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# A RAPID IDENTIFICATION GUIDE FOR LARVAE OF THE MOST COMMON NORTH AMERICAN CONTAINER-INHABITING *AEDES* SPECIES OF MEDICAL IMPORTANCE

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ABSTRACT. Mosquitoes are the single most important taxon of arthropods affecting human health globally, and container-inhabiting *Aedes* are important vectors of arthropod-borne viruses. Desiccation-resistant eggs of container *Aedes* have facilitated their invasion into new areas, primarily through transportation via the international trade in used tires. The public health threat from an introduced exotic species into a new area is imminent, and proactive measures are needed to identify significant vectors before onset of epidemic disease. In many cases, vector control is the only means to combat exotic diseases. Accurate identification of vectors is crucial to initiate aggressive control measures; however, many vector control personnel are not properly trained to identify introduced species in new geographic areas. We provide updated geographical ranges and a rapid identification guide with detailed larval photographs of the most common container-inhabiting *Aedes* in North America. Our key includes 5 native species (*Aedes atropalpus*, *Ae. epactius*, *Ae. hendersoni*, *Ae. sierrensis*, *Ae. triseriatus*) and 3 invasive species (*Ae. aegypti*, *Ae. albopictus*, *Ae. japonicus*).

**KEY WORDS** *Aedes aegypti*, *Aedes albopictus*, *Aedes japonicus*, container mosquitoes, identification key

## INTRODUCTION

Mosquitoes are important global vectors of pathogens and arthropod-borne viruses (arboviruses). Container-inhabiting mosquitoes of the genus *Aedes* are important vectors of arboviruses such as chikungunya (CHIK), dengue (DEN), La Crosse (LAC), West Nile (WN), and yellow fever (YF). Multivoltine *Aedes* species utilize container habitats by ovipositing desiccation-resistant eggs that survive drought for extended periods of time. Natural containers utilized by these species include bamboo nodes, plant axils, rock pools, and tree holes; however, artificial containers that mimic natural oviposition sites, such as discarded tires, also provide suitable habitats. The desiccation-resistant eggs of container *Aedes* have facilitated invasion into new areas, primarily through transportation via the international trade in used tires (Reiter and Sprenger 1987). Increased global travel and trade in used tires are major contributing factors for the dispersal of exotic *Aedes* species of medical importance. Moreover, the ubiquity of used tires and other artificial containers in urban/suburban areas preclude effective control of these medically important species (Farajollahi et al. 2012, Rochlin et al. 2013b). Larvae of invasive container *Aedes* are often superior competitors and may be responsible for reduction of native mosquitoes in overlapping ranges (Juliano and Lounibos 2005, Andreadis and Wolfe 2010, Rochlin et al. 2013a). The public health threat from exotic species introduction into new areas is evident, and proactive measures are needed to identify significant vectors before local establishment. In many cases, vector suppression is the only means to successfully combat exotic diseases. Accurate identification of vectors is therefore crucial for initiation of aggressive abatement measures. However, most vector control and public health officials may not promptly recognize introduced species in expanding ranges, particularly in the larval stage when targeted abatement efforts would be most efficient. We provide a rapid identification guide (see key), a quick reference sheet for important diagnostic characters (Table 1), and current geographical ranges in North America with detailed larval photographs of the most common container-inhabiting *Aedes* in this region (Figs. 1–12). Our key includes 5 native species: *Aedes atropalpus* (Coquillett), *Ae. epactius* Dyar and Knab, *Ae. hendersoni* Cockerell, *Ae. sierrensis* (Ludlow), and *Ae. triseriatus* (Say); and 3 invasive species: *Ae. aegypti* (L.), *Ae. albopictus* (Skuse), and *Ae. japonicus* (Theobald).

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## SYNOPSES OF CONTAINER-INHABITING *AEDES*

### *Aedes* (*Ochlerotatus*) *atropalpus*

*Aedes atropalpus*, the North American rock pool mosquito, occurs primarily in the eastern USA. This species is distributed from northern Alabama in the south to Newfoundland, Canada, in the north, and westward to Missouri (Darsie and Ward 2005, Qualls and Mullen 2006) (Fig. 1). Carpenter and LaCasse (1955) also reported this species as far west as New Mexico and as far south as El Salvador, but those records were complicat-

Table 1. Morphological character comparison of 4th instars of the most common container-inhabiting *Aedes* species in North America. Most distinguishing characters in bold.[1]

| | Native species | | | | | Invasive species | | |
|---|---|---|---|---|---|---|---|---|
| | *Ae. atropalpus* | *Ae. epactius* | *Ae. hendersoni* | *Ae. sierrensis* | *Ae. triseriatus* | *Ae. aegypti* | *Ae. albopictus* | *Ae. japonicus* |
| Head hairs | Box arrangement | Box arrangement | Box arrangement | Box arrangement | Box arrangement | Box arrangement | Box arrangement | **Straight line** |
| U—upper (5-C) | U—single | U—single | U—single | U—single | U—single | U—single | U—single (double) | U—multiple |
| L—lower (6-C) | L—single | L—single | L—triple (multi) | L—double | L—double or triple | L—single | L—single | L—multiple |
| PA—preantennal (7-C) | PA—multiple | PA—multiple | PA—multiple | PA—multiple | PA—multiple | PA—single | PA—double | PA—multiple |
| Pecten teeth (Pt) | Distally detached | Distally detached | Evenly spaced | Evenly spaced | Evenly spaced | Evenly spaced | Evenly spaced | Distally detached |
| Siphonal tuft (1-S) | Multiple | Multiple | Triple | Multiple | Double | Double (multiple) | Double (multiple) | Multiple |
| | Within pecten | Within pecten | Beyond pecten | Beyond pecten | Beyond pecten | Beyond pecten | Beyond pecten | Within pecten |
| Comb scales (CS) | Patch **>34** | Patch **<34** | Partly double row | Patch | Partly double row | **Single neat row** (stout subapical spines) | **Single neat row** (no subapical spines) | Patch |
| Anal saddle (Sa) | Weakly spiculated | Weakly spiculated | Smooth | Smooth | Smooth | Smooth | Smooth | **Heavily spiculated** |
| Lateral hair (1-X) | **Below saddle** | **Below saddle** | On saddle | On saddle | On saddle | On saddle | On saddle | On saddle |
| | Single | Single | Double | Double | Multiple | Double | Double | Single |
| Anal papilla (APP) | Equal and tapering | Equal and tapering | Equal and blunt | Equal and blunt | **Unequal and tapering** | Equal and blunt | Equal and blunt | Equal and tapering |

[1] Parentheses denote abnormal character patterns.

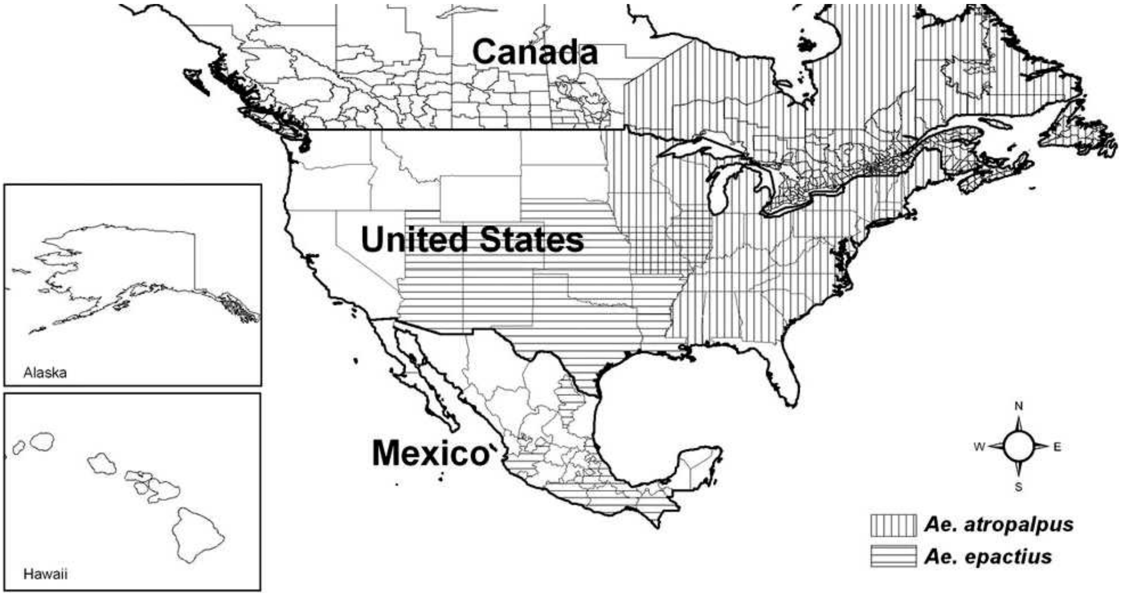


Fig. 1. Geographical distribution of *Aedes atropalpus* and *Ae. epactius* in North America.

