Chapter 14
Lace Bugs (Tingidae)

Marcus Guidoti, Sara I. Montemayor, and Éric Guilbert

Abstract The members of the Tingidae family are commonly known as "lace bugs" because of the lacelike appearance of their pronotum and hemelytra. The family is distributed worldwide and is constituted by three subfamilies, Tinginae, Cantacaderinae, and Vianaidinae; all of them represented in the Neotropical Region being the last one endemic of this region. There are around 300 genera and 2,500 species in this family, but for the Neotropical Region, there are known approximately 70 genera and 600 species; most of them belong to the subfamily Tinginae. All lace bugs are phytophagous and host specific, with a few exceptions. Among them, there are some that have economic importance as crop pests and others that are useful for controlling harmful weeds in field crops. Herein we characterize and diagnose the family, we mention some of the most relevant aspects of their biology and ecology, and we provide a summary of its taxonomy with some comments about its phylogeny. The economically most relevant species of the Neotropical Region are listed; for all of them, we provide information about their host plants, distributions, and related literature. We also developed a key to the most economically important Neotropical genera.

M. Guidoti (✉)
Programa de Pós-graduação em Biologia Animal, Instituto de Biociências, Universidade Federal do Rio Grande do Sul (UFRGS), Av. Bento Gonçalves 9500, prédio 43435, Bairro Agronomia, Porto Alegre, RS 91501-970, Brazil
e-mail: marcus.guidoti@gmail.com

S.I. Montemayor
División Entomología, Museo de La Plata,
Paseo del bosque s/n, La Plata 1900, Buenos Aires, Argentina
e-mail: smontemay@gmail.com

É. Guilbert
UMR7205 MNHN/CNRS/EPHE/UPMC, Muséum National d'Histoire Naturelle,
45 rue Buffon, CP 50, Paris F-75 005, France
e-mail: guilbert@mnhn.fr

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14.1 Introduction

Tingidae is a family of small hemimetabolous, plant-feeding bugs usually called "lace bugs" due to the lacelike aspect of their hemelytra and pronotum of most of its species (Schuh and Slater 1995) (Fig. 14.1). They are unique among the Heteroptera because it is the single family with a high specific richness in which all its members are exclusively phytophagous. They are worldwide distributed and comprise about 2,500 species arranged in 300 genera. The family is composed of three subfamilies: Vianaidinae, Cantacaderinae, and Tinginae (Schuh et al. 2006); all of them are represented in the Neotropical Region, Vianaidinae being endemic of this region (though there are fossil records from the Nearctic Region). Approximately 600 species distributed in around 70 genera are currently known for this region.

The size ranges from 2 to 8 mm, and besides their highly complex morphology, they are poorly colored, generally varying in shades of brown. Tingids are characterized by a low flight activity presenting gregarious and sedentary habits and by being generally host specific (though they feed on a great number of botanical families). Adults and nymphs are usually found on the undersides of leaves (with some exceptions), where they feed on the sap of living plants by piercing the epidermis with their very slender stylets. These stylets are protrusive and retractile and can

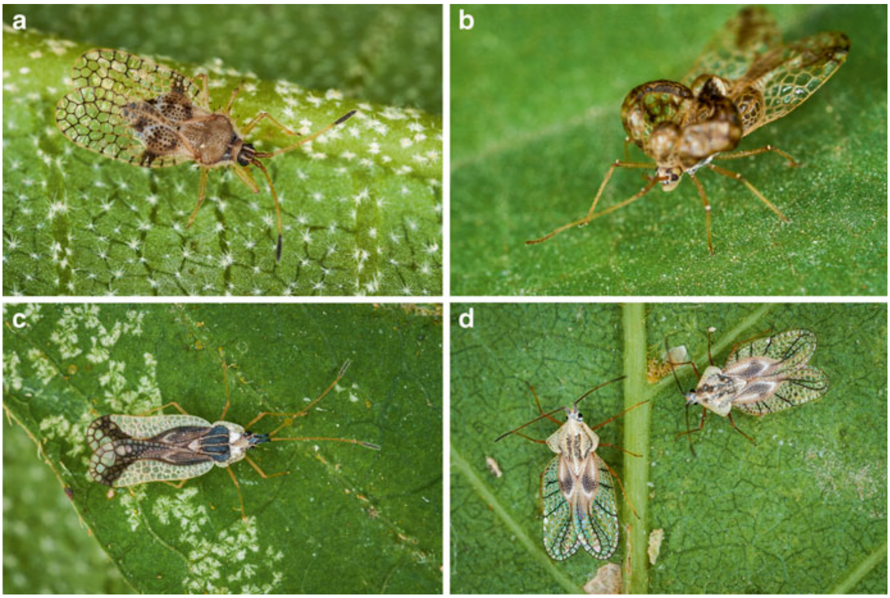

Fig. 14.1 Tingids on the leaves of their host plants: (**a**) *Acanthocheila* sp., (**b**) *Phymacysta* sp., (**c**) *Leptopharsa* sp., and (**d**) *Gargaphia* sp. (Photos by C. D'Haese)

easily penetrate the cellular tissue to extract the sap. Their feeding activities may cause great injury and plasmolysis of the foliage. Many cultivated and wild plants of prime importance in agriculture and horticulture are seriously affected by the feeding activities of these insects (Drake and Ruhoff 1965). The entire life cycle is completed on the same host plant species and on the very same part of the plant in most of the cases.

The members of this family are adapted to a wide range of habitats; some species occur on the ground, associated with the upper parts of the roots or lower parts of stems, some are subterranean, some live in middle height or on the plant canopy, and some non-Neotropical genera induce galls and feed on pollen and moss (Péricart 1983). Some are described as associated with ants, because they were found in ant nests or collected together (Van Doesburg 1977). They are small and difficult to see due to their hyaline structures and then remain poorly known, despite the number of species already described.

14.2 General Characteristics and Diagnosis

Most species are characterized by the lacelike network of areolae (Fig. 14.2a–c), but some species can present punctuations instead (Fig. 14.2d, e). The head is armed with a maximum of nine spines (Fig. 14.3). These spines are extremely relevant for tingid taxonomy, and they are named according to their position. The antennae have four segments as well as the labium which is inserted ventrally in the head. In Vianaidinae, compound eyes can be absent or extremely reduced (Fig. 14.4a), and the ocelli are absent in all but the macropterous forms of this subfamily. The bucculae are well developed (Fig. 14.4b), areolated, and sometimes joined anteriorly. The dorsum and the hemelytra are slightly or heavily punctuated and/or areolated. The pronotum is convex or flat and composed of a collar, a pronotal disk with or without carinae, and a pair of lateral expansions (paranota), with or without a posterior projection covering the scutellum (Fig. 14.2). The paranota and the carinae can be well developed or absent, with different degrees of reflection and numbers of rows of areolae. The collar can be developed forming a hood, which can fully or partially cover the head (Fig. 14.5). The rostral channel forms a groove which is framed with sternal laminae (Fig. 14.6). The dorsal laterotergites are present, but the ventral ones are absent. The abdominal spiracles 2–8 are located on abdominal sterna. The male genitalia are symmetrical; the phallus has some sclerotized eversible structures (Lee 1969). The parameres are usually directed backwards; the ovipositor is laciniate; the connection between the first valvula and first valvifer is lost, as in the Miridae (Schuh and Slater 1995). The spermatheca is absent and the pseudospermathecae present, but it seems to be unrelated with the sperm storage function (Marchini et al. 2010).

