Zootaxa 4136 (2): 247–308
http://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://doi.org/10.11646/zootaxa.4136.2.2
http://zoobank.org/urn:lsid:zoobank.org:pub:51AD5A69-203A-411F-B948-A718B54DCCE4

Morphology of the immature female stages and the wax test of ten species of *Ceroplastes* (Hemiptera: Coccomorpha: Coccidae: Ceroplastinae) from Brazil

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Abstract

This paper describes the development of the waxy test and the microscopic characters of the three female nymphal instars of *Ceroplastes cirripediformis* Comstock, *C. diospyros* Hempel, *C. floridensis* Comstock, *C. flosculoides* Matile-Ferrero, *C. formicarius* Hempel, *C. formosus* Hempel, *C. grandis* Hempel, *C. iheringi* Cockerell, *C. lucidus* Hempel, and *C. stellifer* (Westwood). The discussion compares their morphology and divides the species into three groups according to the pattern of their dermal and wax characters.

Key words: wax scale, soft scale, taxonomy, morphology, female nymphs

Introduction

Scale insects are sap-sucking and some species are considered to be serious economic pests, mainly attacking agricultural and horticultural crops, forestry and ornamental plants. The females are the main cause of damage due to their ability to build up large populations on a plant, thus removing copious amounts of sap. Species in the subfamily Ceroplastinae Atkinson (Hemiptera: Sternorrhyncha: Coccomorpha: Coccidae) are known popularly as the wax scales because the adult females have a thick waxy test that covers the whole of the dorsum. This waxy test is usually divided into plates and these differ in shape, colour, texture and size, according to species (Hodgson & Peronti 2012).

The Ceroplastinae is the second largest subfamily within the Coccidae with 155 species described worldwide (García *et al*. 2016). The geographic regions with the greatest number of species are the Neotropical and Afrotropical regions, with 77 and 58 species respectively, with most species endemic to these regions (García *et al*. 2016).

According to the review by Qin and Gullan (1995), ten genera of wax scales have been proposed since 1828: namely *Baccacoccus* Brain, *Ceroplastes* Gray, *Ceroplastidia* Cockerell, *Ceroplastina* Cockerell, *Cerostegia* De Lotto, *Columnea* Targioni Tozzetti, *Gascardia* Targioni Tozzetti, *Paracerostegia* Tang, *Vinsonia* Signoret and *Waxiella* De Lotto. All, except *Waxiella*, are currently considered to be synonyms of *Ceroplastes*. Qin and Gullan (loc. cit.) undertook a cladistic study based on the morphology of the adult female of 84 species and found that the wax scale insects formed a monophyletic group and that, of the analysed genera, only species in *Waxiella* formed a distinct clade. However, as this clade was supported by only one synapomorphy, they suggested that this group should be considered a species-group and not a genus.

In their review of Ceroplastinae species that occur in the state of São Paulo, Brazil, Peronti *et al*. (2008)

Accepted by D. Ouvrard: 31 Mar. 2016; published: 6 Jul. 2016

synonymized *Vinsonia* with *Ceroplastes* and included all of the 31 species known from this region in the genus *Ceroplastes*. However, the authors observed variations in both macroscopic and microscopic characters that suggested new species-groupings. More recently, Hodgson and Peronti (2012), in their review of the wax scale species known from the Afrotropical region, considered that only *Ceroplastes* and *Waxiella* were valid genera but, nonetheless, they divided the 58 species studied into 19 species-groups based on adult female morphology.

Several phylogenetic studies based on morphological characters of scale insects have now been undertaken, almost all using only the morphological characters of the adult female (Qin & Gullan 1995; Kozár & Miller 2000; Stumpf & Lambdin 2002; Vea & Grimaldi 2012). However, Howell and Tippins (1990) considered that, for a complete understanding of the phylogeny of any group of organisms, characters of all life stages needed to be included in the analysis. Stoetzel and Davidson (1974) studied immature Aspidiotini (Diaspididae) and demonstrated that the morphological characters of these stages were useful in establishing the correct generic placement of the species studied.

Although coccidologists have recently begun describing the nymphal stages of scale insects, these have mainly been to complement systematic studies and to identify vulnerable stages for chemical and biological control. Studies based entirely on the immature stages are scarce, including those of the Ceroplastinae. Microscopically, Kawai and Tamaki (1967) described the female nymphs of *C. pseudoceriferus* Green and Amitai (1969) the female nymphs of *C. floridensis* Comstock; Camporese and Pellizzari (1994) described the immature female stages of *C. japonicus* and Qin and Gullan (1994) described all female stages plus the second- and third-instar males of *C. sinensis* Del Guercio; Marín-Loayza and Cisneros-Vera (1994) described the female nymphs of *C. floridensis* and *C. cirripediformis* Comstock, whilst Wakgari and Giliomee (1998) described all female stages of *C. destructor* Newstead; Rainato and Pellizzari (2008) described the male stages of *C. japonicus* Green, and Pellizzari *et al.* (2010) and Rainato and Pellizzari (2010) described the female and male nymphal instars respectively of *C. rusci* (Linnaeus).

Rosa *et al.* (2011) described the microscopic and macroscopic characters of immature female stages of *Ceroplastes janeirensis* (Gray), a species known only from the Neotropics. These authors found that *C. janeirensis* produced a unique pattern of wax in the first instar which differed from that described for the same stage of other species from other zoogeographic regions (e.g., Silvestri & Martelli 1908; Silvestri 1920; Cilliers 1967; Kawai & Tamaki 1967; Bedford 1968; Xie & Xue 2005).

The ultra-morphology and chemical composition of waxes secreted by *C. ceriferus* (Fabricius) and *C. japonicus* were studied by Xie and Xue (2005), who found that both species have a similar waxy secretion and wax-test forming process. Xie *et al*. (2004) also concluded that three species of *Ceroplastes* (*C*. *japonicus*, *C. rubens* Maskell and *C. ceriferus*) were more similar taxonomically based on their wax secretions than they were to the soft scale insect *Dicyphococcus bigibbus* Borchsenius, showing the significance of wax secretions in the systematics of Coccidae. Rosa *et al*. (2011) suggested that the arrangement of the wax forming the test of *C. janeirensis* may indicate that the structure and timing of wax secretion in each nymphal instar of Ceroplastinae could be important in their classification.

This study describes the development and structure of the waxy test and the microscopic morphology of all three female nymphal stages of ten species of *Ceroplastes* from São Paulo State, Brazil.

Materials and methods

Ten species of the *Ceroplastes* that occur in the State of São Paulo were studied, namely *Ceroplastes cirripediformis*; *C. diospyros* Hempel; *C. floridensis*; *C. flosculoides* Matile-Ferrero; *C. formicarius* Hempel; *C. formosus* Hempel; *C. grandis* Hempel; *C. iheringi* Cockerell; *C. lucidus* Hempel and *C. stellifer* (Westwood).

Ovipositing females of seven species, namely *C. cirripediformis*, *C. diospyros*, *C. floridensis*, *C. flosculoides*, *C. formosus*, *C. grandis* and *C. stellifer* were collected between March 2009 and March 2010 and in December 2013. Each species was placed in a glass tube, closed with cotton wool until the birth of the nymphs. So as to obtain all instars, crawlers were then placed on host plants cultivated in plant pots and maintained at room temperature in individual cages covered with muslin netting, in the entomology laboratory of the Department of Ecology and Evolutionary Biology (DEBE), Federal University of São Carlos, São Carlos, Brazil. The host plants used for rearing the insects were not always the same species as those on which they were collected in the field because some host plants were difficult to cultivate in the laboratory. The host plants are shown in Table 1.

TABLE 1. Data on the *Ceroplastes* species reared in the laboratory.

Name of species	Host plant: collected host/ Host on which reared	Collection site	World Distribution (Region) of wax scale
Ceroplastes cirripediformis	*Tabebuia* sp. (Bignoniaceae) / *Tabebuia* sp. (Bignoniaceae)	São Carlos-SP (22º00'S, 47º54'W)	Widespread
C. diospyros	*Diospyros kaki* (Ebenaceae) / *Punica granatum* (Lythraceae)	Itatiba-SP (23º00'S, 46º50'W)	Neotropical
C. floridensis	*Hedera canariensis* (Araliaceae) / *Schefflera arboricola* (Araliaceae)	São Paulo-SP (23º34'S, 46º40'W)	Widespread
C. flosculoides	*Psidium guajava* (Myrtaceae) / *Psidium guajava* (Myrtaceae);	São Carlos-SP (22º03'S, 47º48'W)	Neotropical
C. formosus	*Myrciaria cauliflora* (Myrtaceae) / *Myrciaria cauliflora* (Myrtaceae);	São Carlos-SP (22º00'S, 47º53'W)	Neotropical
C. grandis	*Duranta repens* var. *aurea* (Verbenaceae); / *Duranta repens* var. *aurea* (Verbenaceae);	São Carlos-SP (21º58'S, 47º52'W)	Neotropical
C. stellifer	*Schefflera arboricola* (Araliaceae) / *Schefflera arboricola* (Araliaceae)	Santos-SP (23º57'S, 46º19'W)	Widespread

Nymphs of the other three species, namely *Ceroplastes formicarius*, *C. iheringi* and *C. lucidus*, were collected directly in the field on their host plants (Table 2), because of difficulty growing any of their host plants in the laboratory.

Specimens of each stage were slide mounted according to procedures of Granara de Willink (1989). Five examples of each stage of each species were mounted on permanent slides and deposited in the DEBE.

For microscopic characterization of immature forms of the species studied, the following characters considered to be of taxonomic importance were studied. *Dorsal characters*: anal plate, clear areas, dorsal setae, loculate and simple dorsal microducts; *Marginal characters*: marginal setae, stigmatic setae and eyespots, and *Ventral characters*: spiracular disc-pores, filamentous ducts, inter-antennal setae, pregenital setae, antennae, clypeolabral shield, metathoracic legs, tarsal digitules, claw digitules and claw denticle. The morphological details for the first-, second- and third-instar nymphs are provided in tables 3, 4 and 5. The morphological terminology follows that of Kawai and Tamaki (1967), Bedford (1968), Rosa *et al*. (2011) and Hodgson and Peronti (2012). The measurements and frequencies are given as ranges.

TABLE 2. Data on the *Ceroplastes* species where the immature stages were collected in the field.

Name of specie	Plant Host: collected host	Place of collection	Distribution (Region)
C. formicarius	*Banisteriopsis oxyclada* (Malpighiaceae)	São Carlos-SP (21º58'S, 47º53'W)	Neotropical
C. iheringi	*Vernonia* sp. (Asteraceae)	Tambaú-SP (21º41'S, 47º18W)	Neotropical
C. lucidus	*Vernonia* sp. (Asteraceae)	Tambaú-SP (21º41'S, 47º18W)	Neotropical

Results

Female *Ceroplastes* develop through three nymphal instars, while the males develop through two nymphal instars plus a pre-pupal and a pupal stage. In our studies, males have only been observed for *C. flosculoides*, *C. formicarius*, *C. grandis* and *C. lucidus*.

After eclosion, the first-instar nymphs or crawlers are active and move in search of a place to settle on the host plant, especially along the leaf veins. Once settled, the nymphs tuck their antennae and legs underneath the body. Later, usually in the third instar, a further dispersal occurs from the leaves to the branches, although this can also occur in the second instar or early on in the adult stage.

Development of the wax test in immature female instars of *Ceroplastes* species

Initially, the crawlers are devoid of wax. However, once they have settled on their hosts, the dermal glands secrete a waxy test over the dorsal region of the body. On the basis of the different patterns of wax secretion by the first-instar nymphs, the ten *Ceroplastes* species were separated into 3 groups.

Group 1: species with the dorsum covered by a glassy test with dry-wax in a series of submarginal and medial waxy filaments. These filaments are probably secreted from primary wax pores, abundant in a dense group in the center of each clear area (Hodgson & Peronti, 2012). This is the most common pattern and has been described previously by Silvestri and Martelli (1908) for *C. rusci*; by Cilliers (1967) for *C. brevicauda* Hall, *C. destructor* and *C. mimosae* Signoret; Kawai and Tamaki (1967) for *C. pseudoceriferus*; Bedford (1968) for *C. sinoiae* Hall and Xie and Xue (2005) for *C. ceriferus* and *C. japonicus*. In the present study, this type of test has been observed on *C. cirripediformis*, *C. floridensis*, *C. formicarius*, *C. grandis* and *C. stellifer.*

Group 2: species with a similar glassy test but without either dry-wax filaments or lateral glassy expansions. This pattern has been described by Rosa *et al.* (2011) for *C. janeirensis* in Brazil and is the pattern observed here in *C. formosus* and *C. lucidus*.

Group 3: species with a similar glassy test to Group 2, i.e., without dry-wax filaments, but with submarginal and medial glassy projections. This pattern is reported here for the first time and has been observed in *C. diospyros*, *C. flosculoides* and *C. iheringi*. The species in this group secrete a wax test with characters intermediate between Groups 1 and 2.

Development of the wax test in Group 1 species

First instar-nymph test. First-instar nymphs secrete a thin, almost imperceptible glassy test which covers the entire dorsum, along with a series of white dry-wax filaments which are probably secreted from primary wax pores. Initially, a semicircle of dry wax is secreted between the eyes in the cephalic region, and then a series of dry-wax filaments appear in the middle of the dorsum forming a distinctive pattern. This pattern is specific for each species —i.e., a different "fingerprint" for each species (Fig. 1). After a few days, either 16 or 18 white waxy points appear around the submargin of the nymph: two anteriorly in the cephalic region between the eyes and 7 or 8 points along each margin. With further development, the dorsal and lateral filaments expand and some become fused, resulting in new patterns of dry-wax filaments (Fig. 2), as follows: two blocks appear on the dorsum, one on the thorax and the other on the abdominal region (except in *C. stellifer* which has only one block on the dorsum (Fig. 2F)); three further blocks appear anteriorly on the head (one medially and two laterally); 3 or 4 along each side of body, and a pair associated with each anal plate (i.e., 4 posteriorly). The stigmatic bands grow from the margin to the first and second pair of lateral filaments (Fig. 2B). Although *C. formicarius* is here included in the Group 1 (because it secretes dry-wax filaments), it differs from other members in this group in that the filaments are shorter and the glassy test is more evident (Fig. 2D).

Second-instar nymph test. After the first moult, the outward appearance of the second-instar nymph remains similar to that of the first-instar nymph (Fig. 3). As stated by Bedford (1968) for *C. sinoiae*, the cuticle splits around the outer margin during the moulting process and the ventral part of the exuviae is expelled but the dorsal part is retained (Fig. 3C). The dorsal exuviae split along predetermined lines between the dry-wax filaments so that, as the insect grows, the exuviae separate into 10 pieces, each piece related to the wax filaments. The dry-wax of the second-instar nymph is secreted below each part of the dorsal exuviae of the first-instar nymph. Each piece of the exuviae from first-instar nymphs form a partition line (Fig. 3C) between the dry-waxes of first- and second-instar nymphs, but these can be difficult to see in some species.

Third-instar nymph test. The second moult occurs as described previously for the first-instar nymph, i.e., the exuviae from the venter is shed but that of the dorsum is retained. The third-instar nymph secretes a wet wax around the dry-wax filaments (Fig. 4) and this becomes thicker and it can change colour as the insect matures (Fig 5). Thus, the dry-wax filaments are surrounded by wet wax so that the test is sometimes divided into nine wax plates each with a central nucleus with dry-wax filaments. The anterior nucleus on the head has three filaments, each lateral nucleus has one filament apart from the last pair which has one or two filaments; the caudal nucleus has two pairs of filaments, while the dorsal nucleus has one or two blocks of filaments. The stigmatic bands lie on top

of the wet wax but, where the stigmatic setae extend along much of the margin, as in *C. formicarius*, a white wax similar with that in the stigmatic band is produced around almost all the margin of the body, apparently secreted by the stigmatic setae (Fig. 5C). *Ceroplastes stellifer* is the only species in which the lateral dry-wax filaments are pushed out to the end of waxy arms, giving the insect the appearance of a star formed by seven rays, with the stigmatic bands growing beneath the first and the second lateral pair of rays (Fig. 5E).

Development of the wax test in Group 2 species

First-instar nymph test. The glassy test is thin, translucent, detachable and comes to cover the entire dorsum. The wax test shows a series of overlapping wax plates, with new larger plates being laid down underneath the old test as the insect enlarges, providing lines similar to growth rings around the body. The stigmatic bands are clearly visible on the wax test (Figs 6A, 6B).

Second-instar nymph test. As in Group 1, the ventral exuviae is discarded when moulting, and the dorsal exuviae remains under the test which does not split into plates. The new wax, secreted by the second-instar nymph, stays beneath the first-instar exuviae, so that the outward appearance of second-instar nymph remains similar to that of the first-instar nymph (Figs 7A, 7B).

Third-instar nymph test. The third-instar nymph initially secretes a wet wax that covers the entire dorsum, apart from areas of derm corresponding to the clear areas, which lack the wax-secreting microducts (Figs 8A, 8B). These clear areas correspond with the postero-lateral and anterior nuclei. As the third-instar nymph grows, it continues to secrete wet wax, so that the glassy wax test (formed by the first- and second-instar nymphs) comes to lie medially on the dorsum, forming the dorsomedial nucleus. The stigmatic bands are broader than on the first- and second-instar nymphs and are found on the wet wax (Figs 9A, 9B).

Development of the wax test in Group 3 species

First-instar nymph test. The first-instar nymphs secrete a thin, detachable glassy wax test similar to that formed by species in Group 2, including the presence of the "growth rings" formed by the secretion of larger plates as the insect grows. However, this group has marginal expansions of glassy wax in the same positions as the dry-wax lateral filaments of Group 1, although *C. flosculoides* and *C. iheringi* still produce expansions medially on the dorsum, each of a different shape, suggesting the beginnings of the dry-wax filaments in this position observed in Group 1 species (Figs 6C, 6D, 6E).

Second-instar nymph test. After the first moult, the second-instar nymph secretes a waxy test similar to that of the first-instar nymph (Figs 7C, 7D, 7E).

Third-instar nymph test. In the third instar, the test splits around the lateral expansions and the nymph starts to secrete wet wax (Figs 8C, 8D, 8E), so that the dorsal glassy test, formed by the previous instars, is displaced to the center of the dorsum, while the lateral expansions are surrounded by the wet wax (Figs 9C, 9E). In *C. flosculoides*, the wet wax is concentrated below the lateral expansions and in three regions between the dorsal test and the lateral expansions, one in the cephalic region and one in each of the latero-posterior regions on the abdomen (Fig. 9D). The stigmatic bands in *C. iheringi* develop in a similar manner to species in the Group 1, i.e., the stigmatic bands lie on top of the wet wax and are restricted to the stigmatic regions (Fig. 9E). However, in *C. flosculoides* and *C. diospyros*, the stigmatic bands are very long and extend laterally free from the test (Figs 9C, 9D).

Microscopic characters of the immature female instars

Key to immature female instars

1. Each stigmatic area with 3 stigmatic setae 2
- Each stigmatic area with more than 3 stigmatic setae. 3

2. Apical seta on each anal plate very long; with a pair of trilocular pores present on dorsum near margin on apex of head; with 2–5 spiracular disc-pores in each spiracular pore band, each with mainly 3 outer loculi (range 3–6); with only 1 pair of setae on anogenital fold. . . . . **first-instar nymph**
- Apical seta on each anal plate short; dorsal setae and pores absent; with 3–12 spiracular disc-pores in each spiracular pore band, each with mainly 5 outer loculi; with 2 pairs of setae on anogenital fold . . . . . **second-instar female**
3. Pregenital (multilocular) disc-pores absent. . . . . **third-instar female**
- Pregenital (multilocular) disc-pores present . . . . . **adult female**

First-instar nymphs (Table 3). Dorsum entirely membranous, with both setae and pores extremely scarce, small and difficult to see but with one pair of trilocular pores near apex of head and one pair of dorsal setae near to center of head (although this could not be detected on *C. formosus* and *C. iheringi*). Note: trilocular pores have also been observed on the dorsum of the first-instar nymphs of *C. rusci* (Pellizzari *et al*. 2010), *C. janeirensis* (Rosa *et al*. 2011), and many other species of Coccidae (Ray & Williams 1982; Hodges & Williams 2003a, 2003b; Kondo & Williams 2004; Kondo 2006), however these pores can also be found near the antennal scape in some species of Coccidae (Pellizzari 2013). Dorsal setae have not been observed previously on first-instar nymphal Ceroplastinae. Because setae and pores are scarce, the presence and position of clear areas could not be determined.

Anal plates very similar to those described by Hodgson and Peronti (2012) for adult Ceroplastinae. Each plate usually roughly triangular and a mirror-image of the other, each with a more or less diagonal anterior margin and rounded posterior margin, generally with 4 dorsal setae (apical seta very long) and 1 ventral seta. Anogenital fold with only 1 pair of setae.

Marginal setae flagellate, with 6–8 (mainly 6) anteriorly between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 laterally between stigmatic areas and 6–7 between posterior stigmatic area and anal lobe. Anal lobe setae usually longer than elsewhere, with 1–2 on each lobe. Generally with three stigmatic setae in each stigmatic area (occasionally some specimens with four setae in one stigmatic area), with central seta usually displaced slightly onto dorsum and of a different shape and/or size from lateral setae. Stigmatic setae of *C. formosus* and *C. lucidus* very similar to those of *C. janeirensis*, possibly indicating that these species are taxonomically close.

Venter entirely membranous, with few spiracular disc-pores and cruciform pores: with only 2–5 disc-pores in each spiracular pore band, each with mainly 3 outer loculi (range 3–6), and only 8 cruciform pores (9 on *C. flosculoides*) on each side of body, restricted to submargin. Ventral setae include: (i) a pair of long setae medially on abdominal segment VII; (ii) a pair of long interantennal setae, located between antennal bases; and (iii) bristle-like ventral setae, mainly present in a longitudinal submarginal row, with 1 seta on the head, 1 or 2 on thorax and 7 on abdomen plus a longitudinal submedial row of 7 on abdomen, one pair of each per segment.

Legs well developed, each without a tibio-tarsal articulation (as also found in some adult female *Ceroplastes* species). All species with a claw denticle and tarsal digitules of (usually) unequal length and thickness, with one shorter and more slender than other but both with a knobbed apex; claws also with one digitule broader than other. All species with 6 antennal segments: with setae as follows: segment I: 3 flagellate setae; II: 2 flagellate setae; III: 3 flagellate setae; IV: 1 fleshy seta; V: 1 fleshy seta and 1 flagellate seta; and VI: 6–8 flagellate setae and 3–5 fleshy setae.

Second-instar nymphs (Table 4). Dorsal region very similar to that of first-instar nymph. Derm entirely membranous, without either dorsal pores or setae visible under an optical microscope. Note: minute dorsal pores have been detected on the dorsum of second-instar nymphs of *C. ceriferus* by Kawai and Tamaki (1967), *C. destructor* by Wakgari and Giliomee (1998) and on *C. japonicus* by Camporese and Pellizzari (1994). Also each anal plate has 4 dorsal setae, but apical seta short and anogenital fold with 2 pairs of setae.

Number of marginal setae as on first-instar nymphs, except that *C. iheringi* has 8 (rarely 9) setae between eyespots and *C. stellifer* has 10–12 between anterior stigmatic areas, and, on each side: 2–6 between stigmatic areas and 7–11 between posterior stigmatic area and anal lobe. In addition, each anal lobe has 2 (some specimens with 1 or 3) anal lobe setae. Each stigmatic area still with three stigmatic setae (occasionally some specimens with four setae in one stigmatic area), but shape of setae slightly different when compared with previous instar. Note: In this instar, it is possible to place these ten species into three groups according with the shape of stigmatic setae. These groups are similar to the groups based on the pattern of wax test of the first-instar nymph. Thus, the species in "group I" have mainly conical stigmatic setae in the second instar, those in "group II" have knob-like stigmatic setae, and "group III" have lateral stigmatic setae that are mainly lanceolate or have an irregular pentagonal shape (Table 4).

Ventrally, spiracular disc-pores, cruciform pores and ventral setae more abundant than on first-instar nymphs, with 3–12 spiracular disc-pores, each with mainly 5 outer loculi (range 3–7) in each stigmatic band; two pairs of interantennal setae (apart from on *C. iheringi*, which has only one pair); bristle-like ventral setae more frequent submarginally and submedially and with a new (third) pair of longitudinal rows of 6–8 setae medially on abdomen; legs generally well developed, but tibia and tarsus fused in *C. stellifer*, and claw denticle absent in some species. Tubular ducts absent in second-instar female nymphs, thus differing from second-instar males which have a submarginal row.

Third-instar nymphs (Table 5). Very great changes occur in this instar. Dorsum remains membranous but a narrow sclerotic area appears around margin of anal plates (which will give rise to the anal process in the adult female); loculate microducts (each with 0–4 satellite loculi) and sometimes also simple microducts frequent on dorsum; dorsal setae cylindrical or conical, each with a variably-shaped apex (dorsal setae not detected on *C. stellifer*); clear areas visible and well defined, with 9 areas on most species: 3 pairs laterally, plus a cephalic and a dorsal area, plus one around anal plates (*C. floridensis* with 12 small clear area: one cephalic, 5 pairs laterally and one around anal plate but no dorsal clear area).