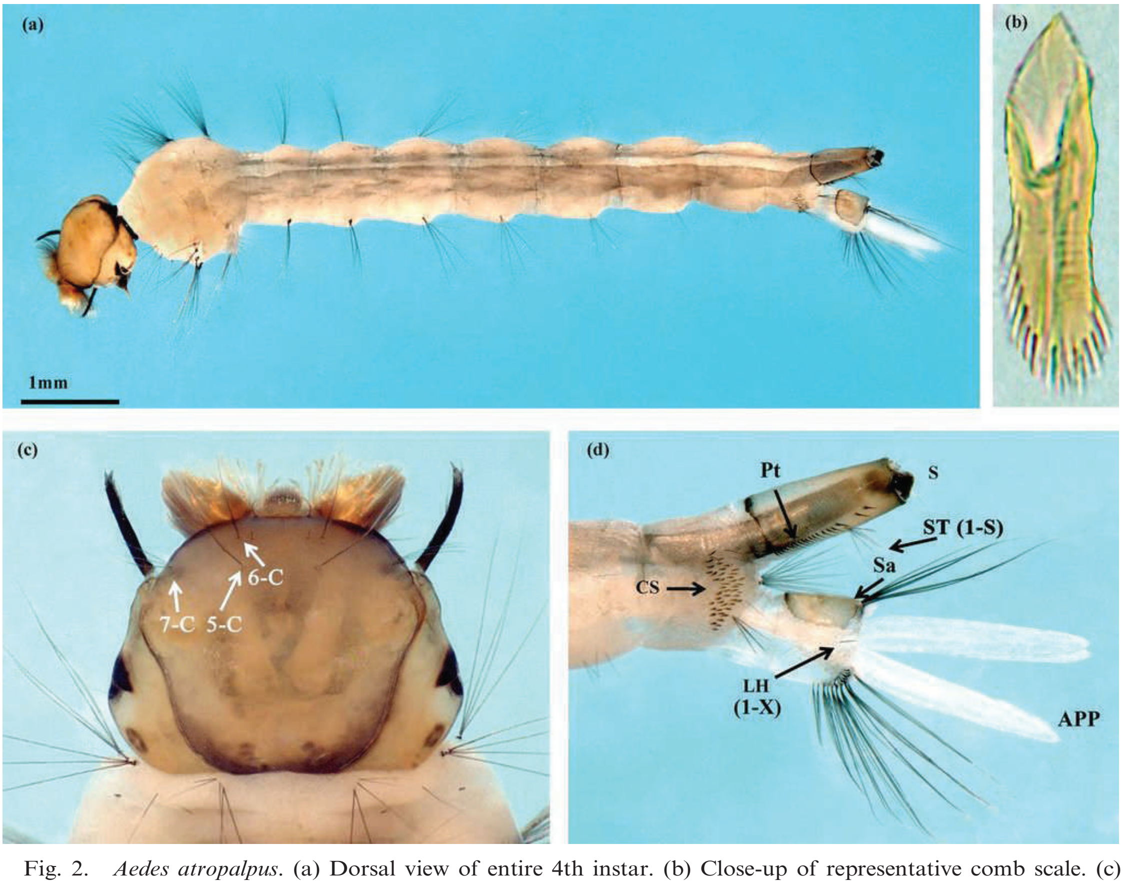


Fig. 2. *Aedes atropalpus*. (a) Dorsal view of entire 4th instar. (b) Close-up of representative comb scale. (c) Dorsal view of head. (d) Lateral view of terminal segment. APP, anal papilla; CS, comb scale; LH, lateral hair (seta 1-X); Pt, pecten teeth; S, siphon; Sa, saddle; ST, siphonal tuft (seta 1-S); 5-C, upper head hair; 6-C, lower head hair; 7-C, preantennal head hair.

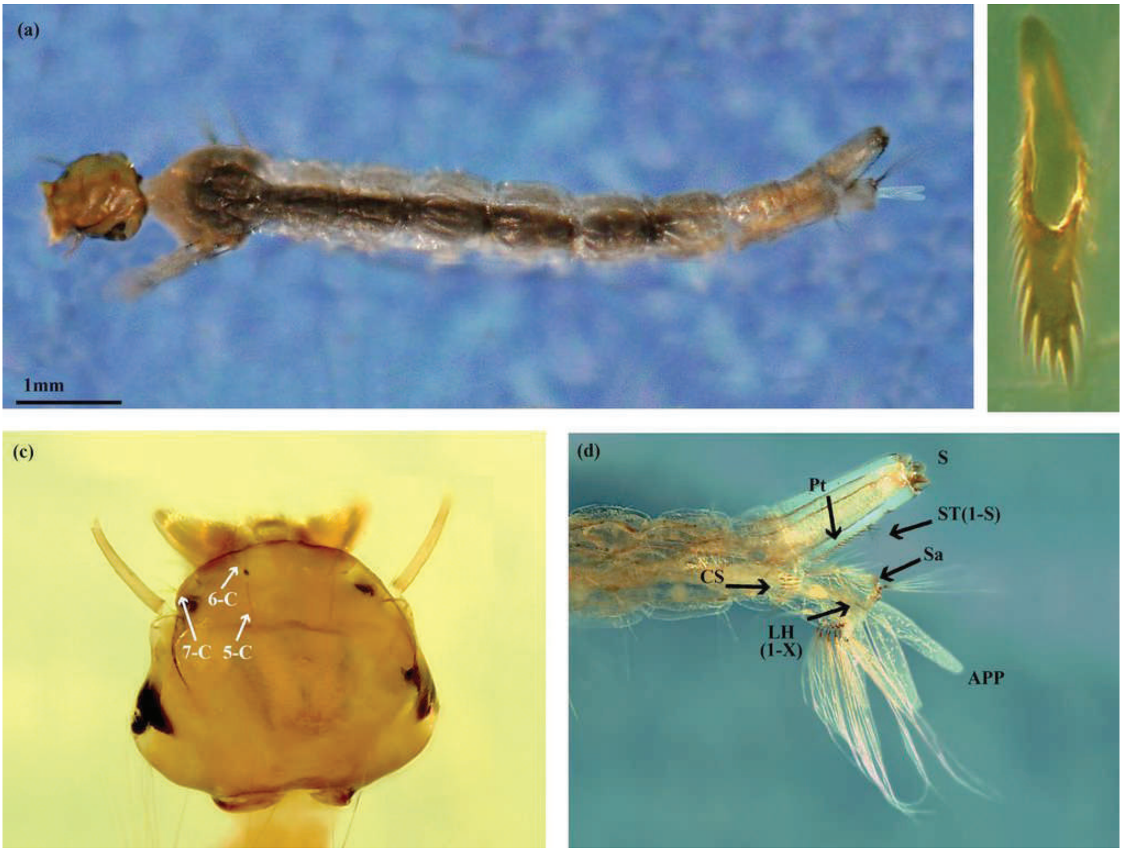


Fig. 3. *Aedes epactius*. (a) Dorsal view of entire 4th instar. (b) Close-up of representative comb scale. (c) Dorsal view of head. (d) Lateral view of terminal segment. APP, anal papilla; CS, comb scale; LH, lateral hair (seta 1-X); Pt, pecten teeth; S, siphon; Sa, saddle; ST, siphonal tuft (seta 1-S); 5-C, upper head hair; 6-C, lower head hair; 7-C, preantennal head hair.

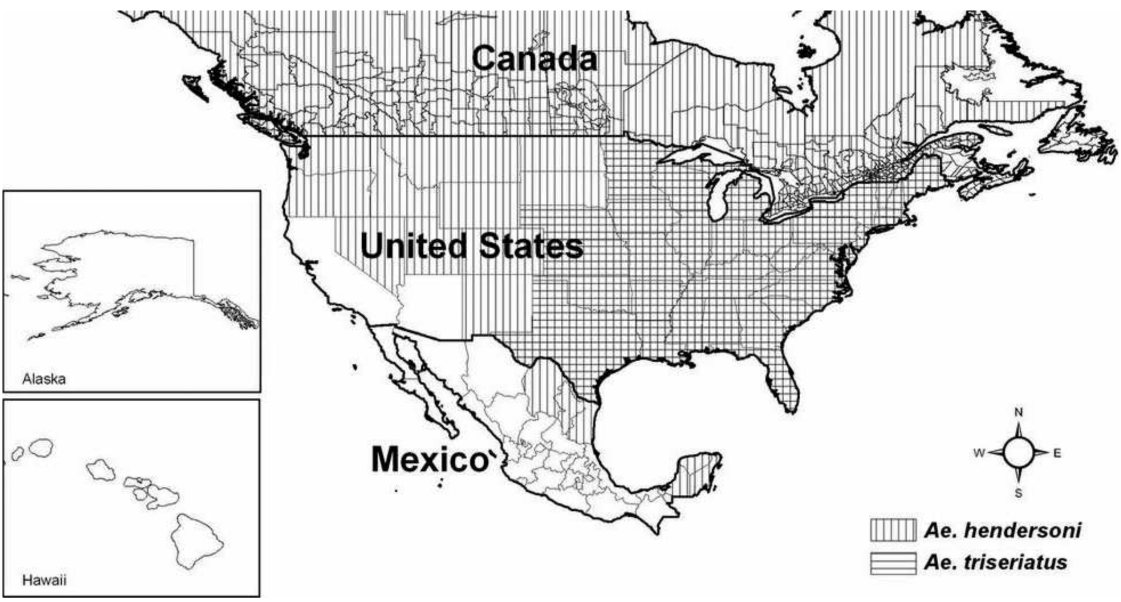


Fig. 4. Geographical distribution of *Aedes hendersoni* and *Ae. triseriatus* in North America.

