y no encapsular al insecto (Cuevas-Reyes, 1998; Fernándes y Price, 1988). Debido a su hábito sedentario, la formación de agallas les proporciona a estos insectos beneficios tales como un microhábitat favorable que facilita los procesos de alimentación, desarrollo y reproducción, confiriéndoles protección ante cambios climáticos, depredación y parasitismo (Ananthakrishan, 1984; Price y Pschorn-Walcher, 1988; Weis y Walton, 1988; Schultz, 1992). Sin embargo, para las plantas, la formación de agallas representa costos fisiológicos en la asignación de recursos a la defensa química, cambios metabólicos en la dirección del crecimiento de los diferentes órganos ya que el crecimiento de la planta es afectado por el desarrollo de agallas (Askew , 1984; Hartley, 1998; Rossi y Stiling, 1998; Hernández Soto, 2015), efectos negativos al reducirse el área y la capacidad fotosintética por la cobertura de agallas (Fay *et al.*, 1993,1996) y efectos negativos sobre el éxito reproductivo de las plantas al reducir la producción de flores, inflorescencias y semillas (Ananthakishan, 1984; Fay *et al.*, 1996; Parra-Tabla y Bullock, 1998).

Actualmente se han reportado más de 13, 000 especies de insectos formadores de agallas agrupados en siete diferentes órdenes: Diptera, Hymenoptera, Homoptera, Coleoptera, Thysanoptera, Lepidoptera y Hemiptera (Shorthouse y Rohfritsch, 1992). Particularmente, el orden Hymenoptera es muy diverso en regiones templadas y el orden Diptera con la familia Cecidomyiidae es el más diverso en el neotrópico. Price (1991) sugiere que la naturaleza adaptativa de la agalla está asociada a ambientes secos debido a que la abundancia y sobrevivencia de estos insectos es mayor en hábitats secos que en ambientes húmedos.

Los patrones generales de diversidad de insectos inductores de agallas se han asociado a factores ambientales como el estrés hídrico (Fernándes y Price, 1988), fertilidad del suelo (Blanche y Westoby , 1995; Cuevas-Reyes *et al.* , 2003; Cuevas-Reyes *et al.*, 2004b) latitud y altitud (Fernándes y Price, 1988, 1991; Price, 1991; Fernándes y Lara , 1993) y a factores bióticos como la riqueza de especies de plantas (Fernándes y Price, 1991; Wright y Samways, 1996; Cuevas Reyes *et al*., 2003; Oyama *et al*., 2003; Cuevas-Reyes *et al.*, 2004a).

La complejidad de la interacción planta-agallero ha llevado a formular una serie de hipótesis para aclarar estas relaciones (Price *et al*., 1987; Abrahamson, *et al.,* 1991; Hartley, 1999). Dichas hipótesis varían en el enfoque y en los mecanismos que se proponen para explicarlo. Algunos autores proponen la interacción planta-agallero como no adaptativa (Bequaert, 1924) y/o mutualista (Cockerell, 1890; Bronner, 1983). Otros autores lo ven desde el punto de vista de la planta, percibiendo la formación de la agalla como un mecanismo de defensa de la planta (Mani, 1964) o bien como un tipo de "rizobia grande" que puede manipular la producción de fenoles que sirven como señales químicas mediadoras de la interacción entre la planta hospedera y el insecto formador de agallas (Hartley, 1998, 1999). Price y colaboradores (1986, 1987, 1988) sugieren que la formación de agallas se encuentra asociada a variables ambientales como el estrés hídrico, en este caso, la cámara de la agalla confiere un microhábitat favorable sin limitaciones de agua aún en ambientes áridos o xéricos. Sin embargo, la elevada incidencia y riqueza de especies de insectos formadores de agallas encontrada en ambientes de gran humedad como bosques tropicales húmedos sugieren que la función principal de las agallas no es la de ofrecer un microclima que proteja a los insectos de la desecación (Cuevas-Reyes *et al.,* 2003; Oyama *et al*., 2003), si no más bien ofrecer un sitio con una alta calidad nutricional. Por ello se ha propuesto una hipótesis alternativa que sugiere que la formación de agallas es considerada una adaptación a la explotación de los tejidos nutricionales de las plantas debido a la formación de una zona celular nutritiva bien determinada en la agalla que presenta un alto contenido de nitrógeno soluble, azúcares y aminoácidos. Además, cada zona forma parches aislados de células organizadas alrededor de las agallas que contienen una gran cantidad de metabolitos secundarios asociados a defensa contra enemigos naturales (Ananthakrishan, 1984; Abrahamson y Weis, 1997). Por lo tanto, la hipótesis nutricional sugiere que la formación de agallas es una adaptación a obtener alimento de alta calidad nutricional químicamente bien defendido (Price *et al*., 1986, 1987; Hartley y Lawton, 1992; Hartley, 1998).

El alto grado de especialización de los insectos formadores de agallas sobre sus plantas hospederas se refleja en la disponibilidad de tejidos indiferenciados de la planta, que están presentes solo en determinado tiempo durante cierta estación, que exista un nivel fuerte de sincronía entre el huésped y la fenología de la formación de la agalla (Weis y Walton, 1988; Yukawa, 2000). Además, los insectos formadores de agallas inducen la formación y controlan la morfología de la agalla, donde cada morfología inducida tiene características muy particulares por lo que se ha sugerido que cada morfoagalla representa a una especie diferente de insecto (Koach y Wool, 1977; Bearsley, 1982; Ananthakrishnan, 1984; Dodson y George, 1986; Price *et al*., 1987; Weis y Walton, 1988; Floate *et al*., 1996; Hartley, 1998; Nyman *et al*., 1998; Nyman y Julkunan-Tiitto, 2000; Cuevas-Reyes *et al*., 2003; Oyama *et al*., 2003). Sin embargo, ninguno de estos estudios ha identificado taxonómicamente la especificidad de esta interacción. Por lo tanto, resulta crucial el reconocimiento taxonómico de los IFA puesto que se ha encontrado que una especie de planta puede estar asociada a diferentes especies de IFA (Fernandes y Price, 1988; Waring y Price, 1989; Fernandes *et al*., 1992). En este estudio se establece una relación taxonómica directa entre los IFA y sus plantas hospederas como base fundamental del análisis químico de hojas con agallas y de las interacciones ecológicas asociadas a este gremio.

HYMENOPTERA:CYNIPIDAE:CYNIPINI

Las avispas formadoras de agallas (Hymenoptera:Cynipidae:Cynipini) pertenecen a un gremio de herbívoros altamente especializados e interesantes como modelos de estudio. Estos insectos endófagos presentan un ciclo de vida partenogenético característico: una generación sexual de primavera-verano y una generación asexual de otoño. En cada una de las generaciones, tienen la habilidad de inducir una amplia diversidad de agallas específicas y complejas sobre miembros del género *Quercus*. Además, se ha reportado alternancia de hospedero (heteroecia) en cada generación para algunas especies de cinípidos (Askew, 1984; Cook *et al.* 1998, 2002).

Relaciones y ubicación taxonómica de los cinípidos

Las avispas formadoras de agallas son miembros de la superfamilia *Cynipoidea*, una de las principales superfamilias de himenopteros, representada principalmente por avispas parasitoides (Nieves-Aldrey y Fontal-Cazalla, 1999; Ronquist, 1995, 1999). Todos los grupos cercanos a los cinípidos son parasitoides que atacan las larvas de insectos, por lo cual se ha sugerido que la inducción de agallas en los cinípidos evolucionó a partir de una forma de vida ancestral de este tipo (Ronquist 1999; Ronquist y Liljeblad, 2001).

Los miembros del grupo de los cinípidos son parásitos obligados de plantas, ya sea que induzcan agallas o bien como inquilinos de las agallas inducidas por otras avispas formadoras de agallas. De acuerdo con Ronquist (1999, 2001), las primeras agallas inducidas por avispas se presentaron en plantas herbáceas, a partir de las cuales divirgieron en seis tribus reconocidas: la tribu Aylacini, en donde la mayoría de sus miembros induce agallas en plantas herbáceas y que dio origen a dos principales linajes monofiléticos.

El primer linaje esta compuesto por cuatro tribus, que forman agallas en plantas leñosas: Diplolepidini (aproximadamente 63 especies, que forma agallas en el género *Rosa*) Pediaspidini (dos especies formadoras de agallas en *Acer* y un número de especies desconocido que forman agallas en *Nothofagus*) Eschatocerini (tres especies que inducen la formación de agallas sobre *Acacia* y *Prosopis*) y Cynipini (inducen la formación de agallas sobre encinos, alrededor de 1000 especies).

Un segundo linaje incluye a la tribu Synergini, con 145 especies que son inquilinos de las agallas de otras avispas agalleras y aunque no son capaces de inducir sus propias agallas, si pueden modificar e inducir tejido nutritivo en las agallas que atacan.

Diversidad y distribución geográfica.

La riqueza de especies reportada en la literatura para la familia Cynipidae varía entre 1000 y 1400 especies (Ritchie, 1993; Ferguson y Hanson, 1995; Liljeblad y Ronquist, 1998) aunque dicho número puede disminuir, considerando que es probable que muchas especies que presentan heterogonía estén descritas en ambas fases como especies distintas, siendo que se trata de una sola especie (Nieves-Aldrey, 2001).

Los miembros de la familia Cynipidae se encuentran en todos los continentes, excepto en Australia, donde solo hay algunas especies que han sido introducidas. El mayor número de especies se distribuye en las zonas templadas del Hemisferio Norte (región holártica).

La mayor cantidad de especies de Cinípidos, pertenecen a la tribu Cynipini y a la tribu de avispas inquilinas, Synergini (constituyen el 80% de las especies), que se asocian exclusivamente a plantas de la familia de las fagáceas, principalmente del género *Quercus*, por lo tanto, el patrón de distribución del grupo está determinado por la distribución de los encinos. En Europa el grupo ha sido estudiado intensamente y se han reportado alrededor de 280 especies de cinípidos, que representan todas las tribus de Cynipidae en las 25 especies de encinos reportadas para Europa.

En México, se han reportado 164 especies en 26 géneros (Kinsey, 1936), de las cuales 134 son exclusivas para el país. Sin embargo, el esfuerzo de colecta no ha sido tan intensivo como para el continente europeo, por lo que los valores aun son inciertos y se ha llegado a estimar hasta la riqueza de especies entre 250 y 700 especies, lo anterior aunado a la gran riqueza de especies que se presenta en México (Nieves-Aldrey, 2001). Entonces resulta importante desarrollar una estrategia para la colecta, crianza e identificación de este grupo de insectos en México, basándose en la distribución de las especies de encinos.

Distribución de las plantas hospederas de los cinípidos.

La mayoría de los miembros de la tribu Cynipini forman agallas sobre encinos (Fagaceae, Fagoidea) y algunos pocos sobre miembros de la subfamilia Castanoidea.

El género *Quercus* (Fagaceae) se encuentra altamente diversificado a nivel mundial, y se divide en dos subgéneros: el subgénero asiático *Cyclobalanopsis* del cual se sabe muy poco acerca de la interacción con cinípidos (Stone *et al*., 2002) y el subgénero *Quercus* que tiene un mayor rango de distribución. Este subgénero se divide en cuatros secciones, la sección *Cerris* que es endémica a la zona Paleártica, mientras que en el Neártico se encuentran tres series, *Quercus* (encinos blancos), *Lobatae* (encinos rojos) y *Protobalanus* (encinos intermedios) (Manos *et al*., 1999).

Los cinípidos forman agallas en prácticamente todas las secciones del subgénero, y con excepción de aquellas que presentan alternancia de hospedero, cada especie de cinípido está asociada a una especie de encino o bien a un grupo de encinos estrechamente relacionados (Abrahamson et al., 1998; Cornell y WAshburn 1979; Stone *et al.,* 2002).

Se considera que los patrones de distribución y de riqueza de especies de encinos son importantes en cuanto a los patrones que presentan las especies de cinípidos, por lo que dependiendo de la distribución del hospedero, habrá una variación en cuanto a la riqueza en la comunidad de cinípidos (Stone *et al*., 2002). Se estima que hay alrededor de 500 especies de encinos en todo el mundo y que la mayor riqueza de especies se encuentra en México (Manos *et al.,* 1999)

México es considerado uno de los centros de diversificación para el subgénero *Quercus* con 161 especies, de las cuales 76 se ubican en la sección *Lobatae* (encinos rojos), que es endémica al Continente Americano y con 61 especies endémicas a México. Además, el género cuenta con 81 especies en la sección *Quercus* (encinos blancos) con 47 especies endémicas y cuatro especies en la sección *Protobalanus* (encinos intermedios) con una especie endémica. (Manos *et al*. 1999; Valencia, 2004). Debido a ésta riqueza específica de encinos, los

Sin embargo, este grupo de insectos y sus interacciones ecológicas han sido poco estudiadas en México. Y a pesar de que se estima que de las aproximadamente 1000 especies de avispas que se conocen para el mundo, 700 se encuentran en México, son pocos los trabajos de tipo ecológico evolutivos que se han realizado (Kinsey, 1936; Weld, 1960; Stone *et al*. 2002). Por lo anterior, existe un hueco en cuanto a la riqueza de especies de cinípidos para México y Centroamérica, a los patrones con respecto a sus hospederos, a la diversidad que se puede encontrar en las diferentes secciones de encinos

Descripción de los capítulos

En el primer capítulo se describe la diversidad de insectos inductores de agallas asociados a los encinos mexicanos. Los datos son el resultado de cinco años de colecta a lo largo de todo el país.

Los insectos inductores de agallas son un gremio de organismos endófagos altamente especializados. Los cinípidos (Hymenoptera: Cynipidae: Cynipini) son avispas inductoras de agallas ampliamente diversificados que se encuentran asociados principalmente a los encinos (Fagaceae: *Quercus*). México es uno de los centros de diversificación para el género *Quercus* con 161 especies descritas de las cuales 109 son endémicas.

El presente estudio contribuyó a identificar la riqueza de agallas, su variación morfológica y el grado de especificidad a los encinos en México. Se realizó una colecta intensiva de marzo a septiembre de cada año de 2008 a 2012 en un total de 80 especies de encinos en 120 localidades en México.

Como resultado de las colectas, se encontraron 224 morfotipos distintos de agallas se asociados a 73 de las 80 especies de encinos estudiadas. El mayor número de morfotipos se encontraron en hojas (125), seguidos por ramas (37), yemas (31), peciolos (20), inflorescencias (5), bellotas (3) y raíces (3). El grado de especificidad entre las avispas inductoras de agallas y sus hospederos fue muy variable; se encontraron entre uno y 20 morfotipos distintos de agallas en cada especie. Únicamente 23 especies de encinos estuvieron asociadas a un solo morfotipo de agalla.

El segundo capítulo se centra en el análisis taxonómico del género Amphibolips, uno de los géneros más representativos de agallas asociadas a los encinos de la sección Lobatae (rojos) en México. La taxonomía de cinípidos es problemática, en parte debido a la falta de especialistas en el mundo y también debido a la presencia de adultos morfológicamente distintos en cada una de las generaciones.

El género *Amphibolips* Reinhard 1865) es un género de avispas inductoras de agallas exclusivo al continente Americano. Actualmente se tiene el registro de 45 especies en toda el área de distribución de este género (desde Canadá hasta Panamá). En México se conocen 12 especies de *Amphibolips* (Kinsey 1937) y los caracteres morfológicos de los adultos y sus agallas son muy uniformes entre la mayoría de las especies conocidas. De acuerdo con la literatura, hay algunas especies de *Amphibolips* que presentan anomalías en algunos caracteres diagnósticos, lo que revela que los límites taxonómicos del género no están todavía claros. Particularmente en México las especies de *Amphibolips* fuera del complejo "*niger*" parecen ser un grupo morfológicamente distintivo. Por lo tanto, resulta importante una revisión taxonómica de las especies de *Amphibolips* de México que no pertenecen a este complejo.

Por lo tanto, en el segundo capítulo se plasman los resultados de la revisión taxonómica de las especies del género *Amphibolips* de México, que no pertenecen al complejo "*niger*". Para ello, se realizó una colecta en varios estados de México. Además, se analizaron materiales "tipo" de tres especies de *Amphibolips* descritas por Kinsey en 1937 y se incluyeron dos especies relacionadas de Panamá. Como resultado de la revisión se describen siete nuevas especies para la ciencia de *Amphibolips*. Además, se generó una nueva clave para la identificación de las especies del grupo.

Diversity of galls induced by wasps (Hymenoptera: Cynipidae, Cynipini) associated with oaks (Fagaceae: *Quercus*) in Mexico

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Abstract

Background: Gall-inducing insects make up a guild of highly specialized endophagous herbivores. The cynipids (Hymenoptera: Cynipidae: Cynipini) are highly diversified gall-inducing wasps that are largely associated with oaks (Fagaceae: *Quercus*). Mexico is one of the centers of diversification for the *Quercus* genus with 161 described species, of which 109 are endemic.

Questions / hypothesis: The present study aims to identify the gall richness, gall morphological variation and degree of specificity to oaks in Mexico.

Methods: An intensive collection was conducted from March to September each year from 2008 to 2012 for a total of 80 oak species in 120 localities in Mexico.

Results: A total of 224 morphologically distinct galls associated with 73 of the 80 oak species were found. The largest number of morphotypes was found in leaves (125), followed by branches (37), buds (31), petioles (20), catkins (5), acorns (3) and roots (3). The degree of specificity between the gall-inducing wasps and their hosts was highly variable; between one to 20 distinct gall morphotypes were found in each species. Only 23 oak species had a single gall morphotype associated.

Conclusions: This study demonstrates the important interaction between oaks and gall-inducing wasps, which is a very complex co-evolutionary process. It also shows the relevance of basic taxonomic studies of little-known groups such as gall-inducing wasps, especially in a highly biodiverse country such as Mexico.

Key words: Cynipidae, herbivore guilds, insect specialization, plant – insect interaction, *Quercus*

Resumen

Antecedentes: Los insectos inductores de agallas son un gremio de organismos endófagos altamente especializados. Los cinípidos (Hymenoptera: Cynipidae: Cynipini) son avispas inductoras de agallas ampliamente diversificados que se encuentran asociados principalmente a los encinos (Fagaceae: *Quercus*). México es uno de los centros de diversificación para el género *Quercus* con 161 especies descritas de las cuales 109 son endémicas.

Preguntas / hipótesis: El presente estudio contribuyó a identificar la riqueza de agallas, su variación morfológica y el grado de especificidad a los encinos en México.

Métodos: Se realizó una colecta intensiva de marzo a septiembre de cada año de 2008 a 2012 en un total de 80 especies de encinos en 120 localidades en México.

Resultados: Un total de 224 morfotipos distintos de agallas se encontraron asociados a 73 de las 80 especies de encinos estudiadas. El mayor número de morfotipos se encontraron en hojas (125), seguidos por ramas (37), yemas (31), peciolos (20), inflorescencias (5), bellotas (3) y raíces (3). El grado de especificidad entre las avispas inductoras de agallas y sus hospederos fue muy variable; se encontraron entre uno y 20 morfotipos distintos de agallas en cada especie. Únicamente 23 especies de encinos estuvieron asociadas a un solo morfotipo de agalla.

Conclusiones: Este estudio demuestra la importancia de la interacción entre los encinos y las avispas inductoras de agallas, el cual es un proceso coevolutivo muy complejo. También muestra la relevancia de estudios taxonómicos básicos de grupos poco conocidos como las avispas inductoras de agallas, especialmente en un país con una alta biodiversidad como lo es México.

Palabras clave: Cynipidae, especialización de insectos, gremio de herbívoros, interacción planta – insecto, *Quercus*

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Galls are atypical growths of plants that offer food, shelter and protection for the gall inducer or its progeny (Cornell 1983, Schönrogge *et al*. 2000, Hernández-Soto *et al*. 2015). Close to 13,000 species of gall-inducing insects have been recorded in plants (Shorthouse *et al*. 2005), although Espírito-Santo & Fernandes (2007) estimated a larger value of gall-inducing species ranging from 21,000 to 211,000 species. The family Cynipidae (Hymenoptera) contributes with approximately 1,400 species, constituting the second-largest source of gall-inducing insects, followed by the family Cecidomyiidae: Diptera (Csóka *et al*. 2005, Liljeblad & Ronquist 1998, Nieves-Aldrey & Fontal-Cazalla 1999, Ronquist & Liljeblad 2001). Each species produces its own gall type, which is anatomically and physiologically distinct from that of other related species (Shorthouse *et al*. 2005).

Nearly a thousand species of gall-inducing wasps have been reported (Hymenoptera: Cynipidae: Cynipini) in oak species (Fagaceae: *Quercus*) (Kinsey 1936, Weld 1960, Stone *et al*. 2002), and they are among the most structurally complex and diverse galls (Liljeblad *et al*. 2008). Gall structures reflect the primary characteristics of the insect inducer, representing an extension of their phenotype (Stone & Cook 1998). The host species of the Cynipini are almost exclusively limited to the *Quercus* genus (Liljeblad *et al*. 2008), although some use other hosts within the Fagaceae family, such as *Castanea*, *Castanopsis*, *Lithocarpus* and *Chrysolepis* (Nieves-Aldrey 2001, Stone *et al*. 2002, Liu & Ronquist 2006).

Each species of wasp from the Cynipini tribe is generally associated with inducing galls in practically all the organs (*e.g*., the leaves, roots, stems, and catkins) of their host species (Weld 1960, Ronquist 1994, 1995, Liljeblad & Ronquist 1998, Nieves-Aldrey 2001, Stone *et al*. 2002, Csóka et al. 2005). This association between wasps and oaks determines the global distribution pattern of this family of insects as well as the richness of the cynipid community in a specific locality (Nieves-Aldrey 2001, Stone *et al*. 2002).

In Europe, approximately 280 cynipid species have been recorded in 25 species of European oaks, which represents all the tribes of the Cynipidae (Nieves-Aldrey 2001, Stone *et al*. 2002, Rokas *et al*. 2003). Most of these endophagous insects have a life cycle with a spring-summer sexual generation and an autumn asexual generation, *i.e*., they exhibit an alternation of generations (Stone *et al*. 2002). During each generation, cynipid species have the ability to induce specific and complex galls on oaks, and in the majority of cases, they form a different gall morphotype each generation (*e.g*., sexual and asexual). Another characteristic in some species of cynipids is host alternation (heteroecy), which occurs every generation (Askew 1984, Cook *et al*. 1998, 2002).

Due to the diversity and structural complexity of the galls induced by cynipids, they are considered to be a microcosm of intense ecological activity since they support at least three trophic levels (gall tissue, gall-inducing wasps and occupants, and parasites and predators), which makes them a complex and interesting community for ecological-evolutionary studies (Nieves-Aldrey 2001, Ronquist & Liljeblad 2001, Hayward & Stone 2005).

It is estimated that there are approximately 500 oak species in the world and that the greatest species richness occurs in Mexico (Manos *et al*. 1999). Mexico is considered one of the centers of diversification for the *Quercus* genus with 161 species, of which 76 are located in the *Lobatae* section (red oaks), and 61 species are endemic to Mexico. In addition, the genus has 81 species in the *Quercus* section (white oaks) with 47 endemic species and four species in the *Protobalanus* section (intermediate oaks), with one endemic species (Valencia-Ávalos 2004).

One issue that is unclear is the specificity of cynipids to their host plants. In some European species, the alternation of hosts from different series of oaks has been reported at each reproductive stage, which indicates that the specificity may not be exclusively limited to a particular host species (Askew 1984, Stone *et al*. 2001, 2002). The specificity of gall-forming wasps has been poorly reviewed in the literature (Stone *et al*. 2002), and in Mexico, this group of insects and their ecological interactions have been poorly studied. Although the collection effort has not been as intense as in other countries, the species richness of cynipids has been estimated to range from 250 to 700 species based on the high richness of Mexican oak species (Nieves-Aldrey 2001). It is thus important to develop a strategy for the collection, breeding and identification of this group of insects in Mexico based on the distribution of oak species.

Based on the above priorities, it is necessary to study the species richness of cynipid species

Contribuciones de los autores
Enrique Pascual-Alvarado conceived the research, collected and analyzed the data, and wrote the manuscript.
José Luis Nieves-Aldrey designed the research project, collected and analyzed the data.
Douhglas Eliseo Castillejos Lemus made the review of the specialized literature and wrote the manuscript.
Pablo Cuevas Reyes conceived and designed the research project.
Ken Oyama conceived and designed the research project, wrote and edited the manuscript.

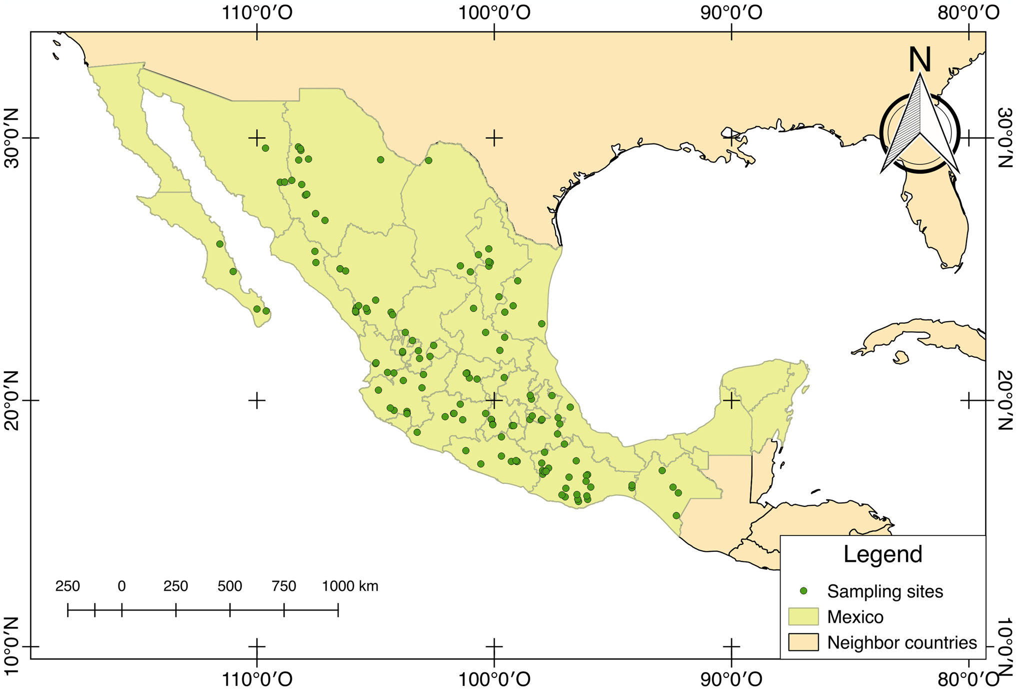
in Mexico, the diversity of gall morphology and the degree of gall specificity to their hosts. Therefore, the specific objectives of this study were to determine 1) the variations in wasp species richness among different oak sections in Mexico; 2) the morphological variation of galls induced by wasps on different oak species; and 3) the relationship between the cynipid species richness and the amplitude in the geographic distribution of the host oak species.

Materials and methods

A literature review of cynipid species associated with oaks was conducted, leading to the construction of a database to locate the species and establish them as starting points for the collection. Sampling was performed from March to August for four years (2008-2012) in 120 localities in total. For each oak species, at least five localities were visited. Geographic coordinates were taken at each location to define the distribution pattern of the cynipids associated with the different *Quercus* species (Figure 1).

Once the different oak species were located, an exhaustive search for galls was conducted at each site by checking each structure (*i.e*., apical buds, leaves, petioles, branches, stems, roots, catkins and acorns) of at least ten trees from each available *Quercus* species. In addition, herbarium specimens were collected to identify the oak species.

Figure 1. Sampling localities of gall morphotypes of oaks in Mexico.



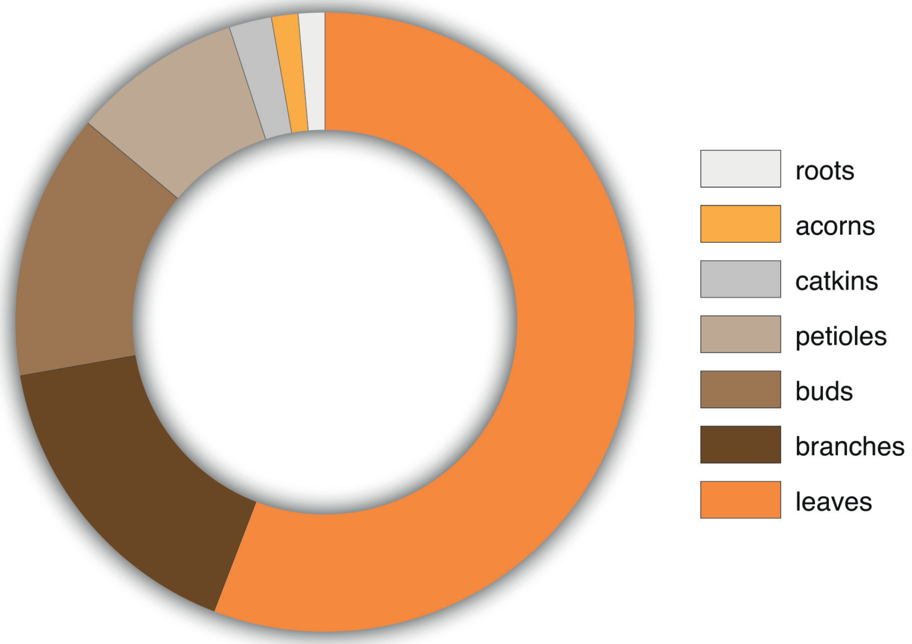
The collection of cynipids was based on gall morphology and was taken from across the country. A total of 80 oak species that were associated with this guild of herbivores was analyzed. For this study, each distinct gall morph is considered a potentially distinct species. We classified the galls according to the number of larval chambers as unilocular (a single chamber) or multilocular (with several chambers) and with or without ornaments (spines, hairs).

The collected galls were brought to the laboratory for growth and subsequent taxonomic determination. The taxonomy of the species is being determined in collaboration with Dr. José Luis Nieves-Aldrey from the National Museum of Natural Sciences in Madrid, Spain.