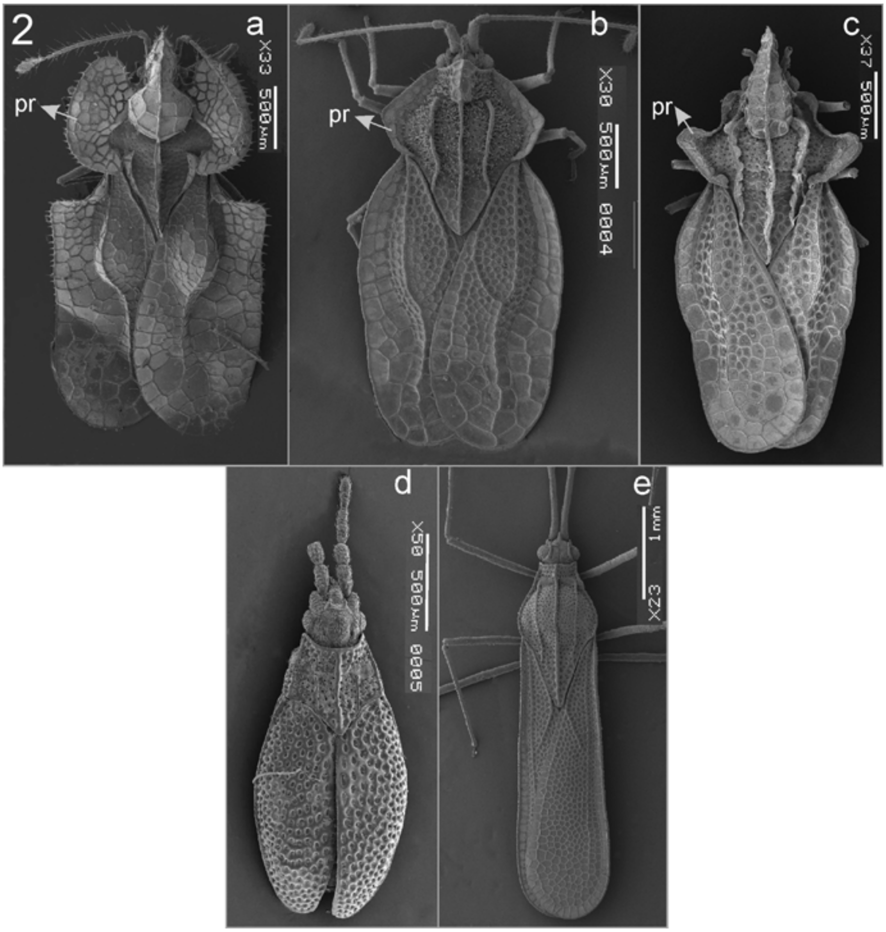

Fig. 14.2 Dorsal habitus, pr: paranota: (**a**) *Corythucha* sp., (**b**) *Gargaphia* sp., (**c**) *Corythaica* sp., (**d**) *Coleopterodes* sp., and (**e**) *Tigava* sp. (Photos by S. Montemayor)

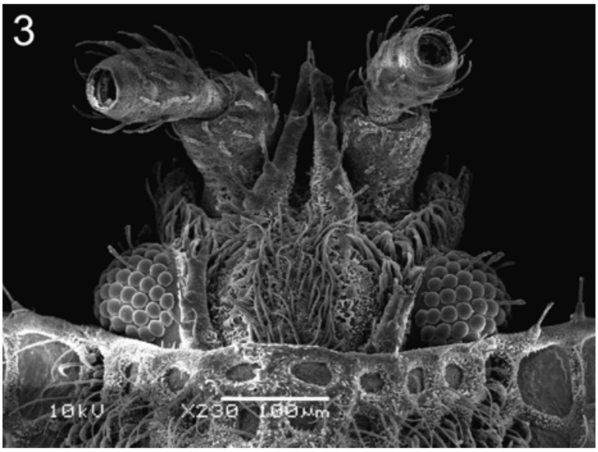

Fig. 14.3 Dorsal view of head of *Tingis americana*, presenting four spines (Photo by M. Guidoti)

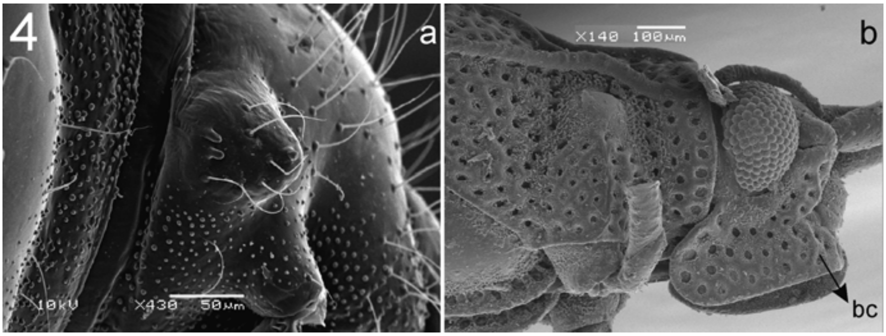

Fig. 14.4 Lateral view of the eye; bc, buccula: (**a**) *Thaumamannia vanderdrifti* Doesburg, 1977 (Vianaidinae), and (**b**) *Tigava* sp. (Photos by M. Guidoti and S. Montemayor)

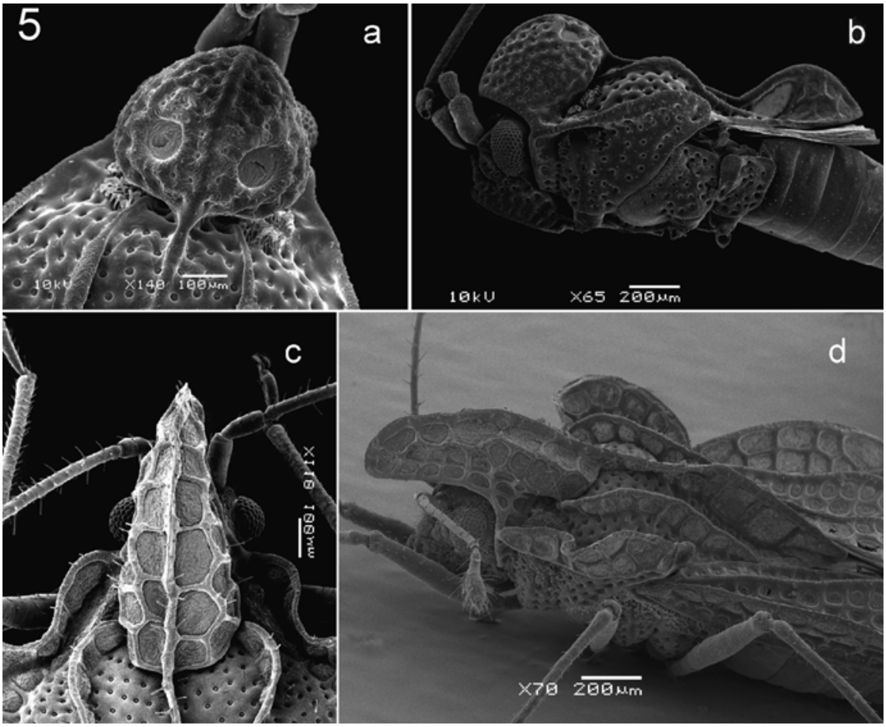

Fig. 14.5 Dorsal and lateral view of the hood: (**a**, **b**) *Sphaerocysta globifera* Stål, (**c**, **d**) *Corythaica* sp. (Photos by M. Guidoti and S. Montemayor)