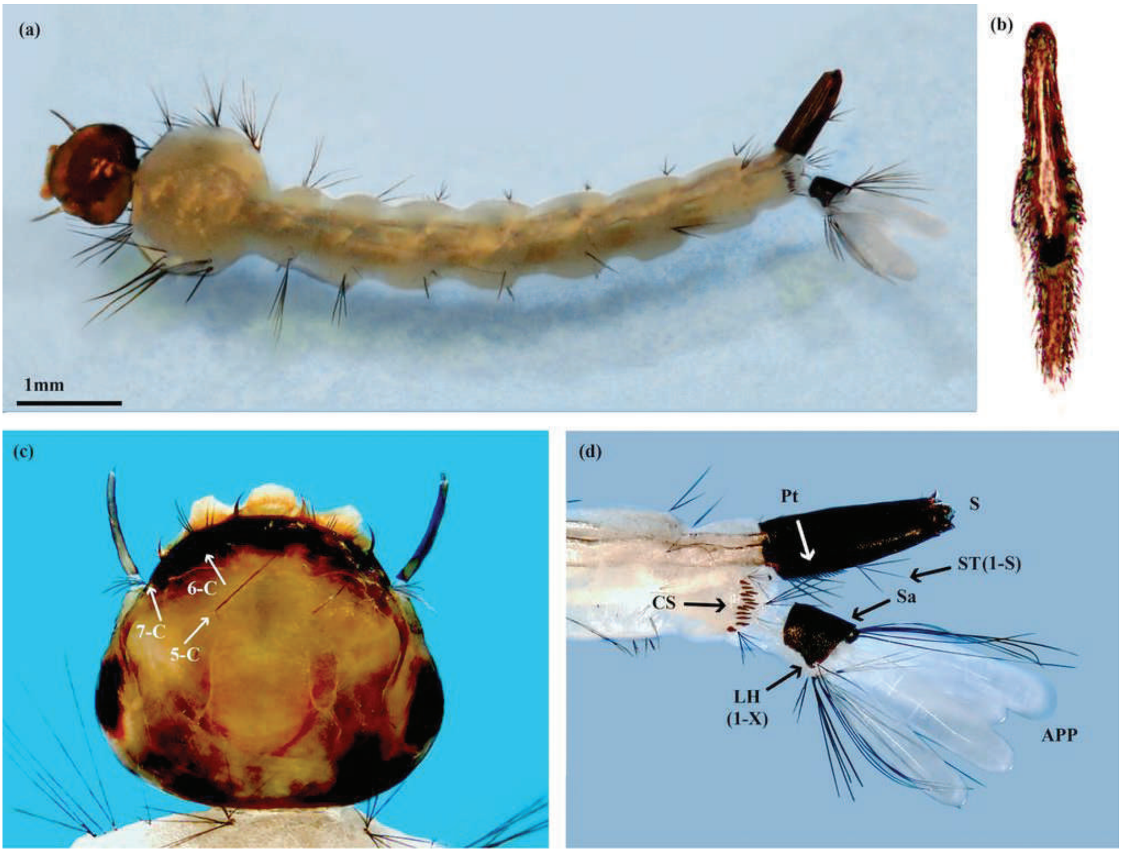


Fig. 5. *Aedes hendersoni*. (a) Dorsal view of entire 4th instar. (b) Close-up of representative comb scale. (c) Dorsal view of head. (d) Lateral view of terminal segment. APP, anal papilla; CS, comb scale; LH, lateral hair (seta 1-X); Pt, pecten teeth; S, siphon; Sa, saddle; ST, siphonal tuft (seta 1-S); 5-C, upper head hair; 6-C, lower head hair; 7-C, preantennal head hair.

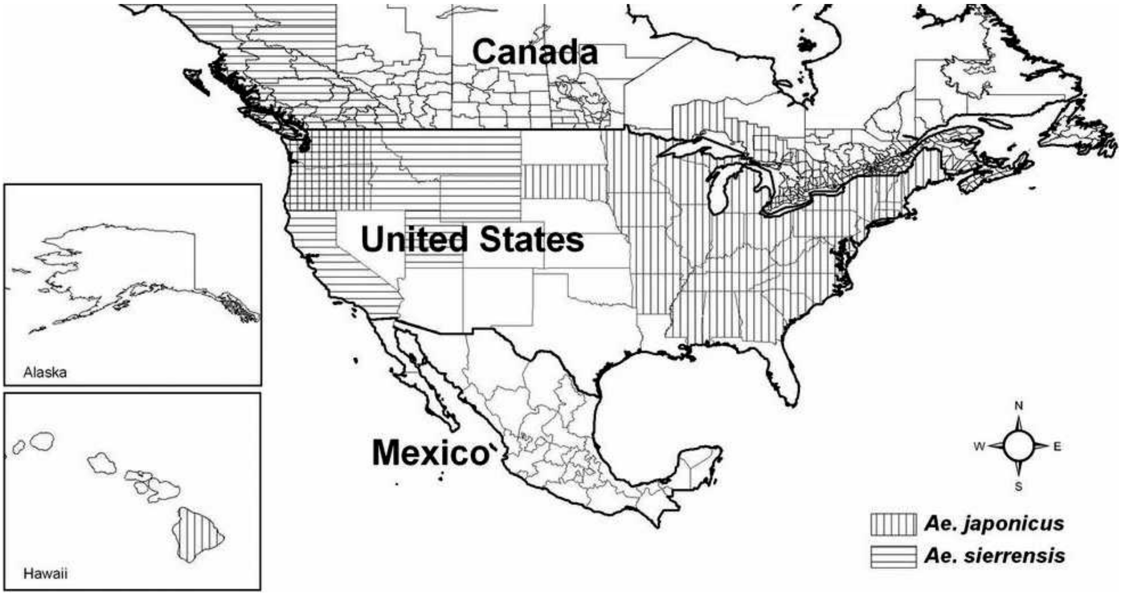


Fig. 6. Geographical distribution of *Aedes japonicus* and *Ae. sierrensis* in North America.

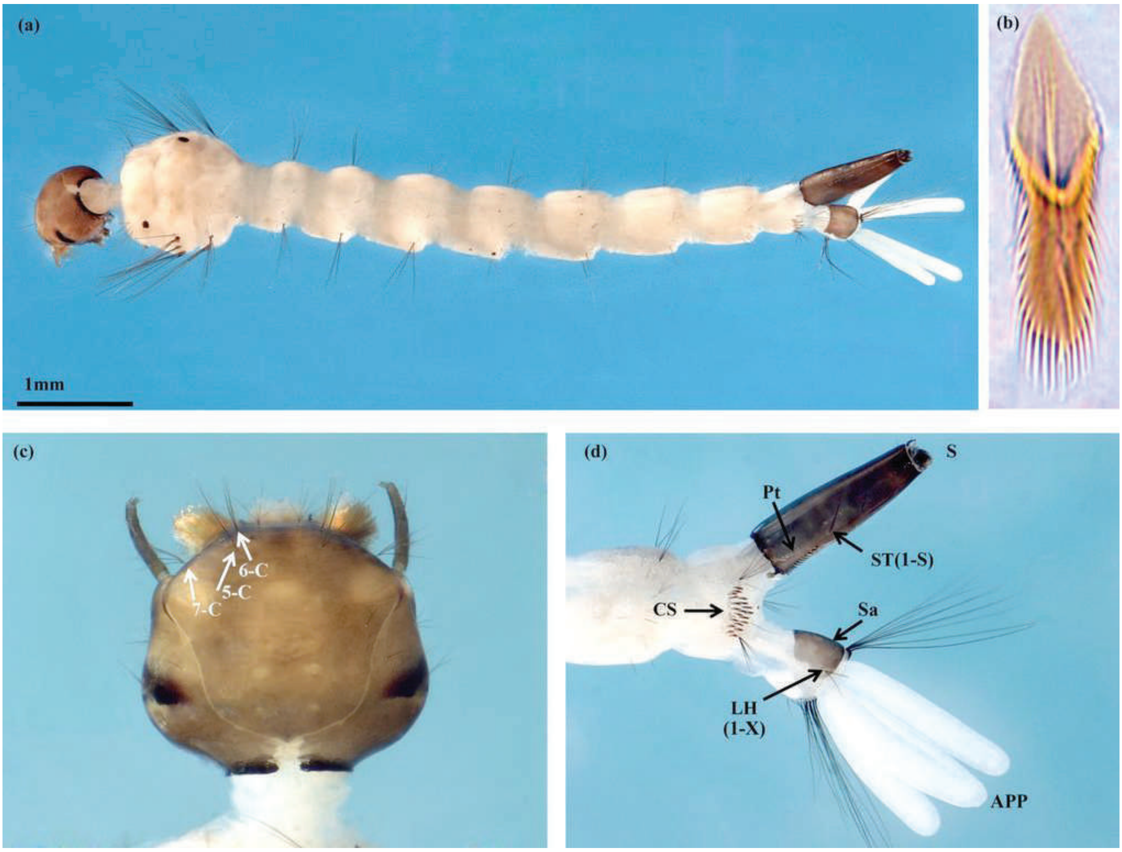


Fig. 7. *Aedes sierrensis*. (a) Dorsal view of entire 4th instar. (b) Close-up of representative comb scale. (c) Dorsal view of head. (d) Lateral view of terminal segment. APP, anal papilla; CS, comb scale; LH, lateral hair (seta 1-X); Pt, pecten teeth; S, siphon; Sa, saddle; ST, siphonal tuft (seta 1-S); 5-C, upper head hair; 6-C, lower head hair; 7-C, preantennal head hair.

ed by the presence of morphologically similar species such as *Ae. epactius* (O'Meara and Craig 1970, Munstermann 1980, Darsie and Ward 2005). Larvae are primarily found in depressions or holes near streams and rivers that become filled with rainwater or when overflow water levels become high. Their geographic distribution is thus sparse and asymmetrical, tending to favor areas where natural rock pools are found. The isolation of populations across a large geographic distribution has facilitated the development of distinct races and species, and in addition to *Ae. atropalpus* and *Ae. epactius*, 2 other taxa have been historically recognized: *Ae. atropalpus nielseni* O'Meara and Craig and *Ae. atropalpus perichares* Dyar (O'Meara and Craig 1970, Zavortink 1972, Brust 1974, Lunt 1977a, Munstermann 1980, Darsie and Ward 2005). However, the latter 2 species are currently considered synonymous with *Ae. epactius* (Darsie and Ward 2005, WRBU 2013). In addition to rock pools, larvae have also been collected from natural (tree hole) and artificial (tire) containers in rural and urban areas (Qualls and Mullen 2006, Yee 2008). Larvae of *Ae. atropalpus* may easily be identified from other common container-inhabiting *Aedes* by the presence of the lateral hair (seta 1-X) of the anal segment (abdominal segment X) occurring below the anal saddle (Sa) (Fig. 2). *Aedes atropalpus* is distinguished from *Ae. epactius* by the presence of 34 or more (usually 34 to 62) comb scales on abdominal segment VIII, whereas the latter species possesses 34 or fewer (usually 18 to 34) comb scales (Darsie and Ward 2005). Also, Darsie and Ward (2005) note that seta 1-M on the larval thorax of *Ae. epactius* is short and barely reaches the base of seta 0-P; whereas seta 1-M is long on *Ae. atropalpus* and reaches the anterior level of seta 0-P. *Aedes atropalpus* is partially autogenous (O'Meara and Craig 1970), capable of ovipositing the 1st batch of eggs without need of a blood meal; however, this behavior requires lengthened periods of larval development for appropriate acquisition of nutrient reserves and may be disadvantageous for the species and lead to displacement by superior competitors (Armistead et al. 2008). Subsequent gonotrophic cycles require nutritional reserves from blood; thus, *Ae.*