Results

A total of 224 distinct gall morphotypes induced by cynipids was found in 73 of the 80 oak species under analysis, of which 40 correspond to the *Lobatae* section (red oaks) and 33 to

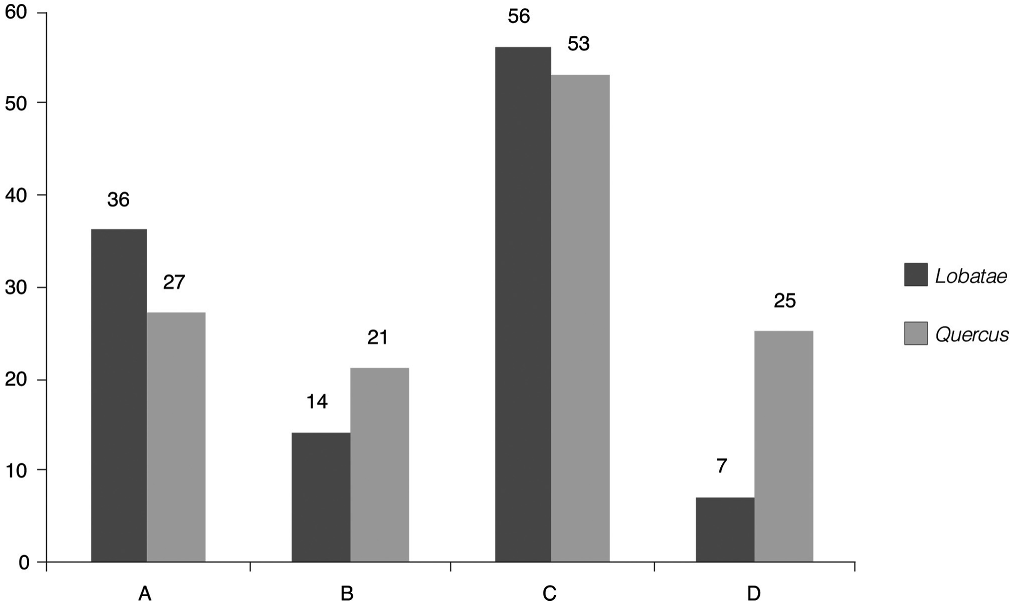
Figure 2. Number of gall morphotypes in each plant organ of oaks. Total number of galls = 224. 1 = leaves (125 galls; 55.8%); 2 = branches (37; 16.5%); 3 = buds (31; 13.8%); 4 = petioles (20; 8.9%); 5 = catkins (5; 2.2%); 6 = acorns (3; 1.3%); and 7 = roots (3; 1.3%).



the *Quercus* section (white oaks). Galls were not found in the following seven oak species: *Q. canbyi*, *Q. gentryi*, *Q. crispifolia* and *Q. hypoleucoides* from the Lobatae section and *Q. glabrescens*, *Q. glaucoides* and *Q. lancifolia* from the *Quercus* section. The largest number of morphotypes was found in leaves (125), followed by branches (37), buds (31), petioles (20), catkins (5), acorns (3) and roots (3) (Figure 2). A total of 126 gall morphotypes were found in the *Quercus* section, and 113 were found in the *Lobatae* section.

The number of gall morphotypes associated with each oak species, their taxonomic section, and the amplitude of geographical distribution and whether they are endemic to Mexico is summarized in Table 1. In the *Lobatae* section (red oaks), the species with the greatest number of morphotypes are *Quercus crassifolia* (11), *Q. castanea* (10) and *Q. mexicana* (7). The remaining species have one to five distinct morphotypes (Figure 3). In the *Quercus* section (white oaks),

Figure 3. Number of gall morphotypes according to the morphology in the two sections of oaks (*Lobatae* and *Quercus*). **A)** Unilocular without ornaments. **B)** Unilocular with ornaments. **C)** Multilocular without ornaments. **D)** Multilocular with ornamentes.



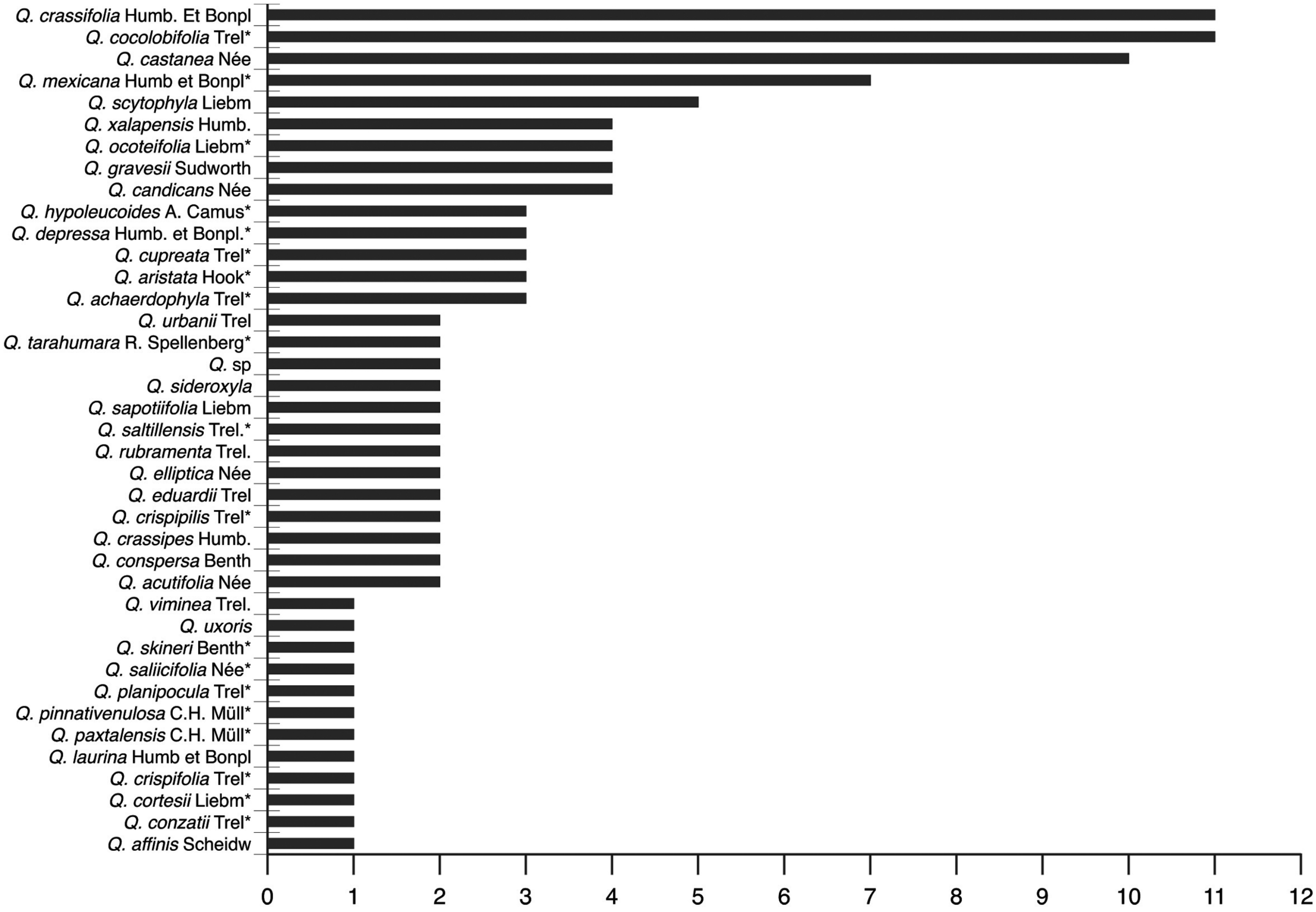


Figure 4. Number of gall morphotypes associated to each oak species in the Section *Lobatae*.

the oak species with the greatest number of gall morphotypes were *Q. microphylla* (20 morphotypes), followed by *Q. resinosa* (17) and *Q. magnoliifolia* (14). The remaining species have one to five distinct associated morphotypes (Figure 4). As in the case of section *Lobatae*, the species with the greatest number of morphotypes are those with a wide geographical distribution.

Only 31.5 % of the 73 oak species (13 red oaks and 10 white oaks) had only a single associated gall morphotype; 24.7 % (12 red and 6 white oaks) had two gall morphotypes, 16.4 % (6 red and 6 white oaks) had three gall morphotypes, and the remainder (27.4 %) had more than 4 morphs. Of the 13 species of red oaks with a single gall morphotype, 9 are endemic to Mexico, and of the 10 white oaks, 6 are endemic.

We found 63 galls with a single larval chamber (unilocular) with smooth surface (without ornaments) (36 in *Lobatae* and 27 in *Quercus*), 35 unilocular with ornaments (14 *Lobatae* and 21 *Quercus*), 109 multilocular without ornaments (56 *Lobatae* and 53 *Quercus*) and 32 multilocular with ornaments (7 *Lobatae* and 25 *Quercus*) (Figure 5).

Discussion

In this study, we found a great diversity of galls induced by wasps on oaks as host species (Figure 6). The assumption that gall-inducing wasps from the Cynipidae family exhibit a high degree of specialization to their host plants in the *Quercus* genus (Weld 1960, Ronquist 1995, Liljeblad & Ronquist 1998, Nieves-Aldrey 2001, Stone *et al*. 2002, Csóka *et al*. 2005) should be reviewed based on the results of this study. Most of the oak species studied here had more than one gall morphotype, and in some cases, they had an unexpectedly high number of gall morpho-

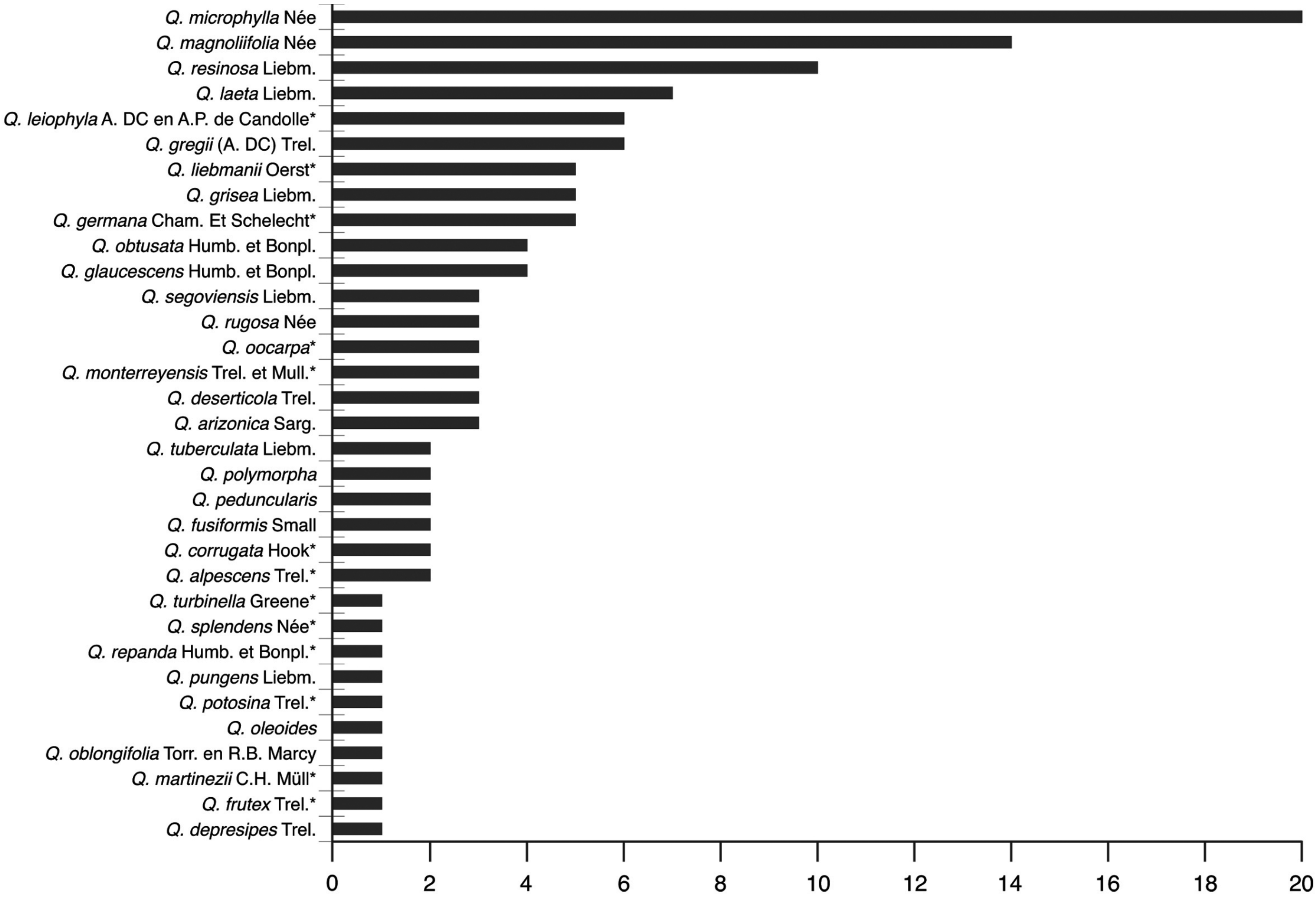


Figure 5. Number of gall morphotypes associated to each oak species in the Section *Quercus*.

types throughout their geographical distribution. In particular, three species of white oaks [*Q. microphylla* (20 morphotypes), *Q. resinosa* (17) and *Q. magnoliifolia* (14)] and three red oaks [*Q. crassifolia* (11), *Q. coccolobifolia* (11) and *Q. castanea* (10)] had a considerable number of galls collected from throughout their broad distribution in Mexico. These oak species have a wide range of geographic distribution occurring in different environmental conditions that could represent diverse ecological niches occupied by different gall wasps. It is also necessary to study the degree of host specialization of these galls through their entire geographic range in future studies.

In these cases, in particular, these oak species could be considered super hosts, since they have galls throughout their entire distribution and because galls occur over the entire structure of the tree. They also have morphotypes that are specific to certain localities, which may indicate endemism.

In the case of the endemic oak species, many have only a single morphotype, and even similar morphotypes had variations in bark texture or the inside the gall itself. It can therefore be assumed that they are distinct species and probably endemic and a detailed ecological and taxonomic study would need to be conducted for each of them.

By contrast, very unique morphs were discovered, which were only found on the leaves of oaks in the *Quercus* section, for example, *Q. magnoliifolia*, *Q. resinosa*, *Q. laeta*, *Q. deserticola*, *Q. rugosa* and *Q. obtusata*. According to Pujade-Villar *et al.* (2010), there is a new genus called *Kinseyella*, although confirming it would require a thorough review of both the gall and the gall inducers to know whether it is the same genus and a distinct species, or whether it is the same species of gall inducer in all the hosts listed here.

Figure 6. Photos of gall morphotypes in different oak species in Mexico. 1. *Quercus conzati* (petiole) Jal. 2. *Q. sideroxyla* (branch) Chih. 3 y 4. *Q.magnoliifolia* (leaves) Gro. 5. *Q. resinosa* (catkin) Mich. 6. *Q. crassifolia* (bud) Chis. 7. *Q. ocoteifolia* (yema) Oax. 8. *Q. uxoris* (leaf) Oax. 9. *Q. sp.* (branch) Ver. 10. *Q. castanea* (branch) Mich. 11. *Q. segoviensis* (catkin) Chis. 12. *Q. polymorpha* (leaf) NL. 13. *Q. arizonica* (leaf) Coah. 14. *Q. segoviensis* (leaf) Chis. 15. *Q. cupreata* (root) NL. 16. *Q. obtusata* (leaf) Dgo. 17. *Q. microphylla* (acorn) Gto. 18. *Q. laurina* (branch) Hgo. 19. *Q. gregii* (leaf) Dgo. 20. *Q. laeta* (bud) Mich. 21. *Q. rugosa* (bud) Jal. 22. *Q. conspersa* (branch) NL. 23. *Q. frutex* (leaf) Pue. 24. *Q. viminea* (bud) Dgo. 25. *Q. deserticola* (leaf) Sin. Abbreviations of each locality (state) as indicated in Table 1.

In the case of *Q. magnoliifoli*a and *Q. resinosa*, recent studies showed that these oak species form hybrids in regions where their geographic distributions overlap (Albarrán-Lara *et al*. 2010), generating new adaptive zones for the formation of new species of gall insects (Pérez-López *et al*. 2016). These zones are also suggested by the *Q. crassifolia* × *Q. crassipes* complex (Tovar-Sánchez & Oyama 2004) in which three gall morphotypes were exclusively associated with the hybrid individuals found there (Tovar-Sánchez & Oyama 2006). However, this pattern cannot be generalized, since in another hybrid complex formed by *Q. affinis* × *Q. laurina* (González-Rodríguez *et al*. 2004, González-Rodríguez & Oyama 2005, González-Rodríguez *et al*. 2005), only one gall morphotype was found in each of the species in this study (see Table 1).

The galls induced by cynipids can be classified according to the number of larval chambers (*e.g.*, unilocular and multilocular) and their ornamentation (*e.g.*, without ornamentation and a

Table 1. Number of gall morphotype associated to each oak species in the section Lobatae (red oaks) and section ***Quercus*** (white oaks). Oak endemic species to Mexico is indicated by an asterisk. The type of gall morphotype: U = unilocular, M = multilocular, s/o = without ornaments and c/o = with ornaments.

Section	Species	Collected states	Number of gall morphotypes	Unique gall in a population	Type of gall morphotype
Lobatae	*Q. acutifolia* Née	Mich., Oax., Jal.	2		Ms/o(2)
	Q. acherdophylla Trel. *	Hgo., Pue.	3		Us/o(1), Ms/o(2)
	Q. affinis M.Martens & Galeotti.	Gto., Pue., Hgo., Ver., S.L.P.	1		Ms/o
	Q. aristata Hook & Arn*	Jal., Nay.	3		Us/o(1), Ms/o(2)
	Q. candicans Née	Chih., Chis., Dgo., Gro., Jal., Mich., Nay., Oax	4		Us/o(1), Ms/o(3)
	Q. castanea Née	Chis., Col., Dgo., Gto., Gro., Hgo., Jal., Mich.,Oax.	10	Us/o (2)	Us/o(3), Ms/o(3), Uc/o(2), Mc/o(2)
	Q. coccolobifolia Trel.*	Chih., Jal., Nay.	11		Us/o(4), Ms/o(4), Uc/o(2), Mc/o(1)
	Q. conspersa Benth.	Chih., Gro., Jal., Mich., N.L.	2		Ms/o(2)
	Q. conzattii Trel.*	Dgo., Jal., Oax., Zac.	1		Ms/o
	Q. cortesii Liebm.*	Chis., Oax., Ver.	1		Ms/o
	Q. crassifolia Bonpl.	Chih., Chis., Dgo., Mich., Oax.	11		Us/o(4), Ms/o(4), Uc/o(2), Mc/o(1)
	Q. crassipes Bonpl.	Col., Gto., Hgo., Mich.	2		Ms/o(2)
	Q. crispifolia Trel.*	Chis., Oax.	1		Ms/o
	Q. crispipilis Trel.*	Chis.	2		Uc/o(1), Ms/o(1)
	Q. cupreata Trel. & C.H.Mull.*	N.L.	3	Us/o(1)	Us/o(1), Ms/o(2)
	Q. depressa Bonpl.*	Hgo.,Oax., Ver.	3		Us/o(1), Ms/o(2)
	Q. eduardi Trel.	Chih., Dgo., Mich., Ver.	2		Us/o(1), Ms/o(1)
	Q. elliptica Née	Chis., Jal., Mich., Sin.	2		Us/o(1), Ms/o(1)
	Q. gravesii (Sarg.) Sudw.	Coah.	4		Us/o(1), Uc/o(1), Ms/o(1)
	Q. hypoleucoides A.Camus*	Chih., Coah., Dgo.	3		Us/o(1), Ms/o(2)
	Q. laurina Bonpl.	Gro., Gto., Hgo., Mich., Pue., Tlax., Ver.	1		Ms/o
	Q. mexicana Bonpl.*	Coah., Hgo., N.L., Tamps., Tlax., Ver.	7	Uc/o(1)	Us/o(2), Ms/o(3), Uc/o(1), Mc/o(1)
	Q. ocoteifolia Liebm.*	Chis. , Oax.	4	Uc/o(1)	Us/o(1), Uc/o(1) Ms/o(2)
	Q. paxtalensis C.H.Müll.*	Chis.	1		Us/o
	Q. pinnativenulosa C.H.Müll.*	N.L. ,Ver.	1		Us/o
	Q. planipocula Trel.*	Mich, Gro., Sin.	1		Us/o
	Q. rubramenta Trel.	Gro., Oax.	2		Us/o(1), Ms/o(1)
	Q. salicifolia Née*	Gro., Jal., Mich.	1		Ms/o
	Q. saltillensis Trel.*	Coah., N.L.	2		Us/o(1), Ms/o(1)
	Q. sapotifolia Liebm.	Chis., Hgo., Oax., Ver.	2		Uc/o(1), Ms/o(1)
	Q. scytophylla Liebm.	Gro., Jal., Mich., Pue.	5		Us/o(2), Ms/o(2), Mc/o(1)
	Q. sideroxyla Bonpl	Ags., Chih. Coah., Dgo., Jal., Zac.	2		Us/o(1), Ms/o(1)
	Q. sp.	Tamps., Ver.	2		Us/o(1), Ms/o(1)
	Q. skinneri Benth.*	Chis., Oax.	1		Us/o
	Q. tarahumara R. Spellenb., J.D. Bacon & Breedlove*	Chih, Sin, Dgo.	2		Us/o(1), Mc/o(1)
	Q. urbanii Trel.	Dgo., Gro., Sin.	2		Us/o(1), Ms/o(1)
	Q. uxoris McVaugh	Col., Jal., Oax.	1	1 Uc/o	Uc/o
	Q. viminea Trel.	Ags., Dgo., Gto., Nay.	1		Ms/o
	Q. xalapensis Bonpl.	Hgo., Ver.	4		Us/o(1), Uc/o(1), Ms/o(2)
Quercus	*Q. alpescens* Trel.*	Hgo., N.L.	2		Ms/o (2)
	Q. arizonica Sarg.	Chih., Coah., Dgo.	3		Us/o (1), Mc/o (2)
	Q. corrugata Hook*	Chis, Gro., Ver.	2		Uc/o(1), Ms/o(1)
	Q. depressipes Trel.	Chih., Zac.	1		Ms/o(1)
	Q. deserticola Trel.	Gto., Jal., Mex., Mich., Oax., Qro., Sin.	3		Uc/o(1), Ms/o(2)
	Q. frutex Trel.*	Hgo., Mex., Oax., Pue.	1		Uc/o(1)
	Q. fusiformis Small	Coah., N.L.	2		Ms/o (2)

Table 1. Continuation.

Section	Species	Collected states	Number of gall morphotypes	Unique gall in a population	Type of gall morphotype
	Q. germana Schltdl. & Cham. *	Oax., Pue., Ver.	5		Us/o(1), Uc/o(1), Ms/o(2), Mc/o(1)
	Q. glaucescens Bonpl.	Gro., Jal., Mich., Sin.	4		Us/o(1), Ms/o(3)
	Q. greggii (A.D.C) Trel.	Coah., Dgo., N.L.	6		Us/o(1), Uc/o(1), Ms/o(2), Mc/o(2)
	Q. grisea Liebm.	Ags., Chih.,Coah., Gto., Jal.	5		Us/o(1), Uc/o(1), Ms/o(2), Mc/o(1)
	Q. laeta Liebm.	Ags., Coah., Dgo.,Gto., Hgo., Jal., Mex., Mich., Zac	7		Us/o(1), Uc/o(2), Ms/o(2), Mc/o(2)
	Q. leiophylla A.D.C. *	Oax., Pue.	6		Us/o(1), Uc/o(1), Ms/o(2), Mc/o(2)
	Q. liebmannii Oerst ex Trel*	Gro.	5		Us/o(1), Uc/o(1), Ms/o(2), Mc/o(1)
	Q. magnoliifolia Née	Col.,Gro., Hgo., Jal., Méx., Mich., Oax., Pue., Sin.	14	Us/o(1), Uc/o(1), Ms/o(1)	Us/o(4), Uc/o(4), Ms/o(4), Mc/o(2)
	Q. martinezii C.H.Mull*	Gro., Jal., Nay., Mich.	1		Mc/o (1)
	Q. microphylla Née	Ags.,Gto., Nay.	20		Us/o(6), Uc/o(4), Ms/o(6), Mc/o(4)
	Q. monterreyensis Trel. & C.H.Mull.*	N.L.	3		Us/o (1), Mc/o (2)
	Q. oblongifolia Torr.	Chih., Coah., Son.	1		Ms/o(1)
	Q. obtusata Bonpl.	Dgo., Gro., Gto., Jal., Mich.	4		Us/o(1), Ms/o(3)
	Q. oleoides Schltdl. & Cham.	Chis., S.L.P., Oax.	1		Mc/o (1)
	Q. oocarpa Liebm.*	Jal., Nay.	3		Us/o (1), Mc/o (2)
	Q. peduncularis Neé	Chis., Col., Nay.	2		Ms/o (2)
	Q. polymorpha Schltdl. & Cham.	Chis., Hgo., N.L.	2	Us/o(1), Ms/o(1)	Us/o(1), Ms/o(1)
	Q. potosina Trel.*	Ags., Dgo., S.L.P.	1		Ms/o(1)
	Q. pungens Liebm.	Chih.	1		Ms/o(1)
	Q. repanda Michx..*	Hgo., Tlax.	1		Ms/o(1)
	Q. resinosa Liebm.	Ags., Dgo., Gto., Jal., Mich.	10	Uc/o(1)	Us/o(2), Uc/o(2), Ms/o(4), Mc/o(2)
	Q. rugosa Née	Ags., Chis., Col., Gro., Gto., Mich., Mor., N.L., Zac.	3		Us/o(1), Uc/o (1), Ms/o(1)
	Q. segoviensis Liebm.	Chis.	3	Ms/o (1)	Us/o (1), Ms/o (2)
	Q. splendens Née*	Nay., Jal., Mich.	1		Ms/o(1)
	Q. tuberculata Liebm.	B.C., Nay., Son.	2		Us/o(1), Ms/o(1)
	Q. turbinella Greene*	B.C., Son.	1		Ms/o(1)

States abbreviations. Ags.: Aguascalientes; BC: Baja California; Coah.: Coahuila; Col.: Colima; Chih.: Chihuahua; Chis.: Chiapas; Dgo.: Durango; Gro.: Guerrero; Gto.: Guanajuato; Hgo.: Hidalgo; Jal: Jalisco; Méx.: Estado de México; Mich.: Michoacán; Mor.: Morelos; Nay: Nayarit; N.L.: Nuevo León; Oax.: Oaxaca; Pue.: Puebla; S.L.P.: San Luis Potosí; Sin.: Sinaloa; Son: Sonora; Tamps.: Tamaulipas; Tlax.: Tlaxcala; Ver.: Veracruz; Zac.: Zacatecas.

smooth surface, or with hair and spines). The highest numbers of galls for both sections are multilocular galls without ornamentation, and they are usually associated with the branch of the host. According to Ronquist (1995, 1999) and Rokas *et al*. (2003), this gall morphotype is the most primitive, suggesting the colonization of the host by cynipids. Confirming this colonization would require a phylogenetic and comparative biological study to locate these species relative to European species and assess their degree of relationship.

There is, however, a peculiar morph in the *Lobatae* section that is unilocular, globular, with or without ornamentation, and similar to galls from the *Amphibolips* genus (Nieves *et al*. 2012). This finding may indicate that there is a particular association between this endemic group of oaks with a genus of cynipid inducers, an interaction so specific that it could be considered a process of speciation that often occurs in the hosts of this section of oaks (Nieves *et al*. 2012).

The collection effort is a key factor in this type of study. Maldonado-López *et al*. (2015a, b, 2016) recorded up to 40 morphologically distinct galls that were induced by wasps on *Q. castanea* throughout its geographic distribution. This finding suggests that studies with both greater temporal and spatial collection intensity, focused on a single species of oak throughout its entire distribution, can produce this type of result.

Conclusions and perspectives

Gall-forming wasps (Hymenoptera: Cynipidae: Cynipini) represent a very diverse group with ecologically interesting characteristics (Nieves-Aldrey 1998, 2001, Ronquist & Liljeblad 2001, Hayward & Stone 2005). In this study, an important effort to add new records to this guild of insects in Mexico was undertaken. However, it is necessary to continue this type of study to determine the total species richness of wasps in Mexico as well as their phylogenetic relationships, and finally, to establish their patterns of diversification. Mexico represents one of the two most important centers of oak diversification in the world, especially for red oaks (section *Lobatae*). These collection efforts must be accompanied by taxonomic studies that elucidate the discovery of new species (Nieves-Aldrey *et al*. 2012) and even genera as observed in some of the collections made in this study.

One important and characteristic aspect of the cynipids associated with oaks is that they are cyclically parthenogenetic, which has been a source of confusion during their taxonomic classification. Thus, studies should focus on finding both morphological (Hernández-Soto *et al*. 2015) and molecular tools to resolve this problem, in addition to elucidating which processes cause this phenomenon.

At the population level, it is important to determine the dispersal distances of individuals and their patterns of colonization in both themselves and their new hosts through either ecological studies (Schönrogge *et al*. 1994, 1999) or genetic studies using molecular markers (Castillejos-Lemus 2016).

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Revision of the *Amphibolips* species of Mexico excluding the "*niger* complex" Kinsey (Hymenoptera: Cynipidae), with description of seven new species

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Abstract

The species of *Amphibolips* Reinhard 1865 (Hymenoptera: Cynipidae: Cynipini) of Mexico not included in the "*niger* complex" Kinsey 1937 are revised. The "*nassa* complex" recently created by Melika *et al.* (2011) for these species is questioned. As a result of faunistic surveys of oak gall wasps in Mexico, seven new species of *Amphibolips* are described: *Amphibolips durangensis* Nieves-Aldrey & Maldonado, *A. malinche* Nieves-Aldrey & Pascual, *A. jaliscensis* Nieves-Aldrey & Pascual, *A. oaxacae* Nieves-Aldrey & Pascual, *A. nevadensis* Nieves-Aldrey & Pascual, *A. tarasco* Nieves-Aldrey & Pascual and *A. michoacaensis* Nieves-Aldrey & Maldonado. The types of *A. dampfi* Kinsey 1937, *A. nebris* Kinsey 1937 and *A. fusus* Kinsey 1937 are revised, redescribed and compared with the new species described herein. A new key for the identification of adults of all species not included in the "*niger* complex" from Mexico, including the related species *A. castroviejoi* Medianero & Nieves-Aldrey and *A. aliciae* Medianero & Nieves-Aldrey from Panama, is presented. Diagnostic characters, distribution data, host plants and species biology are provided for of all of the studied species. The richness and distribution of *Amphibolips* in Mexico and the Neotropical region, their known biological data, and the taxonomic limits of this genus are also discussed.