Anal plates each with 4 dorsal setae and 1 ventral seta, apart from: (i) *C. diospyros* with 5 dorsal setae and 2 ventral setae, (ii) *C. iheringi* with 4 dorsal setae and 2 ventral setae, and (iii) *C. stellifer* with 4 dorsal setae but ventral setae not detected. Anogenital fold with 3 pairs of setae, apart from *C. formosus* which has 2 pairs, as on the second-instar nymphs.

Marginal setae as on second-instar nymphs except more abundant in *C. floridensis* and *C. stellifer.* Each anal lobe with 2–4 setae. Number of stigmatic setae greater than on second-instar nymphs, tending to be more or less confined to stigmatic clefts but in some species extending laterally along margins, as on *C. formicarius* where stigmatic setae present all round margin. As in other instars, central seta of each group usually slightly displaced onto dorsum and often differing in size and shape between species. However, in *C. diospyros*, *C. flosculoides* and *C. iheringi*, there are 3 (rarely 2) setae displaced onto dorsum, each of a slightly different shape to the other stigmatic setae.

Spiracular disc-pores, cruciform pores and ventral setae more abundant than on previous instars: spiracular disc-pores increasing to 7–23, each with mainly 5 outer loculi (range 3–8); cruciform pores and bristle-like ventral setae most abundant submarginally and scarcer medially, particularly on posterior abdominal segments, although cruciform pores often present also in a group near labium. Filamentous ducts present on ventral submargins only in *C. grandis*. All species with well-developed legs, except *C. stellifer*, on which tibia and tarsus fused, as on second-instar nymphs.

The characters of taxonomic importance for the differentiation of each nymphal instar of the 10 species studied are given in Tables 3, 4 and 5.

Discussion and conclusions

The structure of the waxy tests of first- and second-instar nymphs of ten *Ceroplastes* species suggest that they fall into three species group. The third-instar female nymphs are less conservative and most similar to the adults. These nymphal characters appear to be taxonomically important, but have not been used in any phylogenetic studies to-date.

Based on the macroscopic characters of the wax tests of the first- and second-instar nymphs, the species can be separated into the three groups as follows: Group I includes species with dry wax filaments, i.e., *Ceroplastes cirripediformis*, *C. floridensis*, *C. formicarius*, *C. grandis* and *C. stellifer*, described above, as well as *C. rusci* (Silvestri & Martelli 1908), *C. sinensis* (Silvestri 1920), *C. brevicauda*, *C. destructor* and *C. mimosae* (Cilliers 1967), *C. pseudoceriferus* (Kawai & Tamaki 1967), *C. sinoiae* (Bedford 1968), and *C. ceriferus* and *C. japonicus* (Xie & Xue 2005); Group II includes species with a glassy test but which lack both dry-wax filaments and waxy expansions, i.e., *C. formosus* and *C. lucidus* along with *C. janeirensis* (Rosa *et al*. 2011); and Group III with species covered by a glassy wax test intermediate between Groups I and II and with marginal expansions of glassy wax in place of the dry-wax filaments, i.e., *C. diospyros*, *C. flosculoides* and *C. iheringi*.

Microscopically, the morphology of these species is similar but, nonetheless, the shape of the stigmatic setae on the second-instar nymphs suggested groupings similar to those indicated by the wax test characters of first-instar nymphs.

TABLE 3. Microscopic characters of first-instar female nymphs of ten species of *Ceroplastes*.

	Group 1				
1st instar	***C. cirripediformis* (Fig. 10)**	***C. floridensis* (Fig. 11)**	***C. formicarius* (Fig. 12)**	***C. grandis* (Fig. 13)**	***C. stellifer* (Fig. 14)**
Body length	360–630 µm	330–540 µm	420–830 µm	360–800 µm	290–510 µm
Body width	180–340 µm	180–330 µm	230–450 µm	210–390 µm	170–330 µm
Dorsal region					
Dorsal clear areas	Absent	Absent	Absent	Absent	Absent
Dorsal simple pores	Not detected	Not detected	Not detected	Not detected	Not detected
Trilocular pore	One pair, each 2.0–2.5 µm in diameter	One pair, each 3.0 µm in diameter	One pair, each 3.0 µm in diameter	One pair, each 2.0–2.5 µm in diameter	One pair, each 2 µm in diameter
Dorsal setae	A pair of setae with a conical apex, each 0.5–1.0 µm long, basal socket width 2.0 µm.	A pair of cylindrical or slightly conical setae, each 1.0 µm long, basal socket width 1.5–2.0 µm.	A pair of sharply conical setae, each 2.0–3.0 µm long, basal socket width 3.0 µm.	A pair of conical setae, each 1.5–2.0 µm long, basal socket width 2.0 µm.	A pair of sharply conical setae, each 3.0 µm long, basal socket width 2.0 µm.
Measurements of single anal plate (µm)	Length: 45–49 Width: 23–25	Length: 34–44 Width: 20–21	Length: 44–55 Width: 25–30	Length: 43–48 Width: 22–27	Length: 28–32 Width: 11–15
Margin					
Distribution and length of marginal setae and anal lobe setae	6 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 laterally between stigmatic areas and 7 between posterior stigmatic area and anal lobe, each 9–11 µm long. Anal lobe with 1 seta, 16–19 µm long.	6 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 laterally between stigmatic areas and 6 between posterior stigmatic area and anal lobe each 8–10 µm long. Anal lobe with 1 seta, 11–13 µm long.	6 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 laterally between stigmatic areas and 7 between posterior stigmatic area and anal lobe, each 10–19 µm long. Anal lobe with 1 seta, 20–25 µm long.	6 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 laterally between stigmatic areas and 7 between posterior stigmatic area and anal lobe, each about 10–15 µm long. Anal lobe with 1 slightly thicker seta, 18–23 µm long.	8 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 laterally between stigmatic areas and 6 between posterior stigmatic area and anal lobe, each about 9–13 µm long. Anal lobe with 1 seta, 16–21 µm long.
Number, shape and length of stigmatic setae	3 setae; cylindrical with rounded apex; apex slightly wider than base; central seta longer than laterals, 5–6 µm long, and with basal socket 3–4 µm wide; lateral setae each 3–4 µm long with basal socket 2–3 µm wide.	3 setae; all conical with rounded apex; central seta 3–4 µm long and basal socket 2–3 µm wide; lateral setae each 2.5–3.0 µm long and basal socket 3 µm wide.	3 setae, central seta with either a slightly capitate apex or a slightly pentagonal irregular shape, 4–5 µm long with basal socket 4 µm wide; lateral setae cylindrical or slightly conical with apex of one lateral truncated, each 3–4 µm long with basal socket 3 µm wide.	3 (rarely 4) setae; central seta conical with a rounded apex, 4–5 µm long with basal socket 2–3 µm wide; lateral setae cylindrical or slightly conical with rounded apices, each 3–4 µm long with basal socket 2–3 µm wide.	3 setae; central seta sharply conical, 7–8 µm long with basal socket 2–3 µm wide; lateral setae dome shaped, each 2–3 µm long with basal socket 3–4 µm wide.

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TABLE 3. (Continued)

	Group 1				
1st instar	***C. cirripediformis* (Fig. 10)**	***C. floridensis* (Fig. 11)**	***C. formicarius* (Fig. 12)**	***C. grandis* (Fig. 13)**	***C. stellifer* (Fig. 14)**
Width of each lens of eyespots	11–12 µm.	9–10 µm.	12–13 µm	10–12 µm.	9–11 µm.
Venter					
Spiracular disc-pores in each spiracular pore band.	2–4 pores, each with 3 or 5 loculi, each pore 2.0–2.5 µm in diameter.	2–4 pores, each with 3, 4 or 5 loculi, each pore 2 µm in diameter.	2–4 pores, each with 3, 4 or 5 loculi, each pore 2.0–3.0 µm in diameter.	2–5 pores, each with 3 or 5 (mainly 3) loculi, each pore 2 µm in diameter.	3–4 pores, with 3, 4 or 5 (mainly 3) loculi, each 2–3 µm in diameter.
Number and length of inter-antennal setae	One pair: each 30–35 µm	One pair: each 23–27 µm	One pair: each 31–37 µm	One pair: each 32–36 µm	One pair: each 25–30 µm
Length of pregenital setae	23–30 µm	25–30 µm	40–50 µm	20–24 µm	25–30 µm
Total length of antennae	115–128 µm	100–110 µm	135–155 µm	110–124 µm	100–110 µm
Length of clypeolabral shield	90–94 µm	80–90 µm	110–120 µm	84–104 µm	85–90 µm
Legs	Well developed	Well developed	Well developed	Well developed	Well developed
Dimensions of metathoracic legs (µm):					
coxa	36–40	30–35	45–52	36–39	28–30
trochanter + femur	60–69	51–55	77–85	55–62	55–56
tibia	43–51	36–39	58–65	42–47	30–32
tarsus	37–49	29–33	39–48	33–34	25–28
claw	14–16	10–13	17–20	14–16	10–13
Length of tarsal digitules (µm):	Shorter: 24–27 Longer: 37–40	Shorter: 18–20 Longer: 35–37	Shorter: 30–32 Longer: 44–46	Shorter: 23–26 Longer: 35–37	Shorter: 20–22 Longer: 30–31
Length of claw digitules (µm):	13–17	11–15	23–25	16–18	12–15
Denticle on claw	Present	Present	Present	Present	Present

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TABLE 3. (Continued)

	Group 2		Group 3		
1st instar	***C. formosus* (Fig. 15)**	***C. lucidus* (Fig. 16)**	***C. diospyros* (Fig.17)**	***C. flosculoides* (Fig. 18)**	***C. iheringi* (Fig. 19)**
Body length	380–520 µm	435–600 µm	530–700 µm	420–680 µm	380–570 µm
Body width	190–280 µm	210–290 µm	290–400 µm	210–330 µm	210–360 µm
Dorsal region					
Dorsal clear areas	Absent	Absent	Absent	Absent	Absent
Dorsal simple pores	Not detected	Not detected	Not detected	Not detected	Not detected
Trilocular pore	One pair, each 2.0 µm in diameter	One pair, each 3 µm in diameter	One pair, each 3.0 µm in diameter	One pair, each 2.0 µm in diameter	One pair, each 1.5–2.0 µm in diameter
Dorsal setae	Not detected	A pair of sharply conical setae, each 3.0 µm long, basal socket width 2.0–2.5 µm.	A pair of sharply conical setae, each 4.0 µm long, basal socket width 2.0 µm.	A pair of sharply conical setae, each 4.0–5.0 µm long, basal socket width 3.0 µm.	Not detected
Measurements of single anal plate (µm)	Length: 47–50 Width: 24–26	Length: 45–51 Width 22–25	Length: 50–55 Width: 24–28	Length: 38–44 Width: 24–25	Length: 43–50 Width: 25–28
Margin					
Distribution and length of marginal setae and anal lobe setae	6 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 laterally between stigmatic areas and 6 between posterior stigmatic area and anal lobe, each about 10–11 µm long. Anal lobe with 2 setae, one 10–14 µm long and other 14–17 µm long.	6 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 laterally between stigmatic areas and 6 between posterior stigmatic area and anal lobe, each about 6–8 µm long. Anal lobe with 2 setae, both 11–17 µm long.	7 or 8 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 laterally between stigmatic areas and 6 between posterior stigmatic area and anal lobe each 11–15 µm long. Anal lobe with 1 seta, 20–25 µm long.	6 between eyespots, and, on each side, 2 or 3 between eyespots and anterior stigmatic area, 2 laterally between stigmatic areas and 6 between posterior stigmatic area and anal lobe each about 10–15 µm long. Anal lobe with 1 seta, 16–17 µm long.	6 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 laterally between stigmatic areas, 7 between posterior stigmatic area and anal lobe and each anal lobe with 1 seta, each about 9–17 µm long.
Number, shape and length of stigmatic setae	3 setae; knob-like shape; central seta with apex wider than laterals, 3–4 µm long and basal socket 2 µm wide; lateral setae each 2–3 µm long with basal socket 2 µm wide.	3 setae; knob-like; central seta with apex wider than other setae, displaced slightly onto dorsum, 3–4 µm long with basal socket 2–3 µm wide; lateral setae, each 2–3 µm long with basal socket 2–3 µm wide.	3 setae; all central setae cylindrical to slightly conical with rounded or truncated apices and laterals cylindrical with one (rarely two) setae with truncated sides, each 5–6 µm long and with basal socket each 3–4 µm wide.	3 setae; central seta with irregular pentagonal shape, 5–6 µm long and with basal socket 2 µm wide; lateral setae with apex of one lateral truncated, both setae 5–6 µm long with basal socket 2.5–3 µm wide.	3 setae, central seta with pentagonal irregular shape 7–8 µm long with basal socket 3–4 µm wide; lateral setae pentagonal irregular and slightly conical in shape, each 4–5 µm long with basal socket with 3–4 µm wide.

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TABLE 3. (Continued)

	Group 2		Group 3		
1st instar	***C. formosus* (Fig. 15)**	***C. lucidus* (Fig. 16)**	***C. diospyros* (Fig.17)**	***C. flosculoides* (Fig. 18)**	***C. iheringi* (Fig. 19)**
Width of each lens of eyespots	8–11 µm.	10–11 µm.	10–11 µm.	11–12 µm.	10–11 µm
Venter					
Spiracular disc-pores in each spiracular pore band.	2–4 pores, each with 3 or 5 loculi, each pore 1.5–2.5 µm in diameter.	2–4 pores, each with 3, 4, 5 or 6 loculi, each pore 2–3 µm in diameter.	2–4 pores, each with 3 or 5 loculi, each pore 2–3 µm in diameter.	2–4 pores each with 3, 4 or 5 loculi, each pore 2.0–2.5 µm in diameter.	3–4 pores, each with 3, 4 or 5 (mainly 3) loculi, each pore 2.0–2.5 µm in diameter.
Number and length of inter-antennal setae	One pair: each 25–32 µm	One pair: each 28–35 µm	One pair: each 28–32 µm	One pair: each 32–36 µm	One pair: each 25–29 µm
Length of pregenital setae	25–35 µm	27–29 µm	27–33 µm	33–37 µm	34–36 µm
Total length of antennae	107–120 µm	104–117 µm	125–137 µm	113–125 µm	135–144 µm
Length of clypeolabral shield	80–88 µm	80–85 µm	110–120 µm	95–100 µm	103–112 µm
Legs	Well developed	Well developed	Well developed	Well developed	Well developed
Dimensions of metathoracic legs (µm):					
coxa	38–42	37–39	45–50	42–44	33–41
trochanter + femur	58–68	61–65	70–73	65–70	64–75
tibia	45–50	49–51	45–50	47–55	42–50
tarsus	35–37	35–37	40–42	38–40	38–40
claw	14–16	13–15	18–20	15–16	17–18
Length of tarsal digitules (µm):	Shorter: 24–30 Longer: 38–42	Shorter: 25–26 Longer: 38–40	Shorter: 28–31 Longer: 40–45	Shorter: 22–27 Longer: 33–39	Shorter: 28–32 Longer: 42–43
Length of claw digitules (µm):	18–20	17–21	19–21	18–20	19–21
Denticle on claw	Present	Present	Present	Present	Present

TABLE 4. Microscopic characters of second-instar female nymphs of ten species of *Ceroplastes*.

	Group 1				
2nd instar	***C. cirripediformis* (Fig. 20)**	***C. floridensis* (Fig. 21)**	***C. formicarius* (Fig. 22)**	***C. grandis* (Fig. 23)**	***C. stellifer* (Fig. 24)**
Body length	560–770 µm	520–660 µm	910–1030 µm	690–900 µm	500–680 µm
Body width	320–440 µm	330–460 µm	560–640 µm	390–550 µm	340–500 µm
Dorsal region					
Dorsal clear areas	Absent	Absent	Absent	Absent	Absent
Dorsal pores and dorsal setae	Not detected	Not detected	Not detected	Not detected	Not detected
Measurements of single anal plate (µm)	Length: 60–65 Width: 29–32	Length: 50–55 Width: 25–30	Length: 75–82 Width: 42–55	Length: 66–73 Width: 32–37	Length: 42–46 Width: 16–21
Margin					
Distribution and length of marginal setae and anal lobe setae	6 between eyespots, and, on each side, 2 (rarely 3) between eyespots and anterior stigmatic area, 2 between stigmatic areas and 7 between posterior stigmatic area and anal lobe, each 11–15 µm long. Each anal lobe with 2 setae: anterior seta 33–35 µm and posterior seta 13–17 µm.	6 between eyespots, and, on each side: 2 between eyespots and anterior stigmatic area, 2 between stigmatic areas and 6 between posterior stigmatic area and anal lobe, each 7–10 µm long. Each anal lobe with 2 setae each 12–17 µm	6 between eyespots, and, on each side: 2 between eyespots and anterior stigmatic area, 2 between stigmatic areas and 7 between posterior stigmatic area and anal lobe, each 16–35 µm long. Each anal lobe with 2 setae, each 33–60 µm	6 between eyespots, and, on each side: 2 between eyespots and anterior stigmatic area, 2 between stigmatic areas and 7 between posterior stigmatic area and anal lobe, each 14–16 µm long. Each anal lobe with 2 setae, each 15–29 µm long.	10–12 between anterior stigmatic areas, and, on each side: 2–6 between stigmatic areas and 7–11 between posterior stigmatic area and anal lobe, each 5–12 µm long. Each anal lobe with 1 or 2 setae: shorter seta 14–18 µm and longer seta with 25–32 µm.
Number, shape and length of stigmatic setae	3 setae; central seta conical 10–11 µm long, with basal socket 4–5 µm wide, displaced slightly onto dorsum; lateral setae both spinose, each 9–11 µm long with basal socket 3 µm wide.	3 setae; central seta bullet-shaped, 10–12 µm long with basal socket 4–5 µm wide; lateral setae sharply conical, each 6–8 µm long with basal socket 3–4 µm wide.	3 setae; central seta conical or bullet-shaped with a rounded apex, 11–13 µm long with basal socket 6–7 µm wide; each lateral seta spinose, 11–14 µm long with basal socket 4–6 µm wide.	3 setae, conical with rounded apices; central seta longer than laterals, 10–13 µm long with basal socket 3-4 µm wide; each lateral seta 5–8 µm long with basal socket 2–3 µm wide.	3 setae; central seta sharply conical, 12–15 µm long with basal socket 5 µm wide, displaced slightly onto dorsum; lateral setae conical, each 6–9 µm long with basal socket 4–5 µm wide.
Width of lens of eyespots	15–17 µm.	13–15 µm	15–18 µm.	9–11 µm	Eyespots not detected

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TABLE 4. (Continued)

	Group 1				
2nd instar	***C. cirripediformis* (Fig. 20)**	***C. floridensis* (Fig. 21)**	***C. formicarius* (Fig. 22)**	***C. grandis* (Fig. 23)**	***C. stellifer* (Fig. 24)**
Venter					
Spiracular disc-pores in each spiracular pore band.	3–6 pores, with 4, 5 or 7 (mainly 5) loculi, each pore 3 µm in diameter.	5–8 pores, with 3 or 5 (mainly 5) loculi, each pore 2–3 µm in diameter.	6–12 pores, with 3, 5 or 6 (mainly 5) loculi, each pore 2.5–4.0 µm in diameter.	4–6 pores, with 5, 6 or 7 (mainly 5) loculi, each pore 3.0–3.5 µm in diameter.	3–7 pores, with 3, 4 or 5 loculi, each pore 2–3 µm in diameter.
Number and length of inter-antennal setae	Two pairs: longer pair each 37–44 µm, shorter pair each 4–5 µm	Two pairs: longer pair each 30–35 µm, shorter pair each 6–10 µm	Two pairs: longer pair each 34–40 µm, shorter pair each 2–3 µm	Two pairs: longer pair each 36–42 µm, shorter pair each 5–8 µm	Two pairs: longer pair each 25–33 µm, shorter pair each 20–23 µm
Length of pregenital setae	25–31 µm	27–37 µm	37–42 µm	39–43 µm	28–31 µm
Total length of antennae	128–135 µm	103–113 µm	157–170 µm	141–147 µm	79–95 µm
Length of clypeolabral shield	105–119 µm	95–106 µm	150–165 µm	120–128 µm	95–105 µm
Legs	Well developed	Well developed	Well developed	Well developed	Developed but small, with tibia and tarsus fused
Dimensions of metathoracic legs (µm):					
coxa	50–54	39–42	63–72	50–56	20–22
trochanter + femur	75–80	62–65	95–105	75–84	26–30
tibia	55–63	43–47	70–75	51–60	24–35 (tibia + tarsus)
tarsus	43–49	33–37	60–63	44–46	
claw	12–14	8–10	17–21	14–16	5–7
Length of tarsal digitules (µm):	Shorter: 25–28 Longer: 35–40	Shorter: 22–24 Longer: 29–30	Shorter: 30–35 Longer: 37–43	Shorter: 30–32 Longer: 40–43	Shorter: 8–9 Longer: 10–12, without knobbed apex
Length of claw digitules (µm):	18–20	12–15	18–25	19–21	7–8
Denticle on claw	Absent	Absent	Present	Present	Absent

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TABLE 4. (Continued)

	Group 2		Group 3		
2nd instar	***C. formosus* (Fig. 25)**	***C. lucidus* (Fig. 26)**	***C. diospyros* (Fig. 27)**	***C. flosculoides* (Fig. 28)**	***C. iheringi* (Fig. 29)**
Body length	580–700 µm	590–710 µm	670–800 µm	690–810 µm	610–760 µm
Body width	310–440 µm	330–410 µm	360–530 µm	370–500 µm	310–490 µm
Dorsal region					
Dorsal clear areas	Absent	Absent	Absent	Absent	Absent
Dorsal pores and dorsal setae	Not detected	Not detected	Not detected	Not detected	Not detected
Measurements of single anal plate (µm)	Length: 50–58 Width: 25–29	Length: 52–58 Width: 29–34	Length: 60–67 Width: 35–40	Length: 52–61 Width: 29–32	Length: 60–65 Width: 30–35
Margin					
Distribution and length of marginal setae and anal lobe setae	10 between anterior stigmatic areas, 2 between stigmatic areas and 6 between posterior stigmatic area and anal lobe, each 7–10 µm long. Each anal lobe with 2 setae, each same size as marginal setae.	6 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 between stigmatic areas and 6 between posterior stigmatic area and anal lobe, each 5–7 µm long. Each anal lobe with 2 setae, each same size as marginal setae.	7 or 8 between eyespots, and, on each side: 2 between eyespots and anterior stigmatic area, 2 between stigmatic areas and 6 between posterior stigmatic area and anal lobe, each 8–10 µm long. Each anal lobe with 2 setae: anterior seta 50–67 µm and posterior seta 10–13 µm.	6 between eyespots, and, on each side: 2 between eyespots and anterior stigmatic area, 2 between stigmatic areas and 6 between posterior stigmatic area and anal lobe, each 7–11 µm long. Each anal lobe with 2 setae: anterior seta 47–50 µm and posterior seta 11–13 µm	8 (rarely 9) between eyespots, and, on each side: 2 between eyespots and anterior stigmatic area, 2 between stigmatic areas and 7 between posterior stigmatic area and anal lobe, each 12–18 µm long. Each anal lobe with 2 or 3 setae: central seta 38–40 µm, other setae 15–19 µm
Number, shape and length of stigmatic setae	3 setae, knob-like; central seta with apex wider than lateral setae, displaced slightly onto dorsum, 3–5 µm long with basal socket 2.5–4 µm wide; lateral setae, each 2–3 µm long with basal socket 2–3 µm wide.	3 setae, knob-like; central seta with apex wider than others, displaced slightly onto dorsum, 4–5 µm long with basal socket 4–5 µm wide; lateral setae, each 2–3 µm long with basal socket 4 µm wide.	3 (rarely 4) setae; central seta variable in shape: either cylindrical and truncated, with a rounded apex, or spinose; lateral setae cylindrical with one lateral apex truncated, each 9–13 µm long with basal socket 4–6 µm wide.	3 setae; central seta conical with a rounded apex; lateral setae cylindrical with a lateral truncated apex, each 9–12 µm long with basal socket 2–5 µm wide.	3 setae, central seta bullet-shaped, 8–10 µm long with basal socket 6–7 µm wide; lateral setae sharply conical, each 7–10 µm long with basal socket 5–6 µm wide.
Width of lens of eyespots	Eyespots not detected	10–11 µm.	7–8 µm.	9–10 µm.	10–12 µm.