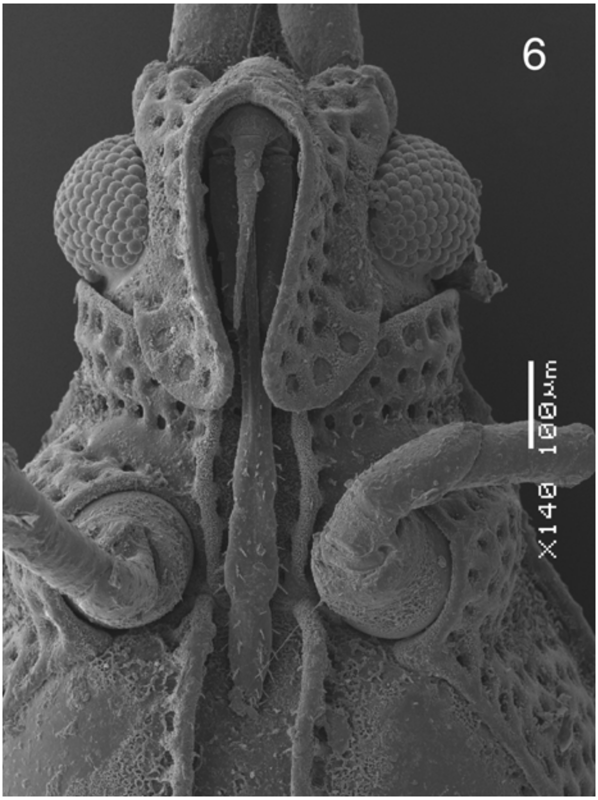

Fig. 14.6 Rostral channel of *Tigava* sp. (Photo by S. Montemayor)

14.3 General Biology and Ecology

14.3.1 Reproduction, Eggs, and Oviposition

The reproductive behavior has been described for very few species [e.g., Kogan 1960 – *Corythaica cyathicollis* (Costa)], and no courtship behavior has been reported. Reproductive parameters, such as fertility and fecundity, could vary in great scale between species, and most of the studies were carried with species from the Palearctic Region (e.g., Stusak 1968) and only a few with Neotropical species (e.g., Cividanes et al. 2004). The development of male and female reproductive organs was described in detail by Eguagie (1976), for *Tingis ampliata* (Herrich-Schaeffer), a non-Neotropical species of a cosmopolitan and probably paraphyletic genera. Generally, there are one or two generations per year (univoltine or bivoltine), although multivoltine species are known (e.g., some *Corythucha* Stål species – Neal and Douglas 1990). The mechanisms that regulate the number of generations in Tingidae are photoperiodic induction of diapause and noncleidoic eggs. The first one was reported in *Corythucha* (Neal et al. 1992) and perhaps is present in genera that overwinter as adults (Neal and Schaefer 2000). The last one was reported for *Stephanitis pyrioides* (Scott) and consists in a dependency on imbibing water from the host for the completion of the embryonic development (Neal and Schaefer 2000). Thus, during development, the absorption of moisture results in an increase in egg size and weight. As a possible consequence of the moisture requirement, seasonal fluctuations in the moisture availability could also affect voltinism (Neal and Schaefer 2000). And a third mechanism present in *Acalypha* Westwood species, a non-Neotropical genus, is to overwinter as nymphs (Pericart 1983).

Eggs have been poorly studied. Their size is around 0.4–0.85 mm (Péricart 1983), and their structure is similar to the one of the other Cimicomorphan families, particularly the Miridae. The posterior part is hemispherical; the sides are slightly compressed laterally and the axis slightly curved; the anterior part is concave and closed by an opercle. The chorion which constitutes the external envelop of the egg is often whitish or clear colored and sometimes brownish at the extremities. The egg shape and structure are quite homogeneous within tingid species.

The oviposition site is variable as there are species that drop their eggs on roots, stems, bud flowers, and/or leafs. The eggs can be inserted on the spongy mesophyll with only the operculum outside the vegetal tissue (endophytic oviposition), partially inserted in the vegetal tissue (pseudo-endophytic oviposition), or placed at the surface of the vegetal tissue (exophytic oviposition). They are usually oviposited in the abaxial surface of the leaf and can be arranged in small or big groups, or they can be isolated, in the midvein or lateral veins or on the leaf surface in several places. Generally, when oviposited on the leaf's veins, they are found on the veins' axillae. The same species can have more than one site for oviposition, so it is difficult to characterize an oviposition strategy at specific level. In some *Gargaphia* Stål species, more than one female oviposits on the same site, forming clusters of eggs from different females. Two Palearctic genera, *Copium* Thunberg and *Paracopium* Distant, are known as gall inducers, and the time and method of laying and fixation of the egg to the corolla are connected with floral cecidogenesis.

14.3.2 Nymph Development and Maternal Care

Most of the species have five instars although four-instar cycle was reported for *Stephanitis rhododendri* Horváth (Johnson 1936). The nymphal morphology varies from simple to highly complex, presenting impressive spinelike structures on the head and on the posterior margins of thoracic and abdominal segments (Fig. 14.7). Some of these cuticular structures present glandular activity, secreting chemical compounds that are related to osmoregulatory functions (Livingstone 1978) and sensorial functions (Aldrich et al. 1991) or have defensive properties (Mason et al. 1991; Scholze 1992). These structures have been described for species of several