Key words: Cynipidae, oak gall wasps, *Quercus*, Mexico

Introduction

The cynipids of the tribe Cynipini (Hymenoptera: Cynipidae), known as the oak gall wasps, form the largest group of gall wasps, including more than 1000 described species, all of which are gall inducers exclusively on plants of the Fagaceae family (Nieves-Aldrey 2001; Liljeblad *et al.* 2008). The oak gall wasp fauna of Mexico has not been well studied and remains poorly known. However, it is estimated that this fauna is potentially very rich because of the great diversity of their host *Quercus* species, 161 species of which are found in México, including 109 endemic species (Valencia-A 2004). A recent inventory of the Cynipidae of Mexico recorded 157 cynipid species (Pujade-Villar *et al*. 2009). However, more recent and ongoing studies on Mexican oak gall wasps are rapidly increasing the number of recorded species.

Amphibolips Reinhard 1865 is a distinctive genus of oak gall wasps (Cynipidae: Cynipini) recorded as being confined to America. The known range of this genus, which was assumed to extend only in the Nearctic, was recently enlarged to the Neotropical region, with three species described from Panama (Medianero & Nieves Aldrey 2010).

At present, forty-five species are known throughout the distribution area of this genus, extending from Canada to Panama. There are 42 species recorded in the Nearctic region, and three are known from Panama: *A. castroviejoi* Medianero & Nieves-Aldrey, *A. aliciae* Medianero & Nieves-Aldrey and *A. salicifoliae* Medianero & Nieves-Aldrey (Medianero & Nieves-Aldrey 2010). Of the 42 Nearctic species, 30 have been recorded from the USA and Canada,

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and 11 species are known only from Mexico (Burks 1979; Melika & Abrahamson 2002; Melika *et al.* 2011). Additionally, one species, *A. niger* Beutenmüller, is known from Mexico and southern Arizona (Burks 1979).

Twelve species are known from Mexico, of which seven species belongs to the "*niger* complex" of species (Kinsey 1937; Melika *et al.* 2011): *A. niger* Beutenmüller 1911, *A. gumia* Kinsey 1937, *A. jubatus* Kinsey 1937, *A. elatus* Kinsey 1937, *A. maturus* Kinsey 1937, *A. nebris* Kinsey 1937 and *A. pistrix* Kinsey 1937. The remaining six species were recently included into the "*nassa* complex" (Melika *et al.* 2011); these include *Amphibolips palmeri* Bassett 1890; three species described by Kinsey, *A. dampfi* Kinsey 1937, *A. nassa* Kinsey 1937 and *A. fusus* Kinsey 1937; and two recently described species, *A. zacatecaensis* Melika & Pujade-Villar 2011 and *A. hidalgoensis* Pujade-Villar & Melika 2011.

The morphological characters of adults and their galls are very uniform among the majority of the known species of *Amphibolips*. These characters include 12–14 segmented antennae in females and 15–16 segmented antennae in males; a robust body with a strong coarsely sculptured head and mesosoma; notauli often obscured by the rugose sculpture; a mesoscutellum often more or less emarginated posteriorly; tarsal claws with a large acute basal lobe or tooth; metasomal tergites usually micropunctate from the posterior part of the second metasomal terguite; forewings usually more or less smoked, often very heavily infuscate, especially in males, with dark bands or spots and a long, narrow radial cell, opened on the wing margin; and the projected part of hypopygium very long and robust (Melika & Abrahamson 2002; Medianero & Nieves-Aldrey 2010; Melika *et al.* 2011). However, there are some *Amphibolips* species that present anomalies in some of these diagnostic characters, thus revealing that the taxonomic limits of the genus are not still clear. This is the case for *A. salicifoliae* Medianero & Nieves-Aldrey from Panama, a species that while presenting most of the diagnostic characters of the genus, exhibits simple metatarsal claws. Another example provided by the species of the "*niger* complex" (Kinsey, 1937) from Mexico, which present 16–17 segmented antennae as well as other morphological and biological characters, such as the sculpture of the mesoscutum and the morphology of their galls, that differ from the typical *Amphibolips* species.

The known *Amphibolips* species from Mexico, out of the "*niger* complex", appears to be a group morphologically distinctive, easily differentiate by their darkest forewing color pattern and emarginated mesoscutellum, from the *Amphibolips* species from USA and Canada.

The understanding of the phylogenetic relationships of *Amphibolips*, both within the genus and with other related Cynipini genera, is still poor. In a recent morphological phylogenetic analysis performed by Liljeblad *et al.* (2008), one *Amphibolips* species was included, but the results were not conclusive with regard to its phylogenic relationships with other genera. Ongoing molecular studies will hopefully contribute to filling this gap in knowledge.

The life cycles of *Amphibolips* species are heterogonic, and both bisexual and asexual forms are known. However, for a great majority of these species, including all of the Mexican and Panamanian species, the complete life cycle is not still known. It is therefore likely that some species described separately based on only either the bisexual or asexual generation could belong to a single species.

All known *Amphibolips* species are associated with *Quercus* species of the section Lobatae (red oaks). The galls induced by species of this genus develops mainly in buds, stems or leaves, rarely also in acorns. They are usually globose to spindle shaped and detachable, with a spongy parenchyma surrounding a central larval cell, sometimes supported by radiating filaments (Beutenmüller 1909; Kinsey 1937; Melika & Abrahamson 2002).

In a recent paper by Melika *et al.* (2011), current knowledge of the Mexican species of *Amphibolips* was updated, and two species new were described: *A. zacatacaensis* Melika & Pujade-Villar and *A. hidalgoensis* Pujade-Villar & Melika. Symmetric to the "*niger* complex" proposed by Kinsey (1937), a second group, the "*nassa* complex" of species, was proposed, and a key for identification of the species of this group was provided. However, this key is not entirely satisfactory in our opinion because the important diagnostic character of forewing colour pattern was neglected or misunderstood. This shortcoming is because the forewing was not examined in the types of some key species described by Kinsey as *A. dampfi*, *A. fusus* and *A. nassa*. As a result, the interpretation of the affinities between species may be incorrect, and their taxonomic separation was not clear in the key.

The objective of this study is to present a revision of the species of *Amphibolips* from Mexico not belonging to the "*niger* complex". As a result of several years of oak gall wasp sampling efforts in a number of states, mainly in the centre of Mexico, new materials were collected containing representatives of seven species new to science, including males of three species, which are described herein. Based on these new materials and examination of Kinsey types, we revise the entire "*nassa* complex" (*sensu* Melika *et al.* 2011), including the related species from

Panama *A. castroviejoi* and *A. aliciae*. A new identification key is provided for all of the species in the group as considered herein. And finally, in the light of the new data and understandings provided in this study, the actual and expected species richness of this genus in Mexico are discussed as well as the taxonomic problems still existing within the group.

Material and methods

Study material. Samplings of *Quercus* species were performed in several states of Mexico from 2007 to 2011, with more intensive samplings of *Quercus castanea* being carried out in selected localities of the state of Michoacan. Galls were collected on the sampled oaks and stored in rearing cages until the emergence of insects. The adult insects emerged from the galls under laboratory conditions. Voucher adult specimens and their galls were deposited in the entomology collections of the Museo Nacional de Ciencias Naturales, Madrid (Spain) and the Laboratorio de Ecología Genética y Molecular, CIEco, UNAM (Mexico). The identification of the *Quercus* species was based on several key references (Govaerts & Frodin, 1998; Valencia-A 2004).

Examination of types

Type materials of three species described by Kinsey from Mexico were examined: *Amphibolips fusus* Kinsey 1937; *Amphibolips nebris* Kinsey 1937; and *Amphibolips dampfi* Kinsey 1937. Kinsey´s type materials were borrowed from the American Museum of Natural History, New York (AMNH) (James Carpenter). Additionally, two paratypes of *A. hidalgoensis* Pujade-Villar & Melika and galls of *A. hidalgoensis* and *A. zacatacaensis* Melika & Pujade-Villar given by the University of Barcelona (Juli Pujade-Villar) were also examined. We could not examine materials of two other species, *Amphibolips palmeri* Basset and *A. nassa* Kinsey 1937. However, some notes on the latter were provided in Melika *et al.* (2011) and have been used here.

Specimen preparation. For observation under a scanning electron microscope (SEM), adult cynipids were dissected in 70% ethanol, air dried, mounted on a stub and coated with gold. Micrographs were obtained with an FEI QUANTA 200, FEI Company (Oregon, USA), operating with high vacuum technique, from several standardised views. Forewings were mounted on slides in Euparal and later examined under a Wild MZ8 stereo microscope. Representatives of some species that were poorly represented in the samples were not dissected but were instead directly observed with the same SEM using a low vacuum (voltage) technique, without coating. Images of the adult habitus and gall dissections were obtained with a NIKON Coolpix 4500 digital camera attached to a Wild MZ8 stereo microscope. Measurements were performed using a calibrated micrometre scale attached to an ocular of the light microscope.

Morphological terms

The terminology of morphological structures and abbreviations follow Ronquist & Nordlander (1989), Nieves-Aldrey (2001) and Liljeblad *et al.* (2008).

Results

Studied species

"*niger* complex" Kinsey, 1937

Amphibolips nebris Kinsey 1937

Figs 1A–B &H, 13C, 14F

Amphibolips nebris Kinsey. *Rev. Entom.*, 7(4): 442

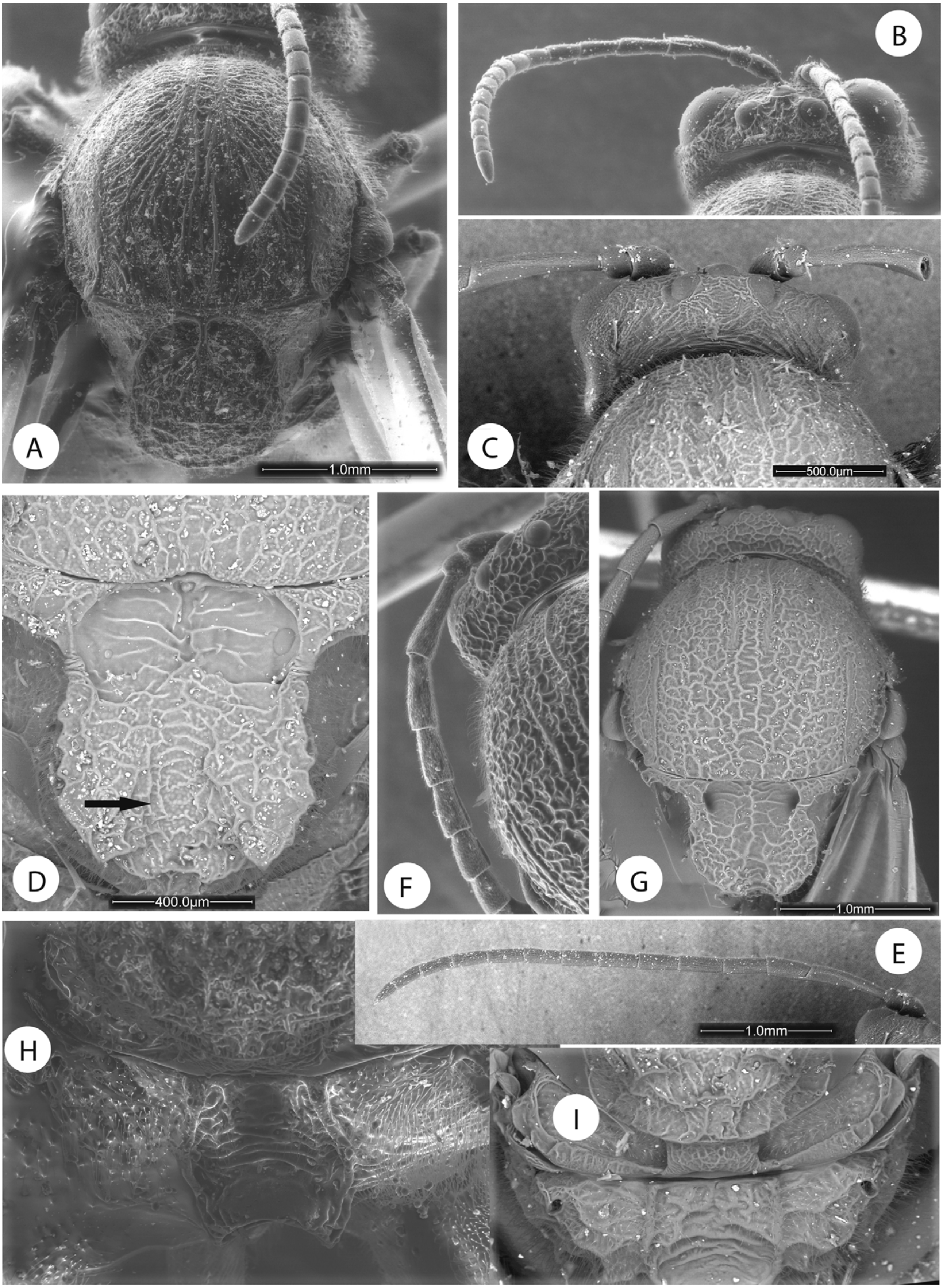

FIGURE 1. *Amphibolips nebris* (A) mesosoma dorsal view; (B) head and antennae dorsal view; and (H) propodeum. *Amphibolips dampfi* (C) head dorsal view; (D) mesoscutellum dorsal view; (E) antenna; and (I) propodeum. *Amphibolips fusus* (F) antenna; and (G) head and mesosoma dorsal view.

Material examined: Holotype female (AMNH).

The holotype, glued to a card point, is in poor condition. The metasoma is missing.

Labels: red Holotype, Parral /2W; Chi 6800; 28–31; 1 ♀, 4.22.32

Quercus eduardi, Kinsey coll.

Here, we present and illustrate some diagnostic characters in addition to those provided in the original description.

Head, dorsal view, 2.7 as wide as long. POL 4 times OOL: OOL shorter than diameter of a lateral ocellus. Antennae with 16 antennomeres (Fig.1B). Pedicel 1.4 as long as wide. F1 1.3 as long as F2. Mesoscutum with longitudinal carinate sculpture, more radiate anteriorly (Fig. 1A). Scutellar foweae ellipsoidal, separated medially by a ridge. Mesoscutellum moderately rugose, rounded posteriorly, not emarginated at its posterior margin (Fig. 1A). Median area of propodeum only slightly rugose laterally; lateral propodeal carinea distinct, slightly divergent (Fig. 1H). Forewing only clouded near anterior margin; first abscisa of radius distinctly projected into radial cell; areolet conspicuously large (Fig. 13C).

Distribution: Chihuahua, Parral

Host: *Quercus eduardi*

Gall: Of the type of galls of the "*niger* complex": a large densely wooly mass containing a hard woody core in which the larval cell is located (Kinsey 1937; Melika *et al*. 2011). In *A. nebris* the gall is large, up to 70 mm; color yellow tan and rosy russet (Kinsey 1937).

Comments

The characters of this species are representative of those shared by the species of the "*niger* complex" (Kinsey 1937), being the most important the 16 segmented antennae, mesoscutellum not emarginated posteriorly, sculpture on mesoscutum not coarsely rugose and forewing less heavily infuscate, which together with its morphologically different galls readily differentiates this species from the remaining Mexican species studied herein.

Species included in the "*nassa* complex" (Melika *et al.* 2011)

The species of *Amphibolips* from Mexico not included into the "*niger* complex" present the following diagnostic characters:

Diagnosis

Head and mesossoma coarsely rugose-reticulate sculptured. Antennae of 13–14 antennomeres in females, 15 segmented in male. Mesoscutellum emarginated in its posterior margin, continued into a submediam impression more or less deep and wide. Forewing moderately to heavily infuscate in females, more entirely in males; with a pattern of clear spots and bands variable extended. Metatarsal claws with a large acute triangular basal lobe or tooth. Sexual forms. Galls from spherical or globose, pointed or not at apex, to more or less fusiform or spindle-shaped.

Comments

The "*nassa* complex" of species was implicitly created by Melika *et al*. (2011), who used this name in a key for the identification of the Mexican species of *Amphibolips*. This convention was confusing because the grouping was not formally described in the referenced paper, as was performed by Kinsey for the "*niger* complex". The only diagnostic character provided for the "*nassa* complex" was a mesoscutellum with posteromedian emargination. However, as we will discuss later, this main character is not discriminant because it is also present in other species from the USA and Panama. Consequently, the "*nassa*" complex should no longer be maintained.

Amphibolips fusus Kinsey 1937

Figs 1F–G, 14C–E

Amphibolips fusus Kinsey. *Rev. entom.*, 7(4): 430

Material examined: Holotype female (AMNH)

The Kinsey description of this species is clear and provided the main diagnostic characters. Some of these characters, such as the forewing colour pattern and the shape of the mesoscutellum, are now illustrated.

Diagnosis

F1 1.3 as long as F2 (Fig. 1F). Mesoscutellum slightly emarginated posteriorly; posteromedian impression shallow and not reaching posterior margins of scutellar foveae (Fig. 1G). Scutellar foveae rounded, with some irregular rugae, the intervals smooth and shining. Forewing (Fig. 14E) with basal half only slightly infuscate; apical half heavily infuscate from the radial cell, which is interrupted by a broad clear cross band extended from antero-apical area of radial cell, to posterior area, into the discoidal cells.

Distribution: Zacatecas: Cantuna

Host: *Quercus eduardi*

Gall. A slender to globose, spindle-shaped oak apple, with the tip and base quite fine. A photograph of the gall was provided in Melika *et al*. (2011).

Life history. Unknown; only females reared from galls in November.

Comments

This species was regarded by Melika *et al*. (2011) as very similar to *A. zacatecaensis*. However, the forewing patterns of the two species are quite different, which is a character that seems to be mistaken or overlooked by that authors. According to the coloration pattern of the forewing and shape of the gall, we consider this species to be more closely allied with the Panamanian species *A. aliciae* Medianero & Nieves-Aldrey 2010. One female that we reared from a globose, apically pointed gall collected in Nuevo León presented a similar forewing pattern (Fig. 21B) and could be identified as *A. fusus*, or more likely, a different closely allied species because of slight differences in the forewing patterns (Fig. 12F). However, other morphological characters are not well differentiated in this specimen, and it is not possible to come to a conclusion regarding its taxonomic status. We also collected galls similar to those of *A. fusus* in Monterrey and Nuevo León (Figs. 20E, 20F), but we unfortunately did not rear any adults from these galls.

Amphibolips dampfi **Kinsey 1937**

Figs 1C–E & I, 13A, 14A–B

Amphibolips dampfi Kinsey. *Rev. entom*., 7(4): 429

Material examined. Holotype male (AMNH)

The holotype is in bad condition. Glued to a card; right antenna and left forewings missing.

Labels: Holotype. *Amphibolips dampfi*. Sierra Juarez between Villa Juarez and Tepan Zacoalco 2.24.32/ 8700 *Quercus ocoteaefolia* Dampf coll.

We present and illustrate some diagnostic characters in addition to those provided in the original description.

Diagnosis

Head, dorsal view 3 as wide as long; with wrinkled reticulate sculpture (Fig. 1C). Antennae with 15 antennomeres (Fig. 1E): Relative lengths of antennal segments as: 10:7:30:16:16:16:16:15:14:14:13:13:12:10:10; F1 1.8 as long as F2, flattened ventrally and slightly enlarged apically. Placodeal sensillae visible in all flagellomeres. Notauli indistinct, obscured by coarse rugose reticulate sculpture of mesoscutum. F1 Scutellar foveae 0.4 as long as mesoscutellum; rounded, with defined margins, medially not well separated by a carina; with some strong transversal carinae, the intervals smooth and shining. Mesoscutellum strongly and widely emarginated posteriorly, V shaped in dorsal view (Fig. 1D); the posteromedial impression deeply and widely extended anteriorly to reach near posterior margins of scutellar foveae. In lateral view with sharp horn projection. Metascutellum reticulate rugose; metanotal trough smooth and pubescent. Median propodeal area coarsely and irregularly carinate, and pubescent; lateral propodeal carinae distinct, subparallel (Fig. 1I). Nucha smooth medially, laterally carinate. Forewing (Fig. 13A) heavily infuscate, with a clear cross band from apical area of radial cell which is extended widening below the radial cell, crossing the Medial vein, but not reaching posterior margin of wing. Radial cell 3.7 as long as wide; veins being visible, R1 and radius not quite reaching anterior margin of wing; Rs1 projected into the radial cell; Rs2 slightly curved.

Distribution: Oaxaca, Sierra Juarez

Host: *Quercus ocoteifolia*, a synonym of *Q. laurina*

Gall. A spongy oak apple similar to that of the American *A. confluentus* (Harris). More or less spherical, thin-shelled, spongy interior dense though soft, larvae central or nearer the base of the gall, galls up to 48 mm in diameter, detachable, on twigs.

Biology

Bisexual; galls mature by February, and adults emerge between February and April

Amphibolips nassa Kinsey 1937

Amphibolips nassa Kinsey. *Rev. entom*., 7(4): 432

Type material: This species was described by Kinsey from a single female and a gall. The female holotype has not been located in the Kinsey collection, actually at the AMNH. A photograph of the gall was provided in Melika *et al.* (2011), but these researchers did not examine the adult type specimen (Melika pers comm.).

Kinsey´s description of the species, with reference to the diagnostic characters of the forewing colour pattern and scutellum, was as follows: wings smoky yellow all over, with a heavy brown cloud on the anterior margin covering most of the basal, first cubital, radial cells and the anterior portion of the third cubital cell, without the clear break in this band found in some other Mexican species of *Amphibolips*.

Scutellum: mesoscutellum broad, square, deeply depressed anteriorly to form a wide, nearly smooth, and almost undivided foveal groove, median longitudinal depression of the mesoscutellum narrow and shallow, except posteriorly, where it cuts a wide, deep notch into the posterior edge of the mesoscutellum.

Gall: A rather large, globose but slightly spindle-shaped oak apple with a fine tip and base. Body of gall quite globose. A photography of the gall was provided by Melika *et al.* (2011).

Distribution: Michoacán, Purépero on *Quercus mexicana* and *Q. castanea* (= *Q. serrulata*).

Comments

Based on its forewing pattern and gall, *A. nassa* is very similar to the recently described *Amphibolips zacatecaensis* Melika & Pujade-Villar 2011. However, according to the descriptions of the two species, the mesoscutellum seems to be more deeply and widely emarginated in *A. nassa*. The galls of *A. nassa* and *A. zacatecaensis* are quite similar, but Melika *et al.* (2011) noted that the galls of *A. nassa* are more elongate and fusiform, with a hard lignified parenchyma, while the galls of *A. zacatecaensis* are globose, with a soft spongy parenchyma. In his key for the identification of the "*nassa* complex", Melika *et al.* (2011) mistakes the forewing pattern of *A. nassa*, in which, according to Kinsey's description and illustration of the forewing, the heavy dark stripe or band along the anterior margin of the wing is not interrupted by any clear cross band. After our analysis, we consider *A. nassa* to be more similar to the new species *A. oaxacae* described here, with the two species being differentiated by their coloration, relative emargination of the mesoscutellum and shape of the gall.

Amphibolips palmeri Basset 1890

Amphibolips palmeri Basset 1890. *Tran. Am. Ent. Soc*., 17:86

This species is cited as the largest known species of gall fly and "oak apple gall" (Beutenmüller 1909). It was described from materials collected in Sierra Madre, Chihuahua, and Guadalajara, Jalisco, Mexico. This species was apparently overlooked by Kinsey in his work addressing the *Amphibolips* of Mexico (Kinsey 1937).

It was not possible to find the type material. However, we reproduce the description provided by Beutenmüller (1909), which is diagnostic with regard to the forewing colour pattern.

Wings dark, smoky brown, with a very dark brown cloud covering the areolet and the lower half of the radial area; beyond this and extending across the radial area to almost the posterior margin is a light colourless spot, and the anterior margin from the dark, broad, first cross-vein to a short distance beyond the second cross-vein is of the same light colour; tip of wing beyond the pale spot is dark smoky brown, as below this spot. Areolet very small but well defined.

Gall. Produced on twigs of an unidentified *Quercus* species. Spherical, with a wrinkly surface with a few scattered very short projections. Internally, the gall is of a spongy consistency. A central rounded larval cell is embedded in the soft internal tissue.

Comments. According to Melika *et al.* (2011), this species may be a synonym of *A. dampfi*. In our opinion, however, although the galls of the two species are similar, the descriptions of the forewing colour patterns of the two species are not in accordance. Thus, we maintain the status of *A. palmeri* as a good species.

Amphibolips hidalgoensis Pujade-Villar & Melika 2011

Amphibolips hidalgoensis Pujade-Villar & Melika. *Zootaxa*, 3105: 53

Material examined. Two female paratypes (MNCN) sent by UB (J. Pujade-Villar).

Diagnosis

Characterised by the forewing colour pattern, presenting a dark infuscate cloud on the anterior margin of the wing, extending from the radial cell to the apical margin. The rest of forewing surface is much clearer, yellowish and slightly infuscate, including the costal cell, first cubital cell and basal cell. Mesoscutellum moderately emarginated posteriorly. F3 as long as F4.

Distribution: Hidalgo state

Gall (Figs 18A, 18B**)**. Spherical, diameter up to 6.5 cm, thin walled, with a smooth and naked surface a with soft, spongious parenchyma and radiating filaments supporting the single central larval cell (Melika *et al.* 2011).

Host: *Quercus crassipes* and *Q. crassifolia*

Life history. Only females are known. According Melika *et al.* (2011), they may represent the asexual generation.

Amphibolips zacatecaensis Melika & Pujade-Villar 2011

Amphibolips zacatacaensis Melika & Pujade-Villar. *Zootaxa*, 3105: 48.

Material studied. Two females. Zacatecas, Tlaltenango, 2400 m. ex gall *Quercus sp*. aff *conzatii* (06/08/2005), adults emerged 09/2005, E. Pascual leg.

Diagnosis and comments. *A. zacatecaensis* has been recently described from a single female reared from galls collected on *Q. eduardi* in Zacatecas. The species is characterised by a combination of characters, including the presence of a dark heavily infuscated band along the anterior area of the forewing, which is not interrupted in the first cubital cell, and the mesoscutellum only slightly emarginated posteriorly. The authors outlined the resemblance of this species with the species *A. fusus* and *A. nassa* described by Kinsey. With regard to the resemblance to *A. fusus*, they indicated that *A. zacatacaensis* and *A. fusus*, both reared from *Q. eduardi*, exhibit a similar pattern of forewing pigmentation. However, that affirmation is erroneous, as we demonstrated by examination of the holotype of *A. fusus*. *A. fusus* presents a quite distinct forewing colour pattern, with a colourless cross band, as is found in *A. dampfi*, *A. durangensis* and *A. castroviejoi*, which is not present in *A. nassa* and *A. zacatecaensis*. Furthermore, that *A. fusus* and *A. nassa* do not closely resemble each other was previously correctly outlined by Kinsey (1937). With regard to the differences from *A. nassa*, in the cited paper, it is affirmed that *A. zacatecaensis* differs from *A. nassa* in its forewing colour pattern, but that affirmation is not correct according the original description and the figure (the types of *A. nassa* could not be found when we requested Kinsey types from the AMNH for direct comparison). According to the original description, the forewing is "everywhere smoky-yellow, with a heavy brown cloud on anterior margin covering most of basal, first cubital, and radial cell and anterior portion of third cubital cell; without the clear break in this band found in some other Mexican species of *Amphibolips*" (it is clear that Kinsey is referring to *A. dampfi* and *A. fusus*, as stated in another paragraph on pp. 434). The above description is coincident with the forewing pattern of *A. zacatecaensis*, except that the forewing drawing of *A. nassa* shows the costal cell as infuscate as the basal cell, differing from *A. zacatecaensis*. In conclusion, it is true that *A. zacatecaensis* closely resembles *A. nassa* (not also *A. fusus*), but it could not be differentiated based on the forewing pattern from *A. nassa*. Because the two species share morphologically similar galls, the only difference between them may be the inner consistency of the gall, which presents a soft, spongious parenchyma, whereas it is hard and lignified in *A. nassa* (Melika pers. comm.). The forewing colour pattern and the moderately emarginated mesoscutellum assigns the materials we studied to *A. zacatacaensis*/*A. nassa*. However, our specimens differ in that the dark smoky band is less heavily infuscate, especially in the first cubital cell, and that veins Sc+R, R1 and Rs are distinct and more visible than in the nominal typical form.

Distribution: Zacatecas state

Gall. Large, globose to slightly spindle shaped, with a nipple at the top (Fig. 18E). The gall is thin walled, very lightweight, internally showing a soft spongious consistency. Internally, the gall exhibits a single hard-walled central larval cell (Melika *et al.* 2011).

Host. *Quercus eduardi*

Life History. Unknown.

New species

Amphibolips durangensis Nieves-Aldrey & Maldonado sp. nov.

(Figs. 2A–G, 11C, 15A)

Type material. Holotype female (Fig. 15A). In the Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), dissected and mounted on a stub. Cat. nº 2246. MEXICO, Durango, Palmito, N 23º 33' 49.4" W 105º 51' 08.8", 1977 m; ex gall *Quercus scytophylla* (Fagaceae), gall collected 08/07/2008, insect emerged 10/2008. Y. Maldonado leg. Paratypes: 1 female Durango, Loberas, 1948 m a.s.l ex gall *Quercus scytophylla*, gall collected 10/07/2008, insect emerged 10/2008, Y. Maldonado leg., dissected and mounted on a stub. In MNCN.

Etymology. Named after the Mexican state, Durango, where the materials were collected.

