In the last 15 years there have been a number of publications on the insects of cloud forests, and it is impossible to include all of them in this update. In particular, it has not been possible to compile all the taxonomic publications that include species occurring in Monteverde, a compilation that would be useful since identification is the principal impediment to studying insects. Nonetheless, I have attempted to mention the most important taxonomic publications (of an order, family or subfamily) as well as some examples of specific investigations.

As in Hanson (2000), this update is organized by taxonomic group. Nonetheless, some publications deal with distinct groups and therefore do not fit this organization, for example the studies of arthropods associated with epiphytes (Yanoviak et al. 2004, 2006). Before commencing with the individual groups, two general comments should be made. First, the estimations of species numbers in each order are too low, but updated estimations are not attempted here. Second, it is important to emphasize that despite the advances reported here, there is still much to learned about the arthropods of cloud forests.

**Small insect orders**

For dragonflies and damselflies (Odonata) there is a very useful website that provides keys and descriptions of the families, as well as photos of all the species known from Monteverde (Haber 2014).

For the order Orthoptera there are two general publications, one on katydids (Tettigoniidae: subfamily Conocephalinae) (Naskrecki 2000) and another on grasshoppers (suborder Caelifera) (Rowell 2013), which provide valuable resources for future research on these groups of insects.

**True bugs, spittlebugs, leafhoppers, treehoppers, etc. (order Hemiptera)**

The vast majority of true bugs (suborder Heteroptera) are predatory or phytophagous, but species in the subfamily Triatominae (Reduviidae) suck blood from vertebrates. In Costa Rica, one species, *Triatoma dimidiata*, is the vector of Chagas disease. One of the few studies of this species in the wild was carried out
in Monteverde (Salas Peña 2010), where it was found principally on trunks of live trees, although it was more abundant in residential areas.

With respect to the suborder Auchenorrhyncha, the principal publication in recent years is one on treehoppers (Membracidae), which includes a guide for identification, photos of all the genera, and summaries of their biology (Godoy et al. 2006). This book should greatly facilitate future studies of these gaudy insects. A publication on the spittlebugs (Cercopidae) associated with pastures (Thompson & León-González 2005) will assist in identifying Monteverde species associated with grasses.

Recently, a study was carried out in Monteverde which examined the responses of six species of Auchenorrhyncha to a model of a redstart (Myioborus, Parulidae), a bird species that hunts insects by first frightening and then pursuing them. Two Membracidae (with structural defenses) were the most sensitive, whereas two Cixiidae (defended by camouflage) were the last to flee; two Cercopidae (with aposematic coloration) showed an intermediate response (Galatowitsch & Mumme 2004).

**Beetles (order Coleoptera)**

Some general works that include aids for identification and summaries of biology are available for Staphylinidae (Navarette-Heredia et al. 2002), Scarabaeidae-Dynastinae (Ratcliffe 2003), Scarabaeidae-Cetoniinae (Solís 2004), Chrysomelidae-Cassidinae (Chaboo 2007) and Chrysomelidae-Chrysomelinae (Flowers 2004).

One of the largest families of beetles is Curculionidae, which includes the phytophagous weevils. Two groups that are found in Monteverde and which have been the subjects of research in recent years are members of the subfamily Baridinae associated with Piperaceae (Prena 2010) and those in the tribe Derelomini (now known as Acalyptini; subfamily Curculioninae). Various members of the latter group are pollinators of palms, but some species have changed host plants and can be pollinators of Cyclanthaceae and Anthurium (Araceae) (Franz 2006).

**Butterflies and moths (order Lepidoptera)**

For butterflies (superfamily Papilionoidea) there is a website providing a list of species known from Monteverde, with more detailed information and photos of the glasswing butterflies (Nymphalidae: Ithomini) (Haber 2001).

In Hanson (2000) there is a summary of the biology of Manataria maculata (Nymphalidae-Satyrinae; now classified as a subspecies of *M. hercyna*), which lays eggs on bamboo in the Pacific lowlands (Murillo & Nishida 2003), but spends most of the year in reproductive diapause at higher altitudes, including Monteverde. This is an unusual butterfly in that it is crepuscular and uses different communal roosts—protected sites near the ground during the day and in the canopy at night, probably to avoid birds during the day and mice during the night (Hedelin & Rydel 2007). Its Vogel’s organ, situated at the base of the front wing, detects ultrasounds of insectivorous bats, allowing this butterfly to respond with evasive flight (Rydel et al. 2003). Although Vogel’s organ is found in the majority of Satyrinae, this is the first case where sensitivity to ultrasound has been demonstrated (other Satyrinae probably use this organ to detect the sounds associated with birds in flight).

As mentioned in Hanson (2000), the only Satyrinae in Monteverde with transparent wings is Cithaerius pireta (cited as *C. menander*). Recently, the larval host plant of this species has been discovered, Philodendron herbaceum (Araceae) (Murillo-Hiller 2009).