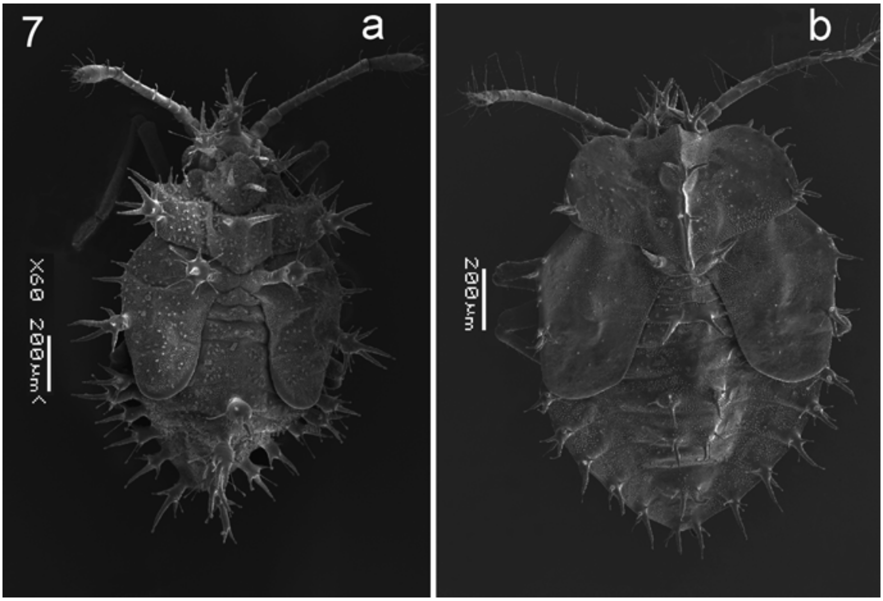

Fig. 14.7 Dorsal habitus of fifth instar nymphs: (**a**) *Corythaica* sp. and (**b**) *Corythucha* sp. (Photos by S Montemayor)

genera and are a reliable source of taxonomic characters (Guilbert 2004a, 2005; Lee 1969). Nymphs also have one pair of abdominal scent glands, which in the subfamilies Tinginae and Cantacaderinae are disposed on the center of the posterior margin of IV and V abdominal segments and in Vianaidinae they are laterally disposed in the posterior margin of the IV segment.

First and second instars are very similar among species; the interspecific differences are more evident from the third instar onwards. Wing pads become conspicuously developed at the fourth or fifth instar, but they are already visible as a small lateral development of the posterior margin of mesonotum in the second instar. Some species belonging to different genera present parental care of nymphs and eggs, sometimes with tricky and aggressive protective behaviors (Tallamy and Denno 1981; Tallamy and Iglay 2004). Very often, nymphs exhibit a gregarious habit; when disturbed and scattered, they quickly group together again. They usually feed and develop to adults on the same plant and even on the same leaf. Some species have all their nymphs fully studied and described, and most of them are from the Palearctic Region (e.g., Livingstone 1976). But only recently (e.g., Guilbert and Montemayor 2010; Guidoti and Barcellos 2013; Montemayor 2009; Montemayor and Dellapé 2010; Montemayor et al. 2011), Neotropical nymphs started to figure in the specialized literature. It has been reported, for example, that an oligophagous Neotropical species, *Tingis americana* Drake, could present different fitness and nymphal development rates in different host plants, due to unequal biological parameters (Moreira et al. 2013). The nymphal morphology is well known for some genera, but little is known about its functionality and evolution (Scholze 1992; Guilbert 2004b). Scholze (1992) studied its functionality, whereas Guilbert (2004b) its evolution and hypothesized nymphal outgrowths as adaptations rather than merely hyperthelic structures. The evolutionary pattern of the development of these structures was studied, and the heterochronic events involved were classified as generally peramorphic, where the next stage (instar) has overdeveloped structures and, in some cases, paedomorphic, where the next stage has underdeveloped structures (Guilbert et al. 2008).

Maternal care of offspring, a rare behavior within Cimicomorpha's families, has been described for three tropical genera, two of them distributed in the Neotropics (*Gargaphia* and *Leptobyrsa* Stål). Chemical compounds were isolated from nymphs and adults, and they seem to play an important role in communication and also as predatory protection strategy (e.g., Aldrich et al. 1991; Mason et al. 1991; Scholze 1992). In *Gargaphia solani* Heidemann, one female takes care of groups of eggs oviposited by several other females until this brood becomes adult (Tallamy and Denno 1981). This probably occurs because the maternal care induces a great survivor rate for the species, but also exposes the female involved in danger. Thus, the smaller is the number of females exposed to predatory activity, the higher is the number of females that could survive (Tallamy 1985). *Leptobyrsa decora* Drake, presents some communal effort to protect the brood (Loeb and Bell 2006), and there are a couple of biological studies where the effect of such maternal care on the brood success through the nymphal development is clear (Melksham 1984). In the Afrotropical species *Compseuta picta* Schouteden, adult females push away the aggressor from the brood and move the wings against the aggressor (Tallamy and Iglay 2004). Besides the mentioned examples, it is expected that more tingids, including Neotropical genera, present these ethological traits.

14.4 Classification and Diversity

The classification of tribes, genera, and species is mostly based on external morphological characters, especially the lacy outgrowths of the pronotum and of the hemelytra. Systematics and taxonomy of the Tingidae are a hard and paradoxal task, due to such particular outgrowths. In contrast to what happens in other families, characters of the genitalia are not frequently used since Drake and Davis (1960) noted that the male genitalia were not of taxonomic value, in spite of Lee's (1969) observation of useful variations of the phallys for the oriental species of the genus *Stephanitis* Stål. Tegumentary structures used to identify the species are not always constant. Today, some genera remain unclearly defined, especially in tropical groups. Drake (with his many coauthors) is the single most prolific author of the group. Drake's latest works were illustrated with habitus views of various tingids, although only few of his works contain aids to identification.

For almost a century, the placement of Piesmatidae within Tingidae has been a case of argument. Tullgren (1918) recognized that Tingidae lacked abdominal trichobothria, whereas Piesmatidae possessed them, and Reuter (1910) classified Piesmatidae and Tingidae together in the superfamily Tingitoidea. Finally, Leston et al. (1954) and Drake and Davis (1960) have clearly shown that these two families are not closely related. Piesmatidae were consistently divorced from the Tingidae and placed in the infraorder Pentatomomorpha. Drake and Davis (1960) proposed the superfamily Miroidea Hahn, based on morphological structures from a global concept, to hold the families Tingidae Laporte and Miridae Hahn, and then systematized the Tingidae into the subfamilies Cantacaderinae Stål, Tinginae Laporte, and Vianaidinae Kormilev. This concept was followed in the catalog of Drake and Ruhoff (1965). Stys and Kerzhner (1975), following Scudder's (1959) conclusion, which was based on a study of the female genitalia of the Heteroptera, treated it as a superfamily including two families: Tingidae (with two subfamilies, Cantacaderinae and Tinginae) and Vianaididae. Owing to its distinct general facies and unique characters, the Vianaidinae were treated as a family by Kormilev (1955) in its original description and later by Scudder (1959), Carayon (1962), and Stys and Kerzhner (1975). Schuh and Stys (1991) and Schuh and Slater (1995) followed Drake and Davis (1960) and Drake and Ruhoff (1965) and treated this taxon as a subfamily of the Tingidae.