Diagnosis and comments. Closely related to *Amphibolips castroviejoi* Medianero & Nieves-Aldrey from Panama, being similar in colour and a majority of morphological characters. The two species share a similar forewing coloration pattern, which is predominantly infuscate, with a clear crossing band extending from the radial cell to the discoidal cell. The new species differ from *A. castroviejoi* in the clear crossing band being narrower as well as the costal cell and discoidal cell being less heavily infuscate. Both *A. durangensis* and *A. castroviejoi* differ from *A. dampfi* in the wide clear band extending across the forewing from the tip of the radial cell to the posterior part of the apical margin (Figs 11A, 11C), whereas the band is smaller and does not extend as far across the ventral margin of the wing in *A. dampfi* (Fig. 13A). Additionally, *A. durangensis* and *A. dampfi* differ from *A. castroviejoi* in exhibiting indistinct notauli, nearly lost in the sculpture, while the last species has a complete notauli, only lost on the coarse surface in the anterior one-third. *Amphibolips dampfi* exhibit the mesoscutellum strongly emarginated posteriorly, with a sharp horn projection in lateral view (Fig. 1D), while in *A. duranguensis*, the mesoscutellum is only moderately emarginated posteriorly (Fig. 2E).

Description. Body length 5.8 mm (N = 2) for females. Head, mesosoma, antenna and legs black. Metasoma chestnut blackish, hipopygium reddish. Forewing predominantly dark infuscate, excepting costal cell and the areas below cubital vein and between medial and cubital veins, which are lighter; an irregular wide clear cross band is present, extending transversally across wing from one third apical of radial cell to posterior margin of wing (Fig 11C).

Female. Head, coarsely rugose, pubescent; in dorsal view about 2 times wider than long. POL about as long as OOL, posterior ocellus separated from inner orbit of eye by 2.5 times its longest diameter. Head in anterior view (Fig. 2A) 1.2 times wider than high, gena slightly broadened behind eye. Vertex, frons, lower face, gena, and occiput with strong reticulate-rugose sculpture, irradiating carinae from clypeus not discernible; head moderately pubescent, with relatively long setae, except vertex and frons with sparse and shorter setae. Clypeus trapezoid, ventral margin strongly projecting over mandibles and slightly sinuate. Anterior tentorial pits well visible; epistomal sulcus and clypeo-pleurostomal lines slightly discernible. Malar space 0.6 times height of compound eye. Toruli situated mid-height of compound eye; distance between antennal rim and compound eye 1.1 times width of antennal socket including rim. Ocellar plate slightly raised.

Mouthparts (Fig. 2A): mandibles strong, exposed; with dense setae in base, right mandible with three teeth; left with two teeth.

Antenna (Fig. 2C–D), of moderate length, as long as 1/2 body length; with 13 antennomeres; last flagellar segment partially divided into two segments; flagellum not broadening towards apex; with relatively long, erect setae, and elongate placodeal sensilla (Fig. 2D). Relative lengths of antennal segments: 15:7:29:19:15:13:11:11:11:9:8:8:20. Pedicel (Fig. 2C), short, small, 0.5 as long as scape; F1 1.5 times as long as F2. F6–F10 longer than wide, F11 2.7 times longer than wide, 2.1 times as long as F10 (Fig. 2D). Placodeal sensillae on F5–F11, disposed in dense rows of 6–8 sensillae, only in half dorsal area of each flagellomere.

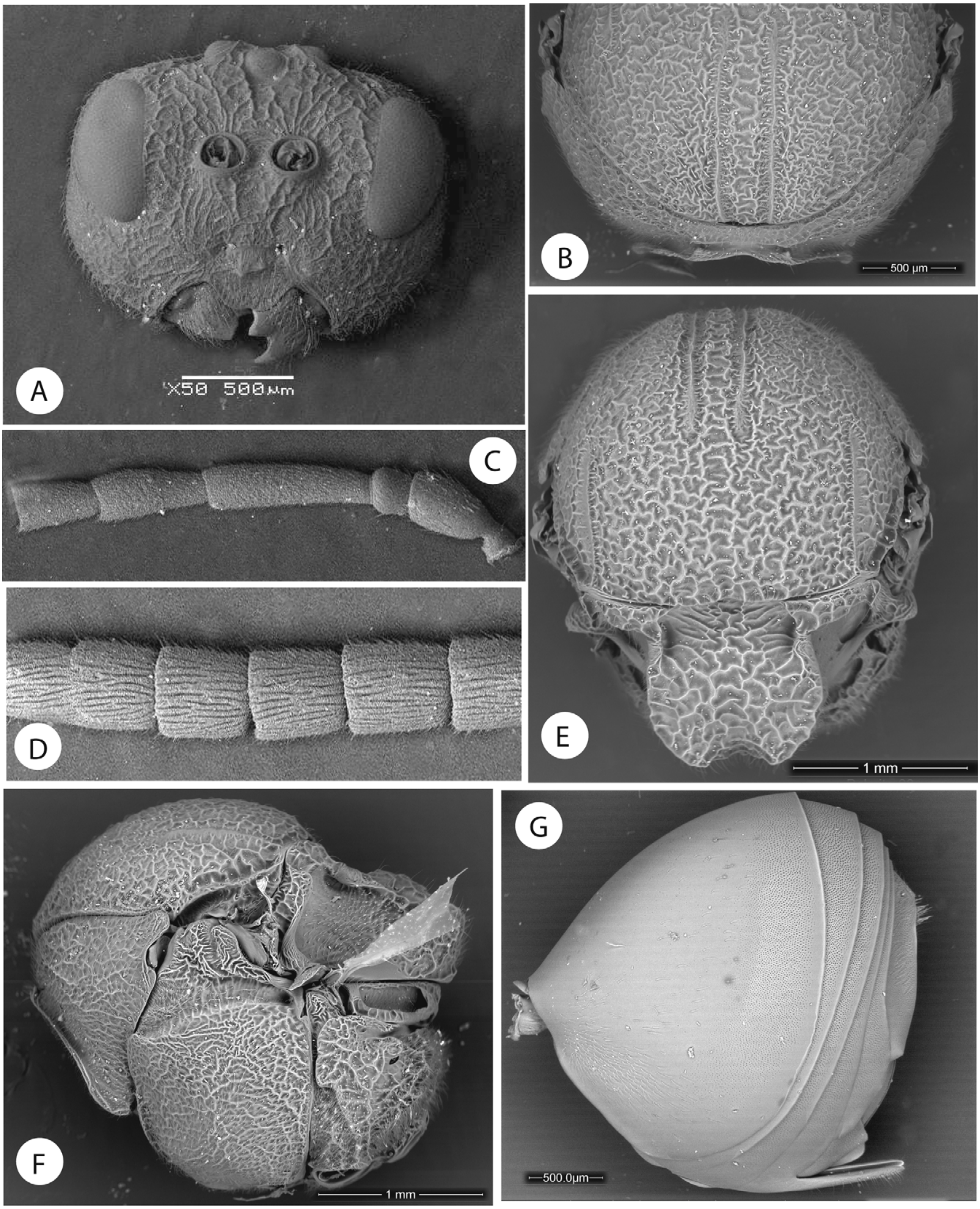

FIGURE 2. *Amphibolips durangensis* sp. nov., female. (A) head anterior view; (B) pronotum anterior view; (C) detail of basal antennomeres; (D) detail of apical flagellomeres; (E) mesosoma dorsal view; (F) mesosoma lateral view; (G) metasoma lateral view.

Mesosoma. Coarsely reticulate rugose, in lateral view as high as long. Pronotum, moderately pubescent; lateral surface of pronotum with strong irregular reticulate rugose sculpture. Pronotum medially short (Fig. 2B); ratio of length of pronotum medially/laterally = 0.20. Pronotal plate indistinct dorsally (Fig. 2B).

Mesonotum. Mesoscutum (Fig. 2E) barely pubescent and with strong rugose-reticulate sculpture. Notauli indistinct. An irregular, shallow, longitudinal median impression, crossed by transversal rugae, visible from anterior to posterior part of mesoscutum. Anteroadmedian signa quite visible, extended back to near one half of mesoscutum; parascutal carinae distinct. Transscutal fissure narrow. Mesoscutellum subquadrate, about 0.6 as long as mesoscutum. Scutellar foveae ellipsoidal about 0.3 as long as mesoscutellum, indistinctly separated medially, deep, crossed by irregular longitudinal rugae, the intervals smooth, posterior margins indistinct. Mesoscutellum strongly reticulate-rugose, with a median longitudinal impression and moderately emarginated at posterior margin (Fig. 2E); the emargination reaching posterior about one sixth of scutellum length. Axillula moderately pubescent, their anterior and posterior margins marked. Mesopleuron coarsely reticulate rugose, the rugae not as strong as mesoscutum. (Fig. 2F).

Metanotum. Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at about mid-height of metapectal-propodeal complex (Fig. 2F). Metascutellum rugose; metanotal trough smooth and pubescent. Median propodeal area reticulate rugose and densely pubescent; lateral propodeal carinae indistinct. Nucha smooth medially.

Legs. Densely pubescent; femora and tibiae robust; metafemur 2.6 as long as wide, strongly curved ventrally. Metatibia about as long as metatarsus; apical margin of metatarsomeres 1–4, with long strong erect setae. Metatarsal claws with strong triangular basal lobe or teeth.

Forewing (Fig. 11C): 1.15 as long as body, radial cell 3.5 times longer than wide; open along anterior margin; areolet small, ovoid, obscured by infuscation. R1, Rs and M nearly straight, not reaching wing margin. Rs+M reaching basalis at its mid-height. First abscissa of radius (2r) and 2r-m curved. Apical margin with obsolete hair fringe.

Metasoma (Fig. 2G), as long as head and mesosoma combined, in lateral view as high as wide. Second metasomal tergite covering about two third of metasoma, with band of micropuntures clearly visible in posterior one third; punctures visible on subsequent tergites; ventral area of second metasomal tergite moderately pubescent. Projecting part of hypopygial spine long (Fig. 2G); about 5 times as long as wide in lateral view; laterally with long setae, longer than spine width but not forming an apical patch.

Male. Unknown

Gall (Figs.18C, 18D). A spindle-shaped gall with an elongated and narrow tip and base. Longitudinally, the surface of the gall is crossed by longitudinal ridges. The gall is monothalamic; the outer shell is thin but firm; internally, it has a spongy consistency, filling the entire gall (Fig. 18D). The larval cell is rounded and is embedded in the soft internal substance. Diameter of 54 x 43 mm on average). Forms on twigs of *Quercus scytophylla*. The gall closely resembles that of *Amphibolips fusus* Kinsey 1937, also described from Mexico, and was illustrated recently by Melike *et al.* (2012). However, the gall of *A. duranguensis* differs from the gall of *A. fusus* due to its much more elongated and narrow points, both at the tip and at base. Another difference is the gall surface, which is smooth in the gall of *A. fusus*, without longitudinal ridges.

Distribution. *A. duranguensis* was found at 1900 m a.s.l. in Durango state, Mexico.

Biology. Only females of the presumably sexual generation are known. The galls were collected in July, and the insects emerged in October.

Comment: We examined one female reared from a gall also developing on *Quercus scytophylla*, but collected in Durango, Loberas, on 18/07/2008, which is very similar to *A. duranguesis* and could be conspecific with this species. However, this specimen differs from *A. duranguensis* in the following ways: the clear crossing band is slightly different, being narrower between the radial and the medial veins and wider and regular between the medial and the cubital. The infuscate area on the apical margin is not as uniform as in the holotype.

Amphibolips jaliscensis Nieves-Aldrey & Pascual sp. nov.

Figs 3A–H, 11D, 13B, 17A–B.

Type material. Holotype female (Fig. 17A). In the Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), mounted on a card Cat. nº 2247. MEXICO, Jalisco, Nevado de Colima, 19º 37' 408” N, 103º 33' 216” W, 2048 m; ex gall *Quercus* aff. *candicans*, gall collected 31/03/2009; insect emerged 04/2009, E. Pascual leg. Paratypes: One male, presenting the same data as the holotype (Fig. 17B). In the MNCN.

Etymology. Named after the Mexican state, Jalisco, where the materials were collected.

Diagnosis and comments. The main diagnostic character of this species is the clear, less infuscate spot on the apical one-third of the radial cell. In most remaining morphological characters, this species is very similar to *A. hidalgoensis* Melika & Pujade-Villar, and the new species is described here as *A. malinche* sp. nov. It further differs from *A. hidalgoensis* in its basal cell, which is more infuscate, and in that due to being a bisexual generation, females and males are both known, while only females are known in *A. hidalgoensis*, and it is presumably an asexual form (Melika *et al*. 2011). From *A. malinche*, the new species differs in the clear spot on the radial cell, which is relatively larger and more extended, and in F1 being 1.4 as long as F2 (1.6 as long as F2 in *A. malinche*).

Description. Body length 7 mm (N = 1) for females; 5.5 mm (N=1) for males. Head, and mesosoma black, excepting base of mandibles and clypeus anteriorly chestnut. Antennae black dorsally, chestnut brown ventrally. Legs black, excepting apical tarsomeres brown. Metasoma red brown in half basal, black in posterior half; hypopigium red brown. Forewing infuscate, with a darker band extended on anterior margin along basal cell, first cubital cell (lightly here), radial cell (heavily in anterior one half), and beyond to posterior margin of wing. The entire costal cell as well as posterior one third of radial cell is colorless.

Female. Head, in dorsal view coarsely rugose, about 2.3 times wider than long, narrower than mesosoma. POL 1.8 OOL, posterior ocellus separated from inner orbit of eye by 1.5 times its longest diameter. Genae strongly broadened behind eye. Head in anterior view 1.2 as wide as high. Vertex, frons, lower face, gena, and occiput with strong reticulate-rugose sculpture; some incomplete and irregular irradiating carinae from clypeus visible. Head moderately pubescent, except vertex and frons with sparse and shorter setae. Genae quite broadened, visible behind eye. Clypeus trapezoid, ventral margin strongly projecting over mandibles and slightly sinuate. Anterior tentorial pits well visible; epistomal sulcus and clypeo-pleurostomal lines slightly visible. Malar space about half height of compound eye. Toruli situated mid-height of compound eye; distance between antennal rim and compound eye as width of antennal socket including rim. Ocellar plate slightly raised.

Mouthparts: mandibles strong, exposed; with dense setae in base, right mandible with three teeth; left with two teeth.

Antenna (Fig. 3A), of moderate length, as long as 1/2 body length; with 13 antennomeres; last flagellar segment partially divided into two segments; flagellum not broadening towards apex; with relatively long, erect setae, and elongate placodeal sensilla. Relative lengths of antennal segments: 18:12:42:30:22:20:17:15:12:12:10:10:22. Pedicel short, small, as long as wide; 0.6 as long as scape; F1 1.4 times as long as F2. F7–F10 about as long as wide, F11 2 times longer than wide, 2 times as long as F10. Placodeal sensillae on F5–F11, disposed in rows of 6–8 sensillae, only in half dorsal area of each flagellomere.

Mesosoma. Coarsely reticulate rugose, in lateral view as high as long. Pronotum, moderately pubescent; lateral surface of pronotum with strong irregular reticulate rugose sculpture. Pronotum medially short; ratio of length of pronotum medially/laterally = 0.20. Pronotal plate indistinct dorsally.

Mesonotum. Mesoscutum (Fig. 3B) barely pubescent and with coarse rugose-reticulate sculpture. Notauli indistinct anteriorly, posteriorly visible by indisctinct, obscured by the irregular sculpture; longitudinal median impression indistinct. Anteroadmedian signa and parascutal carinae distinct. Transscutal fissure narrow. Mesoscutellum squared (Fig. 3B), about 0.6 as long as mesoscutum. Scutellar foveae large, rounded with distinct margins; smooth, excepting by some transversal carinae, and shining. Mesoscutellum roughly reticulate-rugose, with a shallow median longitudinal impression, and deeply emarginated at posterior margin, the incision reaching deeply only one third of distance to posterior margin of scutellar foveae. Axillula moderately pubescent, their anterior and posterior margins marked. Mesopleuron irregularly reticulate rugose, the rugae not as strong as mesoscutum. (Fig. 3C).

Metanotum (Fig. 3F). Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at about mid-height of metapectal-propodeal complex. Metascutellum rugose; metanotal trough smooth and pubescent. Median propodeal area reticulate rugose and densely pubescent; lateral propodeal carinae indistinct, obscured by coarse sculpture. Nucha smooth medially.

Legs. Densely pubescent; femora and tibiae robust. Tarsal claws with strong triangular basal lobe or teeth.

Forewing (Fig. 13B). Slightly longer than body, radial cell 4 times longer than wide; open along anterior margin; areolet distinct. All the veins heavily infuscated; Color as described before. R1, Rs and M nearly straight, not reaching wing margin. Rs+M reaching basalis at its mid-height. First abscissa of radius (2r) and 2r-m curved. Apical margin with very short hair fringe.

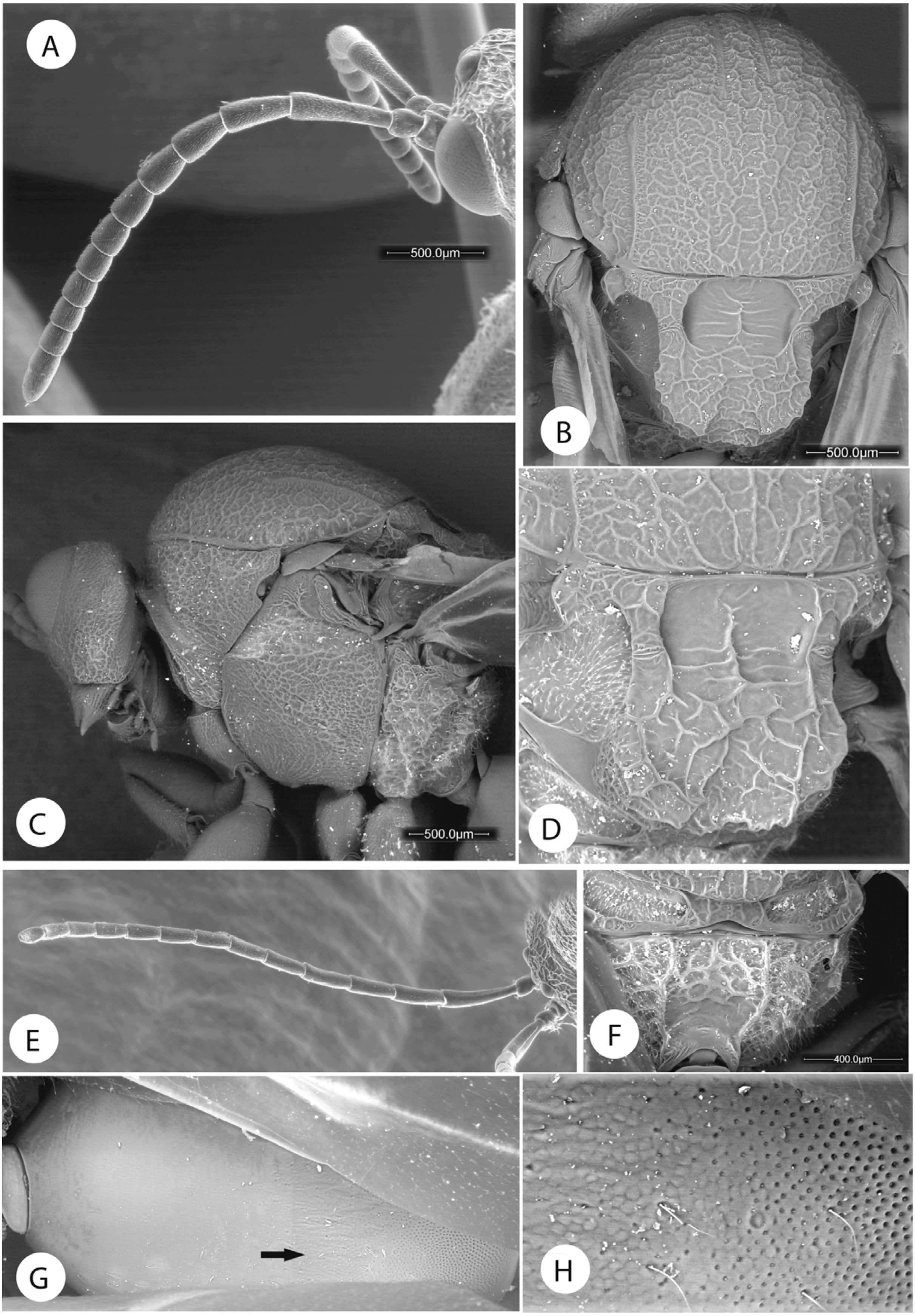

FIGURE 3. *Amphibolips jaliscensis* sp. nov. (A) female, head and antenna; (B) female, mesosoma dorsal view; (C) female, mesosoma lateral view; (D) male, mesoscutellum; (E) male antenna; (F) male propodeum; (G) female, metasoma dorsal view; (H) detail of the sculpture of metasoma in dorsal view.

Metasoma. About as long as head and mesosoma combined; in lateral view 1.2 as long as high. Second metasomal tergite covering about two third of metasoma, with a band of micropuntures clearly visible in posterior one fourth of the large metasomal terguite; anteriorly to the area of micropunctures there is a broad area with weak coriaceous- alutaceaus sculpture, after the anteriormost smooth area of MT2 (Figs 3G–H); micropunctures extended on subsequent tergites; ventral area of second metasomal tergite moderately pubescent. Projecting part of hypopygial spine long; about 4.5 times as long as wide in ventral view; laterally with long setae, longer than spine width but not forming an apical patch.

Male (Fig. 17B). Differs from female as follows. Coloration darker, antenna and metasoma entirely black. Forewing much more strongly infuscate; infuscation extended also on costal cell, and much strongly than in female below the dorsal darker band extended on veins and closed cells (Fig. 13B). Antennae (Fig. 3E) of 14 antennomeres; F1 long, slightly modified, flattened ventrally and slightly broadened toward apex; lateral propodeal carinae distinct.

Gall (Figs 19A, 19B). A globular oak apple gall. Monothalamic; outer shell thin and internally showing a spongy consistency, filling the entire gall. Grows on twigs of *Quercus sp. aff candicans*.

Distribution. *A. jaliscensis* was found at 2370 m a.s.l. at Jalisco state, Mexico.

Biology. Exhibits a sexual generation; both males and females are known. The galls were collected in late March, and the insects emerged in April.

Amphibolips oaxacae Nieves-Aldrey & Pascual sp. nov.

Figs 4A–F, 11F, 17D, 18F

Type material. Holotype female (Fig. 17D). In the Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), mounted on a card. Cat. nº 2249. MEXICO, Oaxaca, S. Pedro Tapanatepec, 16º 22' 34.40” N, 94º 04' 43 11” W, 1300 m; ex gall *Quercus sp*., gall collected 29/03/2006, insect emerged 03/2006, E. Pascual leg.

Etymology. Named after the Mexican state Oaxaca, where the material was collected.

Diagnosis and comments. The forewing colour pattern distinguishes this new species well from other Mexican or Neotropical *Amphibolips* species. The infuscation along the veins is much less heavy than in other Mexican species of *Amphibolips*, with the veins being discernible (Fig. 11F). A slightly darker, more infuscate area extending along the dorsal margin of the wing across the radial cell and reaching the posterior margin of the wing. The infuscate area extends across the costal cell, first cubital cell and basal cell and to the anterior area below the M+Cu1 vein (Fig. 11F). In this forewing colour pattern, the new species resembles A. *nassa* Kinsey, but its coloration, the posterior emargination of the mesoscutellum and the gall are different in these two species. In exhibiting a reddish body and mesoscutellum deeply emarginated and in the shape and size of its gall, this new species also resembles *A. dampfi* and *A. palmeri*. However, the pattern of forewing infuscation distinguishes these species well from *A. oaxacae*; *A. dampfi* exhibits a clear cross-band near the tip of the wing, while *A. oaxacae* does not present this cross-band. The gall is similar in size to that of *A. palmeri*, also described from Mexico and measuring 35–70 mm in diameter. However, the surface of the gall of *A. palmeri* was described and illustrated as uneven, or somewhat wrinkly, sometimes with a few, scattered very short projections, while the surface of the gall of *A. oaxacae* is uniformly smooth.

Description. Female. Body length 6.5 mm (N = 1). Head, and mesosoma black; clypeus, mandibles and areas of mesosoma around tegulae reddish brown. Antennae light brown more light distally and ventrally. Legs and metasoma reddish brown, darker in posterior half; hypopigium red brown. Forewing lightly but entirely infuscate, the veins being clearly visible. A slightly darker band extended dorsally along the costal and basal cells, first cubital cell, and radial cell to postero dorsal area of forewing. The area below basal cell is also more darkened as the anterior band.

Female. Head, in dorsal view strongly reticulate rugose, about 2 times as wide as long. POL as long as OOL, posterior ocellus separated from inner orbit of eye by 1.5 times its longest diameter. Head in anterior view (Fig. 4A) about 1.3 as wide as high, gena broadened behind eye. Vertex, frons, lower face, gena, and occiput with strong irregular reticulate-rugose sculpture, without irradiating carinae from clypeus. Head moderately pubescent. Clypeus trapezoidal, ventral margin strongly projecting over mandibles and slightly sinuate. Anterior tentorial pits conspicuous; epistomal sulcus and clypeo-pleurostomal lines discernible. Malar space 0.5 times height of compound eye. Toruli situated mid-height of compound eye; distance between antennal rim and compound eye as wide as antennal socket including rim. Ocellar plate slightly raised.

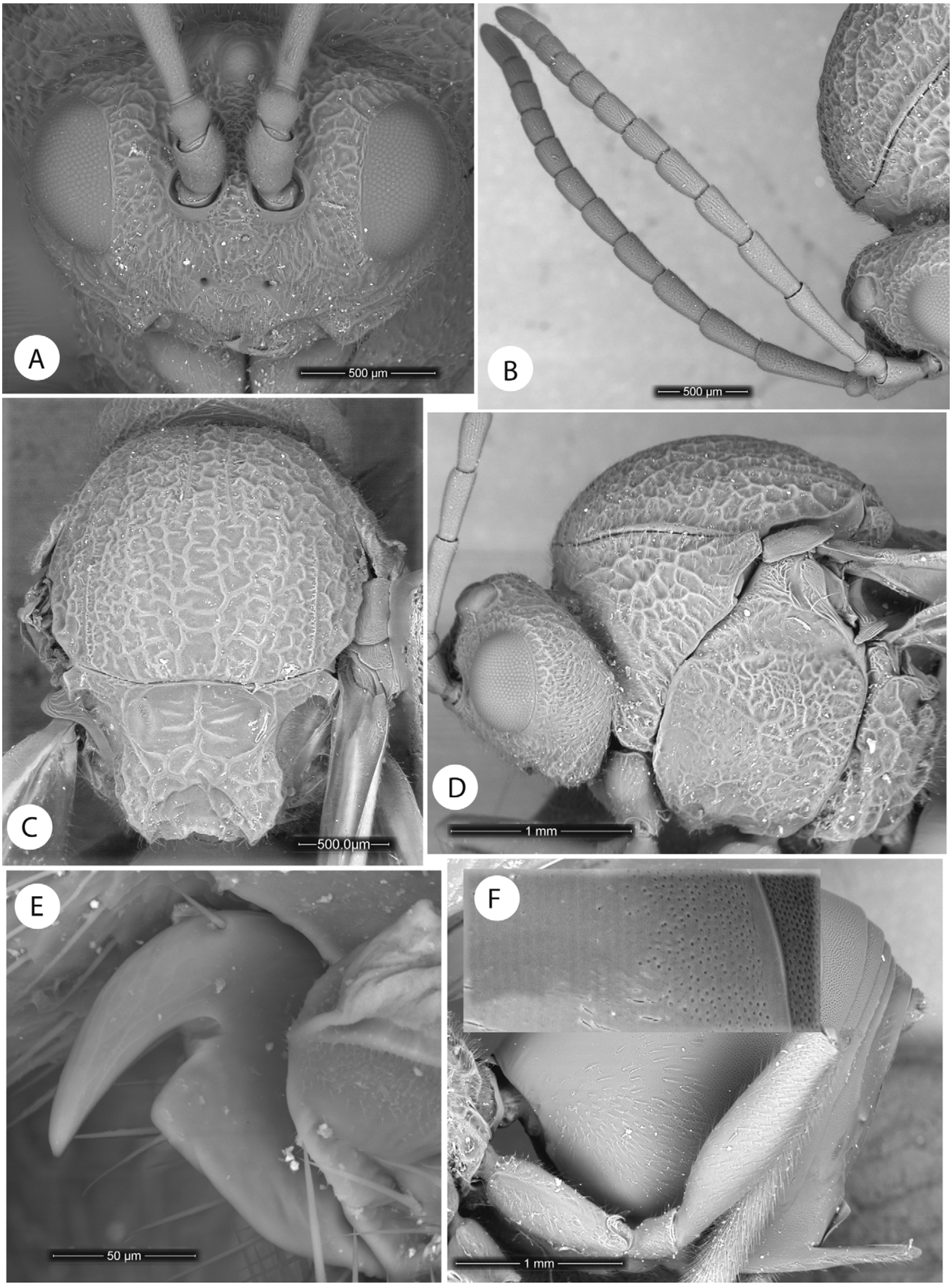

FIGURE 4. *Amphibolips oaxacae* sp. nov., female. (A) head anterior view; (B) antennae; (C) mesosoma dorsal view; (D) mesosoma lateral view; (E) metatarsal claw; (E) male antenna; (F) metasoma lateral view and detail of sculpture.

Mouthparts: mandibles strong, exposed; with dense setae in base, right mandible with three teeth; left with two teeth.

Antenna (Fig. 4B), of moderate length, 0.6 as long as body; with 13 antennomeres; flagellum not broadening towards apex; with relatively long, erect setae, and elongate placodeal sensilla in flagellomeres F3–F11 (Fig. 4B). Relative lengths of antennal segments: 25:10:42:32:30:25:20:18:16:15:12:11:20. Pedicel (Fig. 2C), short, globose, 0.5 as long as scape; F1 1.3 times as long as F2. F6–F10 longer than wide, F11 2 times as long as F10 (Fig. 4B). Placodeal sensillae on F3–F11, disposed in rows of 6–8 sensillae, only in half dorsal area of each flagellomere.