Most families of Lepidoptera are microlepidopterans, but their biology is relatively poorly known. The larvae of many species are leaf miners or leaf rollers. The larvae of a few species induce galls on plants; for example, an undescribed species of Momphidae produces quite large stem galls on Conostegia oerstediana (Melastomataceae).

**Flies (order Diptera)**

Of all the principal insect orders, the inventory of flies is the most advanced, both in Costa Rica as a whole and in cloud forests in particular. The two volumes by Brown et al. (2009, 2010) provide keys for the identification of fly genera and summaries of our knowledge...
of each genus. This valuable work opens doors for future research on flies.

Many of the specialists who collaborated in the production of the two volumes mentioned above are currently carrying out an inventory of the flies found in a cloud forest at Zurquí de Moravia (Zurqui All-Diptera Biodiversity Inventory, ZADBI 2014). Although this cloud forest is located in a different mountain range, the results of this project will be very applicable to the Monteverde cloud forest. When the results of the Zurquí project become available we should have a significantly better understanding of the fly fauna of Costa Rican cloud forests.

The biology of fly larvae is extremely diverse. This order includes the most species-rich family of gall-inducers, Cecidomyiidae (Hanson & Gómez-Laurito 2005). Although there is a large diversity of plant galls in Monteverde, there are very few studies of these insects. In large part this is due to the fact that Cecidomyiidae is probably the largest family of insects and at the same time probably harbors the greatest proportion of undescribed species (more than 99%). Other phytophagous fly larvae include leaf miners, for example, two species of Agromyzidae on Bocconia frutescens (Papaveraceae) (Boucher & Nishida 2014).

The larvae of other flies are predators, one of the best studied families being Syrphidae. The literature gives the impression that nearly all predatory syrphid larvae feed on aphids and other Sternorrhyncha (Hemiptera) on plants. Nonetheless, the biology of predatory syrphids is probably much more diverse in the Neotropics. For example, Ocyptamus luctuosus, a species found in Monteverde, is a predator in the water that accumulates in epiphytic bromeliads (Rotheray et al. 2000). Ocyptamus is one of the most diverse genera of Syrphidae and the evidence suggests that it is not a monophyletic group (Mengual et al. 2012).

Some adult flies are pollinators of certain plants. An unusual example from Monteverde is the fungus gnat, Bradysia floribunda (Sciaridae), which pollinates Lepanthes glicensteinii (Orchidaceae) via a mechanism known as pseudocopulation. This orchid attracts and dupes the male fungus gnats, which confuse the flower for a female gnat and then copulate with it, in the process receiving a pollinarium that becomes attached to its abdomen (Blanco & Barboza 2005).

Wasp, ants and bees (order Hymenoptera)

There are two books in Spanish on the Hymenoptera of the Neotropical region, one that emphasizes identification (Fernández & Sharkey 2006) and the other with detailed summaries of the biology of the order (Hanson & Gauld 2006). Although these books cover the entire region, they provide a good introduction for studies of Monteverde hymenopterans.

The vast majority of hymenopterans are parasitoids of other insects, but in recent years several species have been discovered that have made an evolutionary transition to phytophagy. For example, in Monteverde the larvae of Eurytoma werauhia (Eurytomidae) feed on the floral buds of Werauhia gladioliflora (Bromeliaceae) (Gates & Cascante-Marín 2004). In the Central Valley of Costa Rica the larvae of Allorhogas conostegia (Braconidae) induce galls in the fruits of Conostegia xalapensis (Melastomataceae), but it is possible that in Monteverde another (undescribed) species of the same genus produces these galls (Chavarría et al. 2009a). This deserves more research, and if this hypothesis is correct, it could represent an interesting case of speciation.

The wasps that are best known to the general public are the eusocial wasps which construct paper (carton) nests (Vespidae, subfamily Polistinae). The best studied species in Monteverde is Polybia aequatorialis (O'Donnell et al. 2004, Jones et al. 2009), which is the only species of Polistinae that occurs at very high elevations (more than 3000 m), where they have enormous colonies (Chavarría et al. 2009b).

Ants (Formicidae) continue to be one of the best studied hymenopteran families in Monteverde. Some research deals with the entire ant fauna. For example, utilizing canopy fogging, fewer species were found in secondary forest than in primary forest, but the number of species in pasture trees was similar to that in primary forest (Schonberg et al. 2004). A study of leaf litter ants showed that the complex of species was not very affected by the formation of forest clearings (Patrick et al. 2012). Other studies deal with particular groups of ants and in
recent years army ants (Ecitoninae, now placed in Dorylinae) have received considerable attention, especially with respect to the effects of altitude/temperature and forest fragmentation on the ants (O’Donnell & Kumar 2006, Kumar & O’Donnell 2009, Soare et al. 2014), and the birds that accompany these ants (Kumar & O’Donnell 2007).

Spiders (order Araneae)
A recent study of the arboreal spiders in Monteverde found no differences in the abundance or number of species in primary versus secondary forest. Nonetheless, in both forest types vertical differences were observed, with greater abundance and a greater number of species on tree trunks (from zero to two meters above the ground) than in the canopy (Yanoviak et al. 2003).

Literature cited