On the basis of the first phylogenetic analysis of the Tingidae, Lis (1999) raised the subfamilies Cantacaderinae sensu Drake & Davis and Tinginae sensu Drake & Davis into families: the Cantacaderinae and the Tingidae grouped into the superfamily Tingoidea together with the Vianaididae. Cantacaderinae was divided into two subfamilies, Cantacaderinae and Carldrakeaninae, whereas Phatnomatini sensu Drake & Davis was raised as a subfamily and transferred into the newly raised Tingidae, together with the Tinginae (Tingidae sensu Drake & Davis). In a different phylogenetic analysis, Guilbert (2001) found the Cantacaderinae monophyletic but included into the Tinginae. In a third phylogenetic analysis, including larval characters, Guilbert (2004b) retrieved Cantacaderinae sensu Drake & Davis and Tinginae sensu Drake & Davis. Schuh et al. (2006), on the basis of Lis' study, presented evidences to justify the placement of Vianaidinae as a sister group of Tinginae + Cantacaderinae. Guilbert (2012) validated the groups within Cantacaderinae proposed by Lis (1999), but showed a different relationship within these groups. Guilbert et al. (2014) presented a phylogenetic hypothesis based upon molecular and morphological characters in which Vianaidinae is included in Tingidae, as a sister group of Cantacaderinae + Tinginae, with the Phatnomatini included in Tinginae. In the same contribution, the phylogenetic status of the Tinginae tribes is discussed (Guilbert et al. 2014), as they were in previous contributions (Guilbert 2001, 2004b).

14.5 Economic Importance

14.5.1 Main Genera/Species

***Amblystira* Stål**

This American genus is constituted by 20 species, most of them distributed in the Neotropics. The only member of the genus that has been recorded as a pest is *A. machalana* Van Duzee. It is commonly known as “black lace bug” and feeds on cassava, *Manihot esculenta* Crantz, an important crop of South America. Arias and Belloti (2003) studied the life cycle, behavior, and damage caused by *A. machalana* on cassava. This species is distributed in Venezuela, Colombia, Ecuador, and Peru (Arias and Belloti 2003; Drake and Ruhoff 1965). The only key to species available for the genus is restricted to the South American *Amblystira* (Montemayor 2010a).

***Acanthocheila* Stål**

This is a genus originally constituted by 16 species. Froeschner (1995) reviewed the genus and synonymized some of its species and presented a key to identify them. Currently, it is constituted by seven species distributed in the entire continent, though most of them are known from South and Central America. *Acanthocheila armigera* (Stål) is frequently mentioned because it causes damages in plants of the genera *Nicotiana*, *Ouratea*, and *Pisonia* (Stonedahl et al. 1992; Neal and Schaeffer 2000). It is known from the USA, Mexico, Guatemala, Cuba, El Salvador, Honduras, Haiti, Costa Rica, Panama, Puerto Rico, Trinidad, Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, and Argentina (Froeschner 1995).

***Carvalhotingis* Froeschner**

Froeschner (1995) described this Neotropical genus to accommodate five species originally described as *Acanthocheila*, and, in this same contribution, he provides a key to species. The two species with economic importance are *C. visenda* (Drake & Hambleton) and *C. hollandi* (Drake). *Carvalhotingis visenda* was the first biological control agent approved for release against cat’s claw creeper *Macfadyena unguis-cati* (L.) (Bignoniaceae) in Australia (Dhileepan et al. 2010), and it has also been released in South Africa (King et al. 2011). Cat’s claw creeper, a climbing woody vine, is native from Mexico through Central America to tropical South America including Trinidad and Tobago. In Australia, cat’s claw creeper is a major environmental weed in coastal Queensland and New South Wales, where it is a major threat to biodiversity in riparian and rain forest communities (Dhileepan et al. 2007). *Carvalhotingis visenda* was originally distributed in Brazil, Peru, and

Argentina. *Carvalhotingis hollandi* (Drake), which is also being used as a biological control agent of *Macfadyena unguis-cati* in South Africa (King et al. 2011), was originally distributed in Brazil, Paraguay, and Argentina.

Corythaica Stål

This is an American genus comprised of 21 species, 14 of which are distributed in the Neotropical Region. Hurd (1945) made a comprehensive review of the genus that includes a key to species, redescriptions of all the species known at that moment, and drawings of them. Montemayor and Melo (2012) made a review of the Argentinean *Corythaica* where they describe new species, provide a key to the Argentinean *Corythaica*, and raised from synonymy *C. passiflorae* (Berg). *Corythaica cyathicollis* Costa is frequently mentioned in the literature as a major pest for several solanaceous crops (Kogan 1960; Neal and Schaefer 2000; Stonedahl et al. 1992). Montemayor and Melo (2012) discussed the identity of *C. cyathicollis* Costa and mentioned that probably almost all the citations of *C. cyathicollis* in the literature do not refer to Costa's species and most likely pertain to *C. monacha* (Stål) or *C. passiflorae* (Montemayor & Melo 2012). Because of this identity confusion, the distribution and host plants of these three species must be reevaluated (Montemayor and Melo 2012).

Corythucha Stål

This is a large genus with more than 75 species. It is widely distributed in the Americas, and it has also been accidentally introduced into Europe and Asia. The great majority of its species are from North America (Montemayor 2009). Despite the number of species in this genus, there is a remarkable uniformity among them. One striking feature of the host plants of this genus is that a large number of trees are included, in contrast to the herbaceous plants which predominate as hosts for the majority of tingids (Hurd 1946). Gibson (1918) made a review of the genus in which he described several species and provided a key to 56 species (among them *C. gossypii* F. and *C. ciliata* Say known from the Neotropical Region and with economic importance); this is the last comprehensive study of the genus. *Corythucha gossypii* is a serious pest of beans and cotton, hence the common name "cotton or bean lace bug." However, it has been reported in another 24 host plants including castor bean (*Ricinus communis* L.) (Herney-Varón et al. 2010) and sunflower (*Helianthus annuus* L.). Cotton lace bug damage can be observed on the plant's foliage, ranging from some leaf stippling from considerable yellowing to bleaching. This can reduce plant vigor, and as a consequence, fruit production can be affected or even prevent fruit from forming when infestations are heavy (Miller and Nagamine 2005). All immature stages of this species are described and illustrated by Lopez-Montes et al. (1982). It is known from almost all the New World. *Corythucha ciliata*, commonly known as the sycamore bug, is a pest of the popular ornamental tree *Platanus* *occidentalis* L., sycamore, and of its hybrids. These trees are frequently used as street-side trees in urban areas. In cases of severe infestations, host trees have been observed defoliated in late summer. Several consecutive years of severe *C. ciliata* damage, combined with other stress factors, may kill the trees. It is suspected that *C. ciliata* may serve as vector of two fungi, *Ceratocystis fimbriata* Hell. et Halsted forma *specialis platani* Walter and *Apiognomonia* (= *Gnomonia*) *veneta* (Sacc. and Speg) (Ruiting et al. 2009). It is believed that the pest came from North America, from where it has spread throughout Europe and parts of Asia (Õszi et al. 2005). In the Neotropical Region, it has been only reported for Chile (Prado 1990).