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TABLE 4. (Continued)

	Group 2		Group 3		
2nd instar	***C. formosus* (Fig. 25)**	***C. lucidus* (Fig. 26)**	***C. diospyros* (Fig. 27)**	***C. flosculoides* (Fig. 28)**	***C. iheringi* (Fig. 29)**
Venter					
Spiracular disc-pores in each spiracular pore band.	6–8 pores, with 5 or 6 (mainly 5) loculi, each pore 3–4 µm in diameter.	4–6 pores, with 5–6 (mainly 5) loculi, each pore 3 µm in diameter.	6–11 pores, with 5, 6 or 7 (mainly 5) loculi, each pore 3–4 µm in diameter.	5–7 pores, with 4 or 5 (mainly 5) loculi, each pore 3–4 µm in diameter.	6–8 pores, with 4, 5 or 6 (mainly 5) loculi, each pore 3 µm in diameter.
Number and length of inter-antennal setae	Two pairs: longer pair each 37–45 µm, shorter pair each 4–5 µm	Two pairs: longer pair each 29–32 µm, shorter pair each 7–9 µm	Two pairs: longer pair each 33–38 µm, shorter pair each 4–6 µm	Two pairs: longer pair each 27–32 µm, shorter pair each 3–5 µm	One pair: 23–25 µm,
Length of pregenital setae	37–40 µm	31–46 µm	35–41 µm	30–32 µm	24–29 µm
Total length of antennae	112–123 µm	124–132 µm	148–175 µm	138–145 µm	119–134 µm
Length of clypeolabral shield	120–125 µm	100–105 µm	145–150 µm	120–130 µm	127–131 µm
Legs	Well developed	Well developed	Well developed	Well developed	Well developed
Dimensions of metathoracic legs (µm):					
coxa	49–56	40–48	55–64	50–55	45–47
trochanter + femur	73–75	78–80	90–95	76–84	72–75
tibia	47–52	55–57	55–58	52–55	47–49
tarsus	37–40	44–45	45–51	43–50	45–47
claw	11–13	13–15	13–15	12–14	14–17
Length of tarsal digitules (µm):	Shorter: 20–22 Longer: 31–35	Shorter: 22–26 Longer 35–38	Shorter: 26–28 Longer: 35–37	Shorter: 24–26 Longer: 33–35	Both same length: 28–32
Length of claw digitules (µm):	15–16	15–16	17–20	16–22	16–18
Denticle on claw	Absent	Absent	Present	Present	Present

TABLE 5. Microscopic characters of third-instar female nymphs of ten species of *Ceroplastes.*

	Group 1				
3rd instar	***C. cirripediformis* (Fig. 30)**	***C. floridensis* (Fig. 31)**	***C. formicarius* (Fig. 32)**	***C. grandis* (Fig. 33)**	***C. stellifer* (Fig. 34)**
Body length	730–980 µm	630–970 µm	1020–1330 µm	1000–1430 µm	700–920 µm
Body width	420–630 µm	430–680 µm	700–1120 µm	650–1000 µm	540–800 µm
Dorsal region					
Clear areas	3 lateral pairs, a cephalic, a dorsal, plus one area around anal plate, each without pores or setae.	5 lateral pairs, one cephalic plus one area around anal plate, each without pores or setae.	3 lateral pairs, a cephalic, a dorsal, plus one area around anal plate, each without pores or setae.	3 lateral pairs, a cephalic, a dorsal, plus one area around anal plate, all without pores or setae, except cephalic clear area with one pair of conical setae with truncated or rounded apices, 1.5 µm long, basal socket width 2.5 µm.	3 lateral pairs, a cephalic, a dorsal, plus one area around anal plate, each without pores or setae.
Dorsal setae	Capitate, each 1.5–3.0 µm long, with basal socket width 3.0–3.5 µm.	Setae with slightly convergent sides and a blunt apex, each 2.5–3.0 µm long, basal socket width about 3 µm.	Two shapes: (i) cylindrical with a truncate apex laterally, each 5.0 µm long, basal socket width 3 µm and (ii) conical, each 2–4 µm long, basal socket width 3 µm.	Two shapes: (i) cylindrical or slightly conical with a truncated apex, each 3.0–5.0 µm long, basal socket width 3.0 µm and (ii) cylindrical, but with a chisel-like apex, 3.0–4.0 µm long, basal socket width 3.0 µm.	Not detected
Loculate microducts	1 and 2 satellite loculi; each pore about 2–4 µm wide; those with 1 satellite loculus most abundant throughout.	1, 2 and 3 satellite loculi; each pore about 2.5–5.0 µm wide; those with 1 and 2 satellite loculi most abundant throughout.	1, 2 and 3 satellite loculi; each pore about 2–4 µm wide; those with 2 satellite loculi most abundant throughout.	1, 2, 3 and 4 satellite loculi; each pore about 3–5 µm wide; those with 1 and 2 satellite loculi most abundant throughout.	0, 1 and 2 satellite loculi; each about 1–3 µm wide

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TABLE 5. (Continued)

	Group 1				
3rd instar	***C. cirripediformis* (Fig. 30)**	***C. floridensis* (Fig. 31)**	***C. formicarius* (Fig. 32)**	***C. grandis* (Fig. 33)**	***C. stellifer* (Fig. 34)**
Simple dorsal microducts	Not detected	Present, each 1.5–2.0 µm widest.	Present, each 1 µm wide.	Not detected	Not detected
Measurements of single anal plate (µm)	Length: 80–90 Width: 35–42	Length: 76–83 Width: 37–41	Length:110–120 Width: 60–65	Length: 95–115 Width: 45–60	Length: 52–62 Width: 22–27
Margin					
Distribution and length of marginal setae and anal lobe setae	6 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 between stigmatic areas and 7 between posterior stigmatic area and anal lobe, each about 15–20 µm long. Each anal lobe with 3 (rarely 4) setae: the most anterior 60–65 µm long, central seta 40–47 µm long and most posterior seta 18–23 µm long.	11–13 between eyespots, and, on each side, 4–6 between eyespots and anterior stigmatic area, 5–7 between stigmatic areas and 15–19 between posterior stigmatic area and anal lobe, each about 10–16 µm. Each anal lobe with 3 or 4 (rarely 2) setae: each about 17–32 µm long.	6 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 between stigmatic areas and 6 or 7 between posterior stigmatic area and anal lobe, each about 27–40 µm. Each anal lobe with 2–4 setae: each about 45–60 µm long.	6 between eyespots, and, on each side, 2 or 3 (rarely 4) between eyespots and anterior stigmatic area, 2 or 3 between stigmatic areas and 6 between posterior stigmatic area and anal lobe, each about 13–25 µm. Each anal lobe with 4 (rarely 3) setae, two anterior setae each 31–53 µm long, and two posterior setae each 20–26 µm long.	17–21 between anterior stigmatic areas and, on each side, 6–9 between stigmatic areas and 13–24 between posterior stigmatic area and anal lobe, each about 7–22 µm long. Each anal lobe with 2 or 3 setae: most anterior, with 19–29 µm long (when present), central seta 50–80 µm long and most posterior 100–130 µm long.
Number, shape, length and distribution of stigmatic setae	4–9 setae, each conical to lanceolate, and about 5–8 µm long, basal socket 4–6 µm wide, present mainly as a single row laterad to each stigmatic furrow; plus a central conical seta 9–11 µm long, basal socket 7–9 µm wide, slightly displaced onto dorsum.	6–12 setae, each sharply conical, about 5–10 µm long with basal socket 3–5 µm wide; present mainly as a single row laterad to each stigmatic furrow; plus a central conical seta with 13–15 µm long, basal socket 6–7 µm wide, displaced slightly onto dorsum.	65–140 setae, each sharply pointed, 6–17 µm long. basal socket 4–7 µm wide, present around entire margin, as a single row, but more concentrated in stigmatic cleft regions; central seta, conical, 13–17 µm long, basal socket 9–10 µm wide.	12–19 setae, either conical with a rounded apex or cylindrical with a conical apex; central seta 13–17 µm long, basal socket 8–11 µm wide; other, lateral setae each about 6–12 µm long, basal socket 4–7 µm wide; present mainly in one or two rows in each stigmatic cleft.	3–5 setae, each conical, about 7–15 µm long, basal socket 5–6 µm wide; present mainly as a single row laterad to each stigmatic furrow, plus a central sharply conical seta displaced slightly onto dorsum, 15–20 µm long, basal socket 6–7 µm wide.
Width of lens of eyespots	20–23 µm.	21–22 µm.	18–20 µm	14–21 µm.	not detected

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TABLE 5. (Continued)

	Group 1				
3rd instar	***C. cirripediformis* (Fig. 30)**	***C. floridensis* (Fig. 31)**	***C. formicarius* (Fig. 32)**	***C. grandis* (Fig. 33)**	***C. stellifer* (Fig. 34)**
Venter					
Spiracular disc-pores in each spiracular pore band.	7–12 pores, each with 5 (rarely 3 or 4) loculi, each pore about 3.0–3.5 µm in diameter.	10–17 pores, each with 3 or 5 (mainly 5) loculi, each pore about 2–3 µm in diameter.	15–17 pores, each with 4, 5, 6 and 7 (mainly 5) loculi, each pore about 3–5 µm in diameter.	13–19 pores, each with 5 (rarely 3 or 6) loculi, each pore about 3.0–4.0 µm in diameter.	8–12 pores, each with 4, 5 or 6 loculi, each pore about 3–4 µm in diameter.
Filamentous ducts	Absent	Absent	Absent	Present, pore 1 µm in diameter	Absent
Number and length of inter-antennal setae	Two pairs: longer pair each 35–45 µm, shorter pair each 9–12 µm	Two pairs: longer pair each 42–50 µm, shorter pair each 16–25 µm	Two pairs: longer pair each 45–60 µm, shorter pair each 7–9 µm	Two pairs: longer pair each 41–45 µm, shorter pair each 14–17 µm	8–10: longer setae each 30–50 µm, shorter setae, each 12–25 µm
Length of pregenital setae	26–32 µm	45–52 µm	39–51 µm	54–65 µm	41–50 µm
Total length of antennae	180–205 µm	147–155 µm	212–245 µm	200–235 µm	105–112 µm
Length of clypeolabral shield	143–170 µm	122–130 µm	180–190 µm	150–190 µm	115–127 µm
Legs	Well developed	Well developed	Well developed	Well developed	Developed, but small, with tibia and tarsus fused
Dimensions of metathoracic legs (µm):					
coxa	68–80	53–60	80–95	80–100	30–35
trochanter + femur	95–105	82–87	130–145	100–135	41–45
tibia	66–80	48–54	90–95	79–87	30–36 (tibia + tarsus)
tarsus	57–62	43–47	75–80	61–70	
claw	16–19	12–14	20–25	19–23	6–8
Length of tarsal digitules (µm):	Shorter: 39–42 Longer: 44–50	Shorter: 27–30 Longer: 35–38	Shorter: 33–40 Longer: 45–50	Shorter: 36–47 Longer: 46–58	Shorter: 15–17 Longer: 20–22
Length of claw digitules (µm):	20–25	16–22	30–35	24–30	10–11
Denticle on claw	Absent	Absent	Present	Present	Absent

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TABLE 5. (Continued)

	Group 2		Group 3		
3rd instar	***C. formosus* (Fig. 35)**	***C. lucidus* (Fig. 36)**	***C. diospyros* (Fig. 37)**	***C. flosculoides* (Fig. 38)**	***C. iheringi* (Fig. 39)**
Body length	580–910 µm	680–860 µm	790–1230 µm	750–900 µm	770–980 µm
Body width	370–660 µm	460–650 µm	470–1000 µm	450–650 µm	510–660 µm
Dorsal region					
Clear areas	3 lateral pairs, a cephalic, a dorsal, plus one area around anal plate, all without pores or setae, except cephalic clear area with 2 or 3 dorsal cylindrical setae with rounded apices.	3 lateral pairs, a cephalic, a dorsal, plus one area around anal plate, each without pores or setae.	3 lateral pairs, a cephalic, a dorsal, plus one area around anal plate, all without pores or setae, except cephalic and central clear areas with dorsal cylindrical setae with rounded apex, each 1.5–2.0 µm long, basal socket width 4 µm.	3 lateral pairs, a cephalic, a dorsal, plus one area around anal plate, each without pores or setae.	3 lateral pairs, a cephalic, a dorsal, plus one area around anal plate, all without pores or setae, except cephalic clear area with two conical dorsal setae each 2 µm long, basal socket width 3 µm.
Dorsal setae	Two shapes: (i) cylindrical with a rounded apex, each 1.5–2.0 µm long, basal socket width 2.5–3.0 µm and (ii) conical with pointed apex, each 3.0–3.5 µm long, basal socket width 3.0 µm.	Conical with a truncated apex, each 3 µm long, basal socket width 3 µm.	Three different shapes: (i) cylindrical with a slightly capitate apex, each 3–4 µm long, basal socket width 4–5 µm; (ii) cylindrical with rounded apex, each 1.5–2.0 µm long, basal socket width 4 µm; and (iii) cylindrical with pointed apex, each 6–7 µm long, basal socket width 5 µm.	Conical with a pointed or slightly rounded apex, each 2–4 µm long, basal socket width 3 µm.	Conical, each 2–3 µm long, basal socket width 3 µm.
Loculate microducts	1 and 2 satellite loculi; each pore about 2–5 µm wide; those with 1 satellite loculus most abundant throughout.	1 and 2 satellite loculi; each pore about 3–4 µm wide; those with 1 satellite loculus most abundant throughout.	1 and 2 satellite loculi; each pore about 2–4 µm wide; those with 1 satellite loculus most abundant throughout.	1, 2 and 3 (mainly 2) satellite loculi; each pore about 3–5 µm wide; those with 1 satellite loculus most abundant throughout.	1 and 2 satellite loculi; each pore about 2.0–3.5 µm wide; those with 1 satellite loculus most abundant throughout.

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TABLE 5. (Continued)

	Group 2		Group 3		
3rd instar	***C. formosus* (Fig. 35)**	***C. lucidus* (Fig. 36)**	***C. diospyros* (Fig. 37)**	***C. flosculoides* (Fig. 38)**	***C. iheringi* (Fig. 39)**
Simple dorsal microducts	Not detected	Present, each 1.0–1.5 µm widest.	Present, each 1 µm widest	Not detected	Not detected
Measurements of single anal plate (µm)	Length: 58–65 Width: 35–43	Length: 68–75 Width: 35–38	Length: 78–90 Width: 51–55	Length: 75–80 Width: 42–45	Length: 85–90 Width: 44–49
Margin					
Distribution and length of marginal setae and anal lobe setae	6 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 between stigmatic areas, 6 between posterior stigmatic area and anal lobe, each about 10–11 µm. Each anal lobe with 2 setae, each same size as marginal setae.	6 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 between stigmatic areas, 6 between posterior stigmatic area and anal lobe, each about 10–13 µm long. Each anal lobe with 2 setae, one 10–13 µm long and other 13–15 µm long.	6 or 7 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 between stigmatic areas and 6 between posterior stigmatic area and anal lobe, each about 11–15 µm. Each anal lobe with 3 setae: most anterior 90–105 µm long, central 30–38 µm long and most posterior 15–16 µm long.	6 or 7 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 between stigmatic areas and 6 between posterior stigmatic area and anal lobe, each about 10–17 µm. Each anal lobe with 3 (rarely 4) setae: most anterior 75–95 µm long, central 40–55 µm long and most posterior 18–20 µm long.	8 between eyespots, and, on each side, 2 between eyespots and anterior stigmatic area, 2 between stigmatic areas and 6 between posterior stigmatic area and anal lobe, each about 16–19 µm. Each anal lobe with 3 setae: central seta 37–44 µm long, laterals setae each 18–25 µm long.
Number, shape, length and distribution of stigmatic setae	5–11 setae, either cylindrical or slightly conical with a rounded apex and dome shape, each about 4–6 µm long, basal socket 5–8 µm wide; present mainly as a single row laterad to each stigmatic furrow; central seta sometimes slightly displaced onto dorsum.	8–10 setae , each cylindrical and conical with rounded apex, about 4–6 µm long, basal socket 5–8 µm wide, present mainly in 2–3 rows laterad to each stigmatic furrow.	A group with 6–11 setae, with different apices: either truncated or laterally truncated and toothed; each about 7–11 µm long, basal socket 4–7 µm wide; present as a row laterad to each stigmatic furrow and with 1–3 setae slightly displaced onto dorsum.	A group of 5–9 setae, each either conical, cylindrical with a rounded apex or cylindrical with truncated apex, each about 8–10 µm long, basal socket 5–12 µm wide; present mainly in one or two rows in each stigmatic furrow, and a group of 3 setae each shaped like premolar teeth, each about 7–10 µm long, basal socket 9–12 µm wide, displaced slightly onto dorsum.	Two groups: a group with 3–7 sharply conical stigmatic setae, each about 8–10 µm long, basal socket 3–4 µm wide; present laterad to each stigmatic furrow, and other group of 3 setae, each conical and about 8–12 µm long, basal socket 7–11 µm wide displaced onto dorsum.
Width of lens of eyespots	11–12 µm.	13–15 µm.	11–13 µm.	16–20 µm.	37–43 µm.

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TABLE 5. (Continued)

3rd instar	Group 2		Group 3		
	***C. formosus* (Fig. 35)**	***C. lucidus* (Fig. 36)**	***C. diospyros* (Fig. 37)**	***C. flosculoides* (Fig. 38)**	***C. iheringi* (Fig. 39)**
Venter					
Spiracular disc-pores in each spiracular pore band.	9–16 pores, each with 3, 4 or 5 (mainly 5) loculi, each pore about 3–4 µm in diameter.	9–12 pores, each with 5 loculi, each pore about 3 µm in diameter.	15–23 pores, each with 5, 6 or 7 (mainly 5) loculi, each pore about 3–4 µm in diameter.	11–19 pores, each with 5 and 7 (mainly 5) loculi, each pore about 3–4 µm in diameter.	12–15 pores, each with 5 (rarely 6) loculi, each pore about 3–4 µm in diameter.
Filamentous ducts	Absent	Absent	Absent	Absent	Absent
Number and length of inter-antennal setae	Two pairs: longer pair each 48–55 µm, shorter pair each 6–7 µm	Two pairs: longer pair each 41–43 µm, shorter pair each 16–20 µm	Two pairs: longer pair each 44–49 µm, shorter pair each 9–11 µm	Two pairs: longer pair each 50–55 µm, shorter pair each 6–7 µm	One pair: 22–25 µm
Length of pregenital setae	40–47 µm	44–55 µm	35–39 µm	40–45 µm	37–43 µm
Total length of antennae	135–150 µm	154–167 µm	229–231 µm	190–205 µm	145–152 µm
Length of clypeolabral shield	160–170 µm	133–139 µm	230–232 µm	185–190 µm	139–155 µm
Legs	Well developed	Well developed	Well developed	Well developed	Well developed
Dimensions of metathoracic legs (µm):					
coxa	60–70	71–73	86–103	70–82	52–65
trochanter + femur	80–92	97–102	125–135	115–130	97–100
tibia	50–55	68–70	87–93	75–81	57–59
tarsus	45–49	55–58	69–74	55–60	56–60
claw	15–16	17–19	19–20	17–19	14–19
Length of tarsal digitules (µm):	Shorter: 28–35 Longer: 40–42	Shorter: 31–33 Longer: 40–46	Shorter: 35–40 Longer: 37–44	Shorter: 35–38 Longer: 40–45	Shorter: 36–40 Longer: 41–45
Length of claw digitules (µm):	22–24	22–24	19–25	25–27	25–26
Denticle on claw	Absent	Absent	Present	Present	Present

Group I includes two species that are considered exotic to the Neotropical region, namely *C. floridensis*, thought to be native to the Oriental region (Tang 1991), and *C. stellifer* of uncertain origin. *Ceroplastes cirripediformis*, which falls in this group, was considered to be native to the southern or western United States of America (Nearctic region) by Gimpel *et al*. (1974) but, according to Qin *et al*. (1998), it is native to the Neotropical part of Mexico and/or the Caribbean Islands. *Ceroplastes formicarius* and *C. grandis* are probably native to the Neotropics, as they appear to be restricted to South America (García *et al*. 2016).

All species studied here in groups II and III are probably native to the Neotropical region. However, due to the shape and arrangement of its stigmatic setae, *C. iheringi* (group III), which is only known from the neotropics, should probably be included in *Waxiella*, a genus otherwise restricted to the Afrotropical region, according Qin and Gullan (1995) and Hodgson and Peronti (2012).

Qin *et al*. (1998), in their study on the biogeography of the wax scales, suggested that the Ceroplastinae originated in an area comprising South America, Africa, Madagascar and India, known as West Gondwana. In the Upper Jurassic (Kimmerdigian Stage, 145 mya), Africa, India, South America, Australia, Antarctica and Madagascar were all joined together in the super-continent Gondwana. By 125 mya (Lower Cretaceous, Hauterivian Stage), Gondwana had begun to break up, with proto-India beginning to move North and proto-Australia plus Antarctica moving eastwards. Since then, plate tectonics has caused all these regions to separate, introducing barriers such as the South Atlantic and Indian Oceans and thus dividing the ancestral Ceroplastinae into isolated populations in South America, Africa and India. We suggest, therefore, that Group II, with species restricted to the Neotropical region, is probably more recent than Groups I and III, which includes representatives from other regions.

In addition, although they lack dry-wax filaments, the third-instar nymphs and adult females of Group II have characters that are otherwise similar to those in the corresponding instars of groups I and III species, such as the presence of clear dermal areas without microducts and the presence of the nucleus of the wax plates (Fig. 9A). The presence of these character-states in all three groups suggests that their ancestor should also have had such filaments.

However, more studies will be needed that include further species, particularly from the Afrotropical region, in order to solve the evolutionary origin of each group and to establish other possible groupings.

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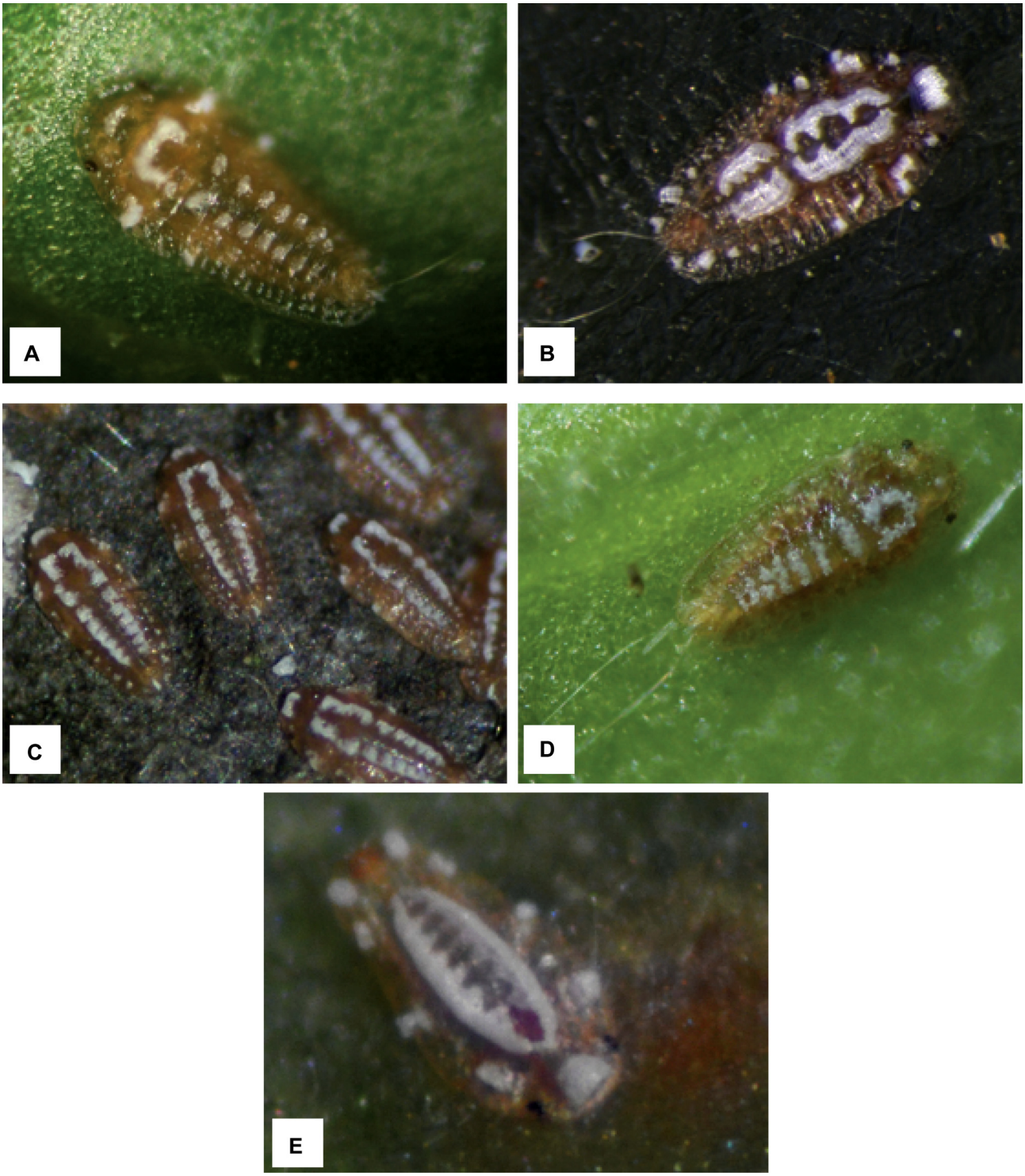

FIGURE 1. Pattern of dry wax tests on early first-instar nymphs: A) *Ceroplastes cirripediformis* Comstock; B) *C. floridensis* Comstock; C) *C. formicarius* Hempel; D) *C. grandis* Hempel; E) *C. stellifer* (Westwood).