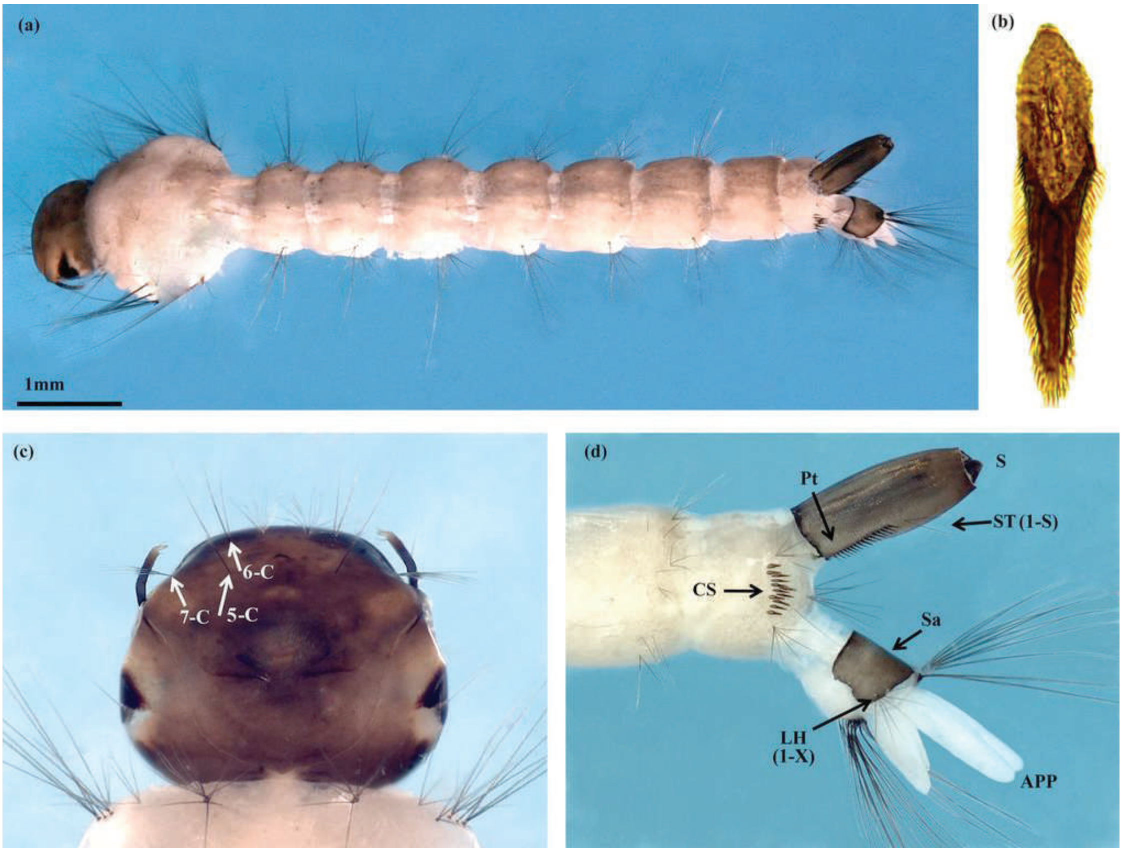


Fig. 8. *Aedes triseriatus*. (a) Dorsal view of entire 4th instar. (b) Close-up of representative comb scale. (c) Dorsal view of head. (d) Lateral view of terminal segment. APP, anal papilla; CS, comb scale; LH, lateral hair (seta 1-X); Pt, pecten teeth; S, siphon; Sa, saddle; ST, siphonal tuft (seta 1-S); 5-C, upper head hair; 6-C, lower head hair; 7-C, preantennal head hair.

*atropalpus* has been considered a persistent daytime biter on mammalian hosts, including humans, particularly near their larval habitats (Carpenter and LaCasse 1955, Means 1979). The significance of *Ae. atropalpus* to public health requires further investigation. Although WN virus has been detected from field specimens (CDC 2013), their sparse and irregular distribution, coupled with autogenous egg development and specialized larval habitat, may limit their contribution to disease cycles.

### *Aedes* (*Ochlerotatus*) *epactius*

*Aedes epactius* is another North American rock pool mosquito with morphological and physiological similarities to *Ae. atropalpus*. The species occurs primarily in the midwestern USA (Fig. 1), with the largest populations being detected in Arizona, New Mexico, Oklahoma, and Texas (Darsie and Ward 2005). *Aedes epactius* have also been collected in Arkansas, Colorado, Illinois, Kansas, Louisiana, Missouri, Nebraska, and Utah (Linley and Craig 1994, Moore 2001, Darsie and Ward 2005). The species has also been collected in Mexico, and their geographic distribution may reach as far south as El Salvador in Central America (Munstermann 1980, Heard et al. 1991, Lozano-Fuentes et al. 2012). Populations of this species from Colorado and Utah have been described as *Ae. ae. nielseni* by some authors and as *Ae. ae. perichares* from Metapan, El Salvador, by others (O'Meara and Craig 1970, Brust 1974, Munstermann 1980); however, current literature accepts these subspecies as synonymous with *Ae. epactius* (Darsie and Ward 2005, Lozano-Fuentes et al. 2012, WRBU 2013). Similar to *Ae. atropalpus*, larvae of *Ae. epactius* are primarily found in depressions or holes near streams and rivers, but have also been collected from other natural (tree holes, ground pools, phytotelmata) and artificial (tires, buckets, flower vases) containers throughout their range (O'Meara and Craig 1970, Heinemann and Belkin 1977, Munstermann 1980, Munstermann and Wesson 1990, Moore 2001, Lozano-Fuentes et al. 2012). Larvae of *Ae. epactius* can be separated from other common container-inhabiting *Aedes* by the

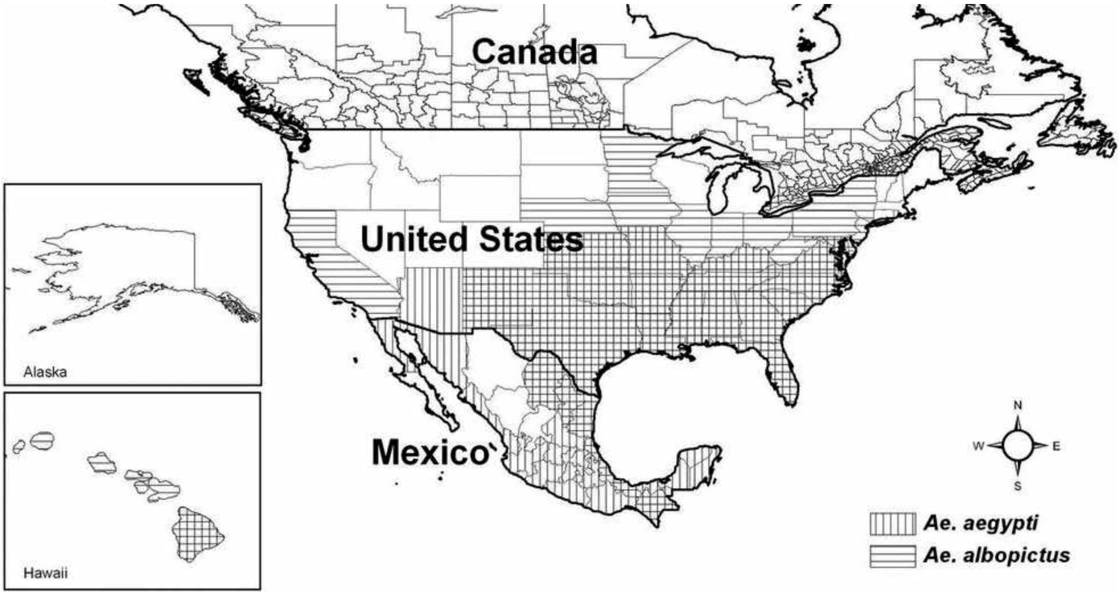


Fig. 9. Geographical distribution of *Aedes aegypti* and *Ae. albopictus* in North America.