Mesosoma. Short, in lateral view slightly higher than long. Pronotum, moderately pubescent; lateral surface of pronotum with strong irregular reticulate rugose sculpture (Fig. 4D). Pronotum medially short; ratio of length of pronotum medially/laterally = 0.20. Pronotal plate indistinct dorsally (Fig.4C).

Mesonotum. Mesoscutum (Fig. 4C) barely pubescent and with strong rugose-reticulate sculpture. Notauli distinct in posterior 2/3 of mesoscutum, crossed by transversal rugae. longitudinal median impression indistinct. Anteroadmedian signa well visible, extended back to near one half of mesoscutum; parascutal carinae distinct. Transscutal fissure narrow. Mesoscutellum subquadrate, about 0.6 as long as mesoscutum. Scutellar foveae rounded, deep, with distinct margins; with some transversal rugae, the intervals smooth and shining; about 0.5 as long as mesoscutellum. Mesoscutellum strongly reticulate-rugose, deeply and widely emarginated at posterior margin, the incision reaching close posterior margins of scutellar foveae (Fig. 4C). Mesopleuron coarsely reticulate rugose, the rugae not as strong as mesoscutum (Fig. 4D).

Metanotum. Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at about mid-height of metapectal-propodeal complex. Metascutellum weakly rugose; metanotal trough smooth and pubescent. Median propodeal area shining reticulate-rugose and densely pubescent; lateral propodeal carinae indistinct. Nucha smooth medially.

Legs. Densely pubescent; femora and tibiae robust. Metatarsal claws with strong triangular basal lobe or teeth (Fig. 4F).

Forewing (Fig. 11F): As long as body, radial cell 3.6 times longer than wide; open widely along dorsal margin; areolet small. R1 straight, not reaching wing margin; Rs+M reaching basalis at its mid-height. First abscissa of radius (2r) angulated and radius curved. Apical margin with short hair fringe.

Metasoma (Fig. 4F), slightly shorter as head and mesosoma combined, in lateral view about as long as high. Second metasomal tergite covering about two third of metasoma, with a band of micropuntures clearly visible in posterior one fourth; punctures visible on subsequent tergites; dorsally the surface of the second metasomal terguite before the band of micropunctures is smooth (Fig. 4F); latero ventral area of second metasomal tergite moderately pubescent. Projecting part of hypopygial spine quite long, in lateral view about 6 times as long as wide; laterally with long setae which not form an apical patch.

Male. Unknown.

Gall (Fig. 18F). A regularly spherical, large oak apple gall measuring approximately 40 mm in diameter. Pale green with darker green spots when fresh. The gall is monothalamic; the outer shell is thin but firm; with a spongy consistency internally, filling the entire gall. The larval cell is rounded and is embedded in the soft internal substance. Forming on twigs of *Quercus sp. aff sapotifolia*. The gall closely resembles that of *Amphibolips palmeri* Basset 1890, also described from Mexico, but for which the host is unknown.

Distribution. *A. oaxacae* was found at 1180 m a.s.l. in Oaxaca State, Mexico.

Biology. Only females of the presumably sexual generation are known. The galls were collected in March, and the insects emerged in the same month.

Amphibolips malinche Nieves-Aldrey & Pascual sp. nov.

(Figs 5A–F, 11E, 15C)

Type material. Holotype. Female (Fig.15C). In the Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), mounted on a card. Cat. nº 2248. MEXICO, Tlaxcala, La Malinche, 19º 12' 29 49” N, 98º 0' 44 47” W, 2800 m; ex gall *Quercus mexicana*, gall collected 16/05/2006, insect emerged 30/05/2006, E. Pascual leg. Paratype, 1 female, with the same data as for the holotype, except that the gall was collected 15/05/2005, and the insect emerged 7/11/2005, E. Pascual leg. In MNCN.

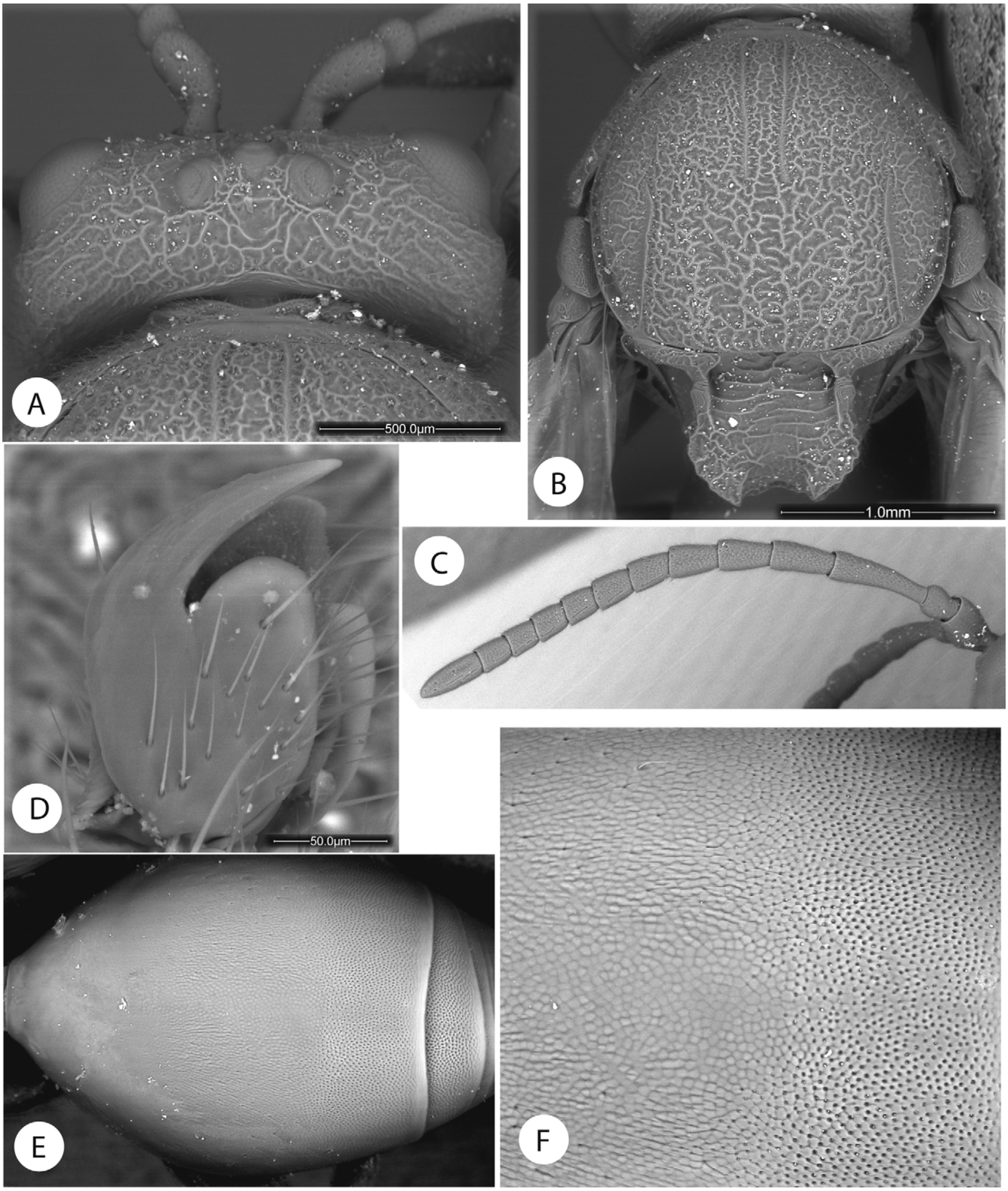

FIGURE 5. *Amphibolips malinche* sp. nov., female. (A) head dorsal view; (B) mesosoma dorsal view; (C) antenna; (D) metatarsal claw; (E) metasoma dorsal view; (F) detail of sculpture.

Etymology. Named after the collection site, referring to Dña Marina, called Malinche, compaigh of Hernán Cortés, two key figures in the birth of modern Mexico.

Diagnosis and comments. Closely resembles *A. jaliscensis* Nieves-Aldrey & Pascual, in its forewing pattern based on the colourless, less infuscate spot situated apically on radial cell. However, this clear spot in *A. malinche* is smaller, only extending to the apex of the radial cell, and the first cubital cell is as colourless as the costal cell (Fig. 11E). Additionally *A. malinche* differs from *A. jaliscensis* in its antennal F1 being 1.6 as long as F2 (Fig. 5C)

[F1 is 1.4 as long as F2 in *A. jaliscensis*], and the general coloration is darker in *A. malinche*, with the antenna and metasoma being black.

Description. Body length 7 mm (N = 2) for females. Head, mesosoma, antennae and legs black. Metasoma in great part black, ventral sides and hypopigium dark chestnut. Forewing infuscate, with a darker band extended dorsally along basal cell, radial cell, and beyond to posterior margin of wing. The entire costal cell as well as first cubital and the apex of radial cell is colorless, not as heavily infuscate.

Female. Head, in dorsal view (Fig. 5A) coarsely rugose, about 2.4 times wider than long, narrower than mesosoma. POL 1.7 OOL, posterior ocellus separated from inner orbit of eye by 1.8 times its longest diameter. Gena strongly broadened behind eye. Head in anterior view 1.2 as wide as high. Vertex, frons, lower face, gena, and occiput with strong reticulate-rugose sculpture; some incomplete and irregular irradiating carinae from clypeus visible. Head moderately pubescent, except vertex and frons with sparse and shorter setae. Genae quite broadened, visible behind eye. Clypeus trapezoid, ventral margin strongly projecting over mandibles and slightly sinuate. Anterior tentorial pits well visible; epistomal sulcus and clypeo-pleurostomal lines slightly visible. Malar space about half height of compound eye. Toruli situated mid-height of compound eye; distance between antennal rim and compound eye slightly shorter as width of antennal socket including rim. Ocellar plate slightly raised.

Mouthparts: mandibles strong, exposed; with dense setae in base, right mandible with three teeth; left with two teeth.

Antenna (Fig. 5C), 0.4 as long as body length; with 13 antennomeres; flagellum not broadening towards apex. Relative lengths of antennal segments: 20:10:40:25:22:20:17:15:13:12:12:13:27. Pedicel (Fig. 2C), short, small, as long as wide; 0.6 as long as scape; F1 1.6 times as long as F2. F7–F10 about slightly longer than wide, F11 2.7 times longer than wide, 2 times as long as F10. Placodeal sensillae on F5–F11, disposed in rows of 6–8 sensillae, only in half dorsal area of each flagellomere.

Mesosoma. Coarsely reticulate rugose, in lateral view 1.1 as long as high. Pronotum, moderately pubescent; lateral surface of pronotum with strong irregular reticulate rugose sculpture. Pronotum medially short; ratio of length of pronotum medially/laterally = 0.20. Pronotal plate indistinct dorsally.

Mesonotum. Mesoscutum barely pubescent and with coarse rugose-reticulate sculpture (Fig. 5B). Notauli only posteriorly visible but indisctinct, obscured by the irregular sculpture; a longitudinal median impression obscurely indicated. Anteroadmedian signa and parascutal carinae distinct. Transscutal fissure narrow. Mesoscutellum squared, about 0.4 as long as mesoscutum. Scutellar foveae (Fig. 5B) squared, with distinct lateral margins; smooth, excepting by some transversal carinae, and shining. Mesoscutellum roughly reticulate-rugose, with a shallow median longitudinal impression, and deeply emarginated at posterior margin, the incision reaching deeply about one half of distance to posterior margin of scutellar foveae (Fig. 5B). Axillula moderately pubescent, their anterior and posterior margins marked. Mesopleuron irregularly reticulate rugose, the rugae not as strong as mesoscutum.

Metanotum. Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at about mid-height of metapectal-propodeal complex. Metascutellum rugose; metanotal trough smooth and pubescent. Median propodeal area reticulate rugose and densely pubescent; lateral propodeal carinae obscured by coarse sculpture but visible. Nucha smooth medially.

Legs. Densely pubescent; femora and tibiae robust. Tarsal claws with strong triangular basal lobe or teeth, apically obtuse (Fig. 5D).

Forewing (Fig. 11E): 1.1 as long as body, radial cell about 4 times longer than wide; open along anterior margin; areolet very small but distinct. Color as described before. R1 and Rs not reaching wing margin; Rs+M reaching basalis at its mid-height. First abscissa of radius (2r) and Rs curved. Apical margin with very short hair fringe.

Metasoma (Fig. 5E), About as long as head and mesosoma combined; in lateral view 1.2 as long as high. Second metasomal tergite covering about two third of metasoma, with a band of micropuntures clearly visible in posterior one fourth of the large metasomal terguite; anteriorly to the area of micropunctures there is a broad area reaching anterior one half of MT2 with coriaceous sculpture, after the anterior smooth area of the metasomal terguite (Fig. 5F); micropunctures extended on subsequent tergites; ventral area of second metasomal tergite moderately pubescent. Projecting part of hypopygial spine long; about 6 times as long as wide in ventral view; laterally with long setae, longer than spine width but not forming an apical patch.

Male. Unknown.

Gall (Figs 19C, 19D). A globular, irregular oak apple gall. Monothalamic; outer shell thin and internally exhibiting a spongy consistency, filling the entire gall. Found on twigs of *Quercus mexicana*.

Distribution. *A. malinche* was found at 2800 m a.s.l. at La Malinche volcano, Tlaxcala state, Mexico.

Biology. Presumably a sexual generation, but males were not reared. The galls were collected in late June, and the insects emerged in July.

Amphibolips nevadensis **Nieves-Aldrey & Pascual sp. nov.**

Figs 6A–F, 7AE, 12B, 13F, 16A–B

Type material. Holotype. Female (Fig. 16A). In the Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), mounted on a card. Cat. nº 2252. MEXICO, Jalisco, Nevado Colima, Ciudad Guzmán, 2300 m; ex gall *Quercus candicans*, gall collected 20/08/2009, E. Pascual leg. Paratypes, 2 males, Nevado Colima, 2370 m, ex gall *Q. candicans* collected 31/03/2009, insect emerged 04/2009, E. Pascual leg. In the MNCN.

Etymology. Named after the collection site, Nevado Colima

Diagnosis and comments. In its forewing pattern, this new species resembles *A. zacatecaensis* and *A. hidalgoensis*. Compared to the former, *A. nevadensis* differs in its mesoscutellum being more deeply emarginated posteriorly; compared to *A. hidalgoensis*, the new species differs in the basal cell of its forewing, which is infuscate, while it is colourless in *A. hidalgoensis*.

Description. Female. Body length 6.5 mm (N = 1). Head and mesosoma black; clypeus, mandibles, antennae anteroventrally, and metasoma ventrally, dark brown. Legs black. Forewing dark infuscate, all the veins obscured by infuscation. A dark heavily infuscate band extended anteriorly along the basal cell, first cubital cell, and radial cell to antero apical of forewing. Costal cell and the area below the described heavily infuscate band is colorless, only slightly infuscate.

Female. Head, in dorsal view strongly reticulate rugose, about 2.4 times as wide as long (Fig. 6A). POL as long as OOL, posterior ocellus separated from inner orbit of eye by 1.5 times its longest diameter. Head in anterior view about 1.3 as wide as high, gena broadened behind eye. Vertex, frons, lower face, gena, and occiput with strong irregular reticulate-rugose sculpture, some irradiating carinae from clypeus visible. Head moderately pubescent. Clypeus trapezoidal, ventral margin strongly projecting over mandibles and slightly sinuate. Anterior tentorial pits conspicuous; epistomal sulcus and clypeo-pleurostomal lines discernible. Malar space 0.5 times height of compound eye. Toruli situated mid-height of compound eye; distance between antennal rim and compound eye as wide as antennal socket including rim. Ocellar plate slightly raised.

Mouthparts: mandibles strong, exposed; with dense setae in base, right mandible with three teeth; left with two teeth.

Antenna (Fig. 6B), relatively short, as long as head and mesosoma combined; with 13 antennomeres; flagellum not broadening towards apex; with relatively long, erect setae, and placodeal sensilla in ventral area of flagellomeres F4–F11. Relative lengths of antennal segments: 26:10:52:33:27:22:20:15:14:14:12:12:21. Pedicel short, globose, shorter than long and 0.5 as long as scape; F1 1.6 times as long as F2. F6–F10 longer than wide, F11 about 2 times as long as F10.

Mesosoma. Coarsely reticulate rugose, short, in lateral view slightly longer than high (Fig.6C). Pronotum, moderately pubescent; lateral surface of pronotum with strong irregular reticulate rugose sculpture. Pronotum medially short; ratio of length of pronotum medially/laterally = 0.20. Pronotal plate indistinct dorsally.

Mesonotum. Mesoscutum barely pubescent and with strong rugose-reticulate sculpture (Fig. 6D). Notauli visible but shallow and indistinct obscured by crossing coarse sculpture. Anteroadmedian signa well visible and parascutal carinae distinct. Transscutal fissure narrow. Mesoscutellum subquadrate, about 0.6 as long as mesoscutum. Scutellar foveae rounded, deep, with distinct margins; with some transversal rugae, the intervals smooth and shining; about 0.5 as long as mesoscutellum (Fig. 6D). Mesoscutellum strongly reticulate-rugose, emarginated at posterior margin, the incision being only moderately deep and wide and not reaching posterior margins of scutellar foveae (Fig. 6D). Mesopleuron coarsely reticulate rugose, the rugae not as strong as mesoscutum. (Fig. 6C).

Metanotum. Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at about mid-height of metapectal-propodeal complex. Metascutellum weakly rugose; metanotal trough smooth and pubescent. Median propodeal area reticulate shining rugose and densely pubescent; lateral propodeal carinae discernible. Nucha rugose medially.

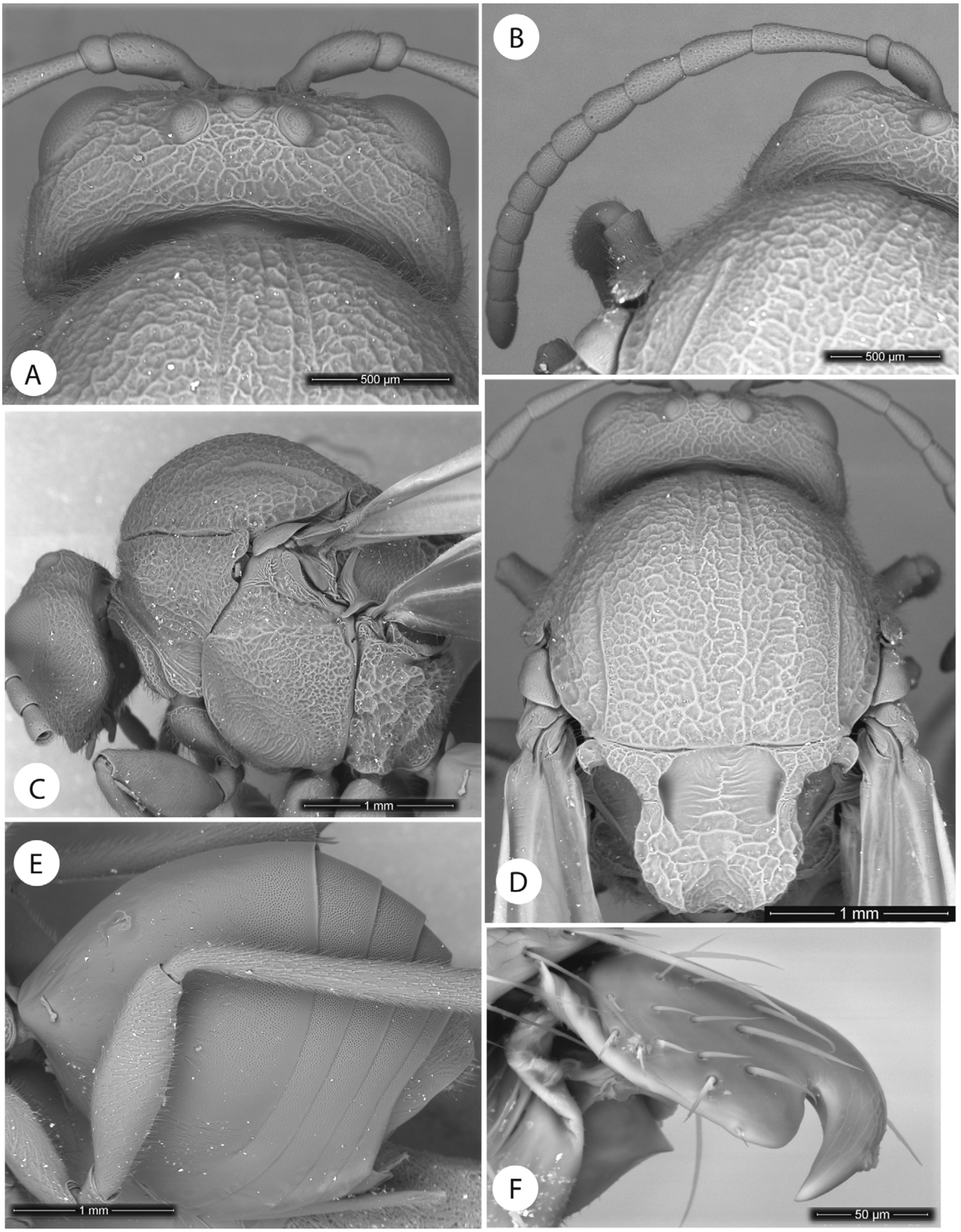

FIGURE 6. *Amphibolips nevadensis* sp. nov., female. (A) head dorsal view; (B) antenna; (C) mesosoma lateral view; (D) mesosoma dorsal view; (E) metasoma lateral view; (F) metatarsal claw.

Legs. Densely pubescent; femora and tibiae robust. Metatarsal claws with strong triangular basal lobe or teeth (Fig. 6F).

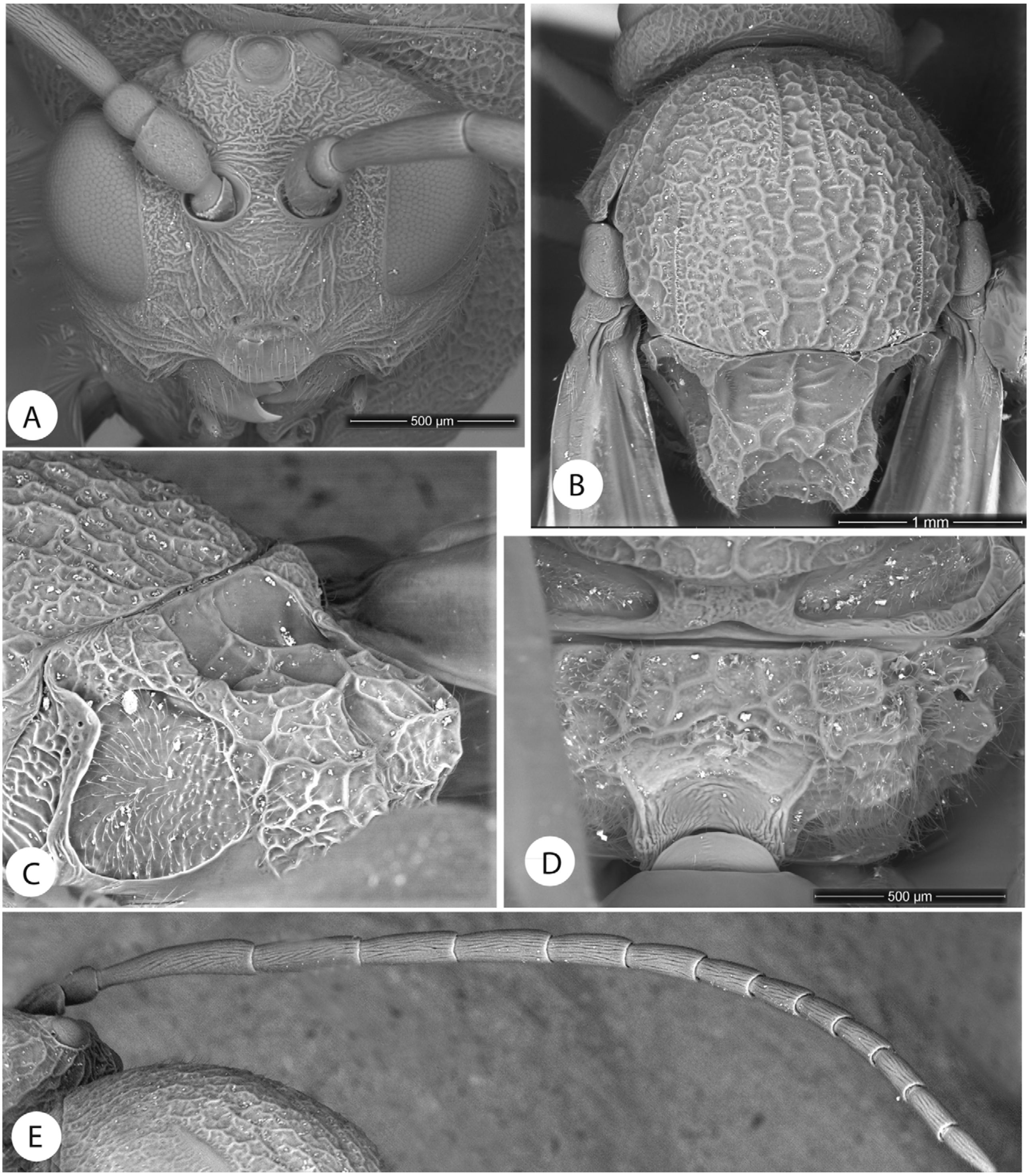

FIGURE 7. *Amphibolips nevadensis* sp. nov., male. (A) head anterior view; (B) mesosoma dorsal view; (C) mesoscutellum lateral view; (D) propodeum. (E) antenna.

Forewing (Fig. 12B): Slightly longer than body; radial cell 4 times longer than wide; open widely along dorsal margin; areolet conspicuous, triangular. R1 straight, not reaching wing margin; Rs+M reaching basalis at its mid-height. First abscissa of radius (2r) obscured by infuscation and radius only slightly curved. Apical margin with short hair fringe.

Metasoma (Fig. 6E), slightly shorter as head and mesosoma combined, in lateral view about slightly longer than high. Second metasomal tergite covering about two third of metasoma, with a band of micropuntures clearly visible in posterior one third; punctures visible on subsequent tergites; dorsally the surface of the second metasomal terguite before the band of micropunctures has coriaceous sculpture; latero ventral area of second metasomal tergite moderately pubescent. Projecting part of hypopygial spine long, in lateral view (Fig. 6E) about 5 times as long as wide; laterally with long setae which not form an apical patch.

Male. Differs from female as follows: antennae with 14 antennomeres (Fig. 7E); F1 slightly modified, flattened on ventral side, elongate placodeal sensillae visible in all flagellomeres. Mesoscutellum more widely and deeply emarginated in posterior margin (Fig. 7B). Forewings more heavily infuscate in all its surface, but the darker anterior band being still visible (Fig. 13F).

Gall (Figs 19E, 19F). A globular gall ending in a obtuse apical point. Monothalamic. Grows on twigs of *Quercus candicans*.

Distribution. *A. nevadensis* was found at 2300 m a.s.l. at Nevado Colima, Jalisco state, Mexico.

Biology. Exhibits a sexual generation. The galls were collected in March, and the male adults emerged in April. The female was collected in August.

Amphibolips tarasco **Nieves-Aldrey & Pascual sp. nov.**

Figs 8A–H, 12C, 13E, 16E–F

Type material. Holotype. Female (Fig. 16E). In the Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), mounted on a card. Cat. nº 2250. MEXICO, Michoacán, Santa María, 2000 m; ex gall *Quercus castanea*, gall collected 12/03/2005, emerged, 22/03/2005, E. Pascual leg. Paratypes, 1 female and 2 males presenting the same data as the holotype. In MNCN.

Etymology. Named after the tarasco Indians, an outstanding indigenous people inhabiting Michoacan prior to Spanish conquest.

Diagnosis and comments. In its lightly infuscate forewing, the new species resembles *A. hidalgoenis* and the new species *A. oaxacae* described herein, but the patterns of infuscation are different, being absent in the costal cell and the basal area below the basal cell in *A. tarasco*, whereas these areas are infuscate in *A. oaxacae*. In *A. hidalgoensis*, the basal cell is not infuscate, whereas infuscation is present on the forewing of *A. tarasco*. This forewing pattern of the new species also resembles *A. nevadensis* and *A. michoacaensis*, but in these species, the infuscation is much heavier than in *A. tarasco*. The mesoscutellum in the new species is deeply, but not widely emarginated posteriorly, especially in males. The gall is a typical large oak apple type, regularly spherical with a smooth surface, which is tinted darker green in spots when fresh.

Description. Female (Fig. 16E). Body length 7 mm (N = 2). Head and mesosoma black; clypeus and mandibles chestnut. Antennae brown with last seven apical flagellomeres chestnut. Metasoma and legs reddish chestnut. Forewing lightly infuscate along a band extended in basal cell, first cubital (lighter here), radial cell and beyond to the antero apical margin of wing. Costal cell and the area below the described infuscate band is colorless, only slightly infuscate.

Female. Head, in dorsal view strongly reticulate rugose, 2.4 times as wide as long (Fig. 8B). POL as long as OOL, posterior ocellus separated from inner orbit of eye by 1.5 times its longest diameter. Head in anterior view (Fig. 8A) 1.3 as wide as high, gena broadened behind eye. Vertex, frons, lower face, gena, and occiput with strong irregular reticulate-rugose sculpture, irradiating carinae from clypeus indistinct. Head moderately pubescent. Clypeus trapezoidal, ventral margin strongly projecting over mandibles and slightly sinuate. Anterior tentorial pits, epistomal sulcus and clypeo-pleurostomal lines discernible. Malar space 0.7 times height of compound eye. Toruli situated mid-height of compound eye; distance between antennal rim and compound eye as wide as antennal socket including rim. Ocellar plate slightly raised.

Mouthparts: mandibles strong, exposed; with dense setae in base, right mandible with three teeth; left with two teeth.

Antenna (Fig. 8D) As long as head and mesosoma combined; with 13 antennomeres; flagellum not broadening towards apex; with relatively long, erect setae, and placodeal sensilla in ventral area of flagellomeres F4–F11; placodeal sensillae on flagellomeres F8–F11 arranged in rows of 7–9 sensillae on ventral area of flagellomere. Relative lengths of first antennal segments: 20:10:36:23:19. Pedicel, short, globose, shorter than long and 0.5 as long as scape; F1 1.5 times as long as F2; F11 about 2 times as long as F10.