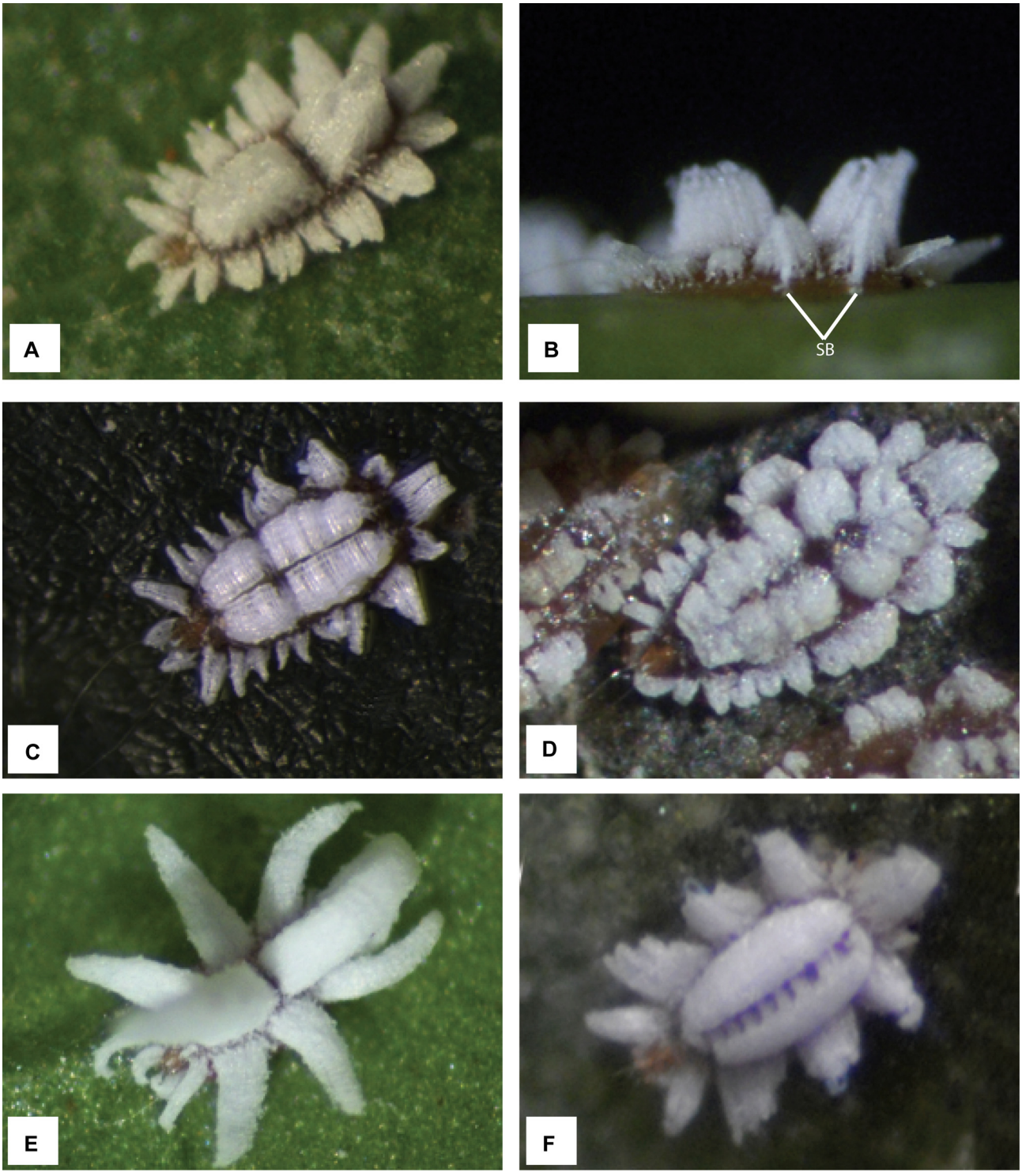

FIGURE 2. Wax test on late first-instar nymphs: A) *Ceroplastes cirripediformis* Comstock; B) *C. cirripediformis* – side view (where: SB = stigmatic band); C) *C. floridensis* Comstock; D) *C. formicarius* Hempel; E) *C. grandis* Hempel; F) *C. stellifer* (Westwood).

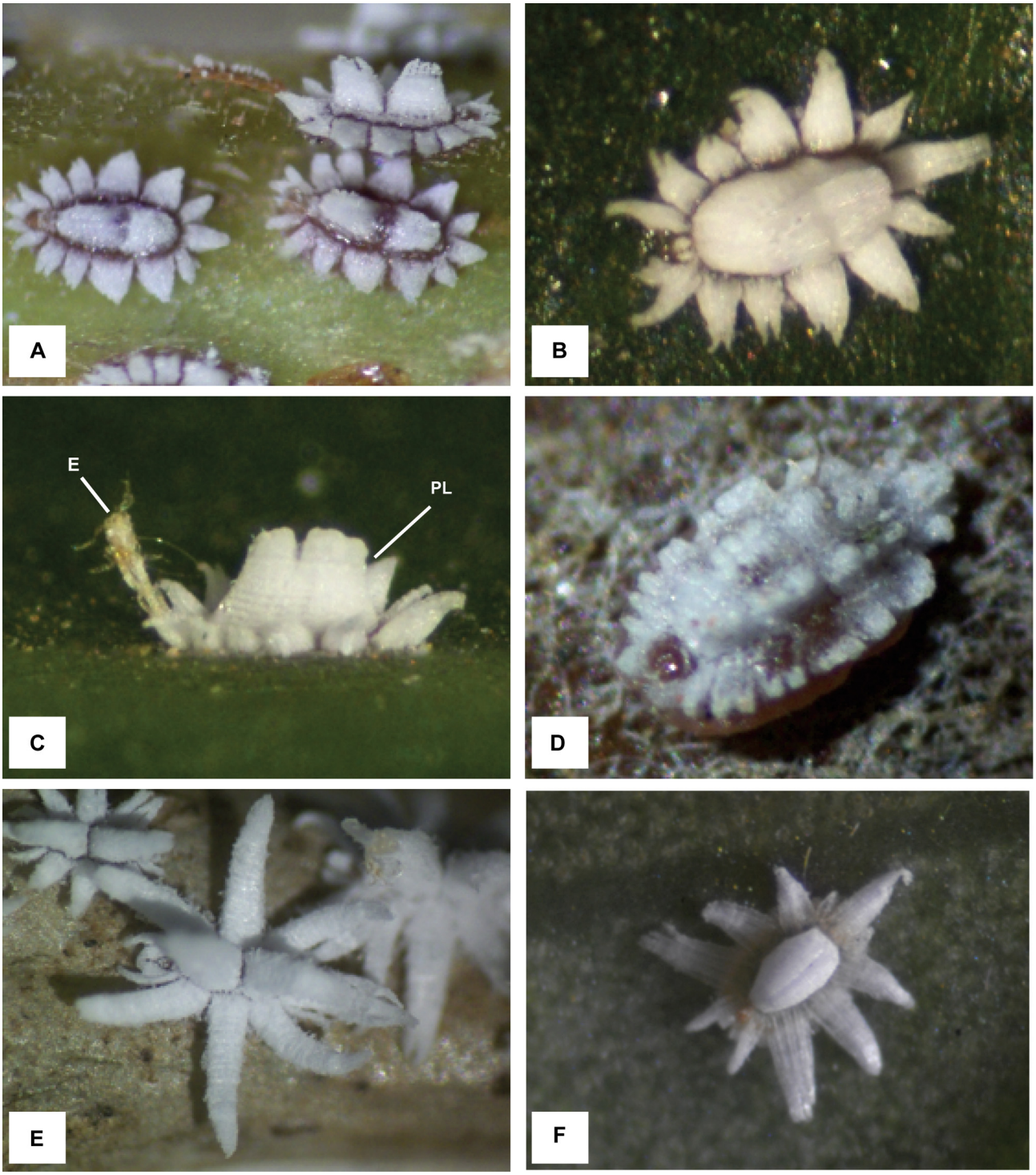

FIGURE 3. Wax tests on second-instar nymphs: A) *Ceroplastes cirripediformis* Comstock; B) *C. floridensis* Comstock; C) *C. floridensis*—side view (where: E = exuviae and PL = partition line) D) *C. formicarius* Hempel; E) *C. grandis* Hempel; F) *C. stellifer* (Westwood).

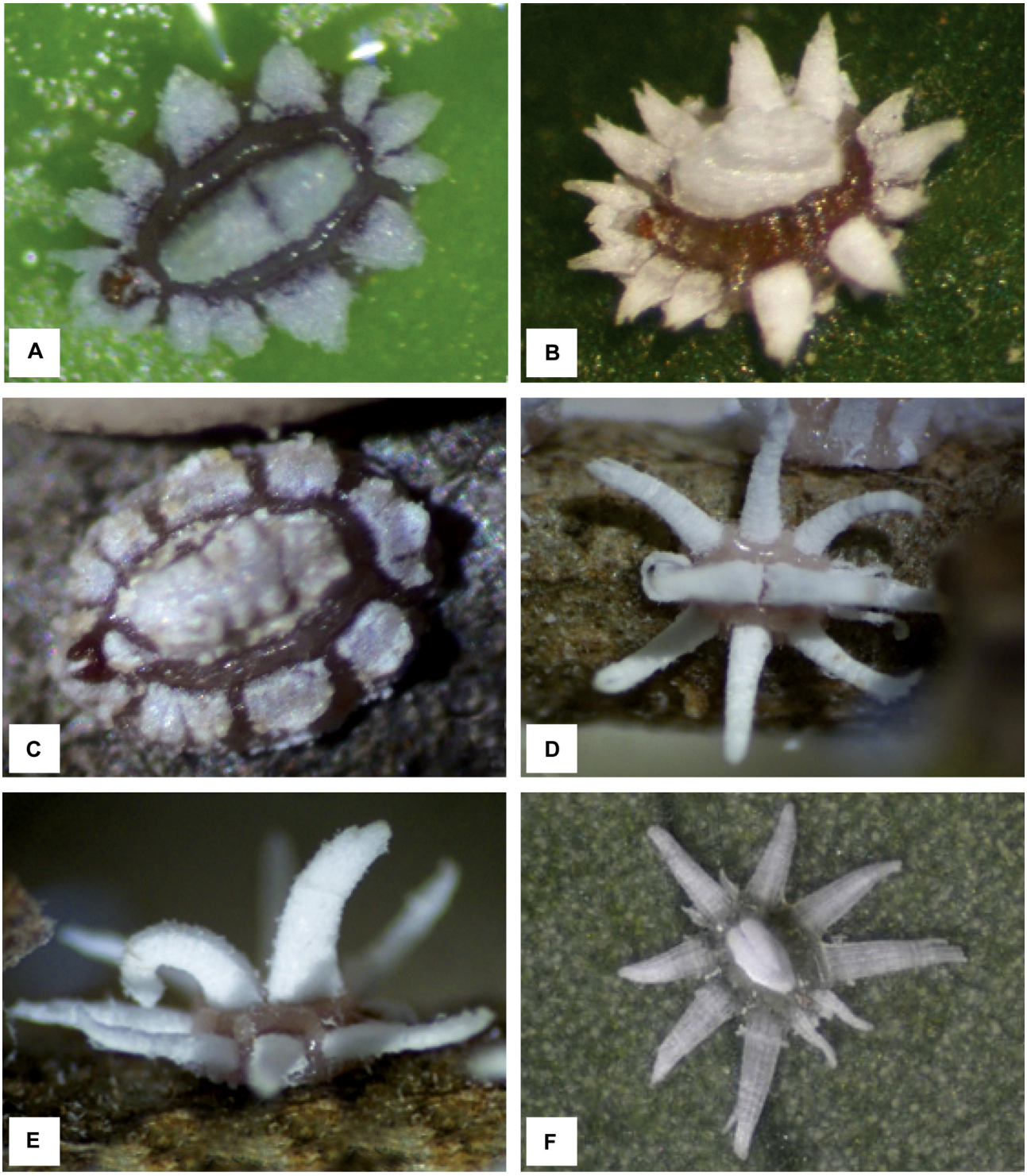

FIGURE 4. Wax tests on early third-instar nymphs: A) *Ceroplastes cirripediformis* Comstock; B) *C. floridensis* Comstock; C) *C. formicarius* Hempel; D) *C. grandis* Hempel; E) *C. grandis* – side view; F) *C. stellifer* (Westwood).

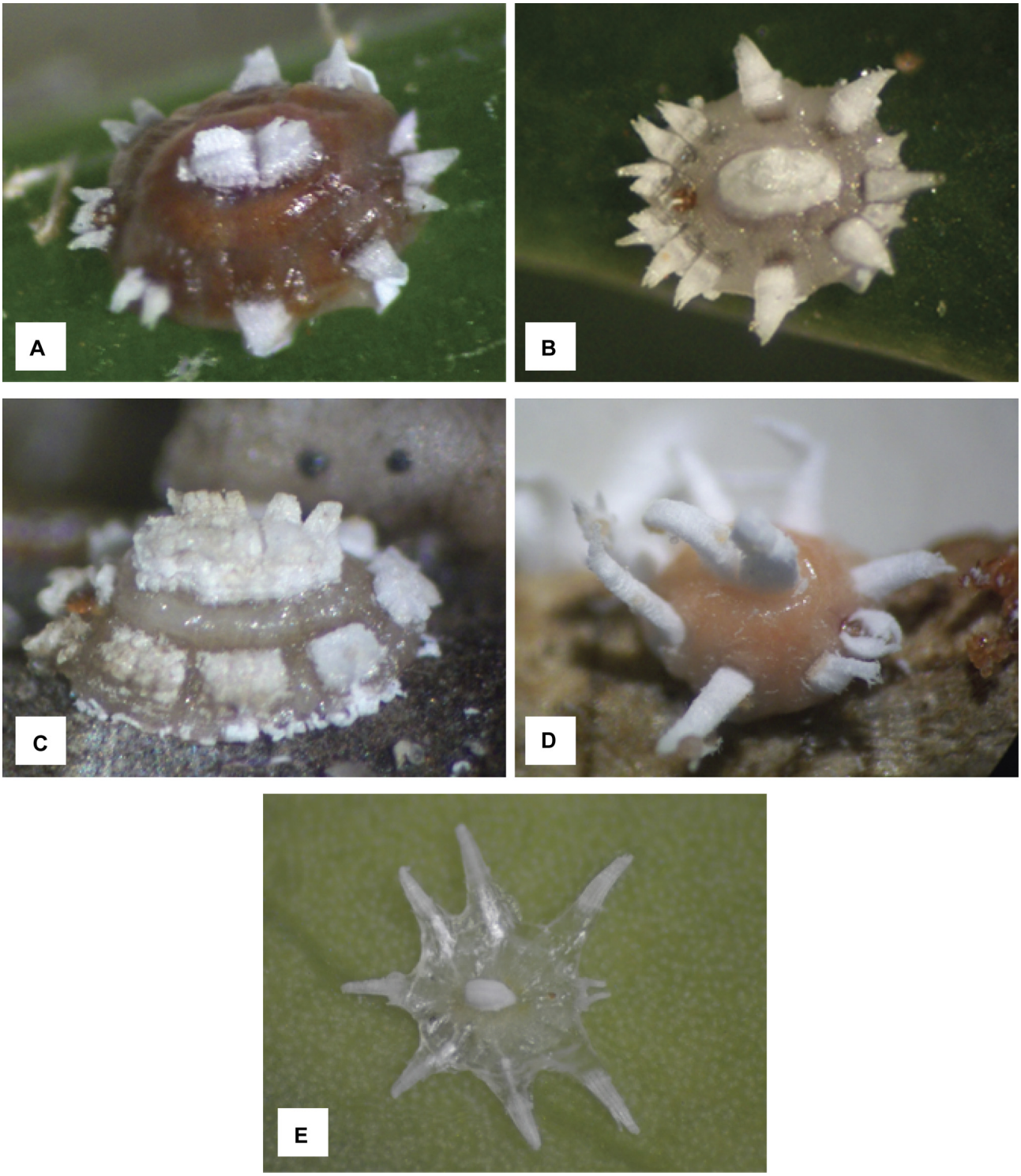

FIGURE 5. Wax tests on late third-instar nymphs: A) *Ceroplastes cirripediformis* Comstock; B) *C. floridensis* Comstock; C) *C. formicarius* Hempel; D) *C. grandis* Hempel; E) *C. stellifer* (Westwood).

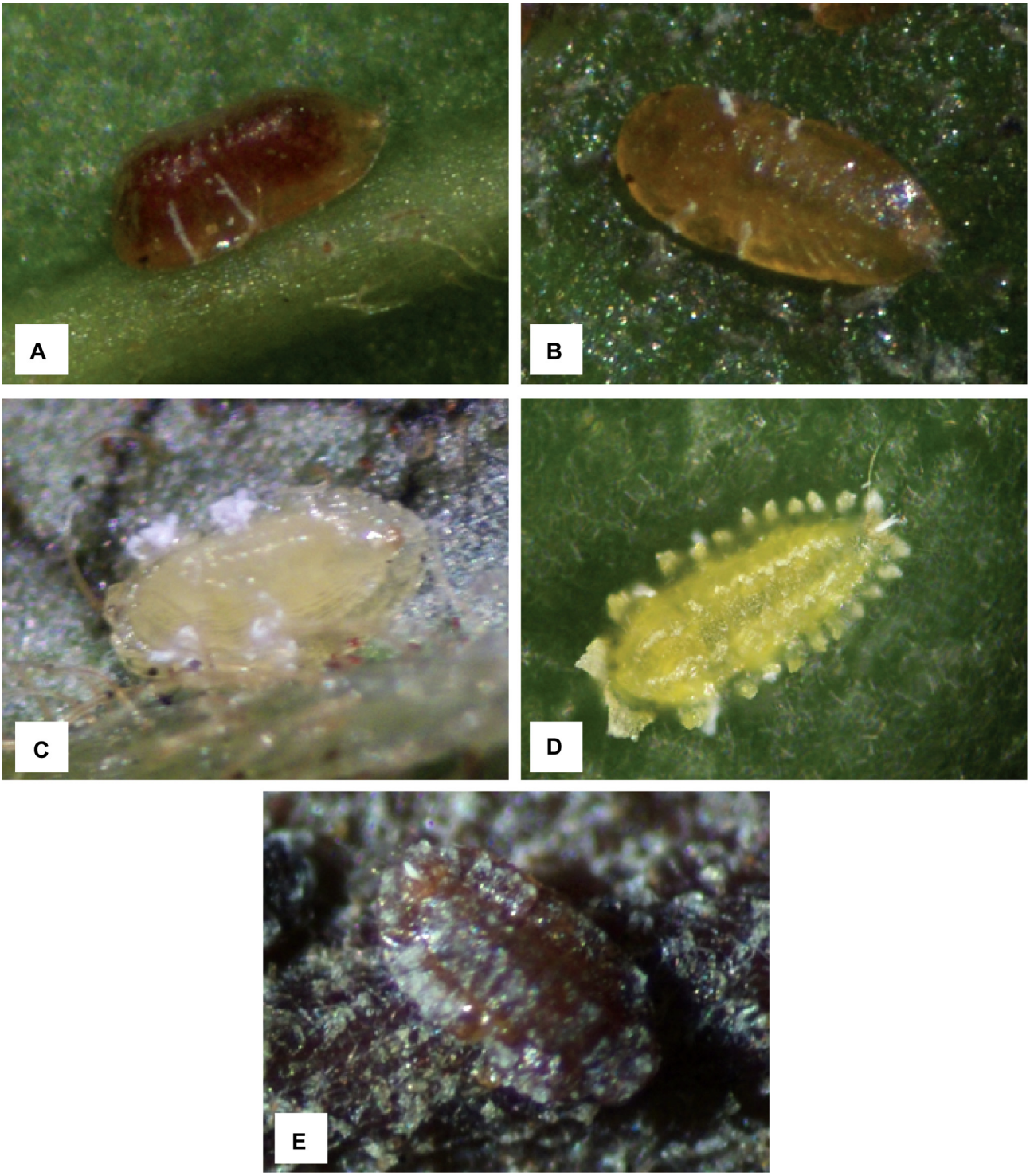

FIGURE 6. Glassy wax tests on first-instar nymphs: A) *Ceroplastes formosus* Hempel; B) *C. lucidus* Hempel; C) *C. diospyros* Hempel; D) *C. flosculoides* Matile-Ferrero; E) *C. iheringi* Cockerell.

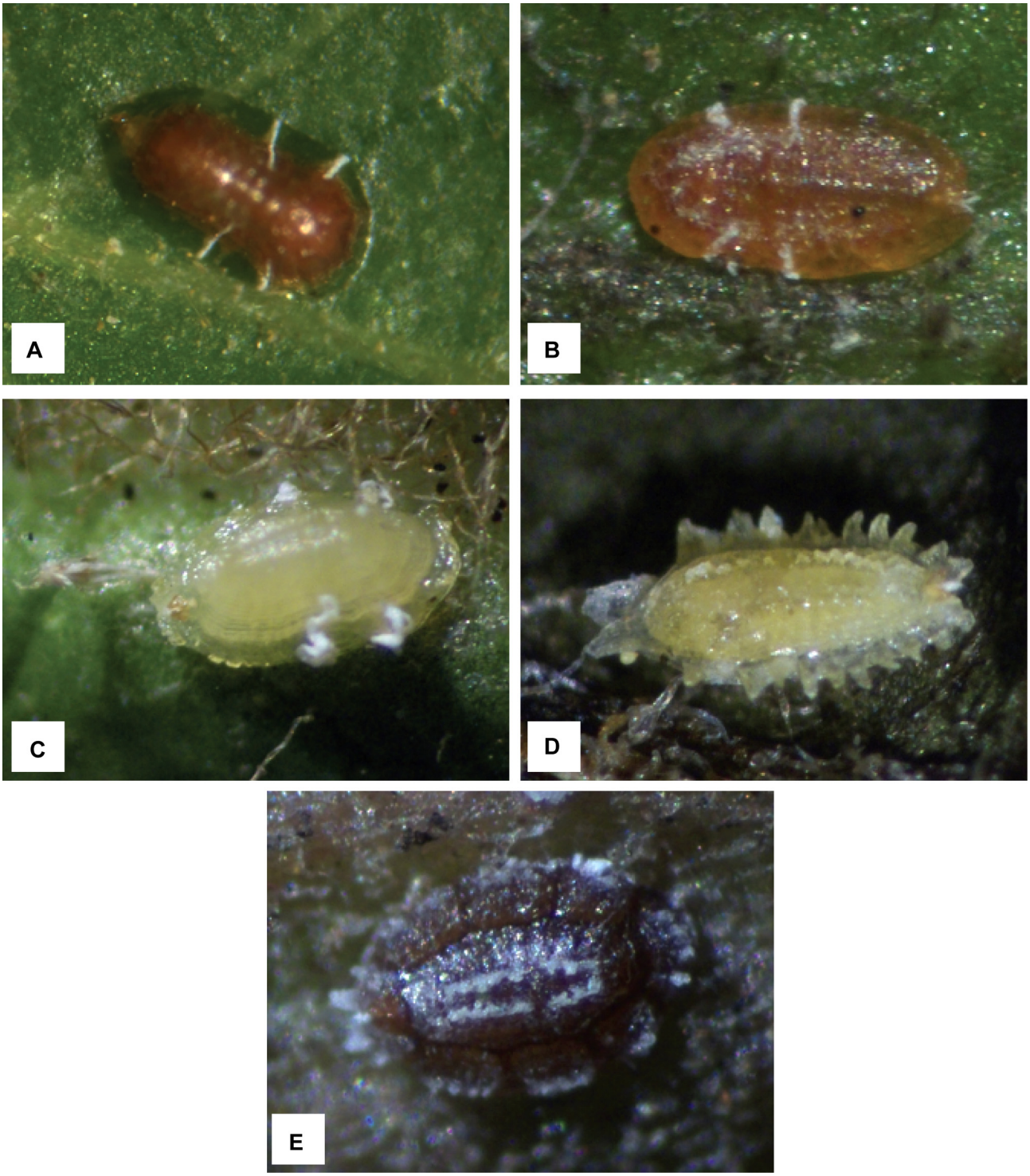

FIGURE 7. Glassy wax tests on second-instar nymphs: A) *Ceroplastes formosus* Hempel; B) *C. lucidus* Hempel; C) *C. diospyros* Hempel; D) *C. flosculoides* Matile-Ferrero; E) *C. iheringi* Cockerell.