Dictyla Stål

This genus is constituted by over 60 species distributed worldwide. There are 17 known species from America and 13 from the Neotropical Region. Brailovsky and Torres (1986) provided a redescription of the genus and mentioned its possible Neotropical origin. The most mentioned species in the literature is *D. monotropidia* (Stål), a Neotropical species that has been frequently reported on *Cordia* spp. (Drake and Ruhoff 1965) as well as on cotton in Argentina (Fenton 1934) and on orchids from Mexico to the boarder of Texas (Swezey 1945; Drake and Ruhoff 1965; Neal and Schaefer 2000). The feeding activities of this insect damage the leaves that fall prematurely causing low flowering and fruiting and a developmental delay of the plants (Arguedas and Fallas 1993). There are some studies about the biology of the species (e.g., Fallas et al. 1993; Martínez et al. 2012). *Dictyla monotropidia* is known from Mexico, Cuba, Costa Rica, El Salvador, Guatemala, Haiti, Honduras, Jamaica, Panama, Puerto Rico, Trinidad, Venezuela, Colombia, Peru, Brazil, Bolivia, Paraguay, and Argentina. Up to now, the known host plants are *Cordia alliodora* (Ruiz & Pav.) Cham., *C. curassavica* (Jacq.) Roem. & Schult., *C. gerascanthus* L., *C. tomentosa* Cham. & Schltdl., *C. trichotoma* (Vell.) Arráb. ex Steud, and *Gossypium* sp. Guilbert and Montemayor (2010) provided a description and illustrations of the fifth instar as well as some comments on the fourth and third instars. There is no key to recognize the species of *Dictyla*, and because of the great number of species that constitute it and its morphological diversity, it is not easy to properly identify them.

Gargaphia Stål

This is a large American genus constituted by over 50 species, most of them distributed in the Neotropical Region. The interrupted rostral channel at meso-metasternal suture with transverse laminae converging medially is a diagnostic character of the genus. It includes several species which are economically important as plant feeders. Drake (1917) developed a key for the Nearctic species of *Gargaphia*. Some years later, Gibson (1919a) made a review of the genus when it was constituted by 25 species and provided a key to 16 of them (none of the Neotropical species with economic importance were included), and this was the last comprehensive study of the genus. The Neotropical species most mentioned as pests are *G. lunulata* (Mayr), *G. sanchezi* Froeschner, and *G. torresi* Costa Lima. *Gargaphia lunulata* feeds on many important South American plants from several families: Euphorbiaceae (*Euphorbia* sp., *Manihot* sp., *Ricinus* sp.), Leguminosae [*Cassia* sp., *Glycine max* (L.), *Phaseolus* spp.], and Malvaceae (*Gossypium* sp., *Hibiscus* sp., and *Urena* sp.) (Stonedahl et al. 1992; Neal and Schaefer 2000). It is also a pest of *Passiflora caerulea* L., a climbing plant with ornamental, medic, and alimentary interest (Ajmat et al. 2003). It is distributed in Colombia, Brazil, Paraguay, Argentina, and Uruguay. *Gargaphia sanchezi* is known from Colombia and attacks beans, *Phaseolus vulgaris* L. The biology of this species was studied by Schoonhoven et al. (1975), and usually the populations of *G. sanchezi* are very high, causing great damage on the plants. Finally, *G. torresi* feeds on several economically important plants such as cotton, sweet potato, bean, corn, and sunflower as well as other plants (*Canavalia* sp., *Gossypium* sp., *Ipomoea* sp., *Helianthus* sp., *Hibiscus* sp., *Parthenium* sp., *Phaseolus*, *Sida* sp., *Triumfetta* sp., *Xanthium* sp., and *Zea* sp.). It has some natural enemies such as *Xylocoris* sp. (Hemiptera: Anthocoridae), *Franklinothrips* sp. (Thysanoptera: Aeolothripidae), and *Bochartia* sp. (Acari: Erythraeidae) (Silva and Barbosa 1986). *Gargaphia torresi* is known from Brazil, Bolivia, Paraguay, and Argentina. The two most important studies that have been performed on the biology of *G. torresi* are related to the effects of temperature on their development, fecundity, and longevity (Domingues-da-Silva 2004) and to different aspects of its life cycle (Arce-de-Hamity et al. 2006).

***Leptobyrsa* Stål**

This genus was described by Stål for *Tingis steini* Stål, and later Champion (1897) redefined the genus to include five more Central American species. Since Champion's modification, 11 more species were added. Drake and Poor (1937) reviewed the genus, and from the 17 species that constituted the genus, only eight were left, all of them Neotropical. Unfortunately, there is no key for the genus. Among the *Leptobyrsa* spp., *L. decora* Drake has importance as a control agent of the weed *Lantana camara* L. to which it causes severe defoliation (Day and Zalucki 2009). Harley and Kassulke (1971) studied the life history of this species as a potential biological control agent of *L. camara*. Melksham (1984) compared the oviposition and maternal care of two populations from Colombia and Peru, and Thomas and Ellison (2000) listed the countries where *L. decora* has been released as a biocontrol agent. This species was described by Drake from Colombia and Ecuador, and later it was reported from Peru (Harley and Kassulke 1971) and the Galapagos Islands (Henry and Wilson 2004). *Leptobyrsa decora* has been introduced widely around the world, including Australia, the Cook Islands, Fiji, Guam, Ghana, Hawaii, Palau, South Africa, and Zambia, to help control *Lantana camara* L. (Thomas and Ellison 2000; Henry and Wilson 2004). A photograph of this species is also available in Henry and Wilson (2004).

Leptocysta Stål

This genus was erected to accommodate *L. sexnebulosa* (Stål), first described in the genus *Tingis*. Currently, the genus includes six species, all distributed in South America. Monte (1946) provided the first key for the genus, when it was constituted by three species, and excellent drawings of these species. Several years later, Montemayor (2010b) provided another revision of the genus with the description of new species and a key to all the currently known species. The only species mentioned feeding on economically important plants is *L. sexnebulosa* (Stonedahl et al. 1992), and the host plants are *Antennaria* sp., *Ipomoea batatas*, *Mikania* sp., and *Parthenium*, and *Vernonia* sp. *Leptocysta sexnebulosa* is distributed in Venezuela, Colombia, Peru, Brazil, Paraguay, and Argentina (Montemayor 2010b). For the remaining species of the genus, there are no records of host plants.

Leptodictya Stål

This genus is confined to the Americas; it is constituted by more than 50 species, most of them distributed in the Neotropical Region. The *Leptodictya* mentioned as pest is *L. tabida* (Herrich-Schaeffer), commonly known as the sugarcane lace bug because it feeds on sugarcane (*Saccharum* spp. hybrids) as well as other species of Poaceae (Setamou et al. 2005). High populations of *L. tabida* reduce plant vigor, cause leaves to senesce prematurely, and reduce the total area of photosynthesis (Neal and Schaefer 2000). It is known from the USA (Florida, Hawaii, and Texas), Mexico, Cuba, Costa Rica, El Salvador, Guatemala, Nicaragua, Panama, and Venezuela (Chang 1986). This author provided a good review with respect to the life cycle, bionomics, damage, and control along with a morphological description of adults and nymphs of *L. tabida*.