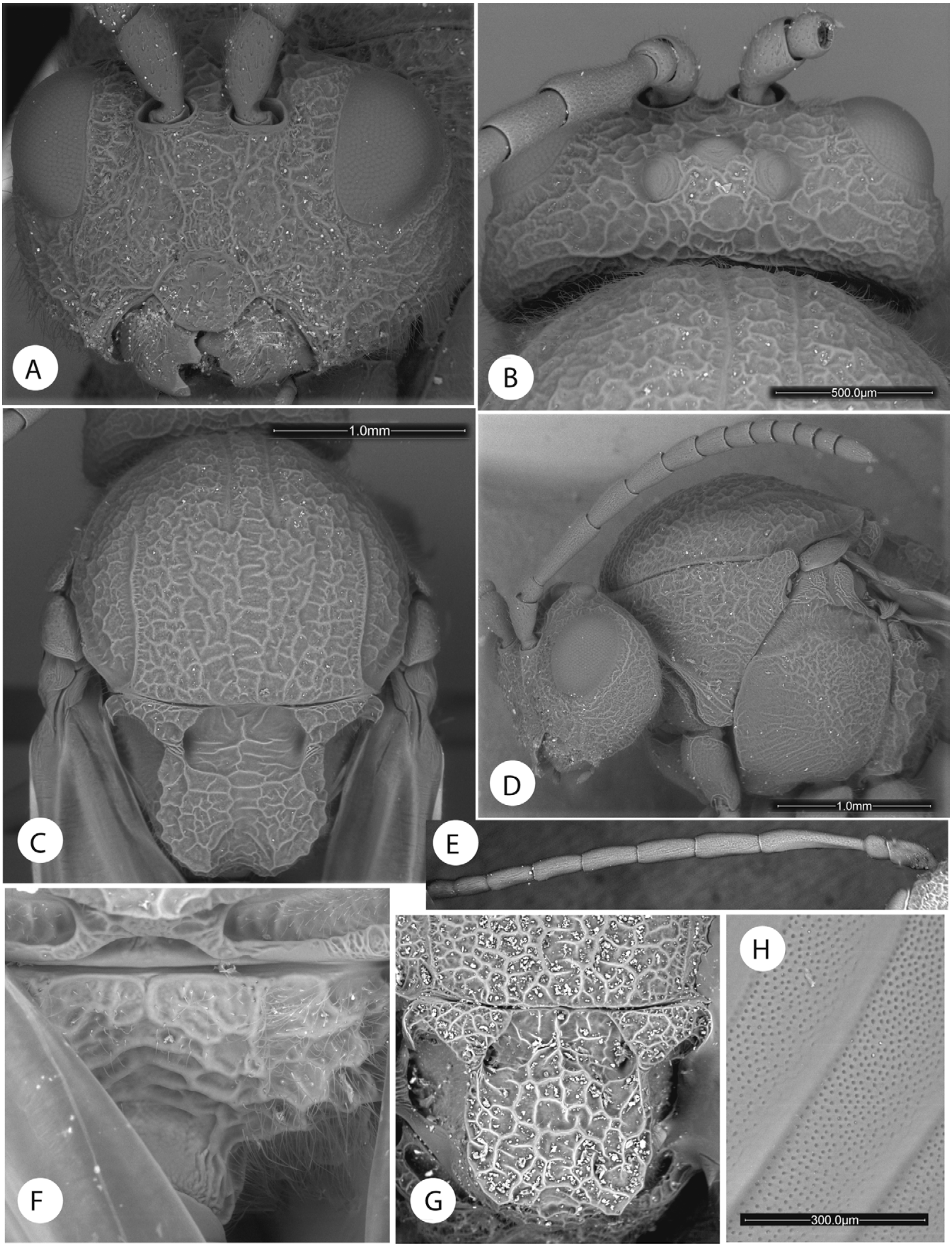

FIGURE 8. *Amphibolips tarasco* sp. nov. (A) female, head anterior view; (B) female, head dorsal view; (C) female, mesosoma dorsal view; (D) female, head and mesosoma lateral view; (E) male antenna; (F) male propodeum; (G) male, mesoscutellum dorsal view; (H) female, metasoma sculpture.

Mesosoma. Coarsely reticulate rugose, short, in lateral view slightly longer than high. Pronotum, moderately pubescent; lateral surface of pronotum with strong irregular reticulate rugose sculpture (Fig. 8D). Pronotum medially short; ratio of length of pronotum medially/laterally = 0.20. Pronotal plate indistinct dorsally.

Mesonotum. Mesoscutum sparsely pubescent and with strong reticulate rugose- sculpture (Fig. 8C). Notauli almost invisible obscured by crossing coarse sculpture. Anteroadmedian signa well visible and parascutal carinae distinct. Transscutal fissure narrow. Mesoscutellum subquadrate, about 0.6 as long as mesoscutum. Scutellar foveae rounded, deep, with distinct margins; with some transversal and oblique rugae, the intervals smooth and shining; about 0.4 as long as mesoscutellum (Fig. 8C). Mesoscutellum strongly reticulate-rugose, deeply emarginated at posterior margin, the incision being 0.3 as wide as scutellum width, extending longitudinally across median area of scutellum to reach, although more shallowly, posterior margins of scutellar foveae (Fig. 8C). Mesopleuron coarsely reticulate rugose, the rugae not as strong as mesoscutum. (Fig. 8D).

Metanotum (Fig. 8F). Metapectal-propodeal complex similar to thes precedent species. Median propodeal area coarsely rugose and densely pubescent; lateral propodeal carinae discernible. Nucha rugose medially.

Legs. Densely pubescent; femora and tibiae robust. Metatarsal claws with strong triangular basal lobe or teeth.

Forewing (Fig. 12C): Slightly longer than body; radial cell about 4 times longer than wide; open widely along dorsal margin; areolet conspicuous, triangular. All veins well visible. R1 straight, not reaching wing margin; Rs+M reaching basalis at its mid-height. First abscissa of radius (2r) angulated; radius only weakly curved. Apical margin with short hair fringe.

Metasoma. Slightly shorter as head and mesosoma combined, in lateral view about slightly longer than high. Second metasomal tergite covering about two third of metasoma, with a band of micropuntures clearly visible in posterior one half of metasomal large terguite; punctures visible on subsequent tergites (Fig. 8H); dorsally the surface of the second metasomal terguite before the band of micropunctures without sculpture, smooth and shinning; latero ventral area of second metasomal tergite moderately pubescent. Projecting part of hypopygial spine long, in lateral view about 4.5 times as long as wide; laterally with long setae which not form an apical patch.

Male. Differs from female as follows: antennae with 14 antennomeres; F1 slightly modified, weakly twisted, flattened on ventral side, and slightly widened towards apex; 1.6 as long as F2; elongate placodeal sensillae visible in all flagellomeres. Mesoscutellum only slightly and shallowly emarginated in posterior margin (Fig. 8G). Forewings completely and more heavily infuscate, the darker anterior band being still visible (Fig. 13E).

Gall (Figs 20C, 20D). A large, regularly spherical, oak apple gall. The surface of gall is smooth, green with darker green spots when fresh. Monothalamic. Grows on twigs of *Quercus castanea.*

Distribution. *A. tarasco* was found at 2000 m a.s.l. at Santa María, Michoacán state, Mexico.

Biology. Includes a sexual generation. The galls were collected in March, and the adults emerged shortly after the galls were collected.

Amphibolips michoacaensis Nieves-Aldrey & Maldonado sp. nov.

Figs 9A–F, 10A–D, 12D, 13D, 16C–D.

Type material. Holotype female (Fig. 16C). In the Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), mounted on a card. Cat. nº 2251. MEXICO, Michoacán, Cuenca del Cuitzeo, Umécuaro, N 19° 32´ 55.4´´ W 101° 15´ 37.2´´. 2140 m; ex gall *Quercus castanea*, gall collected 10/04/2009, emerged 10/2009, Y. Maldonado leg. Paratypes, 2 males and 3 females: 2 males showing the same data as the holotype; 1 female with the same data as the holotype, but gall collected 4/06/2008; 2 females found at Jesús del Monte, 2133 m, ex gall *Q. castanea*, collected 21/04/2009, insects emerged 05/2009, Y. Maldonado leg. In MNCN.

Etymology. Named after the Mexican state including the collection sites.

Diagnosis and comments. In its forewing pattern, this species closely resembles *A. nevadensis* and *A. tarasco*. Compared to *A. nevadensis*, it differs in the first cubital cell of the forewing not being as infuscate and compared to *A. tarasco*, in the dark band being much more heavily infuscate, with all veins obscured by infuscation. The mesoscutellum is moderately emarginated, with the incision not quite reaching the posterior margins of the scutellar foveae. MT3 smooth or only weakly coriaceous prior to the band of micropunctures, which are extended laterally over the posterior 1/3 to ½ of the length of the metasomal terguite. The intervals between micropunctures are strongly coriaceous.

Description. Female. Body length 5.1 mm (N = 4) (range 4.7–5.4). Head and mesosoma black; clypeus, mandibles and antennae anteroventrally chestnut brown. Metasoma blackish to dark chestnut, lighter ventrally. Legs black. Forewing dark infuscate, all the veins obscured by infuscation. A dark heavily infuscate band extended anteriorly along the basal cell, first cubital cell, and radial cell to antero apical of forewing. Costal cell, first cubital cell and the area below the more heavily infuscate band is colorless, only slightly infuscate.

Female. Head, in dorsal view strongly reticulate rugose, 2.3 times as wide as long (Fig. 9B). POL as long as OOL, posterior ocellus separated from inner orbit of eye by 1.5 times its longest diameter. Head in anterior view (Fig. 9A) about 1.3 as wide as high, gena broadened behind eye. Vertex, frons, lower face, gena, and occiput with strong irregular reticulate-rugose sculpture. A pair of irregular carinae running from ventral margin of antennal sockets to anterior tentorial pits and some irradiating carinae from clypeus visible. Head moderately pubescent. Clypeus trapezoidal, ventral margin strongly projecting over mandibles and slightly sinuate. Anterior tentorial pits conspicuous; epistomal sulcus and clypeo-pleurostomal lines discernible. Malar space 0.5 times height of compound eye. Toruli situated mid-height of compound eye; distance between antennal rim and compound eye as wide as antennal socket including rim. Ocellar plate slightly raised.

Mouthparts: mandibles strong, exposed; with dense setae in base, right mandible with three teeth; left with two teeth.

Antenna (Fig. 9C) as long as head and mesosoma combined; with 13 antennomeres; flagellum not broadening towards apex; with relatively long, erect setae, and placodeal sensilla in ventral area of distal flagellomeres. Scape 2 times as long as pedicel; pedicel, as long as wide; F1 1.5 times as long as F2. F9–F10 as long as wide, F11 about 2.5 times as long as wide; 2.5 as long as F10.

Mesosoma. Coarsely reticulate rugose, short, in lateral view 1.2 as long as high. Pronotum, moderately pubescent; lateral surface of pronotum with strong irregular reticulate rugose sculpture (Fig. 9E). Pronotum medially short; ratio of length of pronotum medially/laterally = 0.20. Pronotal plate indistinct dorsally.

Mesonotum. Mesoscutum barely pubescent and with strong rugose-reticulate sculpture (Fig. 9D). Notauli visible but shallow and indistinct anteriorly, obscured by crossing coarse sculpture. Anteroadmedian signa well visible and parascutal carinae distinct. Transscutal fissure narrow. Mesoscutellum subquadrate, about 0.6 as long as mesoscutum (Fig. 9D). Scutellar foveae rounded, deep, with distinct margins; smooth and shining; 0.3 as long as mesoscutellum. Mesoscutellum strongly reticulate-rugose, emarginated at posterior margin, the incision being only moderately deep and wide and not reaching posterior margins of scutellar foveae (Fig. 9D). Mesopleuron coarsely reticulate rugose, the rugae not as strong as mesoscutum. (Fig. 9E).

Metanotum. Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at about mid-height of metapectal-propodeal complex. Metascutellum weakly rugose; metanotal trough smooth and pubescent. Median propodeal area reticulate shining rugose and densely pubescent; lateral propodeal carinae discernible. Nucha rugose medially.

Legs. Densely pubescent; femora and tibiae robust. Metatarsal claws with strong triangular basal lobe or teeth (Fig. 10A).

Forewing (Fig. 12D). Slightly longer than body; radial cell 4 times longer than wide; open widely along dorsal margin; areolet inconspicuous, small. R1 straight, not reaching wing margin; Rs+M reaching basalis at its mid-height. First abscissa of radius (2r) obscured by infuscation and radius only slightly curved. Apical margin with short hair fringe.

Metasoma. Slightly shorter as head and mesosoma combined, in lateral view about slightly longer than high. Second metasomal tergite covering about two third of metasoma, with a band of micropuntures clearly visible in posterior one third; dorsolaterally the puntures being strong with coriaceous sculpture in the intervals. Punctures present on subsequent tergites; dorsally the surface of the second metasomal terguite, before the band of micropunctures, has weak coriaceous sculpture (Fig. 10B); latero ventral area of second metasomal tergite moderately pubescent. Projecting part of hypopygial spine very long, in lateral view about 6.5 times as long as wide; laterally with long setae, more dense apically but not forming an apical patch.

Male (Fig. 16D). Differs from female as follows: antennae with 14 antennomeres; F1 slightly modified, flattened on ventral side, elongate placodeal sensillae visible in all flagellomeres (Fig. 10C). Mesoscutellum only slightly emarginated in posterior margin (Fig. 10D). Forewings more heavily infuscate in its entire surface, but the darker anterior band being still visible (Fig. 13D).

Gall (Figs 20A, 20B). A globular more or less regular gall with spongy interior Monothalamic. Grows on twigs of *Quercus castanea* or nearer the base of the gall, galls up to 48 mm in diameter, detachable, on twigs.

Distribution. *A. michoacaensis* was found at Umécuaro and other sites of Cuenca of Cuitzeo at 2100 m at Michoacán state, Mexico.

Biology. Exhibits a sexual generation. The galls were collected in April, and the adults emerged in May.

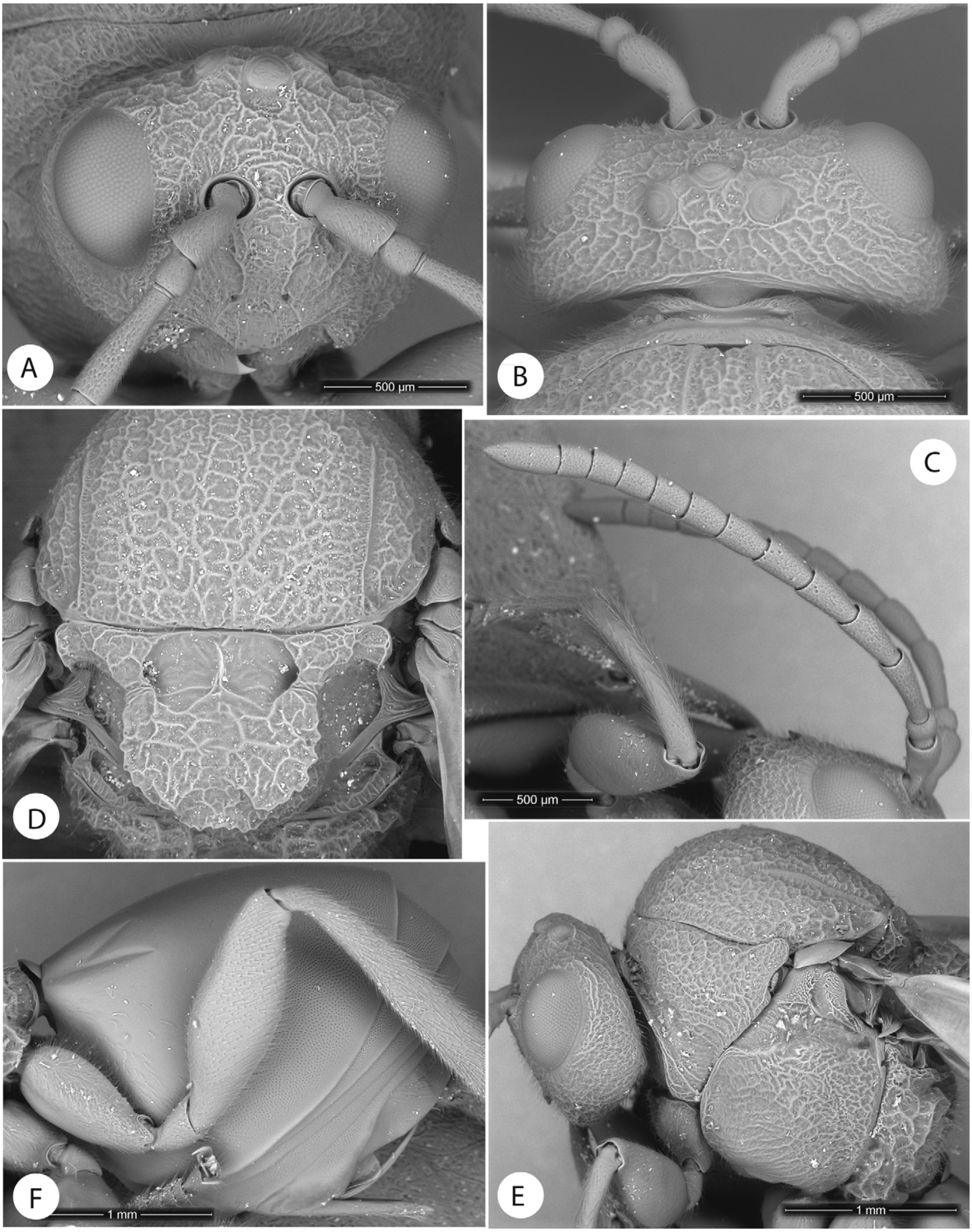

FIGURE 9. *Amphibolips michoacaensis* sp. nov., female. (A) head anterior view; (B) head dorsal view; (C) antennae; (D) mesosoma dorsal view; (E) mesosoma lateral view; (F) metasoma lateral view.

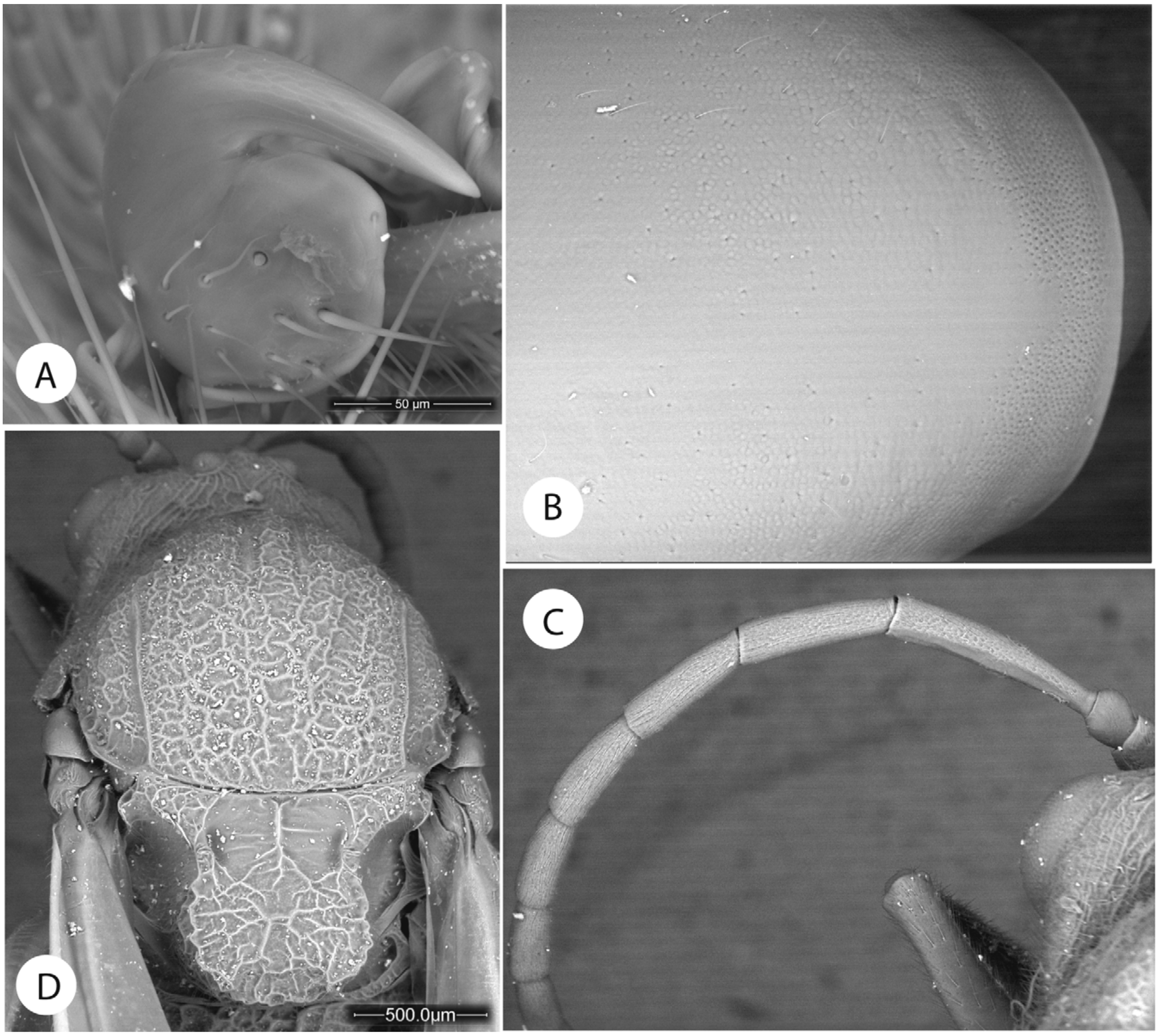

FIGURE 10. *Amphibolips michoacaensis* sp. nov. (A) female, metatarsal claw; (B) female, metasoma dorsal view; (C). male antenna; (D) male, mesosoma dorsal view.

Key to adult *Amphibolips* species of Mexico and related species of Panama (species of "*niger* complex" excluded)

1. Antenna with 16–17 antennomeres. Mesoscutellum rounded posteriorly. Mesoscutum sometimes with carinate longitudinal sculpture (Figs 1A–B). Asexual forms. Galls rounded with a woolly surface and a central hard woody cell . . . . "***niger* complex"** Kinsey

• Antenna with 13–14 antennomeres (females) or 15 antennomeres (males) (Fig. 3A). Mesoscutellum emarginated posteriorly, with the emargination being more or less deep (Figs 7B, 10D). Mesoscutum always with coarse rugose reticulate sculpture (Figs 2E, 6D). Sexual forms. Gall form spherical or globose to spindle shaped. Surface smooth or rugose, never woolly **2**

2. Females **3**

• Males **16**

3. Forewing with a heavily infuscate spot on the basal area of radial cell; remainder of the forewing hyaline to only slightly infuscate (Fig. 11B). . . . . ***aliciae***

• Forewing entirely infuscate, more heavily along a band on anterior margin of wing (Figs. 11C–F) **4**

4. More heavily infuscate band along anterior margin of forewing with a clear cross-band on one-third apical part of radial cell which is more or less extended towards posterior margin of wing (Figs 11A, 11C, 13A, 14E). **5**

• More heavily infuscate band along the anterior margin of the forewing, without a clear cross-band on apical part of radial cell extended towards posterior margin of wing. If there is a clear colourless spot apically on the radial cell, it does not extend below the radial cell (Figs 12A–E) **8**

5. Basal and first cubital cells colourless or only weakly infuscate prior to the heavily infuscate basal half of the radial cell (Fig. 14E). Mesoscutellum weakly emarginate posteriorly. F1 1.2 as long as F2 (Fig. 1F) . . . . ***fusus***

• Basal and first cubital cells as heavily infuscate as basal half of radial cell. F1 1.4–1.5 as long as F2 (Figs 11A, 11C, 13A) . . **6**

6. Clear cross-band narrow, extended below radial cell, but not reaching posterior margin of wing (Fig. 13A). Mesoscutellum strongly emarginated posteriorly (V-shaped in dorsal view (Fig. 1D), with a sharp horn projection in lateral view. . . . . ***dampfi***

• Clear cross-band wide and extended posteriorly to reach posterior margin of wing (Fig. 11A, 11C). Mesoscutellum only moderately emarginated posteriorly (Fig. 2E) **7**

7. Forewing heavily and entirely infuscate outside of the clear cross-band in the anterior area of the radial cell, which is relatively wider; costa cell infuscate (Fig. 11A). Notauli visible; scutellar foveae smooth . . . . ***castroviejoi***

• Forewing not entirely infuscate outside of the clear cross-band in the anterior area of the radial cell, which is relatively narrower; costal cell and posterior half of wing colourless, only weakly infuscate (Fig. 11C). Notauli almost invisible; scutellar foveae with carinate sculpture (Fig. 2E) . . . . ***durangensis***

8. Basal half of forewing uniformly infuscate; the costal cell and the area below basal cell as infuscate as the basal, first cubital and radial cells. **9**

• Costal cell and the area below basal cell and beyond colourless, much less infuscate than the basal and radial cells. **10**

9. Antenna and metasoma predominantly black. Mesoscutellum moderately emarginated posteriorly. F3 1.3 times as long as F4; gall elongate, spindle shaped. . . . . ***nassa***

• Antenna and metasoma predominantly reddish. Mesoscutellum strongly emarginated posteriorly. Gall regularly spherical . . . . ***oaxacae***

10. Heavily infuscate band along the anterior margin of the forewing extended uniformly from basal cell to apical margin of wing, not interrupted in the first cubital cell **11**

• Heavily infuscate band along the anterior margin of the forewing, interrupted in the first cubital cell, sometimes also in the basal cell **12**

11. Mesoscutellum slightly emarginated posteriorly. Heavily infuscate anterior band of forewing quite dark (Fig. 12E). Galls with an acute point. Male unknown . . . . ***zacatecaensis***

• Mesoscutellum strongly emarginated posteriorly (Fig. 7B). Heavily infuscate anterior band of forewing not as dark (Fig. 12B). Galls end in an obtuse point. Bisexual form; male known . . . . ***nevadensis***

12. Colourless, less infuscate spot present on apical area of radial cell (Figs 11D, 11E) **13**

• Colourless, less infuscate spot absent on apical area of radial cell; radial cell uniformly and heavily infuscate (Figs 12A, 12C, 12D). 14

13. All the veins strongly infuscate, basally on the radial cell not being visible. Clear, colourless area on radial cell relatively more extended on one half apical area of radial cell; first cubital cell more heavily infuscate (Fig. 11D). F1 1.4 as long as F2 (Fig. 3A). . . . . ***jaliscensis***

• All the veins less strongly infuscate, all being visible. Clear, colourless area on the radial cell relatively small, extending only on more apical area of the radial cell; first cubital cell only slightly infuscate (Fig. 11E). F1 1.6 as long as F2 (Fig. 5C). . . . . ***malinche***

14. Basal cell not infuscate (Fig. 12A) . . . . ***hidalgoensis***

• Basal cell infuscate (Figs 12C, 12D). **15**

15\. Forewing weakly infuscate, all veins visible (Fig. 12C). Mesoscutellum only slightly emarginated posteriorly (Fig. 8C). . . . . ***tarasco***

• Forewing more heavily infuscate, veins on anterior half of radial cell not visible (Fig. 12D). . . . . ***michoacaensis***

Males

16. Forewing with a heavily infuscate spot in the basal area of the radial cell; rest of the forewing only slightly infuscate. . ***aliciae***

• Forewing entirely and heavily infuscate, more so along a band on the anterior margin of the wing (Figs. 13A–F) **17**

17. More heavily infuscate band along the anterior margin of the forewing, with a clear cross-band on one-third of the apical part of the radial cell, which is more or less extended towards the posterior margin of the wing (Fig. 13A) **18**

• More heavily infuscate band along the anterior margin of the forewing, without a clear cross-band on the apical part of the radial cell, extended towards the posterior margin of the wing. If there is a clear colourless spot apically on the radial cell, it does not extend below the radial cell (Figs 13B, 13D) **19**

18. Clear cross-band wide and extended posteriorly to reach margin of the wing. Mesoscutellum only moderately emarginated posteriorly. . . . . ***castroviejoi***

• Clear cross-band narrow, extended below the radial cell, but not reaching the posterior margin of the wing (Fig. 13A). Mesoscutellum strongly emarginated posteriorly (V-shaped in dorsal view) (Fig. 1D), with a sharp horn projection observed in lateral view . . . . ***dampfi***

19. Mesoscutellum widely and deeply emarginated posteriorly (Fig. 3D). Radial cell with a clear spot apically (Fig. 13B). . . ***jaliscensis***

• Scutellum slightly or moderately emarginated posteriorly (Figs 8G, 10D). Radial cell without a clear spot apically (Figs 13D, 13E) **20**

20 Mesoscutellum only slightly emarginated posteriorly (Fig. 8G); scutellar foveae ellipsoidal. F1 1.6 as long as F2 (Fig. 8E). Costal cell of the forewing relatively clearer, less infuscate than the rest of the forewing (Fig. 13E) . . . . ***tarasco***

• Mesoscutellum moderately to deeply emarginated posteriorly; scutellar foveae rounded. F1 1.4–1.5 as long as F2 (Fig. 10C). Costal cell relatively darker; as infuscate as the remaining forewing surface (Fig. 13D) **21**

21. Mesoscutellum moderately emarginated posteriorly (Fig. 10D). F1 1.4 as long as F2 (Fig. 10C). Radial cell 3.3 as long as wide, second abscissa of radius slightly curved (Fig. 13D) . . . . ***michoacaensis***

• Mesoscutellum deeply emarginated posteriorly (Figs 7B–C). F1 1.5 as long as F2 (Fig. 7E). Radial cell 3.7 as long as wide, second abscissa of the radius only slightly curved (Fig. 13F) . . . . ***nevadensis***

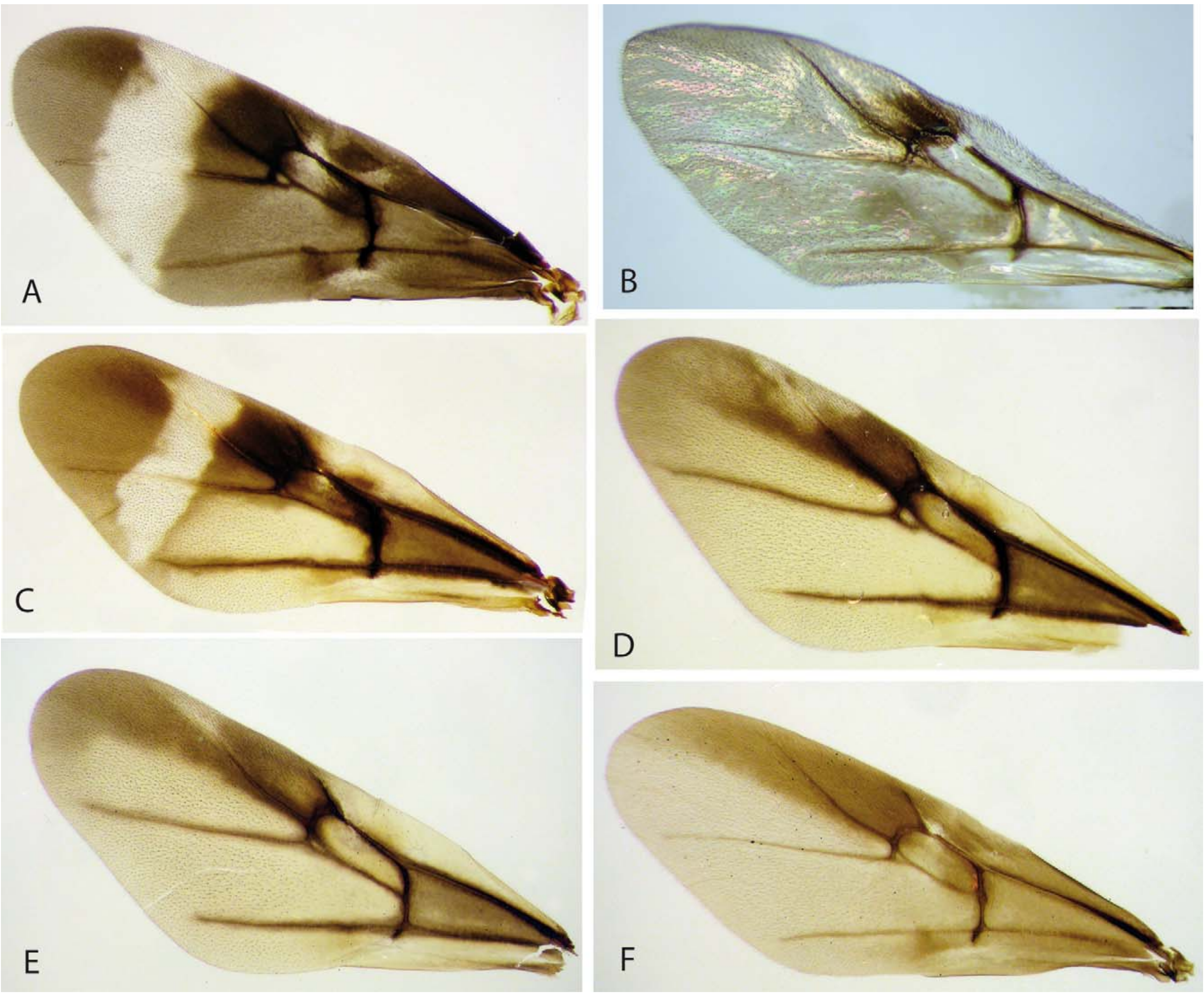

FIGURE 11. Forewings of species of *Amphibolips*, females; (A) *Amphibolips castroviejoi*, from Panama; (B) *A. aliciae,* from Panama*;* (C) *A. durangensis* sp. nov. (D) *A. jaliscensis* sp. nov. (E) *A. malinche* sp. nov. (F) *A. oaxacae* sp. nov.