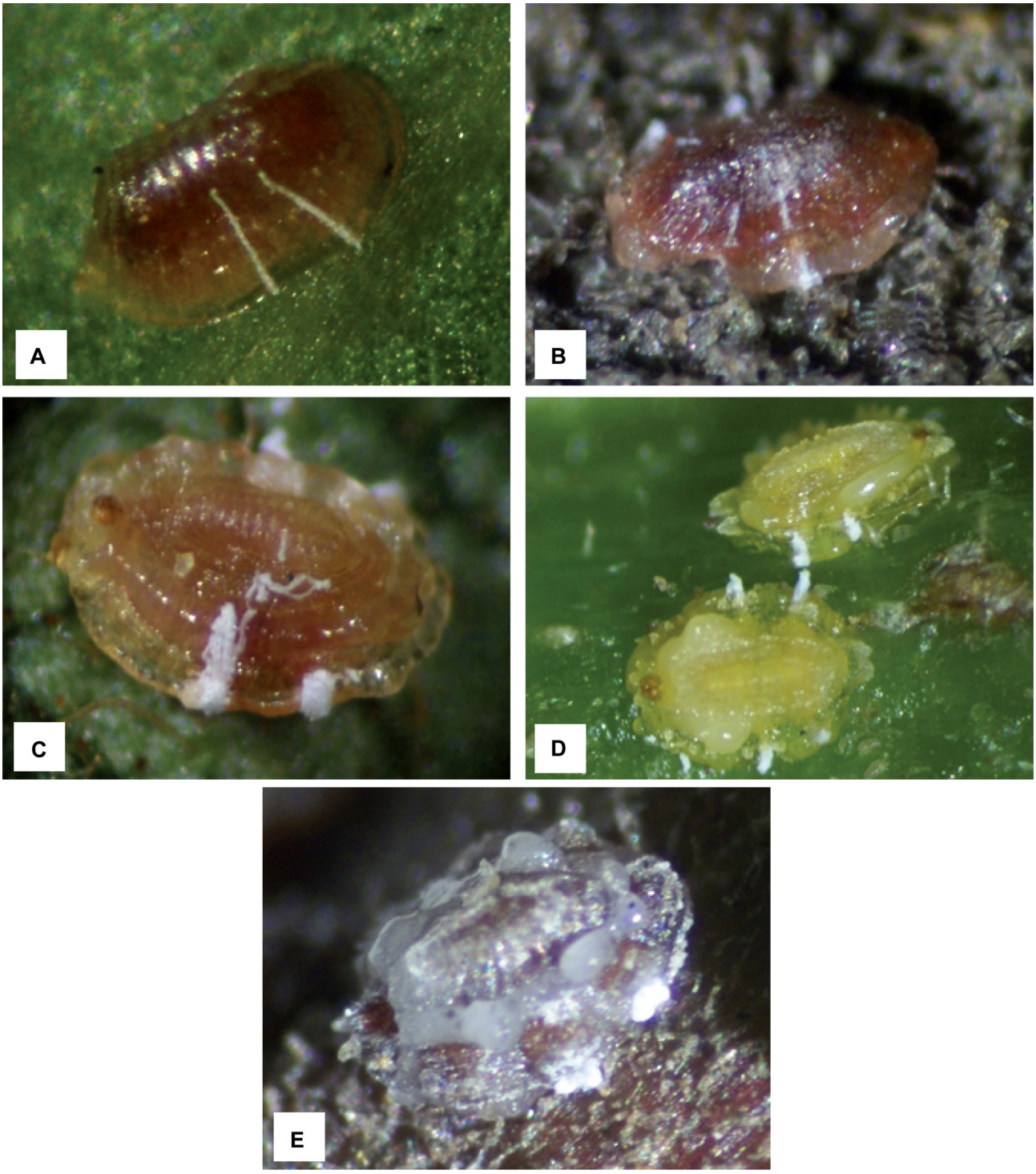

FIGURE 8. Wax tests on early third-instar nymphs: A) *Ceroplastes formosus* Hempel; B) *C. lucidus* Hempel; C) *C. diospyros* Hempel; D) *C. flosculoides* Matile-Ferrero; E) *C. iheringi* Cockerell.

FIGURE 9. Wax tests on late third-instar nymphs: A) *Ceroplastes formosus* Hempel; B) *C. lucidus* Hempel; C) *C. diospyros* Hempel; D) *C. flosculoides* Matile-Ferrero; E) *C. iheringi* Cockerell.

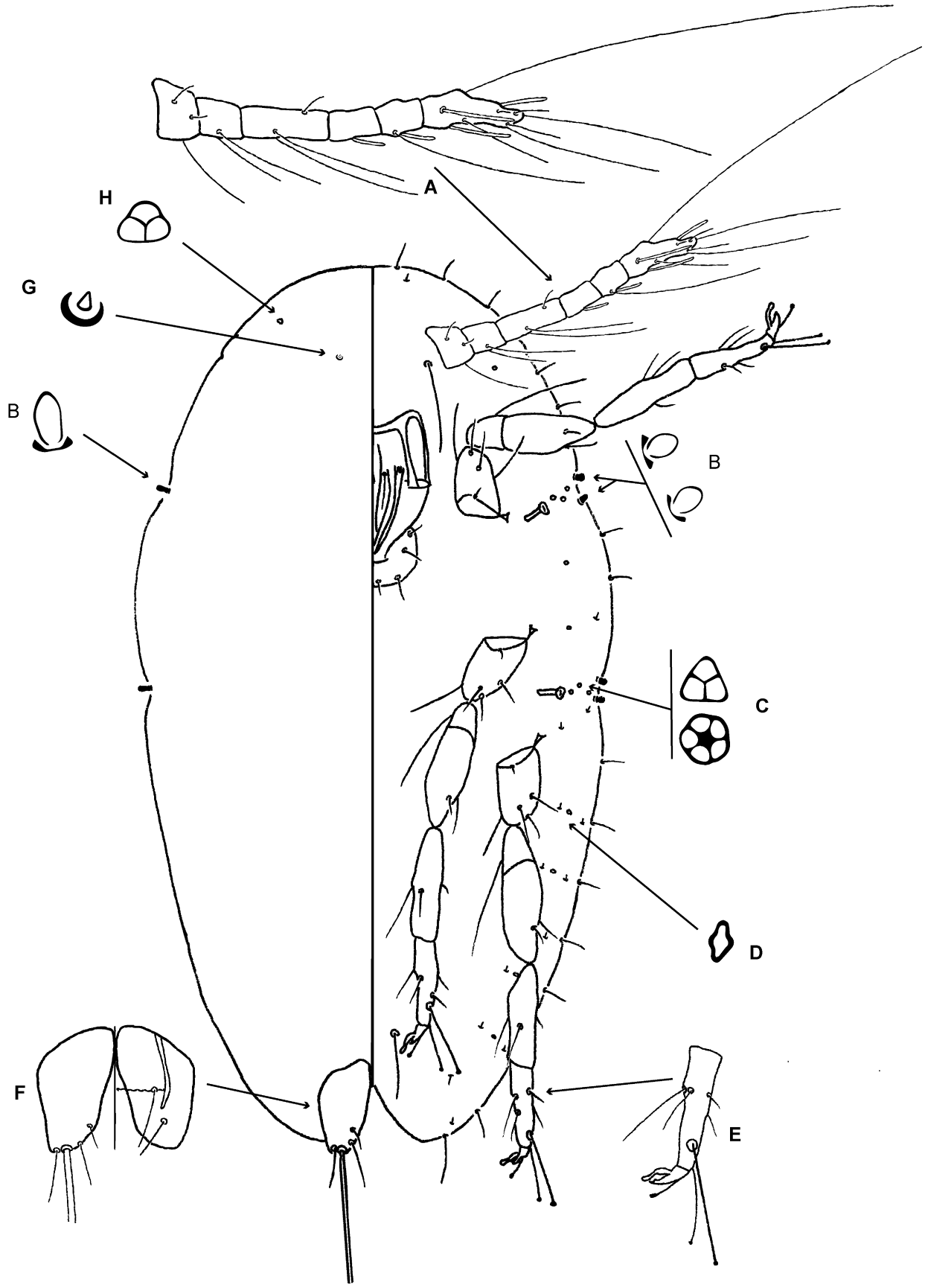

FIGURE 10. *Ceroplastes cirripediformis* Comstock. First-instar nymph. In this and subsequent figures A = antenna; B = stigmatic setae; C = spiracular disc-pores; D = cruciform pore; E = tarsal segment; F = anal plates, dorsal and ventral aspect; G= dorsal setae; H= dorsal pore.

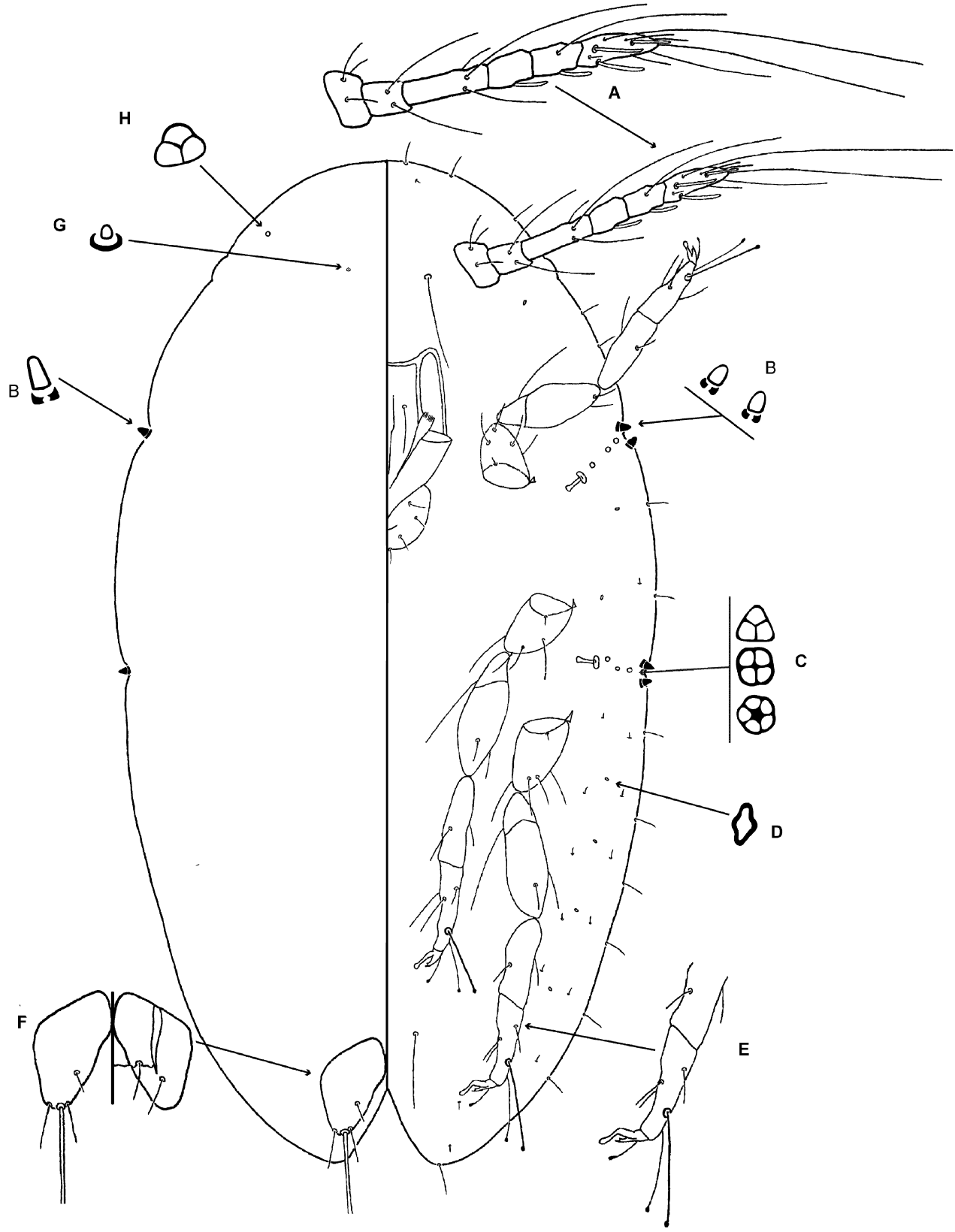

FIGURE 11. *Ceroplastes floridensis* Comstock. First-instar nymph.

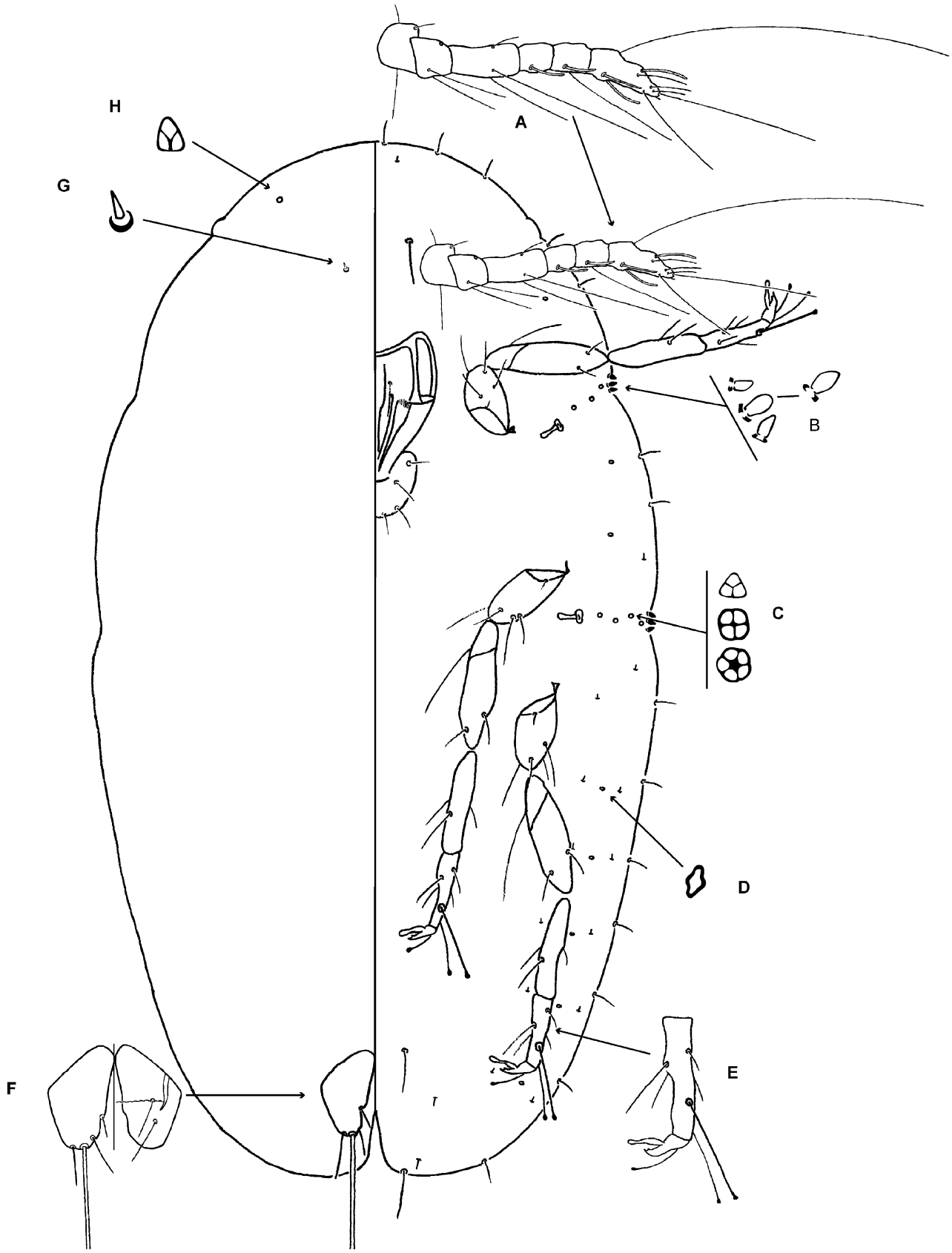

FIGURE 12. *Ceroplastes formicarius* Hempel. First-instar nymph.

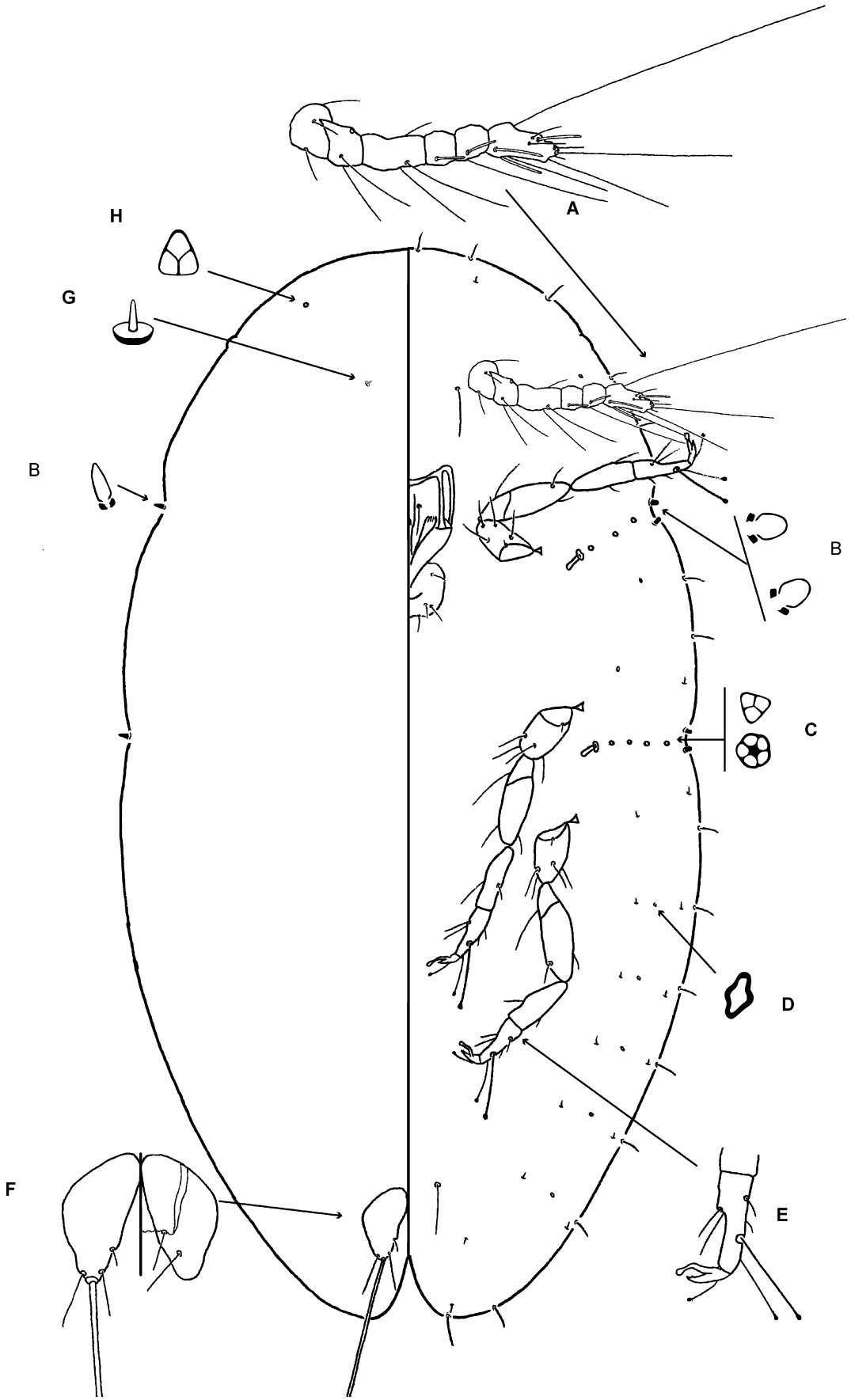

FIGURE 13. *Ceroplastes grandis* Hempel. First-instar nymph.

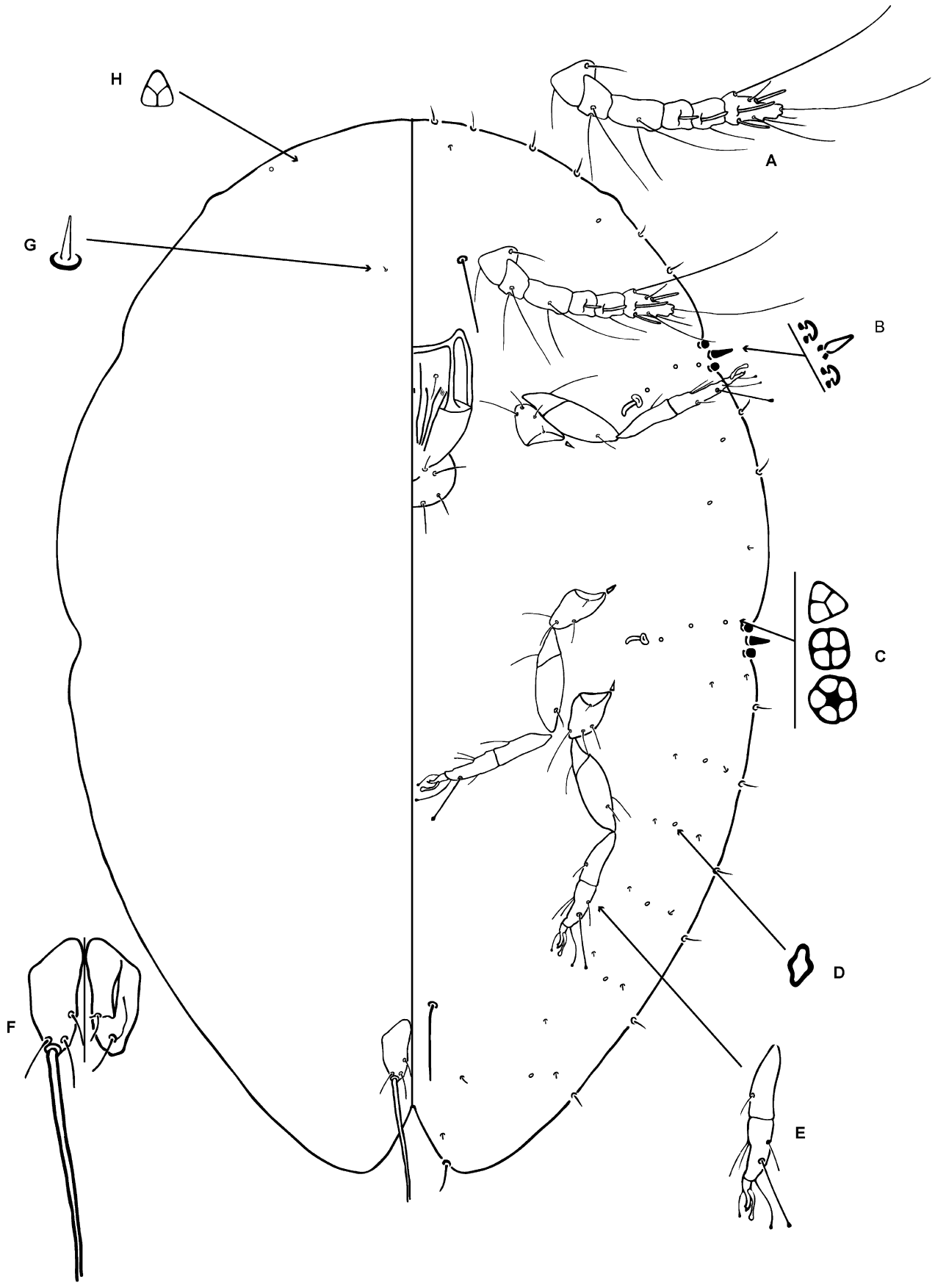

FIGURE 14. *Ceroplastes stellifer* (Westwood). First-instar nymph.