Leptopharsa Stål

This is a very large and diverse genus highly variable in its morphology. Through the years, several genera have been described on the base of species originally described as *Leptopharsa*. It is constituted by over 100 species, most of them from America, except for four African ones and two Australian ones. Most of its members are distributed in the Neotropical Region. There are two Neotropical species well known for their economic importance: *L. gibbicarina* Froeschner and *L. heveae* Drake & Poor. Adults and nymphs of *L. gibbicarina* cause important yield losses in the crops of the African oil palm (*Elaeis guineensis* Jacquin). The lesions caused by the feeding activities of this tingid allow the infestation of the plant by a fungi complex that causes a severe disease called *Pestalotiopsis* or gray leaf blight (Escalante et al. 2010). *Leptopharsa gibbicarina* is distributed in Colombia. The original description (Froeschner 1976) provides very good drawings of the species. The rubber tree lace bug, *L. heveae*, is known from Brazil, and it was described as a pest of *Hevea brasiliensis* Muell. Arg. known as the Pará rubber tree, sharinga tree, or, most commonly, the rubber tree. This tree is of major economic importance because the milky latex extracted from it is the primary source of natural rubber. *Leptopharsa heveae* occurs in high populations in rubber tree plantations, and it is a limiting factor in rubber production due to the loss of photosynthetic tissue (Santos and De-Freitas 2008). The control of the pest has been made mainly with chemical products, which cause environmental contamination. The alternative would be the use of biological control agents; however, information about *L. heveae* natural enemies is scarce. The entomopathogenic fungus Sporothrix insectorum (Hoog & Evans) (Neal and Schaeffer 2000) and the parasitoid *Erythmelus tingitiphagus* (Soares) have been found naturally on eggs of the rubber tree lace bug (Santos and De-Freitas 2008).

***Pleseobyrsa* Drake & Poor**

This is a genus that belongs to the tribe Tingini and was erected to place four species, three previously assigned to the genus *Leptobyrsa* Stål and a new species. After the description of *Pleseobyrsa*, five other species were described for the genus. Until 1969, *Pleseobyrsa* was constituted by nine species, but Froeschner (1969) described a new genus belonging to the tribe Litadeini Drake and Ruhoff, *Stragulotingis*, to place two *Pleseobyrsa* species. In a later publication, Froeschner transferred two other species from *Pleseobyrsa* to *Stragulotingis*, described a new *Pleseobyrsa*, and provided a key to the species of both genera (Froeschner 1991). Some years later, another *Pleseobyrsa* was described, and in this contribution, an updated key to the species of *Pleseobyrsa* was provided as well as illustrations and photographs of adult and fifth nymph of *P. persea* (Montemayor et al. 2011). The genus includes currently seven species, and three feed on avocado tree, causing damage: *P. boliviana* (Drake & Poor), *P. chiriquensis* (Champion), and *P. persea. Pleseobyrsa boliviana* is known from Bolivia; *P. chiriquensis* from Costa Rica, Panama, Venezuela, and Colombia; and *P. persea* from Costa Rica.

***Pseudacysta* Blatchley**

This genus only includes *P. perseae* (Heidemann), first described as *Acysta* Champion, and is commonly known as the avocado bug. As its vernacular name indicates, it is harmful for *Persea americana* P. Miller (avocado). *Pseudacysta persea* destroys leaf cells (Moznette 1922) and causes chlorosis and browning (Medina-Gaud et al. 1991). Other host plants mentioned in the literature are *Comphora officinalis*, *Persea carolinensis*, and *Persea gratissima* (Heidemann 1908). In the original description of the species, egg and nymphs were also described, and drawings of the adult, fifth nymphal instar, and eggs were provided. Hurd (1946) redescribed the genus and discussed some other aspects such as resemblance with *Acysta* and distribution. The known distribution of *P. perseae* includes the USA, Mexico, Cuba, Dominican Republic, Guatemala, Jamaica, Puerto Rico, St. Lucia, St. Thomas, St. John, St. Croix, French Guiana, and Venezuela (Humeres et al. 2009).

Stephanitis Stål

This is a large genus constituted by around 60 species. Hórvath (1912) divided it into four subgenera: *Stephanitis* Stål, *Menodora* Hórvath, *Norba* Hórvath, and *Omoplax* Hórvath; only the first one is present in America (Hurd 1946). One of the species with economic importance is *S. pyrioides* (Scott), an important pest of azaleas (*Rhododendron* spp.). The azalea lace bug has become of increasing importance as azaleas have been more and more popular as ornamentals. Its origin is thought to be Japan, from where it was first described, and it has been accidentally introduced in several countries. The azalea lace bug is considered one of the most important problems affecting azaleas since its introduction (Shakunthala and Braman 2012). Illustrations of *S. pyrioides* are available at Dickerson and Weiss (1917), Weiss and Headlee (1918), Shen et al. (1985), and Gomez-Menor (1954). Shakunthala and Braman (2012) provided an excellent review of all the information available related to the azalea lace bug.

Teleonemia Costa

Teleonemia Costa is a taxonomically complex genus with a high interspecific variation. It is constituted by over 80 species distributed worldwide. *Teleonemia elata* Drake, *T. harleyi* Froeschner, *T. prolixa* (Stål), and *T. scrupulosa* Stål are Neotropical important species because they feed on *Lantana camara* (Winder & Harley 1983) and therefore have been used for the biocontrol of this weed which is considered to be among the world's ten worst invasive weeds. *Teleonemia elata* has been released in Australia, Cook Islands, South Africa, Uganda, and Zambia; *T. harleyi* and *T. prolixa* in Australia; and *T. scrupulosa* in Ascension Island, Australia, Fiji, Ghana, Guam, Hawaii, India, Indonesia, Kenya, Madagascar, Micronesia, New Caledonia, Niue, Northern Mariana Islands, Palau, Papua New Guinea, Samoa, Solomon Islands, South Africa, St. Helena, Tanzania, Tonga, Uganda, Vanuatu, Zambia, Zanzibar, and Zimbabwe (Thomas and Ellison 2000). Photographs of adults and nymphs of *T. elata* as well as comments on the species are provided by Harley and Kassulke (1971). The original distribution of this species is Brazil, Chile, Paraguay, and Peru (Drake and Ruhoff 1965). Harley and Kassulke (1973) provided SEM photographs of adults, fifth instar, and egg of *T. harleyi*. This species is distributed in Trinidad. *Teleonemia prolixa* has not only been considered for the biological control of *L. lantana* but also for *Mikania micrantha* Kunth, a Neotropical vine that is causing great damage to crops of tea, teak, rubber, oil palm, and coconut in Southeast Asia (Cock 1982). It is distributed in the Neotropical Region in Guatemala, Jamaica, Panama, Surinam, Trinidad and Tobago, British Guiana, Venezuela, Colombia, Ecuador, Peru, Brazil, Bolivia, Paraguay, and Argentina. *Teleonemia scrupulosa* eggs, nymphs, and adults are described and illustrated by Roonwal (1952), and more recently, SEM photographs and redescriptions of the nymphs were provided (Guidoti and Barcellos 2013). It is distributed in the Neotropical Region in the following countries: Cuba, Costa Rica, Guatemala, Haiti, Jamaica, Netherlands Antilles (Aruba, Curacao, Klein Bonaire, Bonaire), Panama, Trinidad, Windward Islands (Grenada, St. Vincent), French Guiana, British Guiana, Venezuela, Peru, Brazil, Colombia, and Paraguay.