Discussion

In his pioneer study of the *Amphibolips* of Mexico, Kinsey (1937) separated the Mexican species of this genus into two groups. He described the new species *A. dampfi*, *A. fusus* and *A. nassa*, but without constructing any formal or informal taxonomic grouping for them. Of these three species, only *A. dampfi* exhibits a demonstrated bisexual generation, as both males and females have been described. The other two species, *A. fusus* and *A. nassa*, have been described based only on females, and Kinsey doubted whether they presented bisexual or agamic generations. For instance, he recorded the life history of *A. nassa* as unknown. However, he formally proposed the group "*niger* complex" (asexual generations) for six new species he described from Mexico, including the species *Amphibolips nigra* Beutenmüller 1911, which he included in the "*niger* complex" under the name *Amphibolips* (niger) *niger* Beutenmüller. One last Mexican *Amphibolips* species, *A. palmeri* Basset 1890, which was in fact the first *Amphibolips* species described from Mexico, was not mentioned in Kinsey (1937) and was not formally included in any group.

The species of the "*niger* complex" are well characterised according to Kinsey (1937) based on their morphology and biology. With regard to morphology, the main diagnostic character separating the species of this group from other *Amphibolips* species is their 16–17 segmented antennae, which typically exhibit 13–14 antennomeres in the majority of species of this genus (Medianero & Nieves-Aldrey 2010; Melika *et al*. 2011).

Other morphological characters are less clear because they present mixed character states and are shared by other *Amphibolips* species, such as heavily infuscate wings, the sculpture of the mesoscutum and mesoscutellum and the shape and sculpture of the scutellar foveae. Melika *et al.* (2011) provided some additional diagnostic characters of the "*niger* complex" as follows: the surface sculpture of the head and mesosoma is less rugose and smoother; the mesoscutellum is rounded posteriorly, without a median posterior depression; all metasomal tergites with white setae posterolaterally; and the projecting part of the ventral spine of the hypopygium shorter and thinner. However, some of these diagnostic characters, especially the mesoscutellum character, which is supposedly rounded posteriorly in species of the "*niger* complex", were not mentioned in Kinsey´s original description, and we ignore whether or not these additional diagnostic characters were examined in all of the species of the "*niger* complex". The character of the mesoscutellum was examined and illustrated in at least two *Amphibolips* species: one of the "*niger* complex", *Amphibolips pistrix* Kinsey, 1937 and another outside of this group, *A. quercuscinereae* (Ashmead, 1881), both of which present a posteriorly rounded mesoscutellum. We have examined this character in one additional species of the "*niger* complex", *Amphibolips nebris* Kinsey, whose mesoscutellum is also rounded posteriorly (Fig. 1A), as in the cases illustrated by Melika *et al.* (2011).

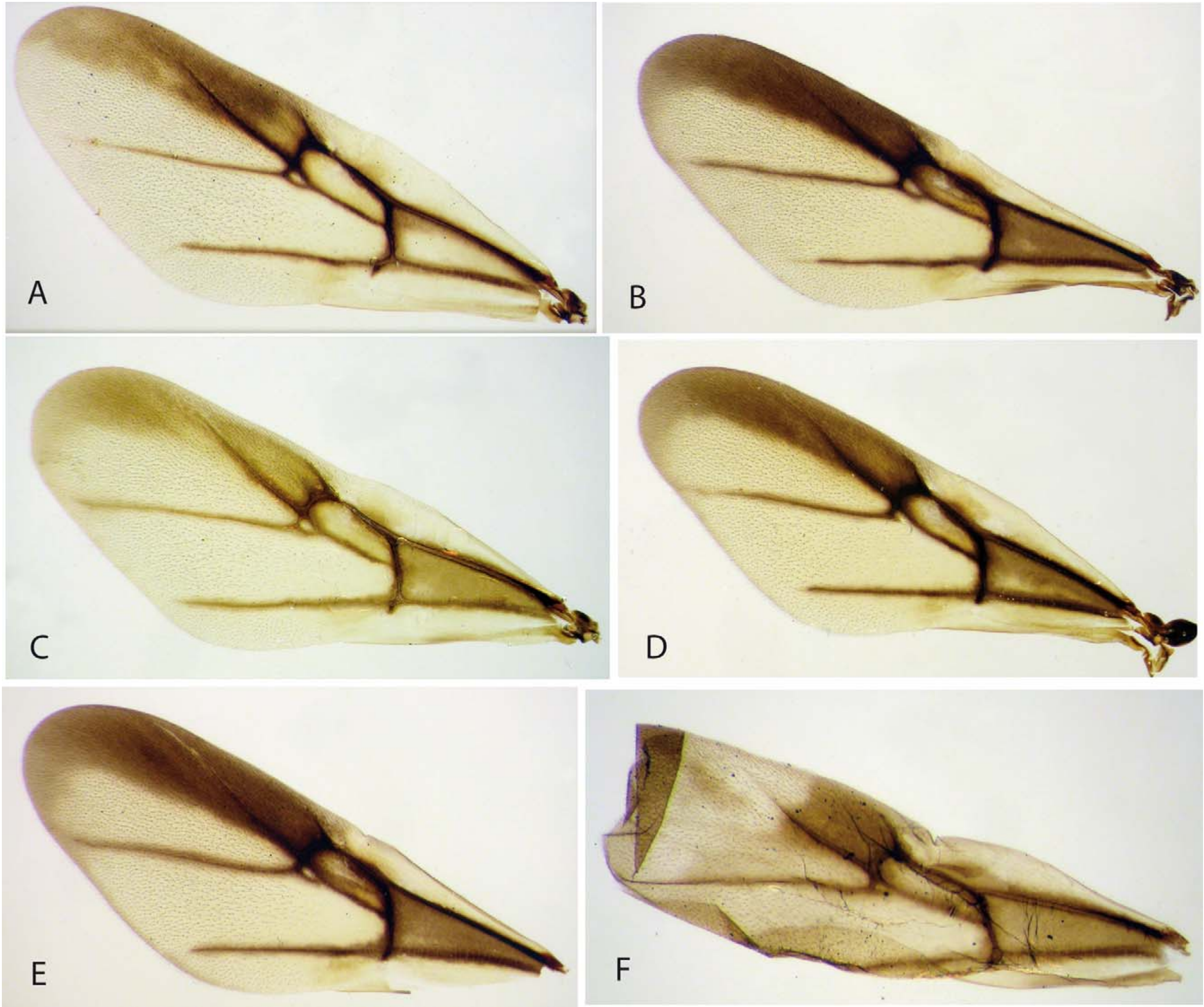

FIGURE 12. Forewings of species of *Amphibolips*, females; (A) *Amphibolips hidalgoensis*; (B) *A. nevadensis* sp. nov. (C) *A. tarasco* sp. nov. (D) *A. michoacaensis* sp. nov. (E) *A. zacatecaensis*; (F) *Amphibolips sp*., from Nuevo León.

However, Melika *et al.* (2011) omitted the most important diagnostic character of the "*niger* complex" mentioned in Kinsey´s original description, that is, the 16–17 segmented antennae. We have examined this character in the female holotype of a species of this group, *A. nebris* Kinsey. This specimen in fact exhibits a 16 segmented antenna (Fig. 1B). The cited authors questioned whether all seven species of the '"*niger* complex" are distinct biological entities or are simply varieties based entirely on different collection localities. After this study, we will go further, asking whether the entire "*niger* complex" should be excluded from *Amphibolips* because its members differ strongly, both morphologically and biologically, from the core species of this genus. A revision of the entire complex, as well as biological and molecular analyses, should provide us with initial crucial information for solving this problem.

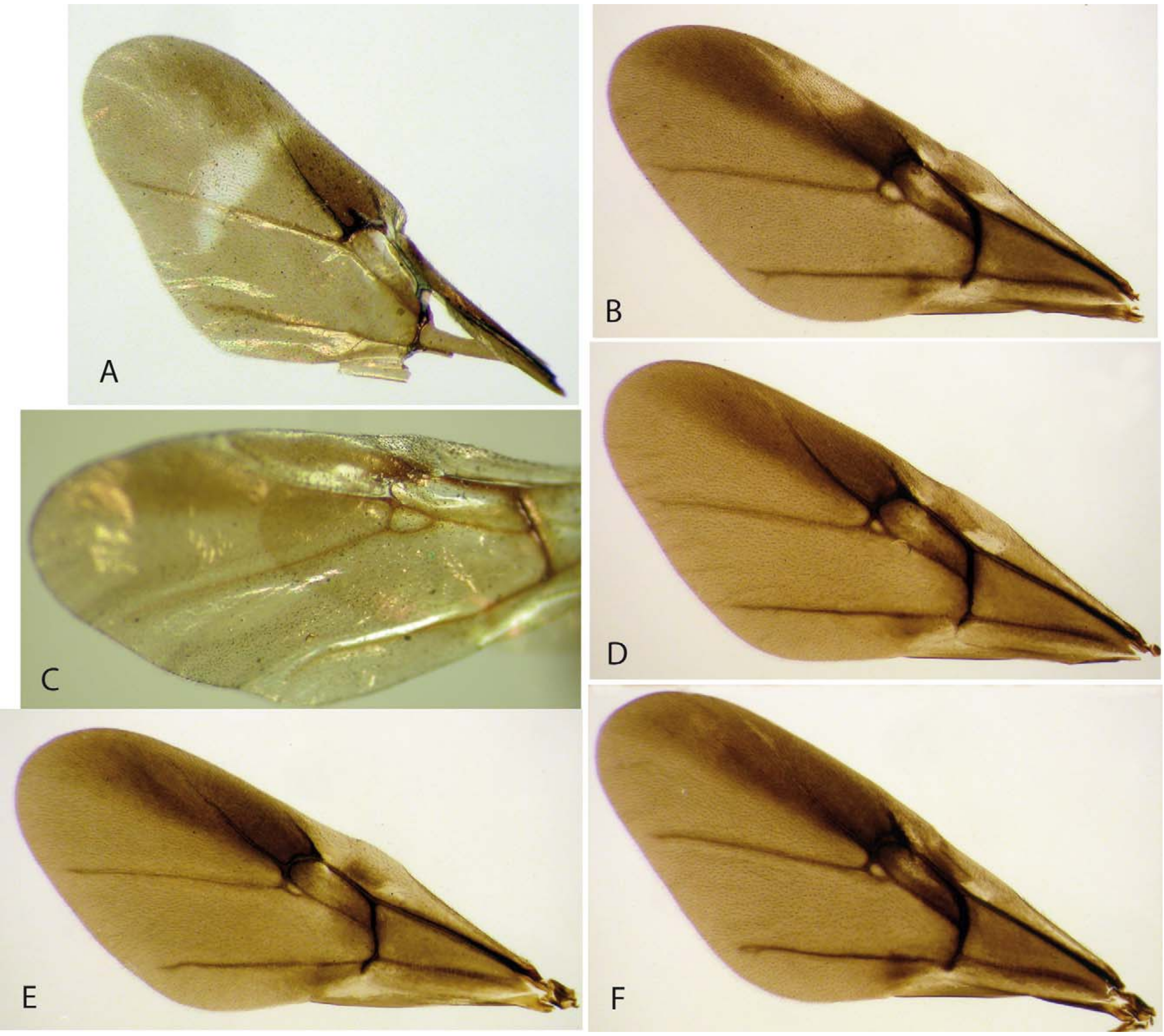

FIGURE 13. Forewings of species of *Amphibolips*, males except as indicated; (A) *Amphibolips dampfi*; (B) *A. jaliscensis* sp. nov. (C) *A. nebris*, female; (D) *A. michoacaensis* sp. nov. (E) *A. tarasco* sp. nov. (F) *Amphibolips nevadensis* sp. nov.

Melika *et al.* (2011) erected a new group, the "*nassa* complex", for the six Mexican species not included in the "*niger* complex", including the three described by Kinsey plus *A. palmeri* and two species described as new. However, they did not formally describe the "*nassa* complex" in the same way that was used by Kinsey, despite providing a key for the identification of these species. We do not follow this informal taxonomic proposal here due to the reasons presented below.

The species included by Melika *et al.* (2011) in the "*nassa* complex" are characterised, according the identification key provided by the above-cited authors, by presenting a mesoscutellum with a posteromedian emargination. The other couplet included the species of the "*niger* complex" and all known *Amphibolips* species from the USA and Panama. However, this couplet is clearly erroneous because at least three species of *Amphibolips* from the USA (*A. confluentus* (Harris, 1841), *A. quercusinanis* (Osten Sacken, 1861) and *A. melanocerus* (Ashmead, 1885)) and two from Panama (*A. castroviejoi* Medianero & Nieves-Aldrey, 2010 and *A. aliciae* Medianero & Nieves-Aldrey, 2010) also present a mesoscutellum emarginated posteriorly (Beutenmüller 1909; Medianero & Nieves-

Aldrey 2010). This morphological character cannot then be used as diagnostic for defining the “*nassa* complex”. Other characters shared by the species included in the “*nassa* complex” are as follows:

-Antennae with 13–14 antennomeres in females; 14–15 in males.
-Forewings always more or less deeply infuscate, with bands or spots variably extended to the anterior margin of the forewing or/and to the radial and cubital cells.
- Ventral projection of the spine of the hypopygium quite long, more than five times as long as wide in lateral view.
- Head and mesoscutum with a strong reticulate rugose sculpture.
- Second metasomal terguite covering approximately two-thirds of the metasoma, ventrolaterally pubescent and with a band of micropunctures posteriorly.
- Galls of the “oak-apple” type, spherical or globose, pointed or not, to more or less fusiform or spindle shaped.

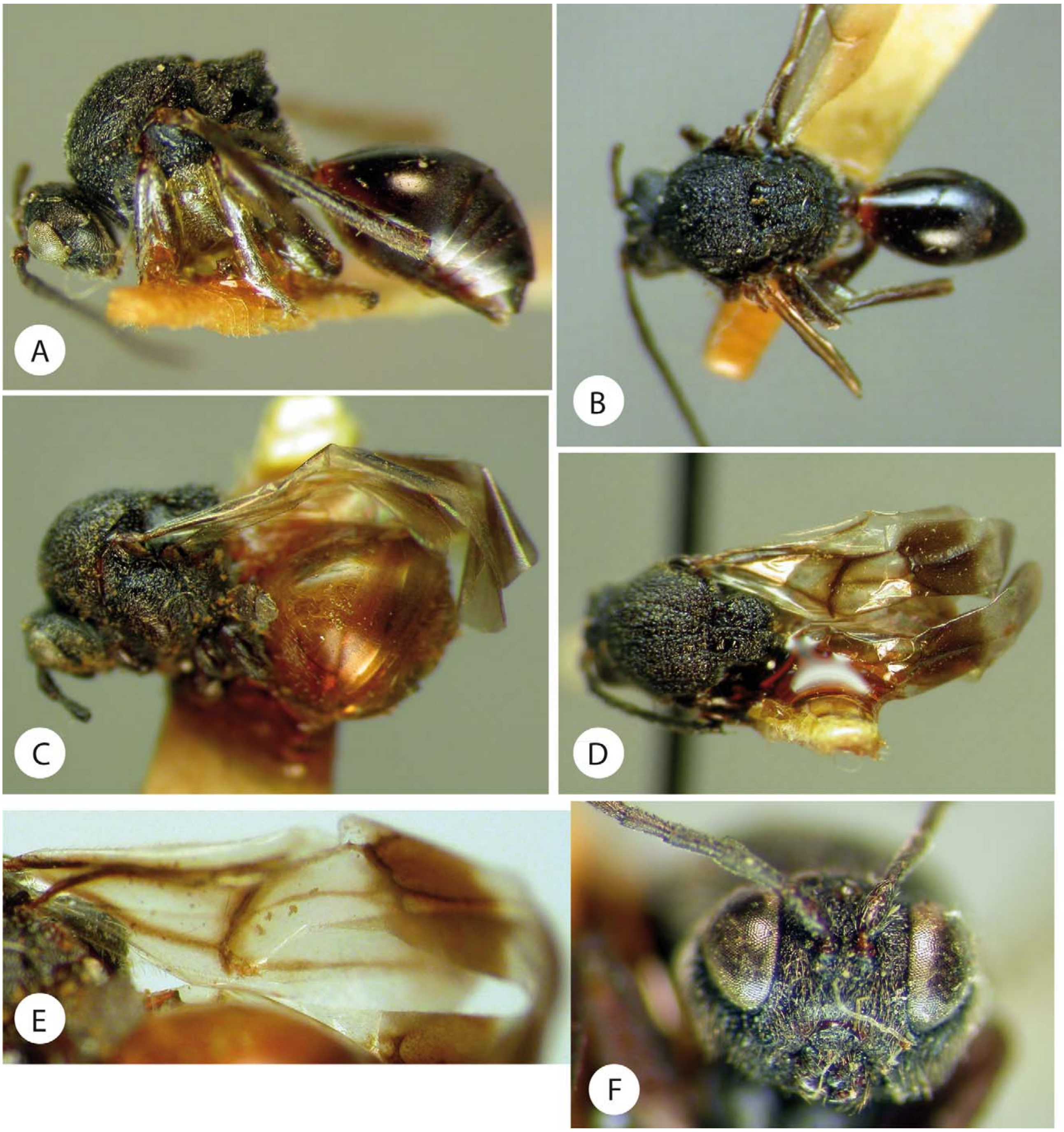

FIGURE 14. Type material examined of species of *Amphibolips* (A) *Amphibolips dampfi*, holotype male, lateral view; (B) *Amphibolips dampfi*, holotype male, dorsal view; (C) *Amphibolips fusus*, holotype female, lateral view; (D) *Amphibolips fusus*, holotype female, dorsal view; (E) *A. fusus*, forewing; (F) *Amphibolips nebris*, head anterior view.

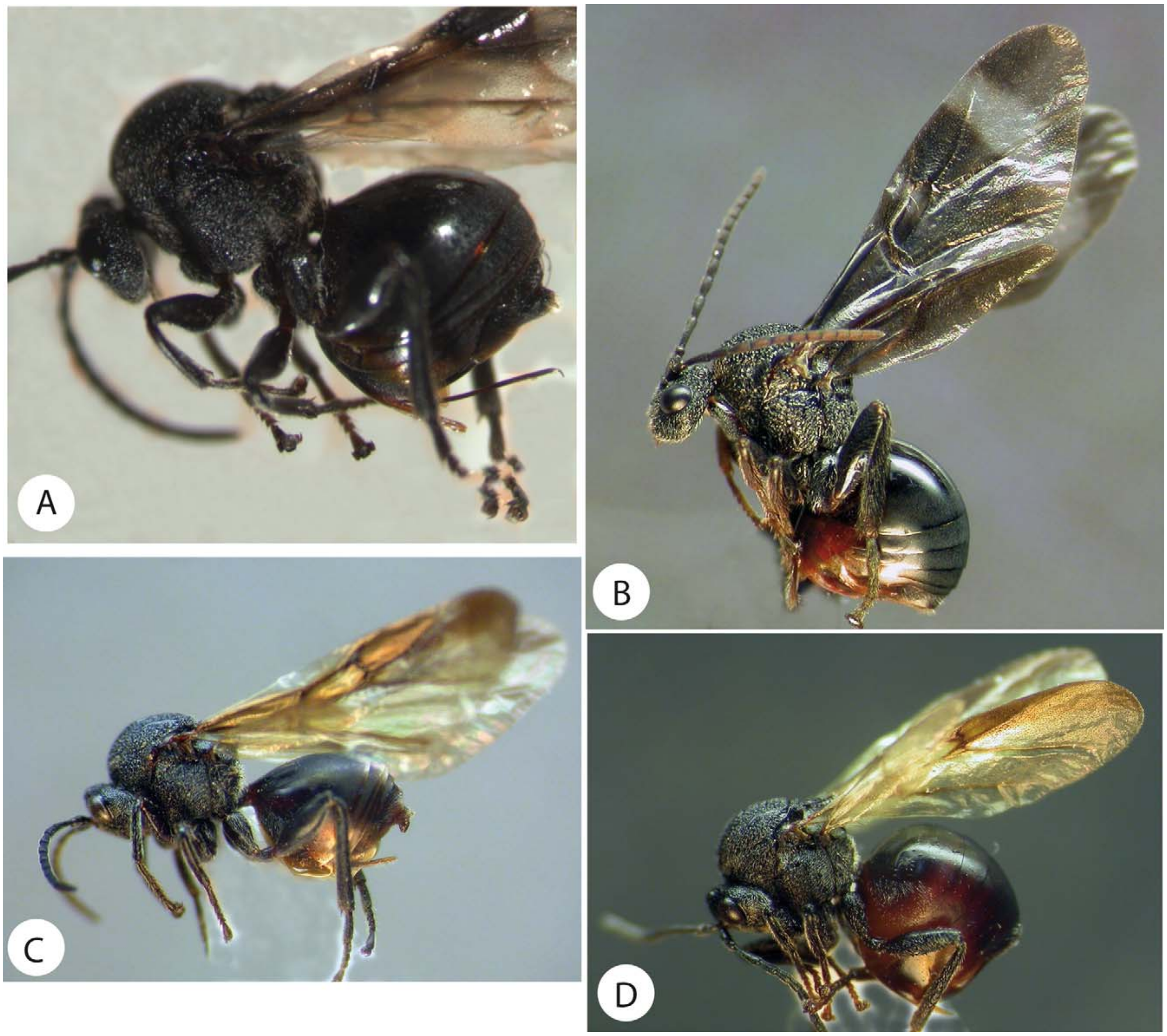

FIGURE 15. Habitus of species of *Amphibolips*, females. (A) *Amphibolips durangensis* sp. nov. (B) *A. castroviejoi*. (C) *Amphibolips malinche* sp. nov. (D) *Amphibolips hidalgoensis*.

Nevertheless, all of these characters are also shared, at least in part, by *Amphibolips* species from the USA and Panama and may not be used to readily define the "*nassa* complex" in the sense used by Melika *et al.* 2011. By example darker clouds or smoky brown transverse bands on the forewings are also present in the North American species *Amphibolips gainesi* Basset, 1900 and *A. trizonata* Ashmead, 1896 (Beutenmüller 1909).

In conclusion, the "*nassa* complex" appears to us to be an useless taxonomic group that is not supported and not well defined with regard to morphology and should no longer be maintained. Further morphological and molecular studies will elucidate whether this hypothesis is or is not supported by additional data.

The Mexican *Amphibolips* species not belonging to the "*niger* complex" comprise a group of species that are closely related and are weakly differentiated morphologically. Gall morphology, which is a distinctive feature used for differentiation of these species as an extended phenotype in many oak gall wasps, appears to be not as discriminant in this group of *Amphibolips* species. There are two main types of gall morphologies, ranging from spherical or globose, pointed at the end or not, to fusiform or more or less spindle shaped. However, morphologically different insects, supposedly belonging to different species, sometimes emerge from similar galls. This fact, together with the extreme morphological similarity within the group, poses the taxonomic problem of the limits of the extant species with respect to whether they represent widely variable single species or closely related different species. The species analysed in the present study, including the species described as new, are all only slightly differentiated with regard to the morphology of adults and galls. They appear to form a group of closely related sibling species. Ongoing molecular phylogeographic studies may eventually elucidate the real, objective limits of the geographic variability within a given species or between two different species.

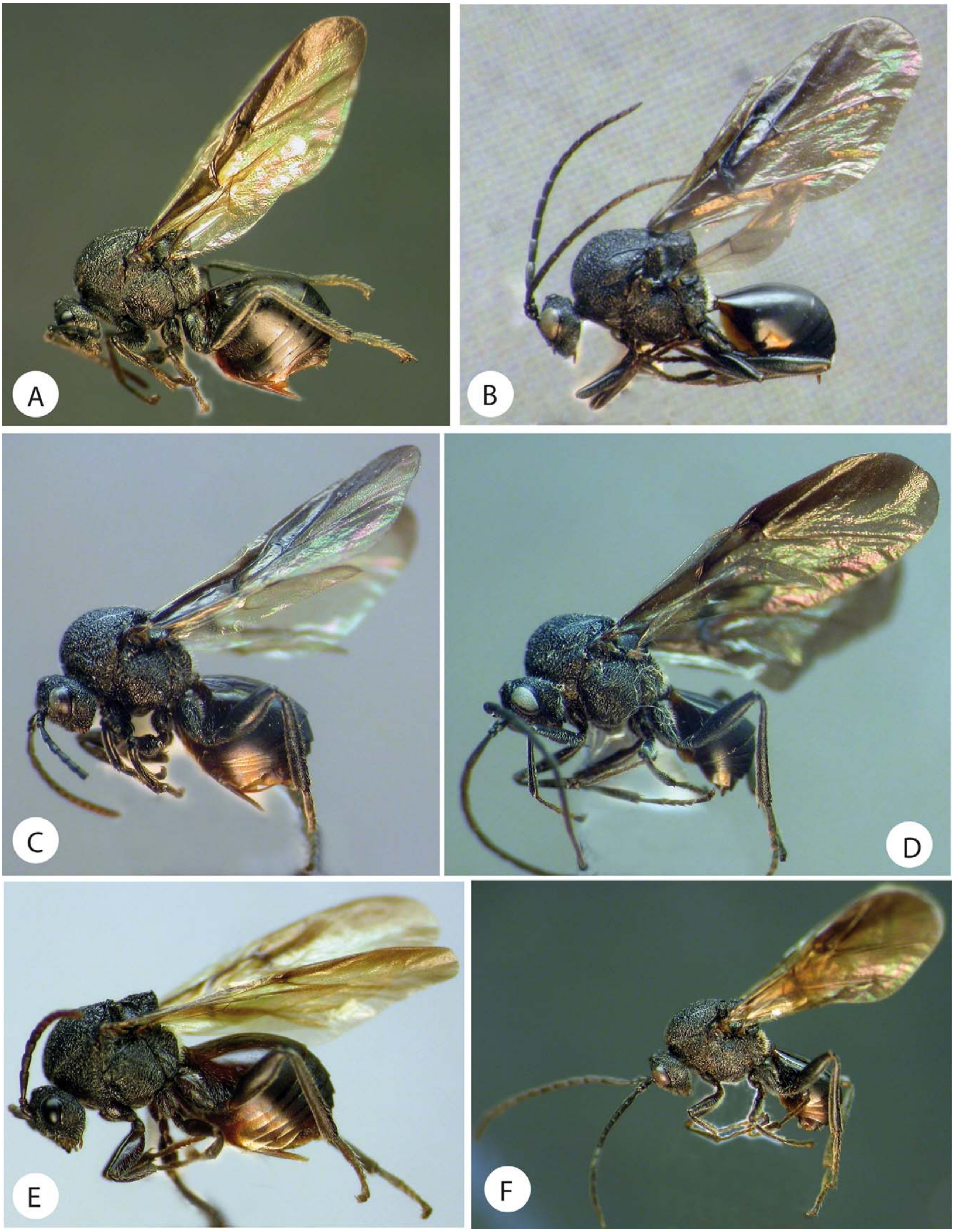

FIGURE 16. Habitus of species of *Amphibolips*. (A) *Amphibolips nevadensis* sp. nov., female. (B) *A. nevadensis*, male. (C) *Amphibolips michoacaensis* sp. nov., female. (D) *A. michoacaensis*, male. (E) *Amphibolips tarasco* sp. nov., female. (F) *A. tarasco*, male.