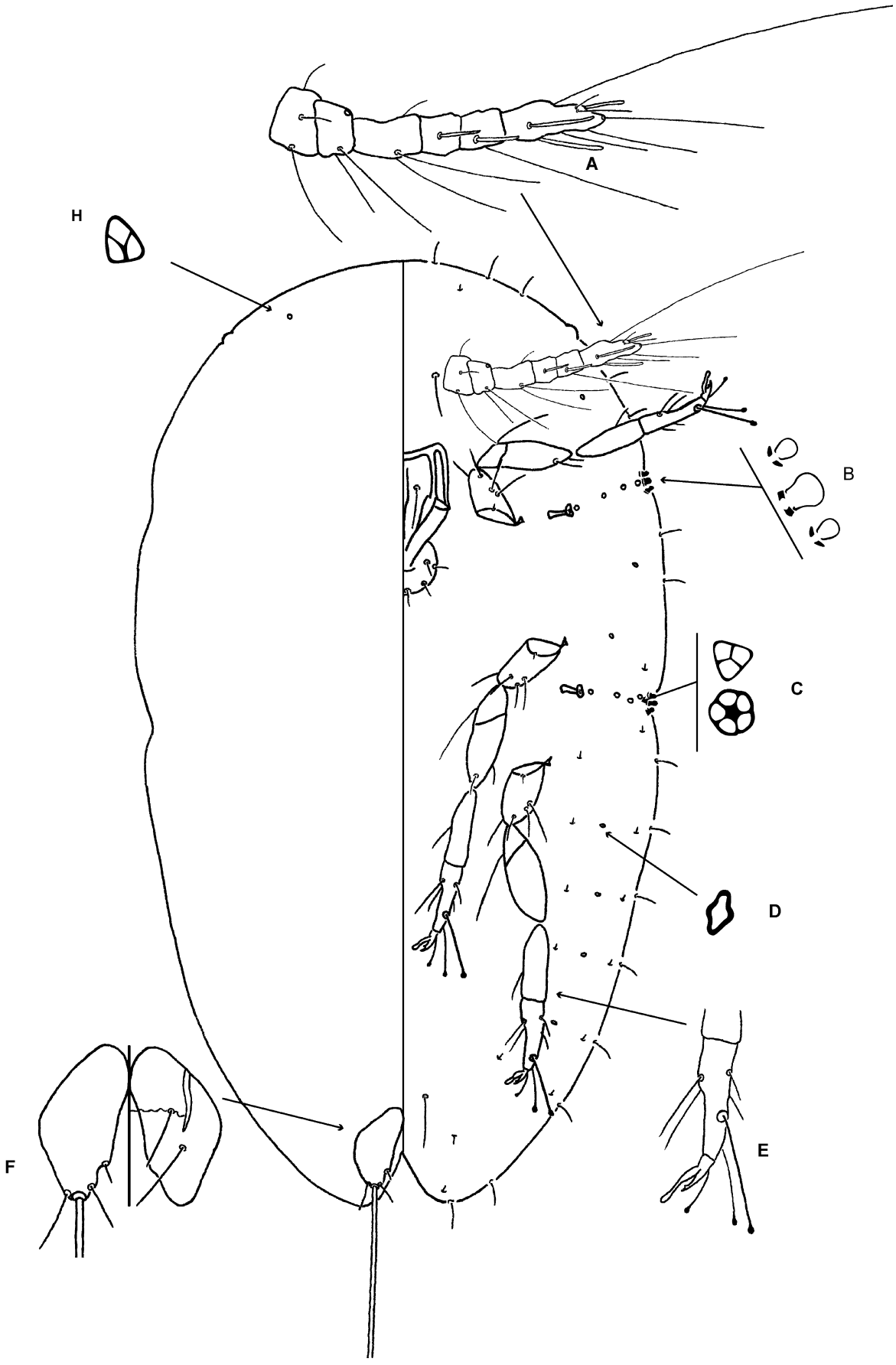

FIGURE 15. *Ceroplastes formosus* Hempel. First-instar nymph.

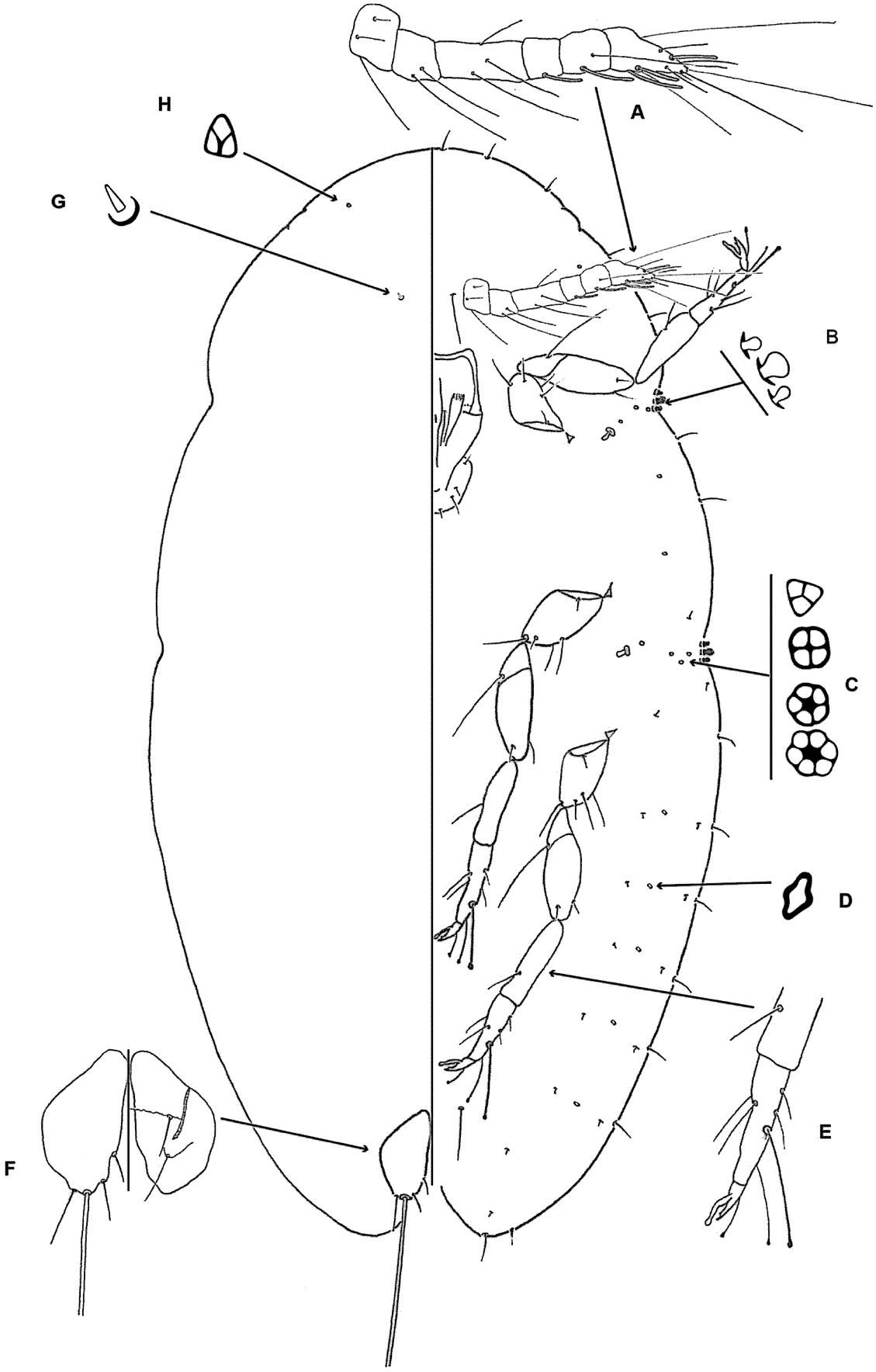

FIGURE 16. *Ceroplastes lucidus* Hempel. First-instar nymph.

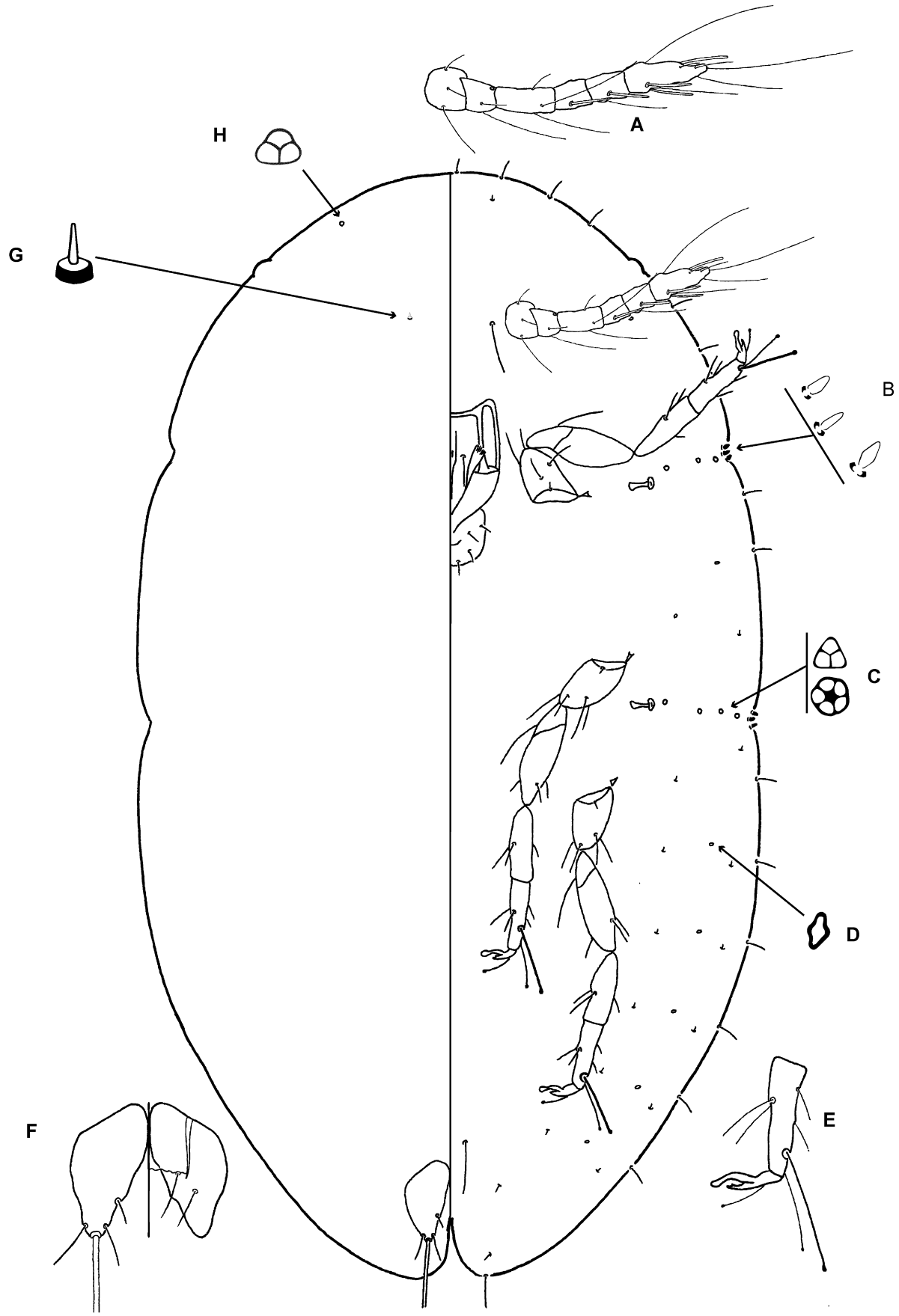

FIGURE 17. *Ceroplastes diospyros* Hempel. First-instar nymph.

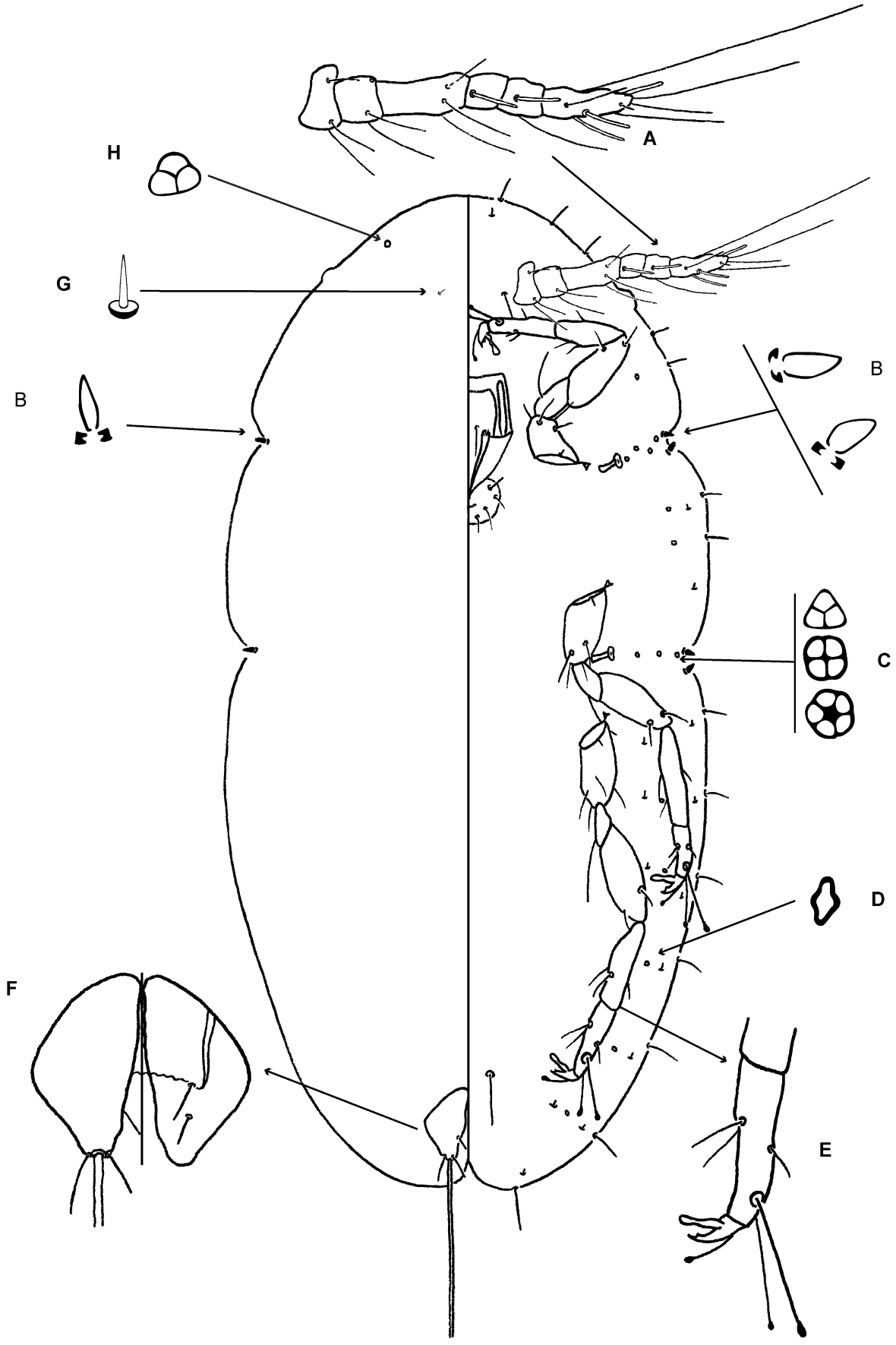

FIGURE 18. *Ceroplastes flosculoides* Matile-Ferrero. First-instar nymph.

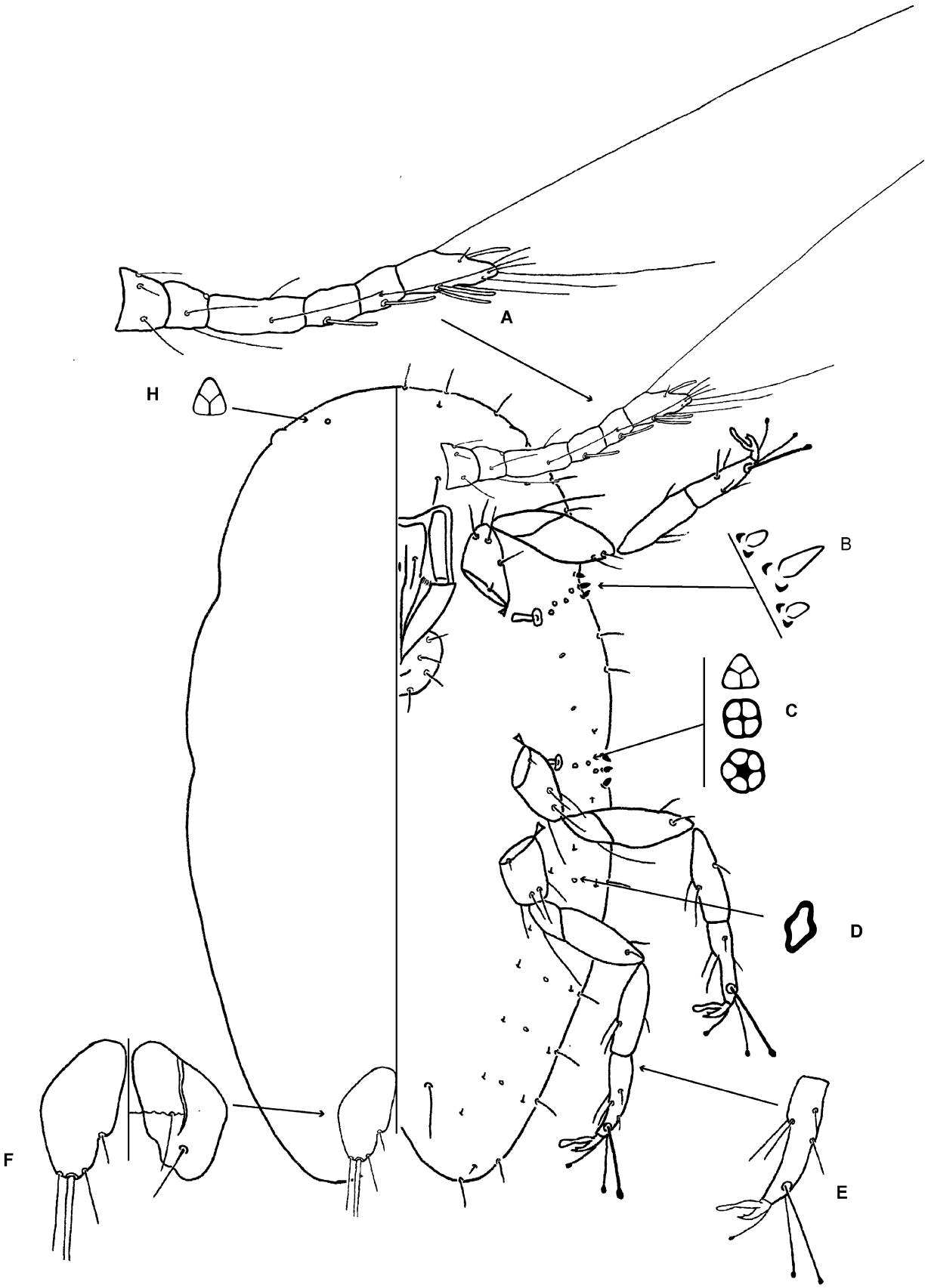

FIGURE 19. *Ceroplastes iheringi* Cockerell. First-instar nymph.

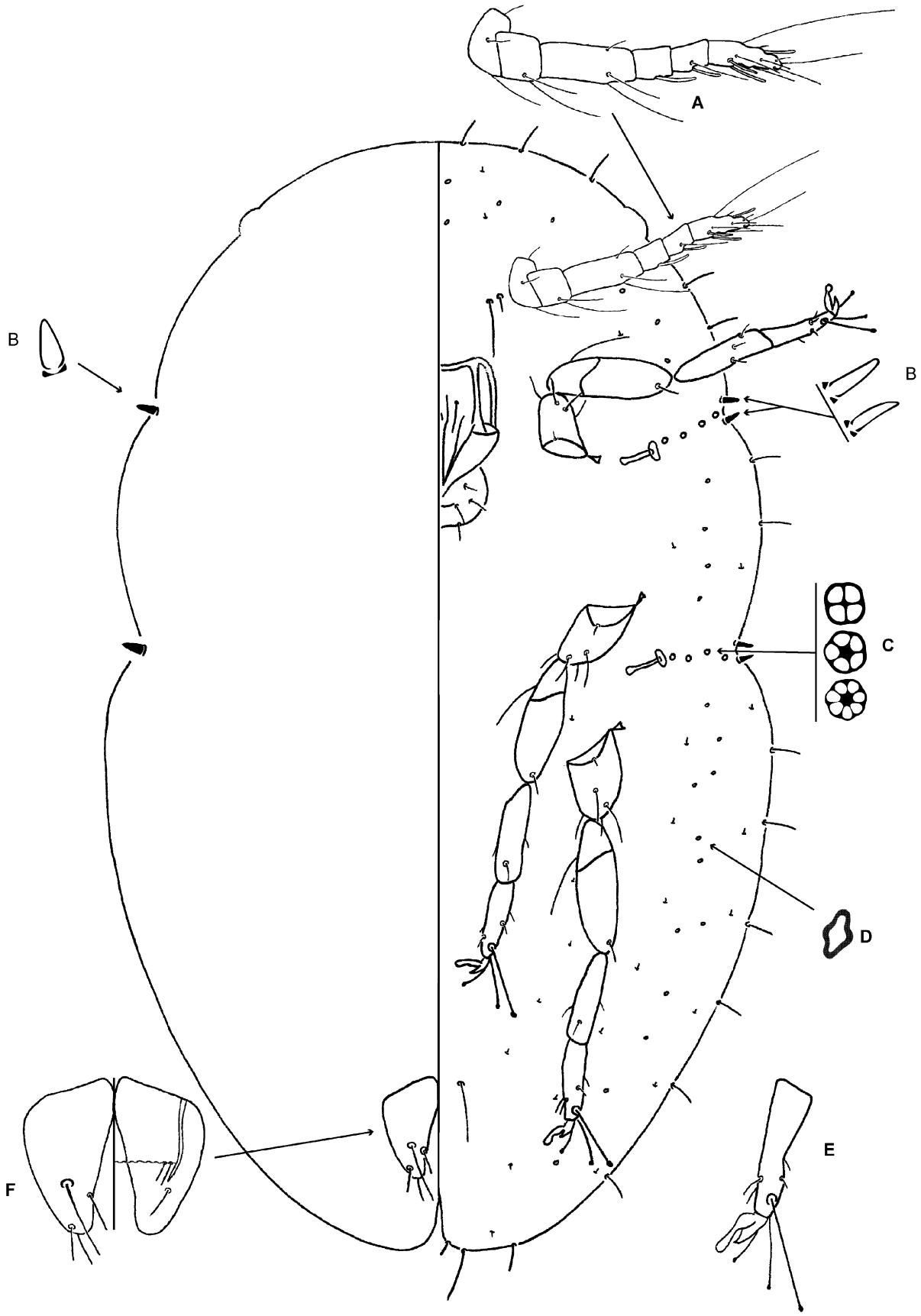

FIGURE 20. *Ceroplastes cirripediformis* Comstock. Second-instar nymph.

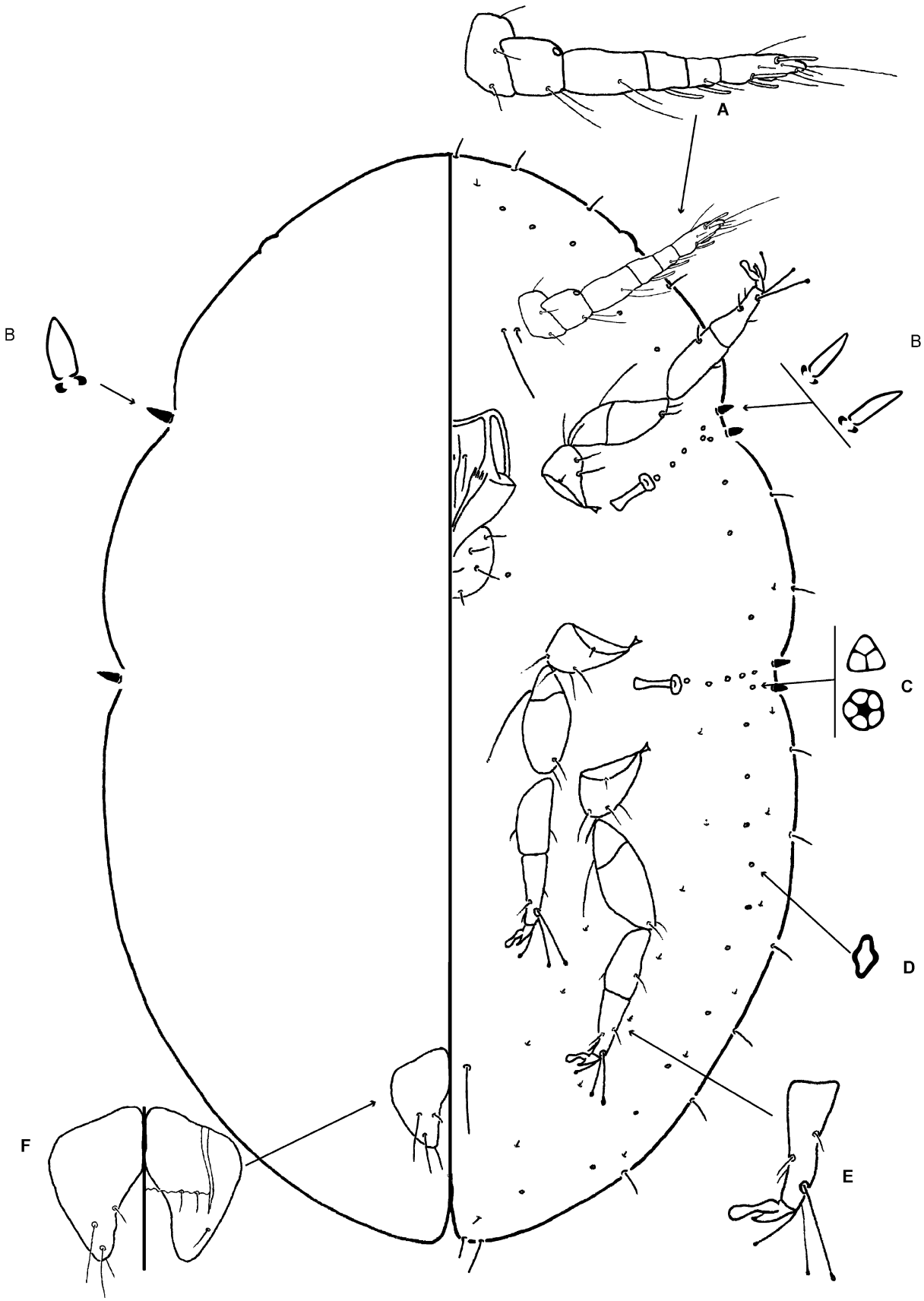

FIGURE 21. *Ceroplastes floridensis* Comstock. Second-instar nymph.