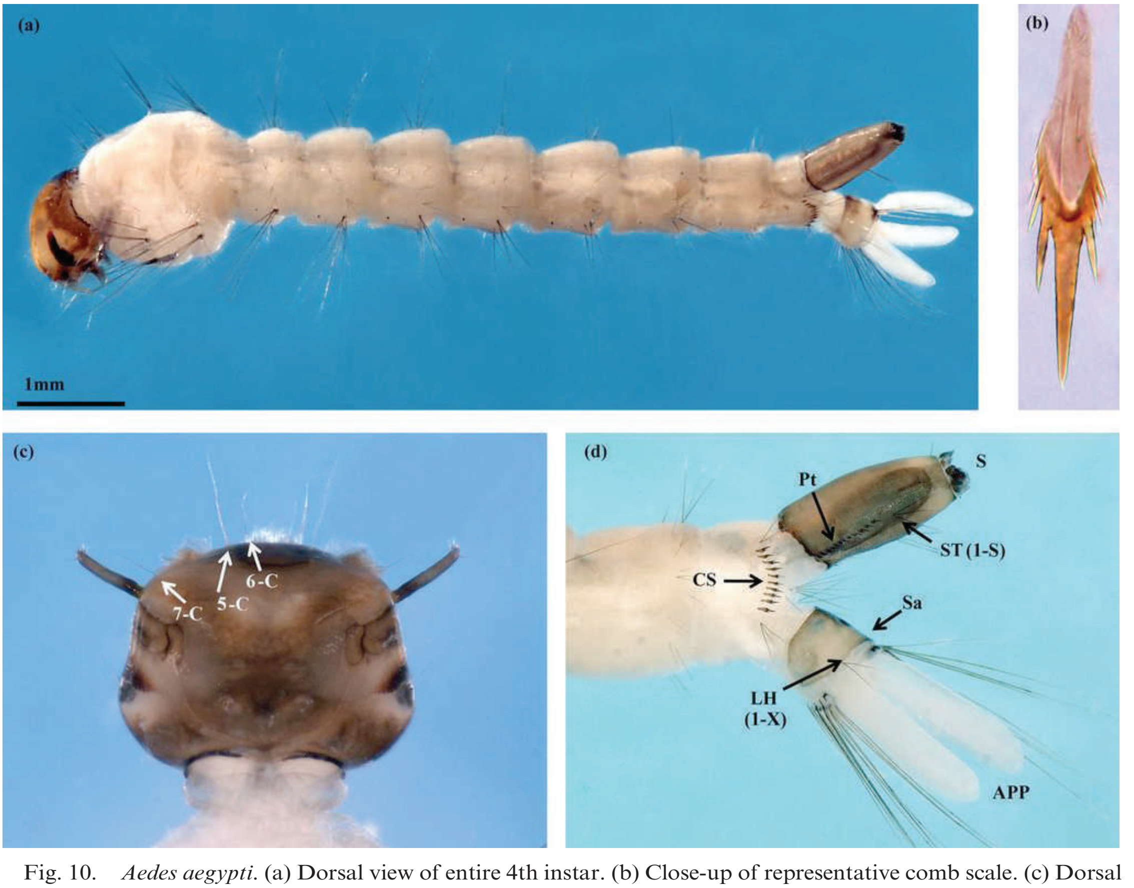


Fig. 10. *Aedes aegypti*. (a) Dorsal view of entire 4th instar. (b) Close-up of representative comb scale. (c) Dorsal view of head. (d) Lateral view of terminal segment. APP, anal papilla; CS, comb scale; LH, lateral hair (seta 1-X); Pt, pecten teeth; S, siphon; Sa, saddle; ST, siphonal tuft (seta 1-S); 5-C, upper head hair; 6-C, lower head hair; 7-C, preantennal head hair.

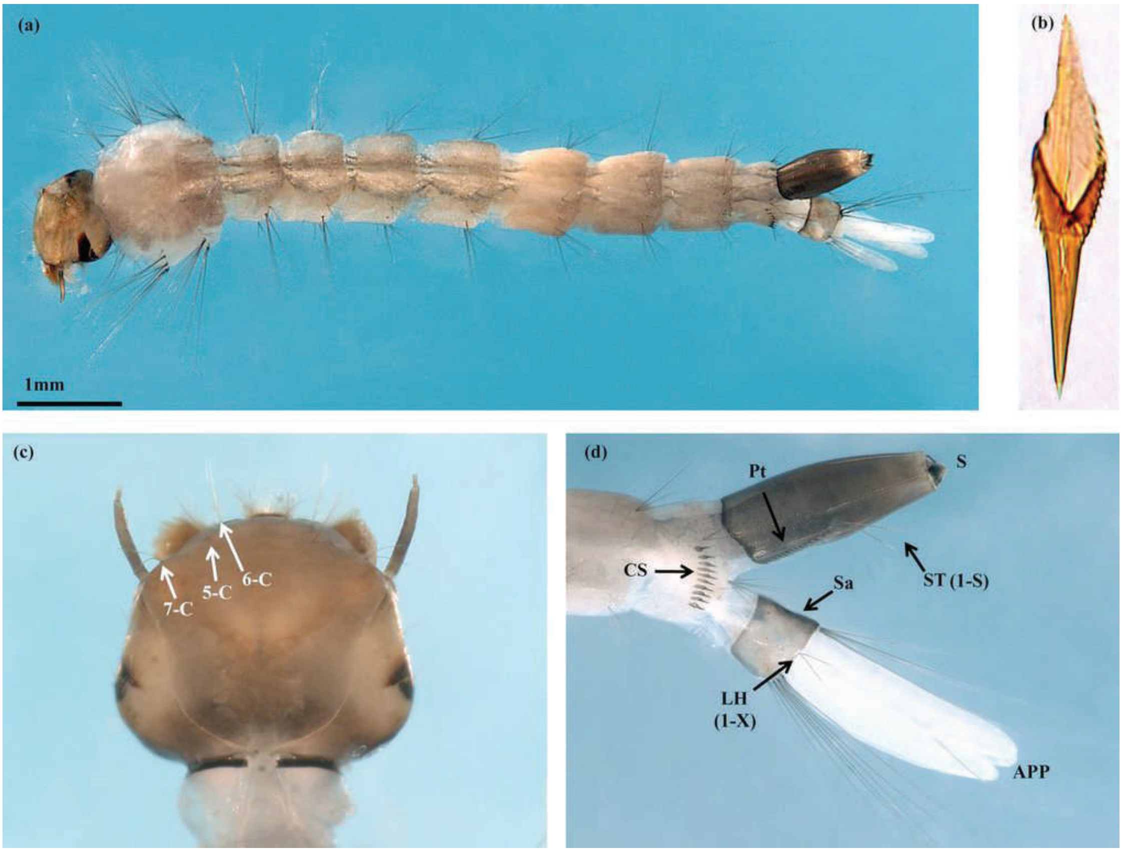


Fig. 11. *Aedes albopictus*. (a) Dorsal view of entire 4th instar. (b) Close-up of representative comb scale. (c) Dorsal view of head. (d) Lateral view of terminal segment. APP, anal papilla; CS, comb scale; LH, lateral hair (seta 1-X); Pt, pecten teeth; S, siphon; Sa, saddle; ST, siphonal tuft (seta 1-S); 5-C, upper head hair; 6-C, lower head hair; 7-C, preantennal head hair.

presence of the lateral hair (seta 1-X) of the anal segment (abdominal segment X) occurring below the anal saddle (Sa). The species is also distinguished from *Ae. atropalpus* by the presence of 34 or fewer (usually 18 to 34) comb scales (CS) on abdominal segment VIII (Zavortink 1972, Darsie and Ward 2005) (see key and Fig. 3). Darsie (1974) has also reported that the total number of comb scales on *Ae. epactius* may range from 14–21 with an average of 16.8, while O'Meara and Craig (1970) report that usually fewer than 25 comb scales are present on this species. Also, Darsie and Ward (2005) note that seta 1-M on the larval thorax of *Ae. epactius* is short and barely reaches the base of seta 0-P; whereas seta 1-M is long on *Ae. atropalpus* and reaches the anterior level of seta 0-P. *Aedes epactius* is multivoltine and has been reported as an avid bloodfeeder, exhibiting anautogenous behavior in contrast to *Ae. atropalpus* (O'Meara and Craig 1970, Brust 1974, Munstermann 1980, Lozano-Fuentes et al. 2012). Although the exact host preference of *Ae. epactius* is currently unknown, the species likely feeds on mammals (similar to *Ae. atropalpus*), particularly in areas proximal to larval habitats. The potential significance of *Ae. epactius* as a vector of arboviral diseases or its threat to public health importance is poorly understood. Laboratory strains of *Ae. epactius* have been shown to biologically transmit Jamestown Canyon virus (Heard et al. 1991) and to transovarially transfer St. Louis encephalitis virus to their progeny (Hardy et al. 1980) under experimental settings. However, it is apparent that further research is necessary to further elucidate the biology and ecology of this species in North America.

### *Aedes* (*Protomacleaya*) *hendersoni*

*Aedes hendersoni* is a tree hole mosquito that is distributed throughout North America, extending from Canada to Mexico and from the East to the West coasts (Fig. 4). It often occurs sympatrically with *Ae. triseriatus* and bears a notable morphological resemblance to that species. Hybridization is known to occur between the 2 species, thus making accurate identification even more difficult (Truman and Craig 1968, Grimstad et al. 1974).