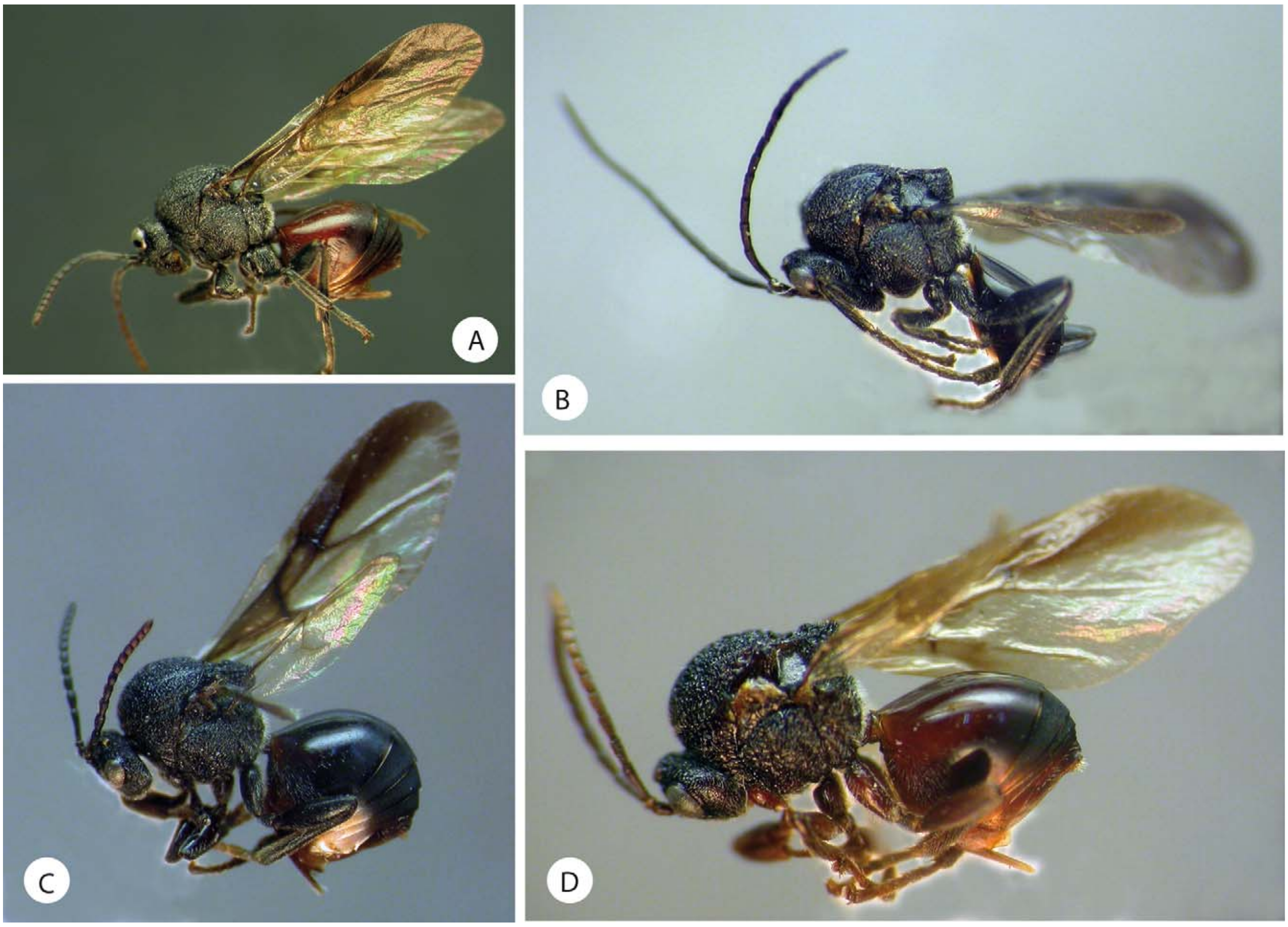

FIGURE 17. Habitus of species of *Amphibolips*. (A) *Amphibolips jaliscensis* sp. nov., female; (B) *A. jaliscensis*, male*;* (C) *Amphibolips zacatecaensis,* female; (D) *Amphibolips oaxacae* sp. nov., female.

In this work, a far from exhaustive sampling revealed a great number of unknown species of *Amphibolips* in Mexico. However, these findings were not surprising, given the great number of potential host species present in the study area and the limited studies performed on this gall wasp fauna to date, which referred only to the expeditions of Kinsey in the past century.

We collected galls of unknown/unidentified species of *Amphibolips* at several sites in Mexico on several *Quercus* species (Figs 21A–H), though unfortunately, no adults were reared to allow identifications to be made. However, this gall diversity reveals that the fauna of *Amphibolips* species may be quite rich in Mexico and that many other species could remain to be described. It is clear that a much greater sampling effort is still necessary to understand this fauna, as is the case for the Cynipidae of Mexico in general.

Acknowledgements

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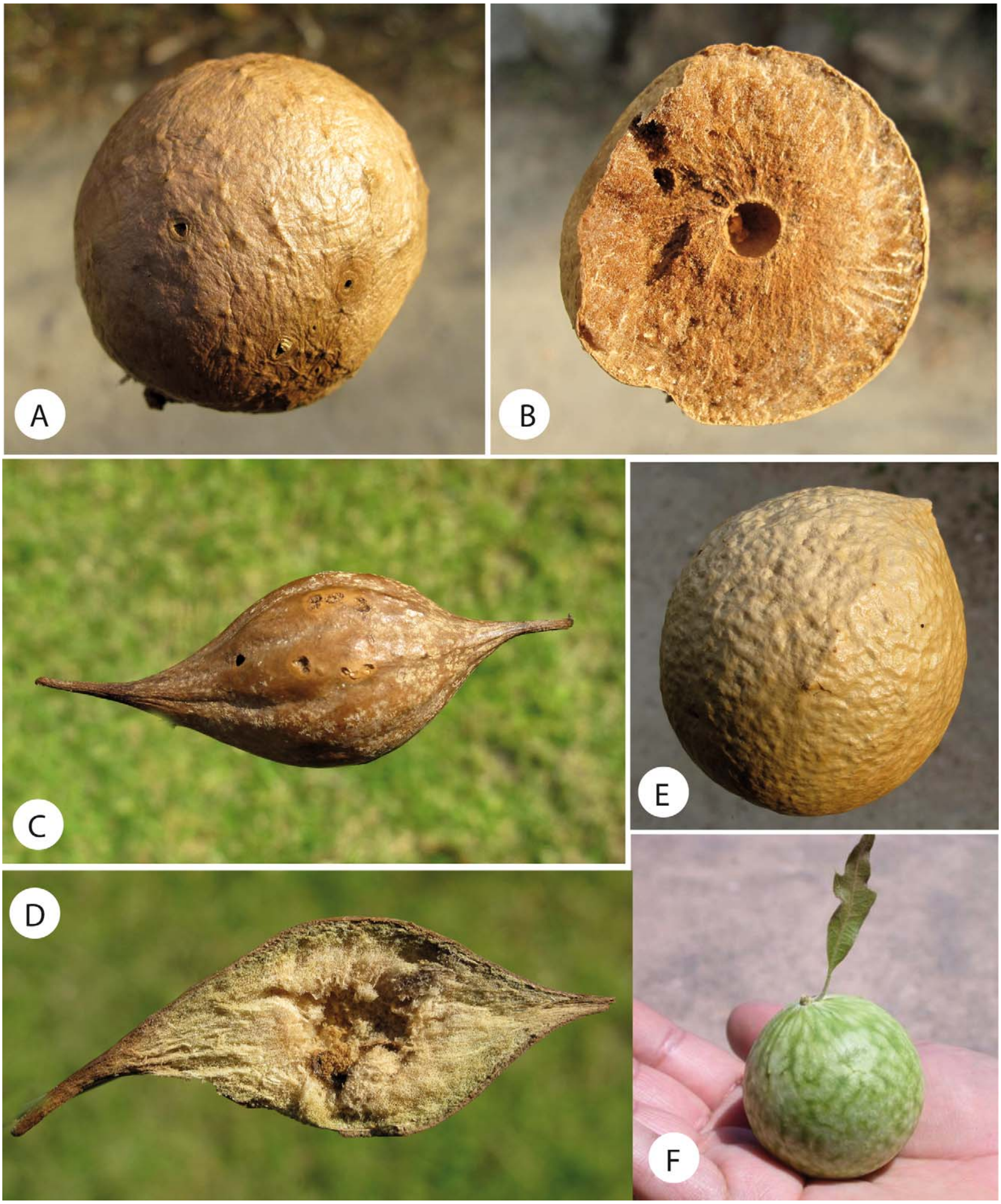

FIGURE 18. Galls of species of *Amphibolips*. (A) *Amphibolips hidalgoensis;* (B) section of a gall; (C) *A. durangensis* sp. nov. (D) section of a gall; (E) *A. zacatecaensis*; (F) *A. oaxacae* sp. nov.

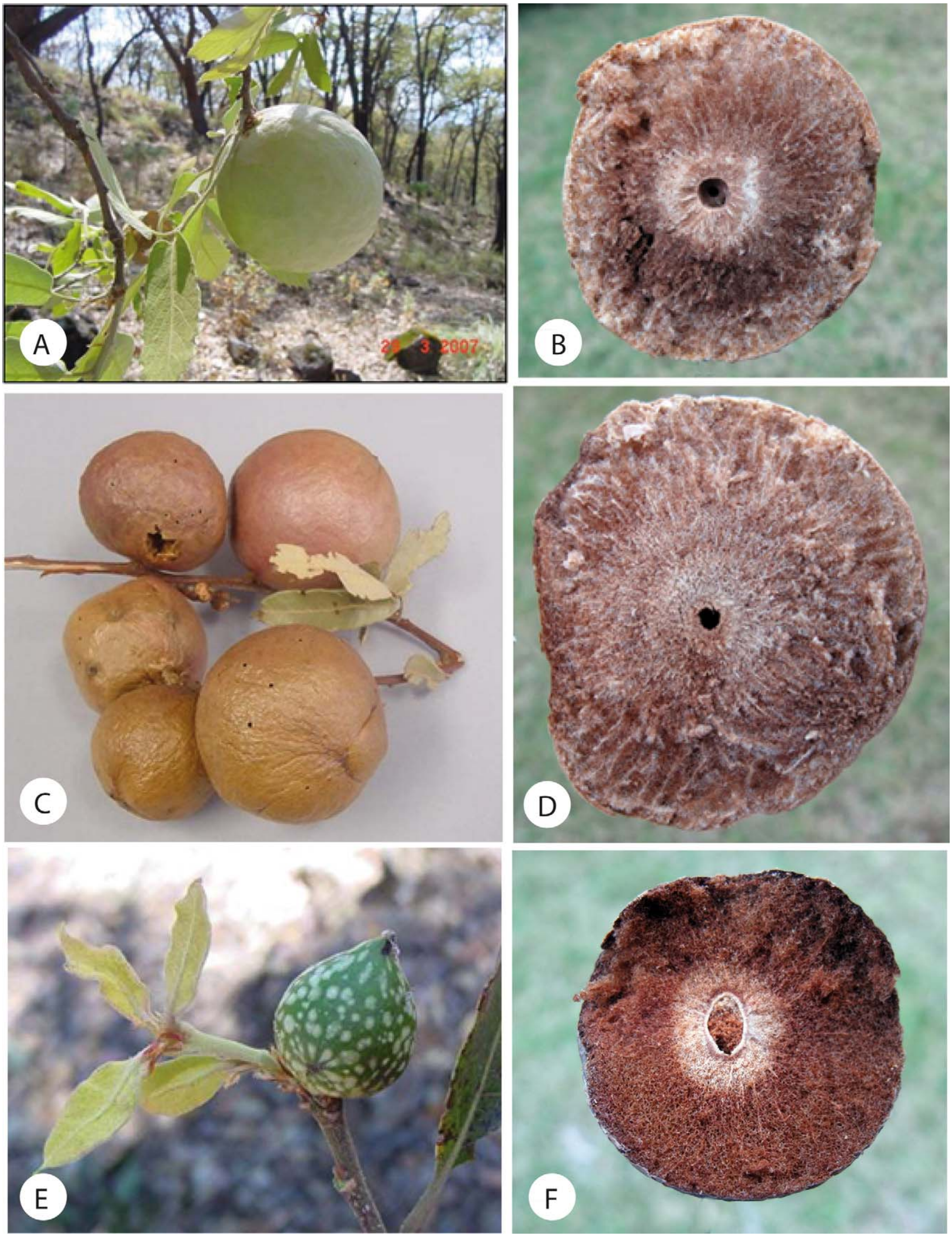

FIGURE 19. Galls and sections of galls of species of *Amphibolips*. (A–B) *Amphibolips jaliscensis* sp. nov. (C–D) *A. malinche* sp. nov. (E–F) *A. nevadensis* sp. nov.

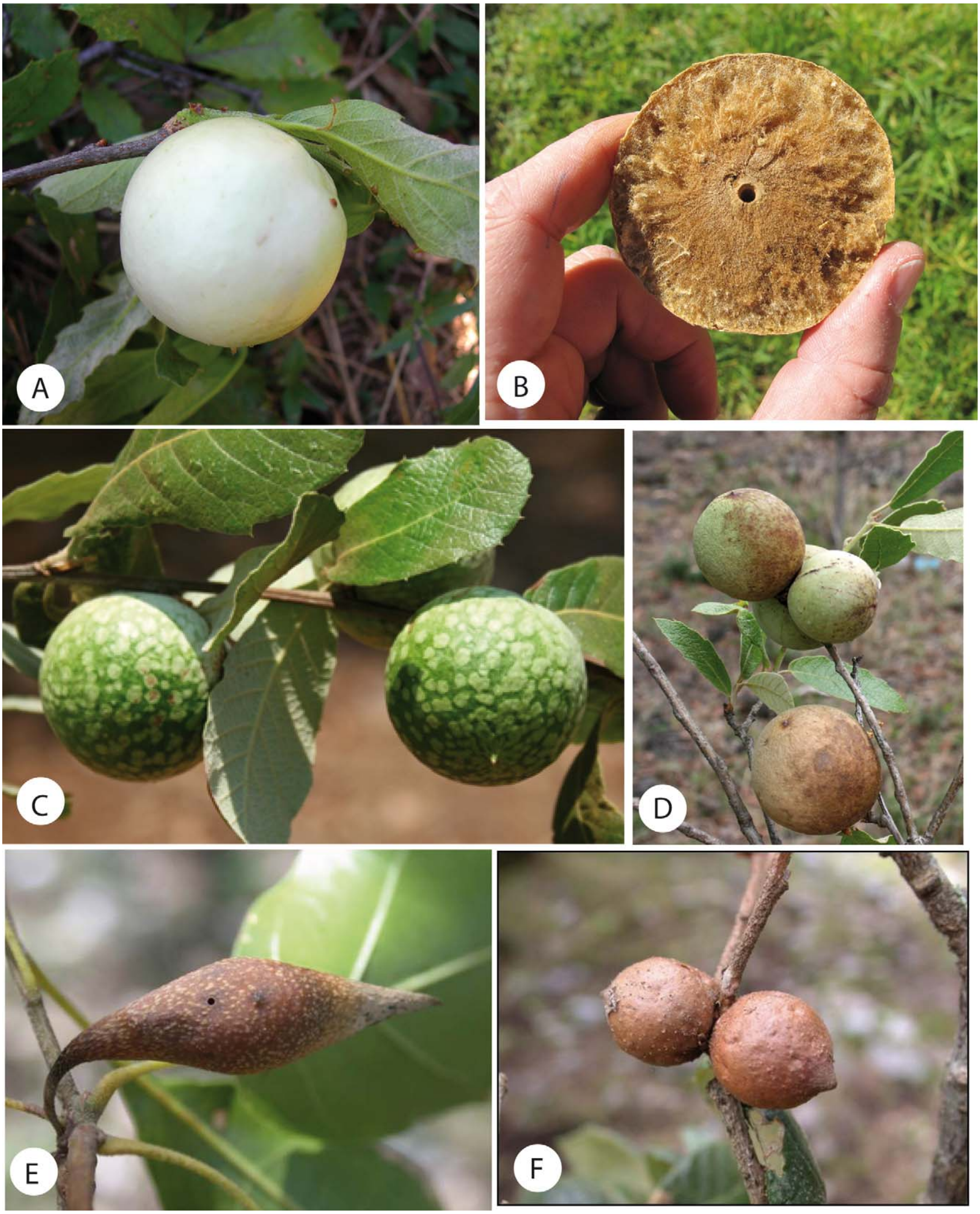

FIGURE 20. Galls of species of *Amphibolips*. (A) *Amphibolips michoacaensis* sp. nov. (B) section of a gall. (C–D) *A. tarasco* sp. nov. (E–F) *Amphibolips sp.*, Nuevo León.

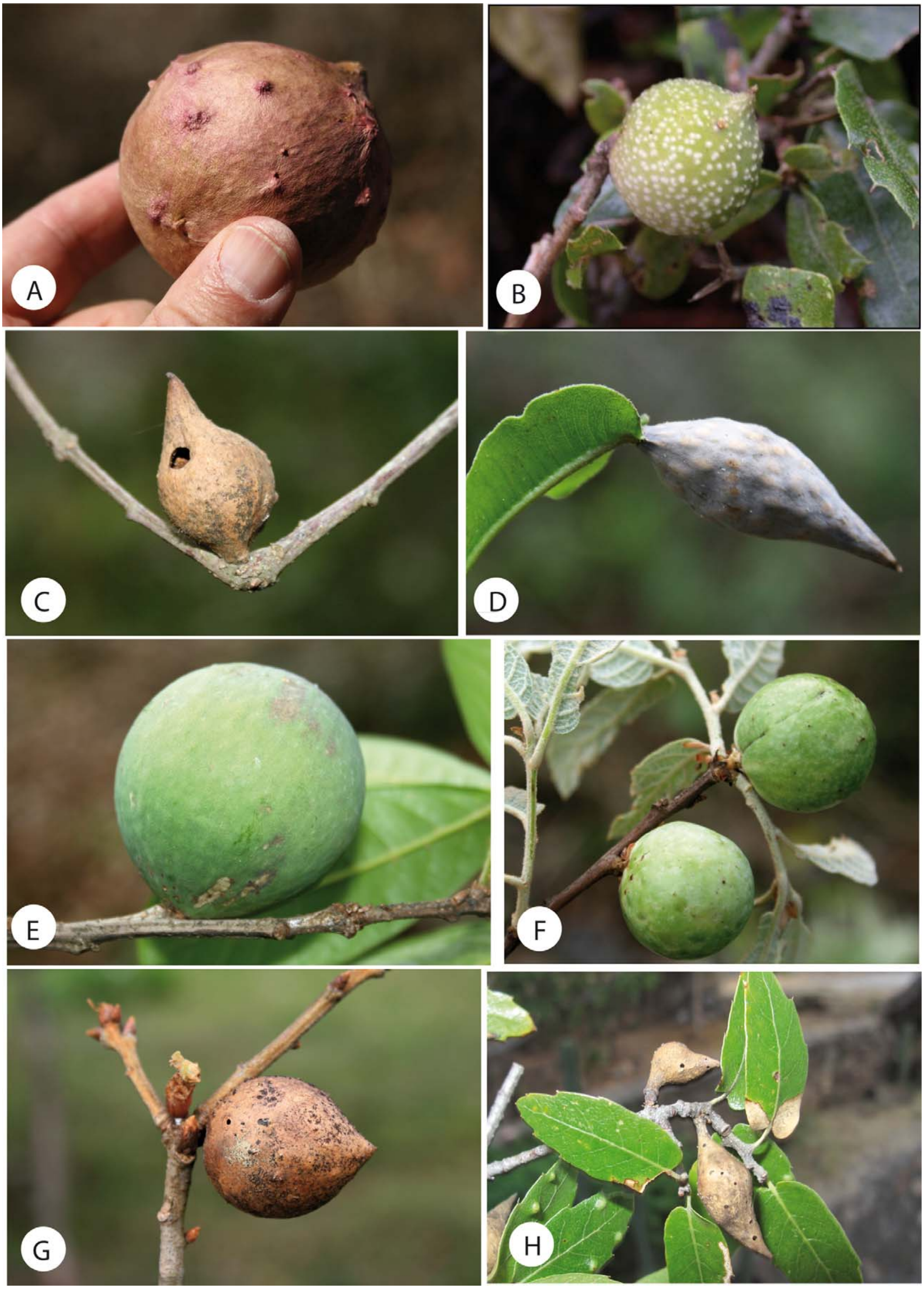

FIGURE 21. Galls of undetermined species of *Amphibolips* from Mexico (collected on 23–28 April, 2008 and 27–28 November, 2010, Pascual & Nieves leg.). (A) Umécuaro on *Q. castanea*. (B) Nuevo León on *Quercus sp*. (C) Xico, on *Quercus sp*. (D) Xalapa, on *Quercus sp*. (E) Xico, on Q. sp. (F) Xalapa on *Quercus glaucoides*. (G) Xalapa on *Quercus sp*. (H) Guanajuato, on *Q. microphylla.*

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DISCUSIÓN GENERAL

El alto grado de especialización de las avispas inductoras de agallas de la familia Cynipidae sobre sus plantas hospederas del género *Quercus* (Weld, 1960; Ronquist, 1995; Liljeblad y Ronquist, 1998; Nieves-Aldrey, 2001; Stone *et al*., 2002, Csoka *et al*., 2005) debe de revisarse en base en los resultados obtenidos en este trabajo. La mayoría de las especies de encinos estudiadas presentaron más de un morfotipo de agalla y en algunos casos, un número alto no esperado de morfotipos de agallas a lo largo de su distribución geográfica. En general, las especies de la sección Quercus presentan un mayor número de morfotipos asociados, lo cual puede estar relacionado con el hecho de que son las especies que colonizaron primero en los sistemas montañosos del país, por lo que el patrón podría ser similar para los inductores y además presentar patrones de especiación de los inductores en cada una de las especies hospederas. Resaltan tres especies de encinos blancos [*Q. microphylla* (20 morfotipos), *Q. resinosa* (17) y *Q. magnoliifolia* (14)] y tres de encinos rojos [*Q. crassifolia* (11), *Q. cocolobifolia* (11) y *Q. castanea* (10)] en las que se colectaron un número considerable de agallas a lo largo de su amplia distribución en México.

En estos casos en específico, se podría considerar a las especies de encinos como súper hospederos, ya que presentan agallas en toda su distribución y prácticamente hay agallas en toda la estructura del árbol, además de presentar morfotipos específicos para ciertas localidades, lo que podría tratarse de endemismos. Es probable que el elevado número de morfotipos encontrados en estas especies esté directamente relacionado con su rango de distribución, De acuerdo con Valencia (2004), estas especies presentan un rango amplio de distribución, tanto longitudinal como altitudinal, por lo que se encuentran en un rango de características ambientales variadas, lo cual puede representar un nicho ecológico para colonizar por las especies de inductores.

En el caso de las especies de encinos endémicas, muchas de ellas presentan un solo morfotipo, si bien similar, con algunas variaciones en cuanto a la textura de su corteza o bien del interior de la propia agalla. Por lo anterior, se puede asumir que se trata de especies distintas y probablemente endémicas, para lo cual habría que realizar un estudio ecológico y taxonómico detallado para cada una de ellas. Debido a que se ha reportado que algunas especies de cinípidos inducen agallas en la etapa de otoño-invierno, en las especies de hospederos que presentan uno o ningún morfotipo asociado, es recomendable hacer una observación y colecta en todo el patrón fenólógico de las mismas.

Por otro lado, existen morfotipos que son muy peculiares y que solamente se encuentran sobre hojas de encinos de la sección Quercus, por ejemplo en *Q. magnoliifolia, Q. resinosa,Q, Q. laeta, Q. desertícola, Q. rugosa y Q. obtusata.* De acuerdo con Pujade et al. (2010), se trata de un nuevo género denominado *Kinseyella*, aunque se requiere de una revisión exhaustiva tanto de la agalla como de los inductores para saber si se trata del mismo género y diferentes especies o bien si se trata de la misma especie de inductor en todos los hospederos mencionados.

En el caso de *Q. magnoliifolia* y *Q. resinosa*, estudios recientes muestran que estas especies de encinos forman complejos híbridos en regiones donde su distribución geográfica se sobreponen (Albarrán-Lara et al., 2010) generando nuevas zonas adaptativas para la formación de nuevas especies de insectos agalleros como se sugirió en el complejo *Quercus crassifolia* X *Quercus crassipes* (Tovar-Sánchez y Oyama, 2004) en donde se encontraron tres morfotipos de agallas asociados exclusivamente a los individuos híbridos (Tovar-Sánchez y Oyama, 2006). Esto podría ser el caso de *Quercus magnoliifolia* X *Quercus resinosa*, en donde se encontraron morfotipos particulares, por lo que habría que realizar una revisión puntual de los cinípidos asociados a este complejo de encinos. Sin embargo, este patrón no puede generalizarse ya que en otro complejo híbrido formado por *Q. affinis* y *Q. laurina* (González-Rodríguez et al., 2004; González-Rodríguez y Oyama, 2005; González-Rodríguez et al., 2005) sólo se encontró un morfotipo de agalla en cada especie en el presente estudio (ver Tabla 1).

Las agallas inducidas por cinípidos pueden clasificarse de acuerdo al número de cámaras larvales (e.g., unilocular y multilocular) y a las ornamentaciones que presentan (e.g., sin ornamentaciones y superficie lisa, y con vellosidades y espinas). En este sentido, el mayor número de agallas para ambas secciones se trata de agallas de tipo multilocular sin ornamentaciones, generalmente asociados a la rama del hospedero. De acuerdo con Ronquist (1995, 1999) y Rokas *et al.* (2003), este tipo de morfoagallas son las más primitivas, por lo que en este caso podría tratarse de un proceso de colonización de los cinípidos a los hospederos, por lo que se requiere un estudio filogenético y de biología comparada para ubicar estas especies con especies europeas y evaluar su nivel de parentesco.

Sin embargo, en el caso de la sección Lobatae se presenta un morfo peculiar, unilocular, con o sin ornamentaciones pero todos de tipo globular, agallas parecidas al género *Amphibolips* (Nieves *et al.* 2012). Esto puede ser un indicio de una asociación particular entre este grupo de encinos endémicos a México con un género de cinípidos inductores, de una interacción tan específica que se trate de procesos de especiación que se llevan a cabo en hospederos de esta sección de encinos.

El esfuerzo de colecta es un factor clave en este tipo de trabajos. Maldonado-López et al. (2015a, b) reportaron hasta 40 morfotipos diferentes de agallas inducidas por avispas sobre *Q. castanea* a lo largo de su distribución geográfica indicando que estudios con mayor intensidad de colecta tanto temporal como espacialmente, y enfocados a una sola especies de encino a lo largo de toda su distribución pueden dar este tipo de resultados.

Las especies de *Amphibolips* que se encuentran en México, que no pertenecen al complejo "*niger”,* son especies relacionadas y con variaciones morfológicas muy sutiles. Uno de los factores a destacar, es que se considera que la morfología de la agalla es un factor que se usa como diferenciador entre especies. Sin embargo, en el caso de éste género, esta característica podría no ser determinante en la identificación taxonómica. Lo anterior reafirma lo expuesto por Pujade-Villar *et al.* (2001), que indican que la taxonomía de cinípidos es problemática, y en lugares como México aún hay muchas especies de cinípidos sin describir.

Conclusiones y perspectivas

Las avispas formadoras de agallas (Hymenoptera: Cynipidae: Cynipini) representan un grupo muy diverso y con características ecológicas muy interesantes (Nieves-Aldrey, 1998, 2001; Ronquist y Liljeblad, 2001; Hayward y Stone, 2005). En el presente estudio, se realizó un esfuerzo importante para aportar nuevos registros de este gremio de insectos para México. Sin embargo, es necesario continuar con este tipo de estudios para conocer la riqueza total de especies de avispas para México así como sus relaciones filogenéticas y establecer los patrones de diversificación de los mismos. México representa uno de los dos centros de diversificación más importantes de encinos en el mundo particularmente para los encinos rojos (sección Lobatae). Estos esfuerzos de colecta deben de ir acompañados con estudios taxonómicos que permitan dilucidar el descubrimiento de nuevas especies (Nieves-Aldrey *et al*., 2012) e incluso géneros como ha ocurrido con parte de las colectas realizadas en este estudio.

Un aspecto importante y característico de los cinípidos asociados a los encinos es que son cíclicamente partenogenéticos, aspecto que ha causado confusión en la clasificación taxonómica. Al respecto, los trabajos deben de encaminarse a encontrar herramientas tanto morfológicas (Hernández *et al*., 2015) como moleculares que ayuden a solucionar el problema, además de dilucidar que procesos provocan dicho fenómeno.

A nivel poblacional, es importante conocer las distancias de dispersión de individuos y sus patrones de colonización tanto a sus mismos como a nuevos hospederos ya sea través de estudios ecológicos (Schönrogge *et al*., 1994, 1999) o genéticos con marcadores moleculares (Castillejos-Lemus, 2016). Por ejemplo, en *Amphibolips michocaensis*, cinípedo endémico de México, se encontraron altos valores de diversidad genética y de flujo génico a nivel regional (Castillejos-Lemus, 2016).

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