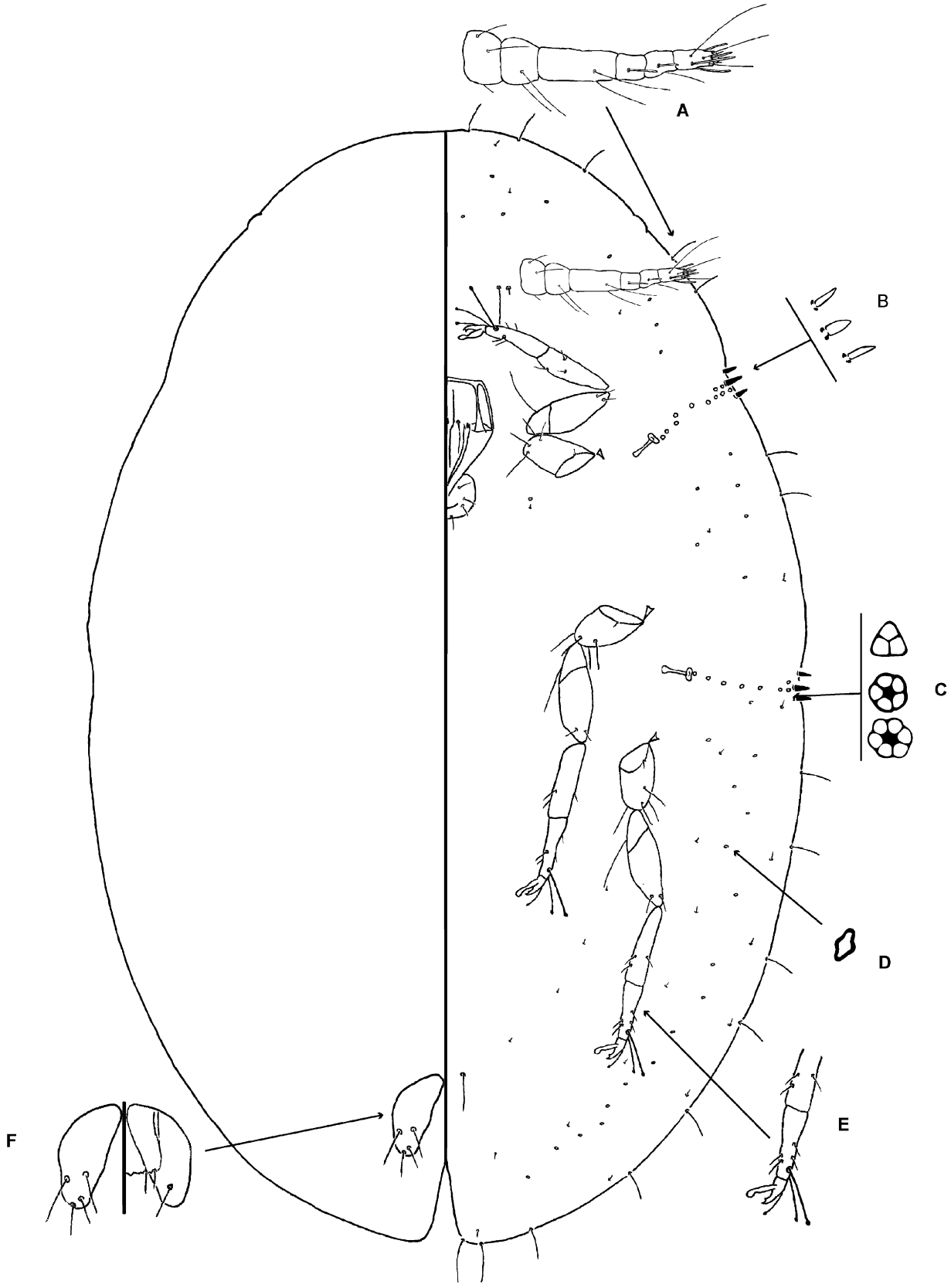

FIGURE 22. *Ceroplastes formicarius* Hempel. Second-instar nymph.

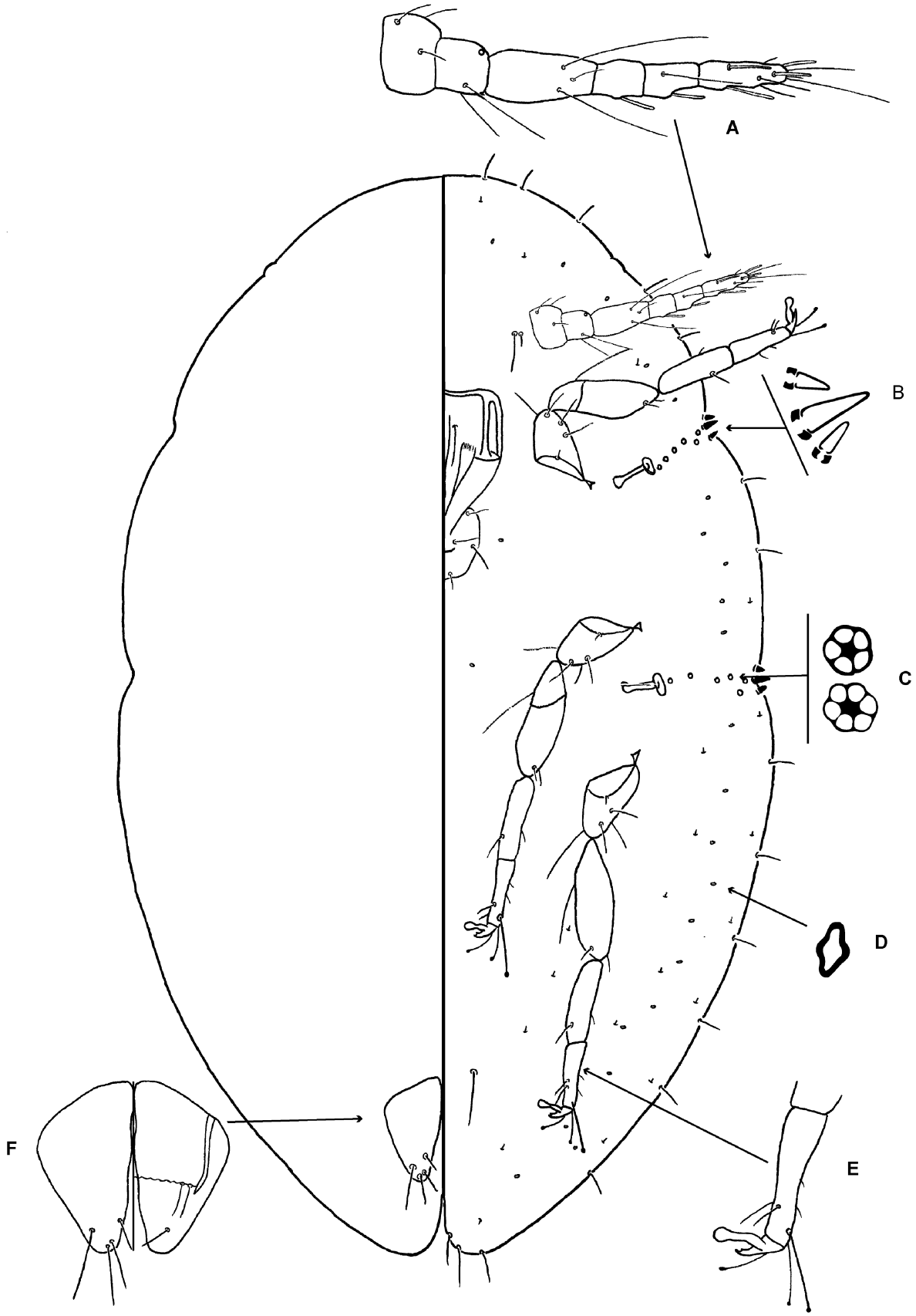

FIGURE 23. *Ceroplastes grandis* Hempel. Second-instar nymph.

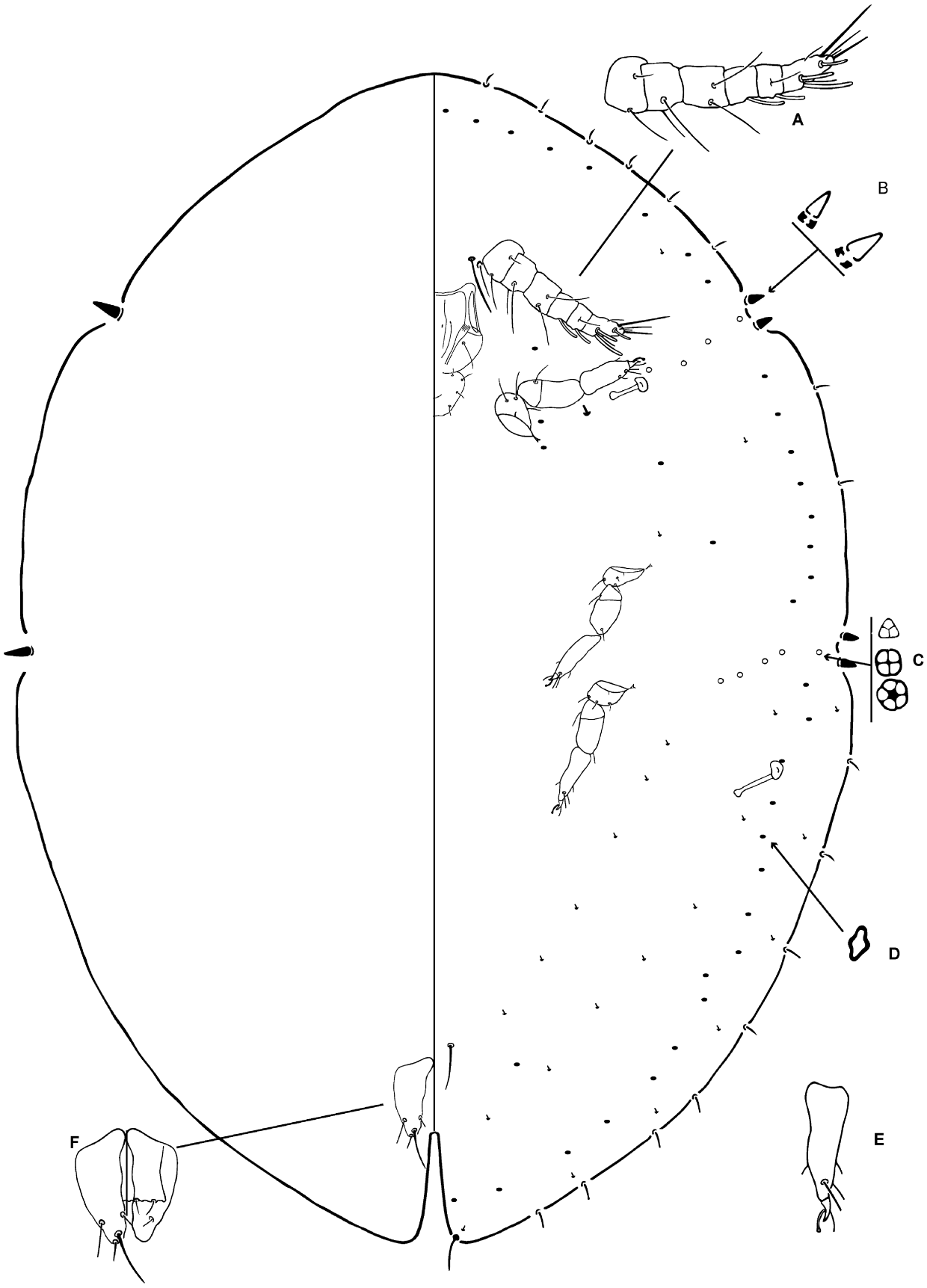

FIGURE 24. *Ceroplastes stellifer* (Westwood,). Second-instar nymph.

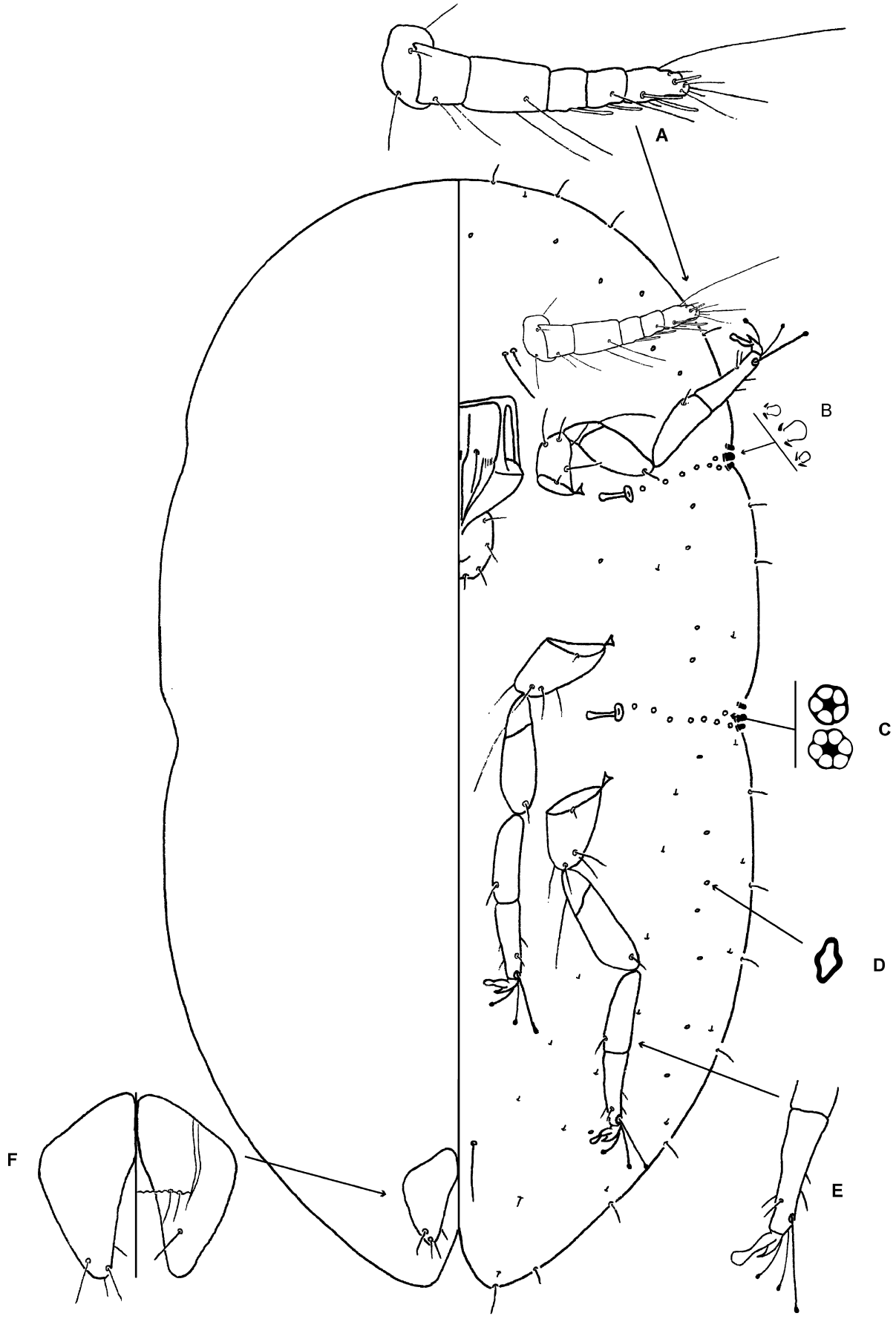

FIGURE 25. *Ceroplastes formosus* Hempel. Second-instar nymph.

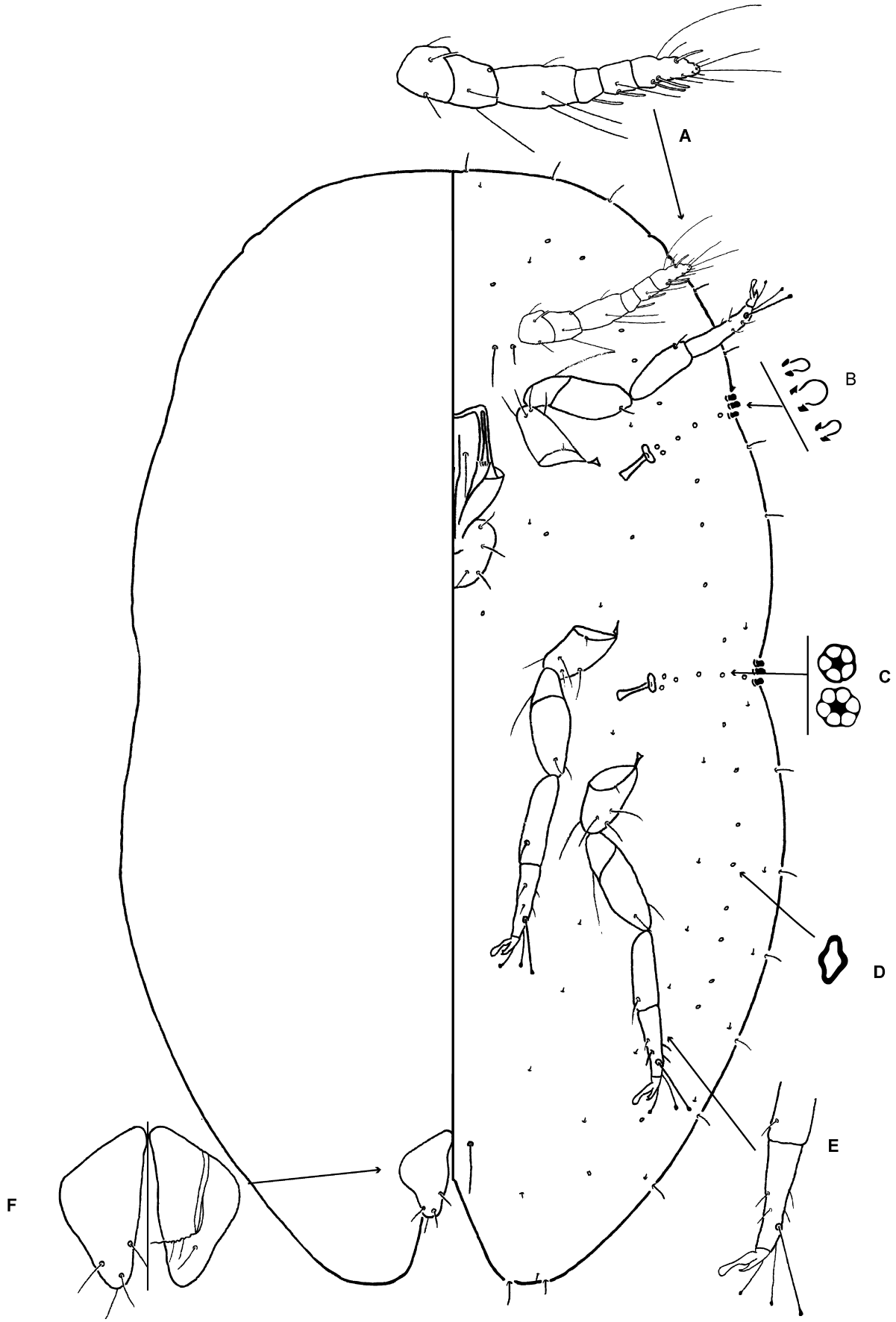

FIGURE 26. *Ceroplastes lucidus* Hempel. Second-instar nymph.

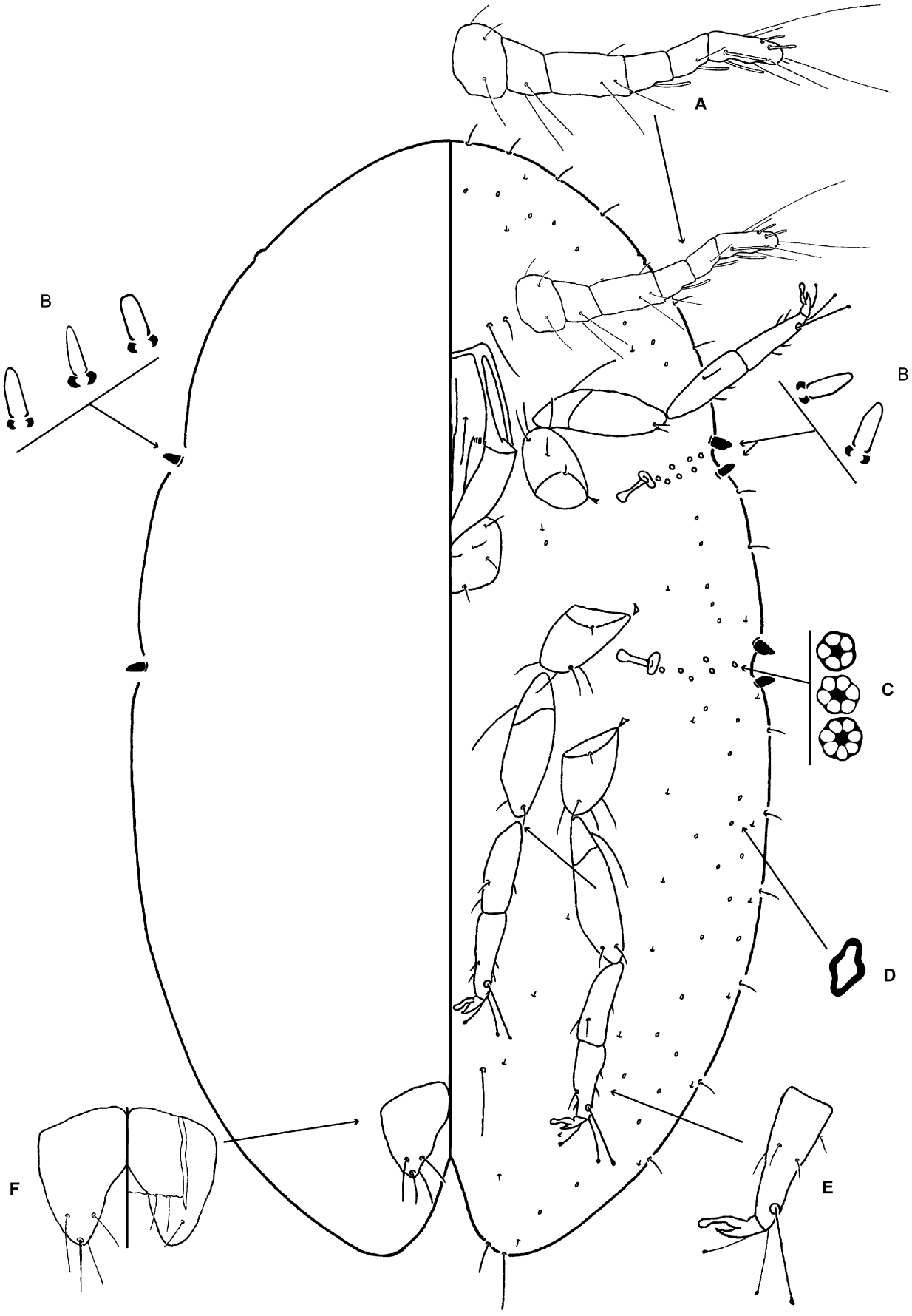

FIGURE 27. *Ceroplastes diospyros* Hempel. Second-instar nymph.