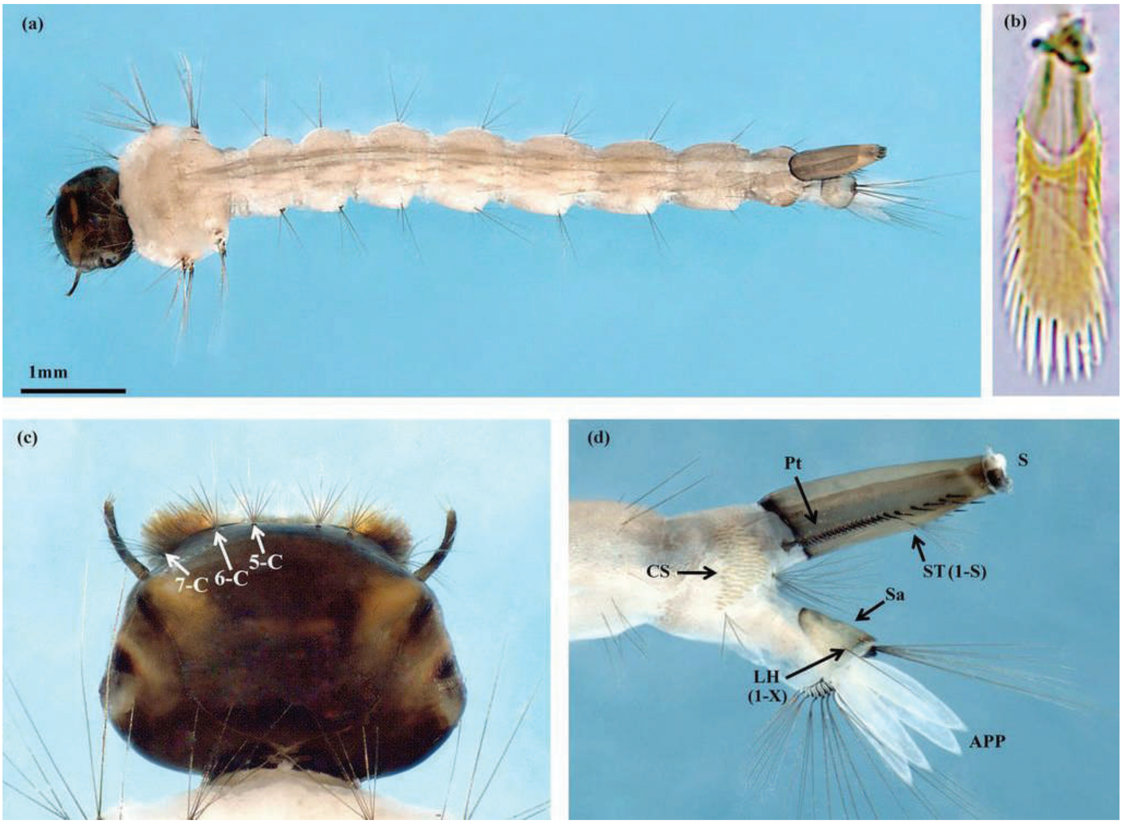


Fig. 12. *Aedes japonicus*. (a) Dorsal view of entire 4th instar. (b) Close-up of representative comb scale. (c) Dorsal view of head. (d) Lateral view of terminal segment. APP, anal papilla; CS, comb scale; LH, lateral hair (seta 1-X); Pt, pecten teeth; S, siphon; Sa, saddle; ST, siphonal tuft (seta 1-S); 5-C, upper head hair; 6-C, lower head hair; 7-C, preantennal head hair.

Larvae are found in a wide variety of natural and artificial containers, and there are several generations each year (Means 1979, Yee 2008). *Aedes hendersoni* is also occasionally found in the same larval habitat as *Ae. triseriatus*, but the former has been traditionally reported to favor tree holes in the canopy and is not as readily encountered in larval habitats near the ground (Loor and DeFoliart 1970, Scholl and DeFoliart 1977, Sinsko and Grimstad 1977). However, this conventional paradigm of vertical distribution may not be as clear between these 2 species, as others have shown that *Ae. hendersoni* may also oviposit at ground level (Scholl and DeFoliart 1977, Schreiber et al. 1988, B. Byrd, personal communication). Further investigations are warranted to decipher the niche shifts and interspecific competition between *Ae. hendersoni* and *Ae. triseriatus*, which may not be solely based on vertical oviposition preference, but also on predation, susceptibility to parasites, and larval habitat type/quality. Overall, the larvae of *Ae. hendersoni* may easily be identified from other container-inhabiting *Aedes* by the presence of comb scales (CS) arranged in a partly double row, and multibranched lateral hair (seta 1-X) on anal saddle (Sa) (see key and Fig. 5). Also, Siverly (1972), Grimstad et al. (1974), Lunt (1977b), Darsie and Ward (2005), and Byrd (2013) provide detailed morphological characters that distinguish *Ae. hendersoni* from *Ae. triseriatus* larvae. These include a siphonal acus (SA) detached and removed from base of siphon, equal length and blunt anal papilla (APP), a 3-branched siphonal tuft (1-S), and 2-branched lateral hair (1-X) of saddle on *Ae. hendersoni*; whereas *Ae. triseriatus* larvae possess a SA usually attached to siphon (but situated close to siphon base, if removed), unequal and tapering APP, a 2-branched siphonal tuft (1-S), and multibranched lateral hair (1-X) on saddle. Byrd (2013) also notes that because of hybridization between the 2 species, incomplete morphology may exist and multiple characters should be accounted for before a specimen is positively identified. Although little is known about the biology and hosts of *Ae. hendersoni*, adults are purported to primarily feed on mammals (Means 1979, Nasci 1985). The public health significance of *Ae. hendersoni* is poorly understood, perhaps further confounded by its morphological similarity to *Ae. triseriatus*; however, although the latter species is an efficient vector of LAC virus, *Ae. hendersoni* can only transmit LAC virus at very low rates (Grimstad et al. 1985). This reduced vector competence has been attributed to an inability of the virus to escape from the salivary gland barriers (Paulson et al. 1989). *Aedes hendersoni* may also possess veterinary importance, as the species has been experimentally shown to be biologically capable of supporting infective-stage larvae of *Dirofilaria immitis* (Leidy), the dog heartworm (Rogers and Newson 1979).

### *Aedes* (*Ochlerotatus*) *sierrensis*

*Aedes sierrensis*, the western tree hole mosquito, occurs primarily on the West Coast of North America (Fig. 6). It is distributed from southern California to British Columbia in the north, and westward to Utah (Darsie and Ward 2005). Larvae of *Ae. sierrensis* may be distinguished from other species by the arrangement of comb scales (CS) in a patch, a double lateral hair (seta 1-X) occurring on the saddle (Sa), and anal papilla (APP) which are equal in size and blunt (Fig. 7). *Aedes sierrensis* was reduced to synonymy with *Ae. varipalpus* (Coquillett) until Belkin and McDonald (1956) resurrected the former to species status (Arnell and Nielsen 1972). Larvae are primarily found in natural tree hole cavities, although specimens have occasionally been collected from artificial containers with ample organic detritus present (Bohart and Washino 1978). *Aedes sierrensis* may be considered a univoltine species because larvae develop slowly, but additional broods may be possible following excessive rainfall and subsequent egg hatch (Carpenter and LaCasse 1955). The species readily feeds on humans and other mammals during the day, and is considered an important pest in recreation and wooded areas (Carpenter and LaCasse 1955, Bohart and Washino 1978). *Aedes sierrensis* has been experimentally infected with California encephalitis, Japanese B encephalitis, and western equine encephalitis viruses (Bohart and Washino 1978). The species is also implicated as an important vector of *Dirofilaria immitis* in domestic and wild animals (Bohart and Washino 1978, Scoles et al. 1993).

### *Aedes* (*Protomacleaya*) *triseriatus*

*Aedes triseriatus*, the eastern tree hole mosquito, is the most common tree hole mosquito in North America (Fig. 4). It occurs primarily in the eastern USA and is distributed from Florida to Canada, and westward to Texas and Oklahoma (Darsie and Ward 2005). Larvae are found in a wide variety of natural and artificial containers at ground level, and there are several generations each year. Larvae of this species may easily be identified from other container-inhabiting *Aedes* by the presence of comb scales (CS) arranged in a partly double row, multibranched lateral hair (seta 1-X) on anal saddle (Sa), and anal papilla (APP) of unequal length (Fig. 8). It is closely related to *Ae. hendersoni* (see section above for further information regarding these 2 species). The public health significance of *Ae. triseriatus* has been well documented and the species is the principal vector of LAC virus in the USA. The species has also been implicated in transmission of *Dirofilaria immitis*, Cache Valley, eastern equine encephalitis, Highlands J, Jamestown Canyon, and WN viruses (Rogers and Newson 1979, Andreadis et al. 2005, Erickson et al. 2006, Scheidler et al. 2006).

### *Aedes* (*Stegomyia*) *aegypti*

*Aedes aegypti*, the yellow fever mosquito, has been an invasive species in North America for centuries. The species was most likely introduced via the slave trade in the 16th century in water barrels intended to collect rainwater on the docks and ships during voyage (Spielman and D'Antonio 2001). The native range of *Ae. aegypti* is tropical and subtropical areas of Africa; however, it is now endemic in South America and parts of temperate North America (Fig. 9). In North America it is primarily concentrated around the southeastern USA and Mexico; however, it has been detected as far west as Arizona, and as far north as Indiana and New Jersey (Darsie and Ward 2005). The northern range of *Ae. aegypti* is limited by its inability to survive during cold winter months and establishment of permanent populations in these areas has been unsuccessful; thus, the species should not be included as an endemic species in northern states (Farajollahi and Crans 2012). Populations of *Ae. aegypti* are also particularly sparse in Kentucky, Maryland, Missouri, North Carolina, Tennessee, and Virginia. Additionally, in the state of Hawaii, although the species was previously detected on most of the main islands, it is now only considered endemic on the island of Hawaii; nevertheless, imminent dispersal to other main islands is expected (Nishida 2002, Promed 2012, D. Fonseca and P. Yang, personal communication). Larvae are primarily peridomestic and are almost always found within artificial containers in the close vicinity of humans. Larvae of this species, along with *Ae. albopictus*, may readily be identified from other common container-inhabiting *Aedes* by the presence of a single straight row of comb scales (CS) on abdominal segment VIII (Fig. 10). *Aedes aegypti* are primarily anthropophilic, but may feed on domestic animals when available. These mosquitoes are a nuisance, feeding mostly in the shade during daytime, and have been shown to prefer lower parts of the body. They are skittish during the host feeding process, often flying away when disturbed, only to return a short while later. Interrupted blood-feeding increases host probing and may increase *Ae. aegypti* vectorial capacity because of increased host contact and potential to transmit pathogens with each probe. The public health significance of *Ae. aegypti* is well documented and the species is considered the primary vector of YF, and an important vector of CHIK, DEN, and several other arboviruses. Although WN virus has been detected from field specimens in the USA (CDC 2013), their high preference for human blood may limit their contribution to this disease cycle and they are probably not an important bridge vector of this disease. However, the importance of this mosquito as a major vector of CHIK, DEN, and YF, coupled with globalization of cargo trade and air travel, underscores the need for surveillance and control to prevent outbreaks of human epidemics. Locally acquired infections of DEN in the Florida Keys, driven by *Ae. aegypti*, during multiple years in 2009–10 (MMWR 2010) further highlight the importance of a vigilant detection and response plan.