Vatiga Drake & Hambleton

The species of the genus *Vatiga* are native to the Neotropics and exhibit a decided preference for plants of the genus *Manihot* Miller, mainly *Manihot esculenta* Crantz, commonly known as cassava and one of the most important crops in Africa, Central and South America, and Asia. Froeschner (1993) reviewed the genus, provided a key to species, synonymized some species, and elevated to species status a subspecies, so as a result of Froeschner's study, the genus is currently constituted by five species. *Vatiga illudens* (Drake) is one of the species most frequently mentioned in the literature and also most frequently misidentified. It is mentioned from Brazil, Colombia, Cuba, Dominican Republic, Ecuador, Guyana, Haiti, Jamaica, Lesser Antilles, Puerto Rico, Reunion Island, Trinidad and Tobago, USA, and Venezuela. Oliveira et al. (2001) studied the biology of this species in experimental conditions, and Fialho et al. (2009) evaluated the economic damage caused in cassava root and foliage yield. *Vatiga manihotae* (Drake) is the second most mentioned species, and it is also the most widely distributed. According to Froeschner (1993), it is known from Cuba, Trinidad, Venezuela, Colombia, Peru, Brazil, Paraguay, and Argentina. The other species of the genus have more restricted distributions, such as *V. cassiae* (Drake & Hambleton), only known from Brazil; *V. pauxilla* (Drake & Poor), from Argentina; and *V. varianta* (Drake), restricted to Brazil and Colombia.

Phatnoma Fieber

This genus occurs in several geographic regions of the world. Most of the 27 species of the genus are similar in structure and intraspecific variability and therefore are difficult to separate (Froeschner 1996). For this genus, only a very outdated partial key exists (Gibson 1919b). *Phatnoma* is distributed in South and Central America, Africa, Asia, and Oceania. For the Neotropics, the species that has been reported feeding on plants with economic importance is *P. marmorata* Champion. It feeds on cacao and pineapple, and it is distributed in Costa Rica, Honduras, Panama, Trinidad, Brazil, and Ecuador. Its fifth nymph has been described by Guilbert (2005); however, very little is known about its biology.

14.5.2 Key to the Most Economically Important Neotropical Genera

The key below is valid for the genera of economic importance, and it may lead to erroneous results if used for other genera.

1. Seven cephalic spines, anterolateral paranotal angle projecting as a distinct angle or spiniform process..*Phatnoma* Fieber
– Less than seven cephalic spines, paranota otherwise... 2
2. Hood absent or scarcely developed.. 3
– Hood well developed 10
3. Radio-cubitus vein "C" shaped, paranota folded over pronotum .... *Dictyla* Stål
– Radio-cubitus vein not "C" shaped, paranota not folded over pronotum 4
4. Paranota lacking or poorly developed... 5
– Paranota well developed 6
5. None or two rudimentary cephalic spines present (occipital pair), paranota represented by a small pale earlike appendage at each lateral angle, discoidal area not closed behind ....*Pseudacysta* Blatchley
– Two cephalic spines present (occipital pair), paranota absent or very slender carina like, discoidal area closed behind .... *Amblystira* Stål
6. Paranota projected forward, much broader anteriorly.. ....*Pleseobyrsa* Drake & Poor
– Paranota not projected forward, same width in all its length or posteriorly broader 7
7. Paranota armed with spines, lateral carinae absent or only posteriorly developed 8
– Paranota without spines, lateral carinae fully developed..................................... 9
8. Without occipital spines, paranota armed with 7–10 long, stout spines.. *Carvalhotingis* Froeschner
– With occipital spines, paranota armed with 5–10 long, stout spines..*Acanthocheila* Stål
9. Generally five cephalic spines (sometimes less), elytra broadening from base, discoidal area not surpassing middle of hemelytra.....................*Leptopharsa* Stål
– Between two and five cephalic spines; elytra elongated, parallel margined; discoidal area generally surpassing middle of hemelytra ....*Teleonemia* Costa
10. Hood not surpassing length of head.. 11
– Hood surpassing length of head... 14
11. Mesosternal rostral laminae deeply constricted at mesosternum........................ ....*Vatiga* Drake & Hambleton
– Mesosternal rostral laminae subparallel.. 12
12. Rostral channel interrupted at meso-metasternal suture by the metasternal laminae that converge and contact to each other.........................*Gargaphia* Stål
– Rostral channel not interrupted at meso-metasternal suture 13
13. Hood tectiform shaped, paranota folded over pronotum, posterior process fully developed, elytra and paranota..*Leptodictya* Stål
– Hood globose or subglobose, paranota not folded, projected forward in front, posterior process abbreviated, elytra and paranota armed with hairs and/or spines ....*Leptobyrsa* Stål
14. Paranota not projected forward.. 15
– Paranota projected forward 16

15. Hood gradually narrowing toward apex, tip surpassing antennal segment I; paranota with basal folds wider at the callus .... *Corythaica* Stål
– Hood tectiform, not surpassing antennal segment I; paranota without basal fold, produced evenly ....*Leptopharsa* Stål
16. Hood compress, slightly wider backwards, narrow through all its length; discoidal area not raised, surpassing middle of hemelytra ....*Leptocysta* Stål
– Hood globose or subglobose, much wider backwards, narrower anteriorly; discoidal area raised, not surpassing middle of hemelytra 17
17. Hemelytra rectangular shaped abruptly widened at base, broadest anteriorly, margins parallel or slightly concave .... *Corythucha* Stål
– Hemelytra gradually widening toward apex, broadest apically, margins rounded .... *Stephanitis* Stål

14.6 Concluding Remarks

Tingidae are exclusive plant feeders and usually monophagous, features that make them particularly interesting from an economical point of view. However, there is a noticeable lack of information about this group of insects. The economic importance of lace bugs will continue increasing as species emigrate (e.g., as concealed eggs) and as minor crops gain importance and expand to serve a burgeoning world population (Neal and Schaefer 2000).

Among the Neotropical lace bugs are some potential pests for different economically important crops, though usually only large populations cause serious damage. It is not easy to control and manage lace bug populations because of their different reproductive strategies (e.g., oviposition strategies), the annual number of generations, and the habit of living in the underside of the leaf. The ecology and behavior of most of the species remain unknown, and the knowledge of these different aspects of their biology is fundamental for the establishment of management strategies of their populations. Another little known aspect of these complex insects is their chemical communication, which seems to play an important role in intraspecific interactions, particularly between females and offspring. Predator and parasitoid information are scarce, and it could be useful when establishing control strategies for Tingidae populations.

The taxonomy of Tingidae is mostly based on external morphological characters which exhibit a high diversity of shapes. As such, relationships within Tingidae subfamilies and tribes are far from known. Suprageneric taxa have been currently discussed without highly supported hypothesis proposed so far. Immature forms seem to present very important characters that should be more explored in a taxonomic and phylogenetic framework. Morphological studies on unexplored structures could reveal important source of information. The tingid taxonomy and systematics are still in need of further studies to improve our knowledge on biological, ecological, ethological, and evolutionary questions.

Behavior and ecological parameters are the keys to understand economic problems raised by tingid species. As such, they will help provide the adequate solution. Considering that this chapter focused on Neotropical tingids, a more comprehensive work should be done since the last worldwide contribution was published 13 years ago (Neal and Schaeffer 2000).

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