### *Aedes* (*Stegomyia*) *albopictus*

*Aedes albopictus*, the Asian tiger mosquito, is among the most invasive of all animal species, and without question the most invasive of all mosquitoes. The mosquito is considered as one of the "*100 of the World's Worst Invasive Alien Species*" by the World Conservation Union (ISSG 2013). *Aedes albopictus* has dispersed widely from its native range in Southeast Asia, and is now found in close to 30 countries in Africa, the Middle East, Europe, the Pacific, and South and North America (Benedict et al. 2007). *Aedes albopictus* was 1st established in the USA in Texas during 1985 via used tires shipped from Japan (Sprenger and Wuithiranyagool 1986). Within the last 20 years, the species has spread to 30 states and continues to expand its range, presumably aided by human activities and scrap tire movement on interstate highways (Enserink 2008). In North America it is primarily concentrated around the southeastern USA, with a westward range into Texas, and northward into Illinois and New Jersey (Darsie and Ward 2005) (Fig. 9). *Aedes albopictus* was also collected in Southern California during 2001 (Linthicum et al. 2003, Madon et al. 2003) and was thought to have been extirpated; however, it was once again detected during 2011–13 (Metzger and Hu 2012, K. Fujioka, personal communication). Local public health and vector control officials believe that the recent detections may have been derived from smaller remnant populations of the initial infestation that survived locally (Metzger and Hu 2012), but major efforts are currently underway to curb the infestation to prevent further spread of the species. However, given the current global climate change patterns, predicted range expansion of *Ae. albopictus*, and difficulty in suppressing populations of this peridomestic pest (Moore and Mitchell 1997, Benedict et al. 2007, Bartlett-Healy et al. 2011, Unlu et al. 2011, Farajollahi et al. 2012, Fonseca et al. 2013, Rochlin et al. 2013b), we have updated our distribution map to include California (Fig. 9). Additionally, the species is now endemic on all 7 of the major Hawaiian Islands (Hawaii, Kaua'i, Lāna'i, Maui, Moloka'i, Ni'ihau, O'ahu), generally with an elevation of under 1,000 m, and may further spread into the smaller islands in the coming years (Nishida 2002, D. Fonseca and P. Yang, personal communication). However, much like *Ae. aegypti*, the northern range of *Ae. albopictus* is limited by its inability to survive extreme cold (Nawrocki and Hawley 1987), but the species appears to be more temperate and is slowly expanding its geographical range near its northernmost limits (Farajollahi and Nelder 2009, Rochlin et al. 2013b). Larvae are predominantly peridomestic and thrive in artificial containers, but may also be found in rural areas inhabiting natural containers such as tree holes. Larvae of this species, along with *Ae. aegypti*, are distinguished from other common container-inhabiting *Aedes* by the presence of a single straight row of comb scales (CS) on abdominal segment VIII (Fig. 11). *Aedes albopictus* larvae are superior competitors to *Ae. aegypti* and in Florida, they have caused local extinctions of *Ae. aegypti* (O'Meara et al. 1995, Juliano and Lounibos 2005). Although *Ae. albopictus* are superior competitors to *Ae. triseriatus* under the laboratory conditions, they coexist in tree hole habitats where larval predators such as *Corethrella appendiculata* Grabham are present (Kesavaraju et al. 2008). Differential antipredatory behavior may be the mechanism behind the coexistence (Kesavaraju et al. 2008). *Aedes albopictus* females are opportunistic feeders and adults in urban areas tend to be found in shade near gardens and landscaping. They are primarily diurnal feeders, preferring to attack large mammals, including humans and livestock, but also feed on birds (Savage et al. 1993). The public health significance of *Ae. albopictus* has been well documented, and the species is considered not only a vector of several arboviruses but also a significant nuisance where it is abundant. The mosquito has been documented as an efficient laboratory vector of more than 30 arboviruses, including 7 alphaviruses (such as eastern equine encephalitis and Ross River viruses), 8 bunyaviruses (such as LAC and Rift Valley fever viruses), and 4 flaviviruses

(Japanese encephalitis, DEN, WN, and YF) (Estrada-Franco and Craig 1995, Gratz 2004). Field populations of *Ae. albopictus* have been found naturally infected with CHIK, DEN, Japanese encephalitis, Potosi, Keyston, Tensaw, Cache Valley, eastern equine encephalitis, WN, and YF viruses (Gratz 2004, Enserink 2008). *Aedes albopictus* is implicated as a bridge vector in the transmission of WN virus (Farajollahi and Nelder 2009), and is also an efficient vector of DEN virus (all 4 serotypes), *Dirofilaria immitis*, and CHIK virus (Gratz 2004, Charrel et al. 2007). The recent outbreak and reemergence of CHIK virus in the Indian Ocean were driven primarily by *Ae. albopictus* and attributed to a viral mutation that enhanced the vector competency and transmission efficiency by this species (Tsetsarkin et al. 2007). Also, autochthonous transmission of CHIK virus in temperate northern Italy and southeastern France were both driven by invasive *Ae. albopictus* populations (Carrieri et al. 2011, Grandadam et al. 2011). Ultimately, increased human travel and dispersal of mosquito vectors will allow a viremic patient to meet a competent vector in a new environment and exotic diseases will undergo establishment, amplification, and dispersal. Expanded surveillance and subsequent control are urgently needed within the urban landscape where the potential for introduction of an exotic arbovirus is high.

### *Aedes* (*Finlaya*) *japonicus*

*Aedes japonicus*, the Asian bush mosquito, is the most recently introduced invasive container *Aedes* in the USA. The species was 1st detected in the northeastern USA in 1998, but quickly expanded its range and is now established in 33 states (Peyton et al. 1999, Andreadis et al. 2001, Cameron et al. 2010) (Fig. 6). Introduction via international trade in used automobile tires is suspected as the primary cause for the initial introduction. The species is native to Japan, Korea, and eastern China, where it is found in a wide variety of natural and artificial containers, including rock pools (Tanaka et al. 1979). In North America it is primarily concentrated around the eastern USA, ranging from Canada and Maine in the north to Mississippi in the south and westward to South Dakota (Andreadis et al. 2001, Mullen 2005, Gallitano et al. 2006, Dunphy et al. 2009, Johnson et al. 2010, Gaspar et al. 2012, Kaufman et al. 2012, Thorn et al. 2012). Isolated introductions on the Pacific Coast have also been detected in Oregon, Washington, and Hawaii on separate occasions, and the species is now considered endemic on the big island of Hawaii from sea level to elevations of about 5,000 m (Roppo et al. 2004, Larish and Savage 2005, D. Fonseca and P. Yang, personal communication). A complete listing of American states where *Ae. japonicus* is now endemic includes Alabama, Arkansas, Connecticut, Delaware, Georgia, Hawaii, Illinois, Indiana, Iowa, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, New Hampshire, New Jersey, New York, North Carolina, Ohio, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Vermont, Virginia, Washington, West Virginia, and Wisconsin (Fig. 6). Temperate strains of *Ae. japonicus* are more tolerant of cold temperatures than other invasive *Aedes* species, with eggs and larvae successfully overwintering in northern geographic ranges. Eggs of this species also hatch earlier than other container mosquitoes in the Northeast, and larvae persist much longer during the fall season, despite near-freezing water temperatures (Scott 2003). In a survey of rock pools conducted in Connecticut, Andreadis and Wolfe (2010) reported *Ae. japonicus* as the dominant mosquito collected from these habitats, except from pools where water temperatures exceeded 30°C. They have theorized that a temperature barrier may exclude *Ae. japonicus* from expansion into southern states with high summer temperatures (Andreadis and Wolfe 2010). However, despite limiting environmental barriers, *Ae. japonicus* appears as a dominant invader and may be competitively displacing native species in certain habitats (Bevins 2007, Armistead et al. 2008, Andreadis and Wolfe 2010, Rochlin et al. 2013a). In the USA, larvae of *Ae. japonicus* are readily found in domestic and sylvan habitats, in a wide variety of natural and artificial containers (Peyton et al. 1999, Scott 2003, Juliano and Lounibos 2005, Bartlett-Healy et al. 2012). Larvae of this species may readily be identified from other common container-inhabiting *Aedes* by the arrangement of the head hairs (5-C, 6-C) in a straight line near the anterior margin of head (Fig. 12). North American populations of *Ae. japonicus* appear to be primarily mammalophilic, with a substantial proportion of human bloodfeedings from field-collected specimens in the Northeast (Apperson et al. 2004; Molaei et al. 2008, 2009). The public health significance of *Ae. japonicus* has been a significant topic of research in recent years. Laboratory studies have shown it to be an efficient vector of WN virus and St. Louis encephalitis virus, and a moderately efficient vector of eastern equine encephalitis and LAC encephalitis viruses (Sardelis and Turell 2001, Sardelis et al. 2002a, Sardelis et al. 2002b, Sardelis et al. 2003, Turell et al. 2005). Furthermore, WN virus has been detected from field-collected specimens of *Ae. japonicus* from multiple states and from each year since 2000 (CDC 2013). The vectorial capacity of *Ae. japonicus* for several established and emerging arboviruses, its rapid spread across the USA since it was introduced, and a competitive advantage over native species emphasizes the pressing need for implementing surveillance and control measures against this species.

## MATERIALS AND METHODS

Morphological characters used in the key are based on observation of specimens and previous usage in published literature (Carpenter and LaCasse 1955, Stojanovich 1961, Siverly 1972, Bohart and Washino 1978, Rueda 2004, Andreadis et al. 2005, Darsie and Ward 2005). Drawings were adapted from Bohart and Washino (1978), Andreadis et al. (2005), and Darsie and Ward (2005). Terminology used in the key follows Stojanovich (1961), Harbach and Knight (1980), and Darsie and Ward (2005). Immature stages of *Ae. aegypti*, *Ae. atropalpus*, *Ae. japonicus*, and *Ae. triseriatus* were obtained from laboratory colonies maintained at the Center for Vector Biology, Rutgers University. *Aedes albopictus* larvae were collected from wild populations in Mercer County, NJ. *Aedes sierrensis* specimens were obtained as eggs on oviposition substrate collected from wild populations in Lake County, CA. Specimens of *Ae. epactius* (Brewster County, TX) and *Ae. hendersoni* (Jackson County, NC) were provided by Brian Byrd, Western Carolina University. Only 4th instars of all specimens were used for photographic plates.

Photomicrographs of mosquito specimens were taken with a Leica MZ16 stereomicroscope (Leica Microsystems, Bannockburn, IL) outfitted with a Leica type 10411597 (f = 100 mm) objective, 62-mm circular polarizer (Tiffen Company, Hauppauge, NY), and Leica DFC-480 digital camera. Images were acquired with Image-Pro MC v.6 software (Media Cybernetics, Bethesda, MD). Software Z-stacking based on maximum local contrast criteria was used to assemble image layers taken at different focal depths. The terminal segment was dissected from larvae and cleared in 10% NaOH solution. Comb scale patches were then further dissected and mounted in euparal on glass microscope slides. Scales were photographed with a Zeiss Axioplan microscope (Carl Zeiss AG, Jena, Germany) equipped with a 40× Plan-Neofluar objective and ProgRes CF Scan digital microscope camera (Jenoptik Laser, Jena, Germany). Adobe Photoshop CS3 (Adobe, San Jose, CA) was used to further crop image layers and adjust final photographs for visual quality.

## KEY TO 4TH-STAGE LARVAE OF CONTAINER *AEDES* IN NORTH AMERICA[1]

1. Pecten teeth on siphon distally detached, siphonal tuft (seta 1-S) inserted within pecten teeth (Fig. 13a) . . . . . . . . 2
   Pecten teeth on siphon evenly spaced, siphonal tuft (seta 1-S) inserted beyond pecten teeth (Fig. 13b) . . . . . . . . 4
2. Head hairs 5-C and 6-C multibranched and arranged in a straight line near anterior of head (Fig. 14a), lateral hair 1-X long and originating on anal saddle . . . . . . . . *Ae. japonicus*
   Head hairs 5-C and 6-C single and not arranged in a straight line (Fig. 14b), lateral hair 1-X short and originating below anal saddle (Fig. 13a) . . . . . . . . 3
3. Abdominal segment VIII with 34 or more (usually 34 to 62) comb scales (Fig. 15a), seta 1-M on thorax long and reaching anterior level of seta 0-P . . . . . . . . *Ae. atropalpus*
   Abdominal segment VIII with 34 or fewer (usually 18 to 34) comb scales (Fig. 15b), seta 1-M on thorax short and reaching base of seta 0-P . . . . . . . . *Ae. epactius*[2]
4. Comb scales aligned in a single straight row (Fig. 16a) . . . . . . . . 5
   Comb scales aligned as a partly double row or patch (Fig. 16b) . . . . . . . . 6
5. Comb scales with prominent subapical spines resembling a pitchfork (Fig. 17a), head hair 7-C single (Fig. 17b), lateral sides of thorax with prominent black hooks (setal support plate of setae 9–12-M,T) . . . . . . . . *Ae. aegypti*
   Comb scales with straight and long median spine, resembling a thorn (Fig. 17c), head hair 7-C double (Fig. 17d), lateral sides of thorax with small hooks or no hooks (setal support plate of setae 9–12-M,T) . . . . . . . . *Ae. albopictus*
6. Comb scales arranged in a patch (Fig. 18a) . . . . . . . . *Ae. sierrensis*[3]
   Comb scales arranged in a partly double row (Fig. 18b) . . . . . . . . 7

[1] Key only includes the most common container-utilizing *Aedes* mosquitoes in North America. Only species with large geographic distributions and/or significant public health importance were included.

[2] Darsie (1974) has also reported that the total number of comb scales on *Ae. epactius* may range from 14 to 21, while O'Meara and Craig (1970) report that usually fewer than 25 comb scales are present on this species.

[3] Larvae of *Ae. sierrensis* may also be distinguished from *Ae. triseriatus* based on the ventral brush (seta 4-X). In *Ae. sierrensis* seta 4-X is sparsely developed with the 2 most caudal setae single or double; whereas in *Ae. triseriatus* seta 4-X is well developed with the 2 most caudal setae multibranched.

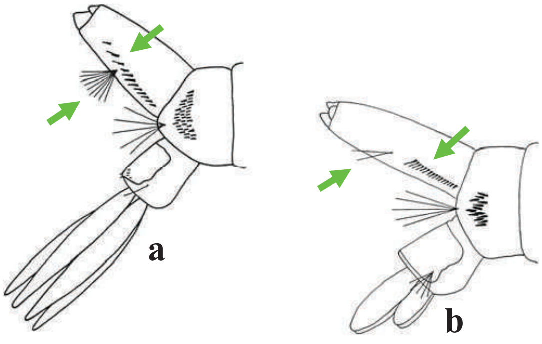


Fig. 13.

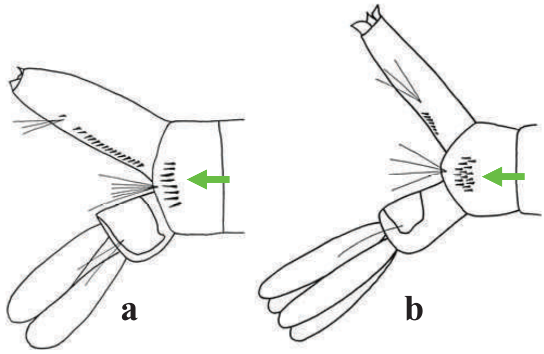


Fig. 16.

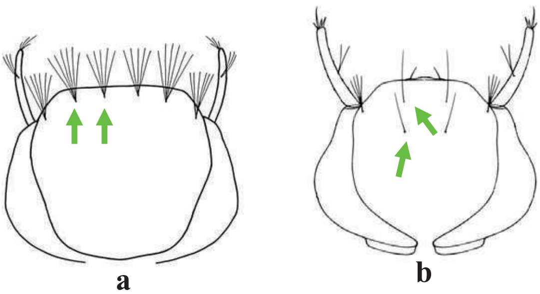


Fig. 14.

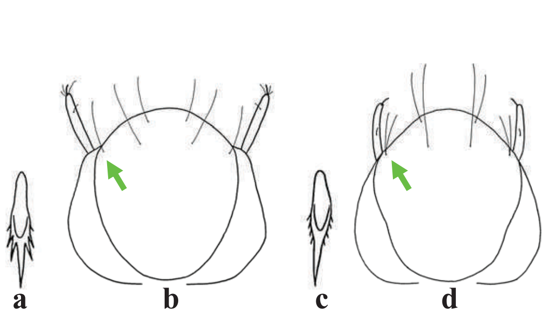


Fig. 17.

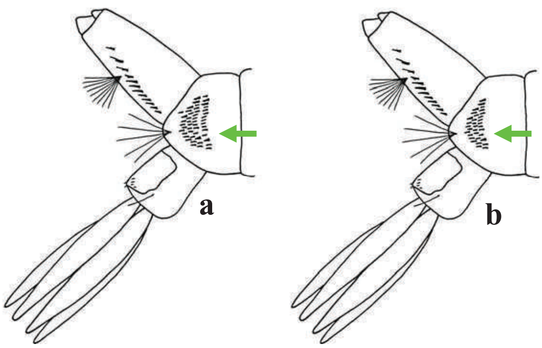


Fig. 15.

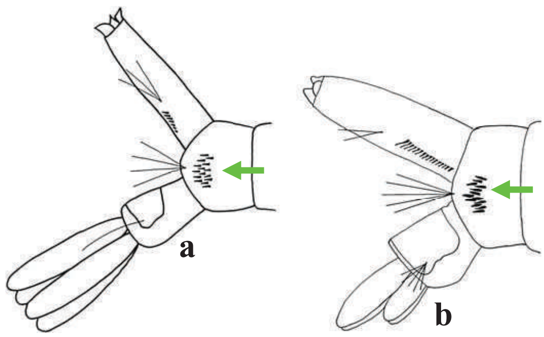


Fig. 18.

7. Siphonal acus (SA) usually attached to siphon or situated close to siphon base if removed, unequal and tapering anal papilla, a 2-branched siphonal tuft 1-S, multibranched lateral hair 1-X on saddle (Fig. 19a) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Ae. triseriatus*
Siphonal acus (SA) usually detached and removed from base of siphon, anal papilla equal in size and blunt, a 3-branched siphonal tuft 1-S, 2-branched lateral hair 1-X on saddle (Fig. 19b) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Ae. hendersoni*

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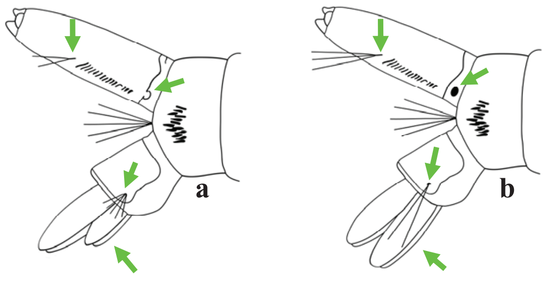

Fig. 19.

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