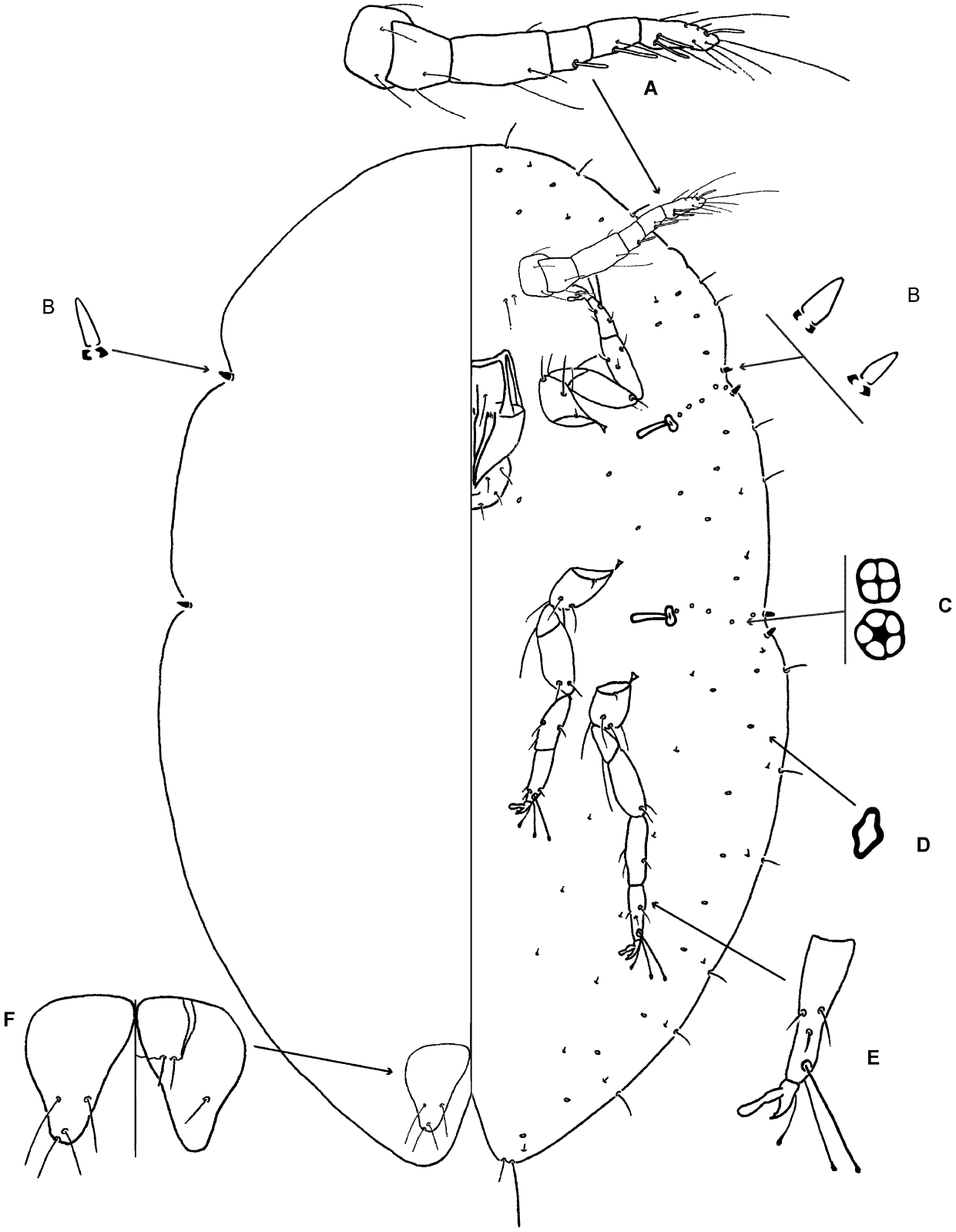

FIGURE 28. *Ceroplastes flosculoides* Matile-Ferrero. Second-instar nymph.

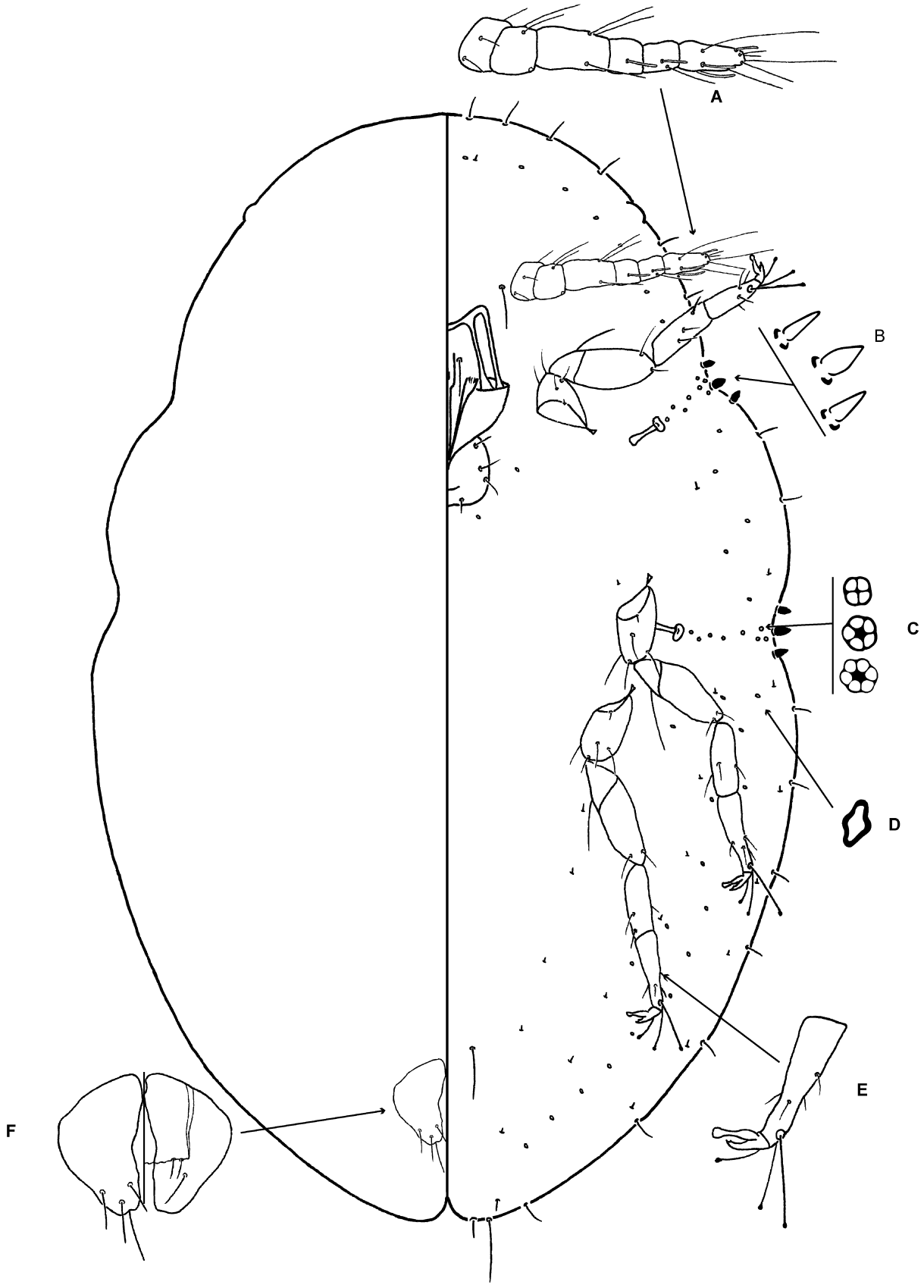

FIGURE 29. *Ceroplastes iheringi* Cockerell. Second-instar nymph.

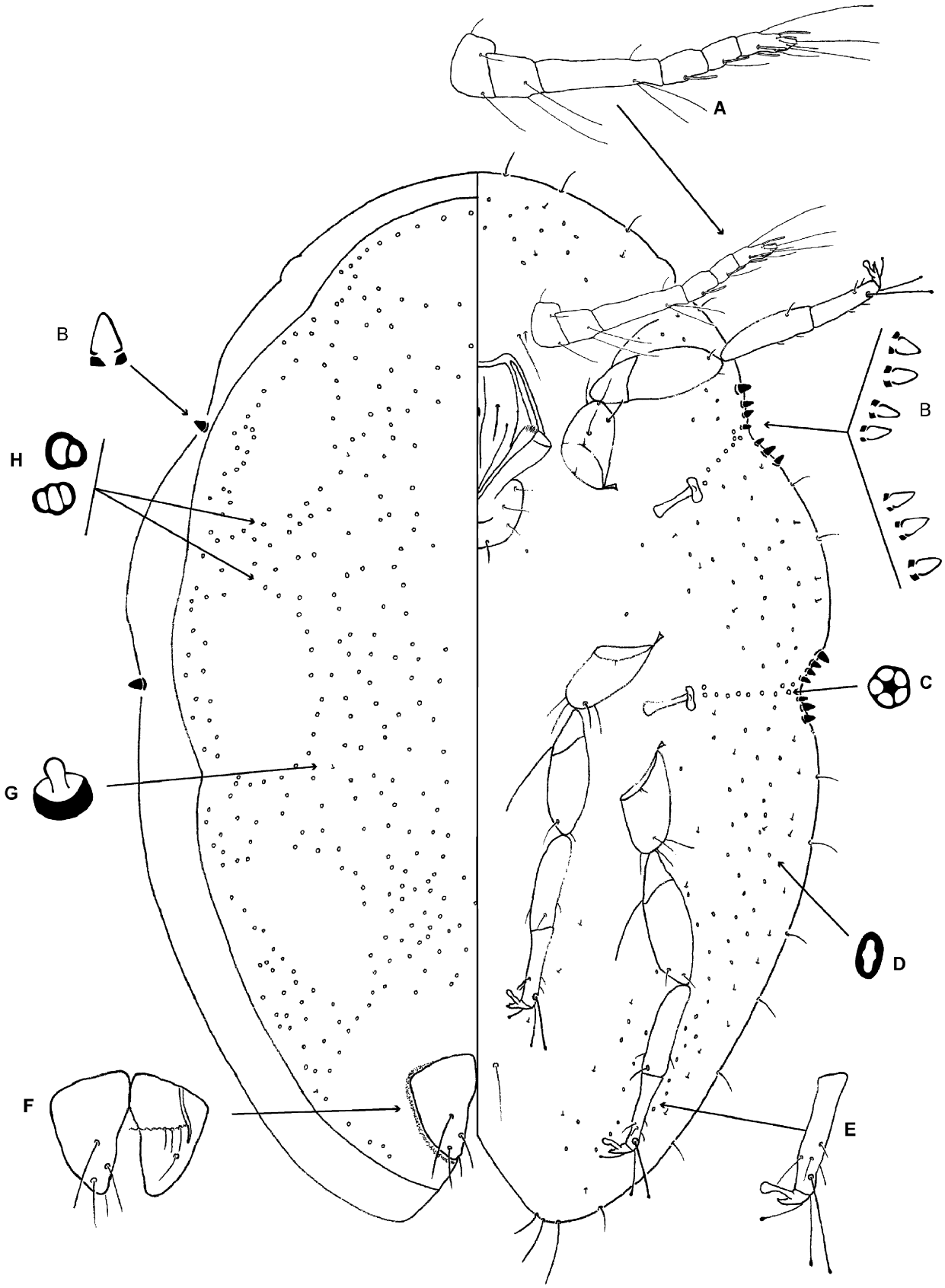

FIGURE 30. *Ceroplastes cirripediformis* Comstock. Third-instar nymph.

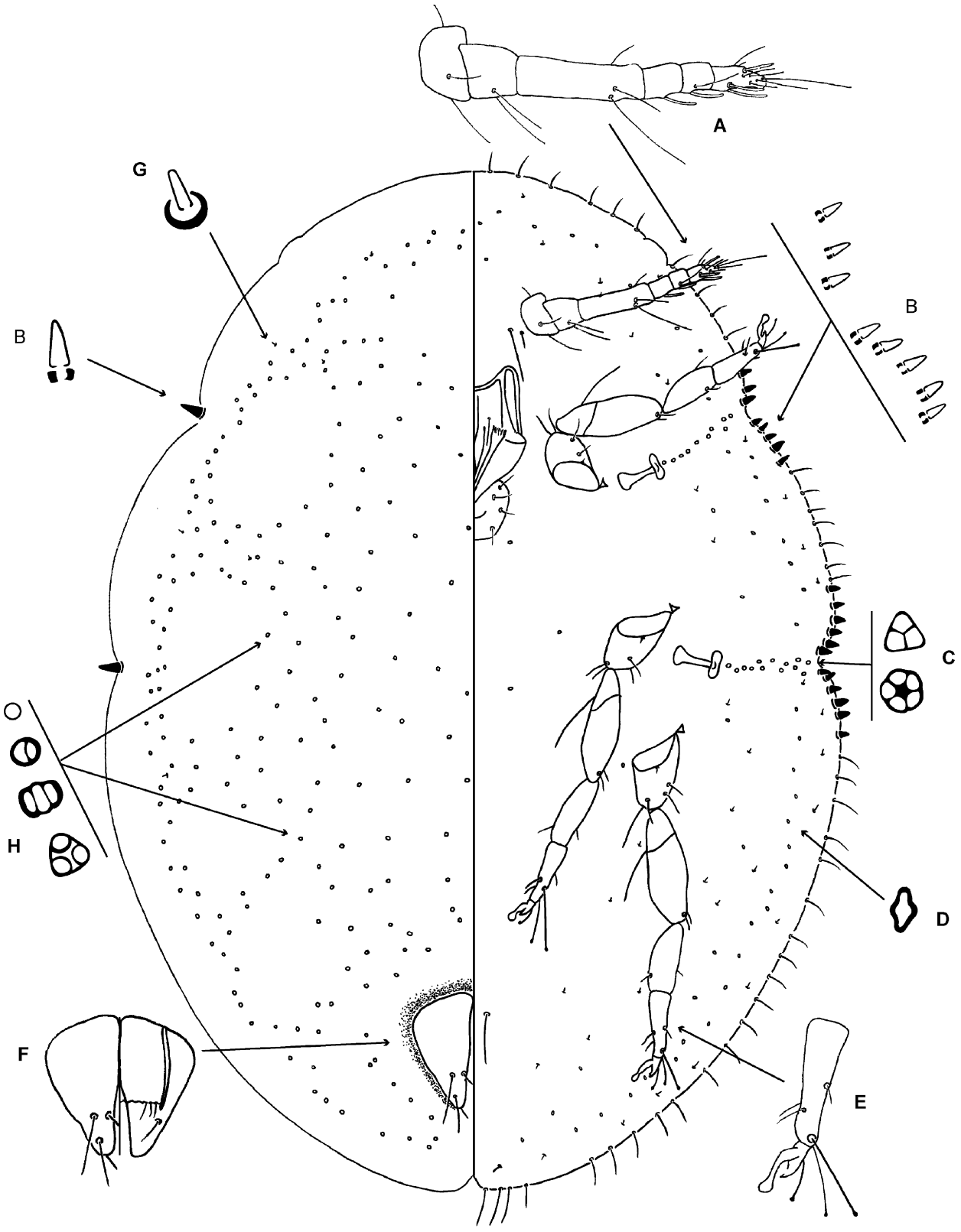

FIGURE 31. *Ceroplastes floridensis* Comstock. Third-instar nymph.

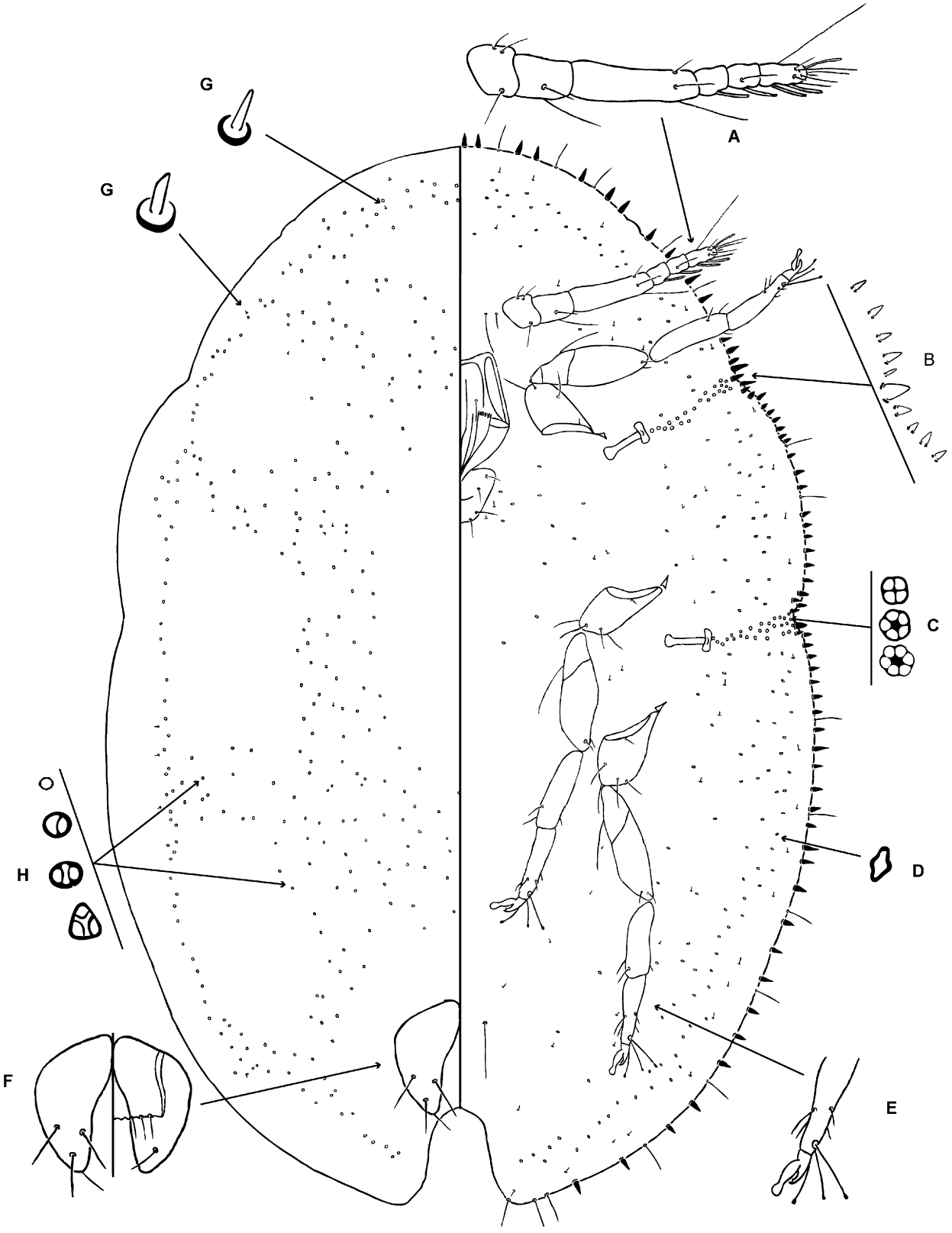

FIGURE 32. *Ceroplastes formicarius* Hempel. Third-instar nymph.

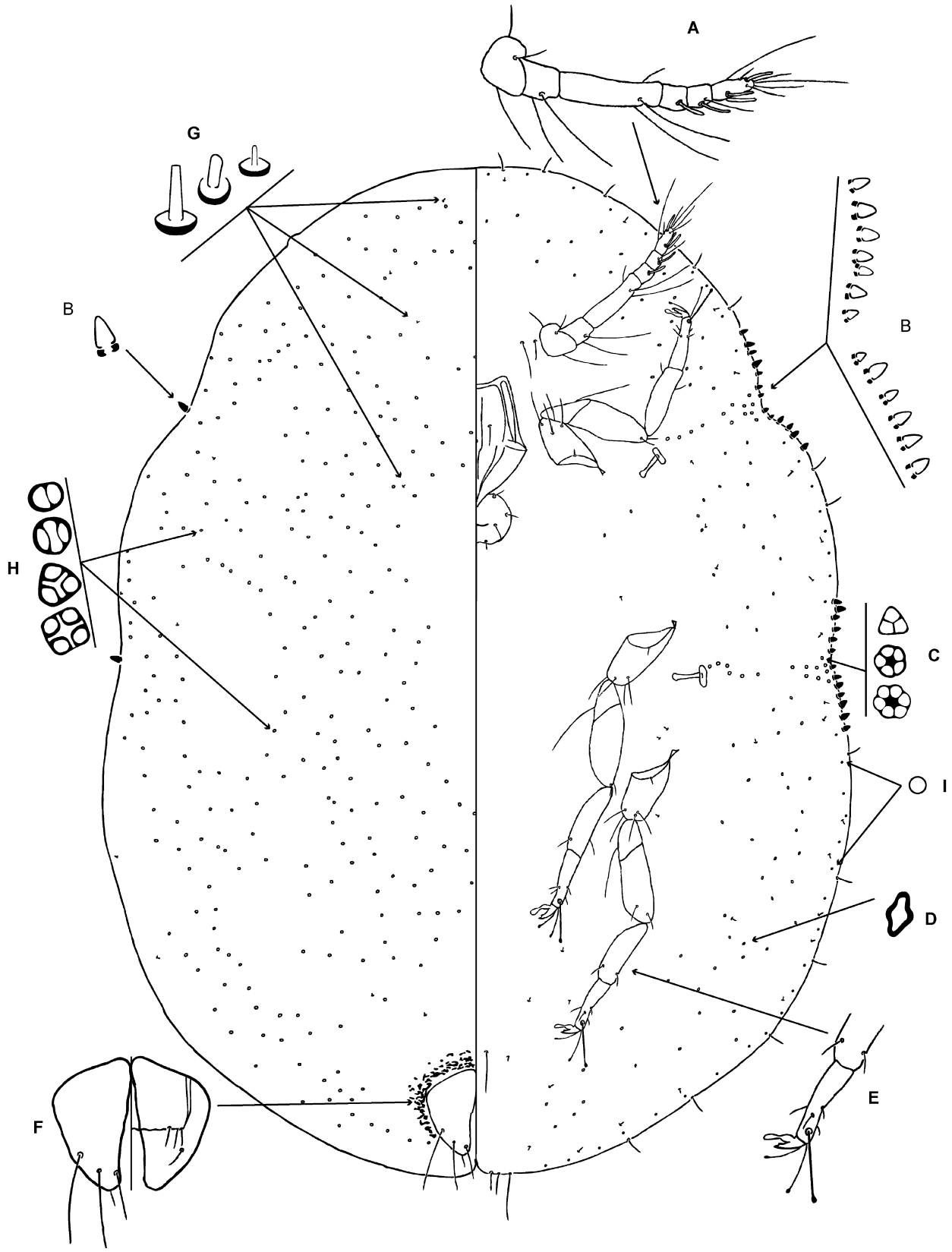

FIGURE 33. *Ceroplastes grandis* Hempel. Third-instar nymph, where I = filamentous ducts.

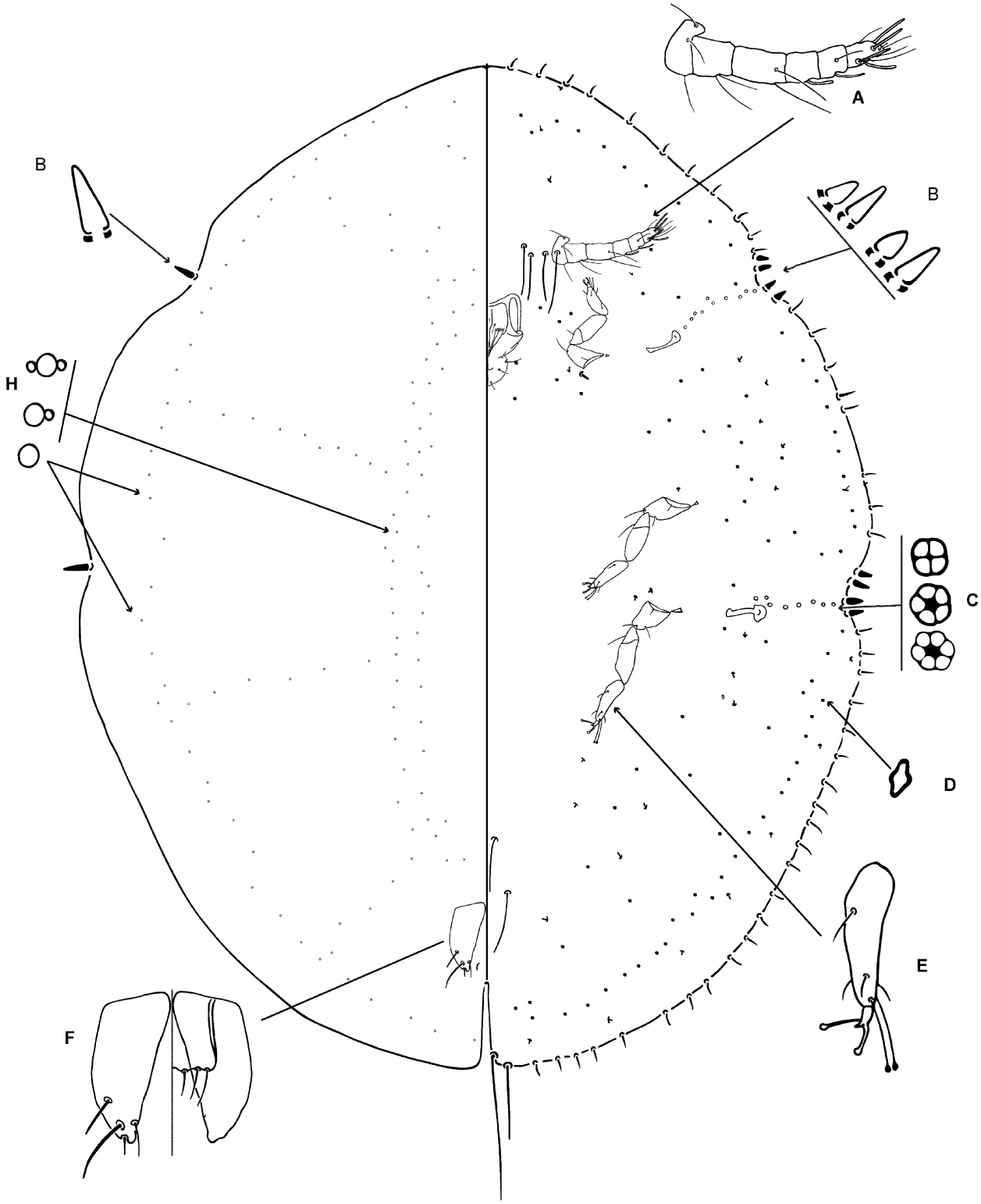

FIGURE 34. *Ceroplastes stellifer* (Westwood). Third-instar nymph.

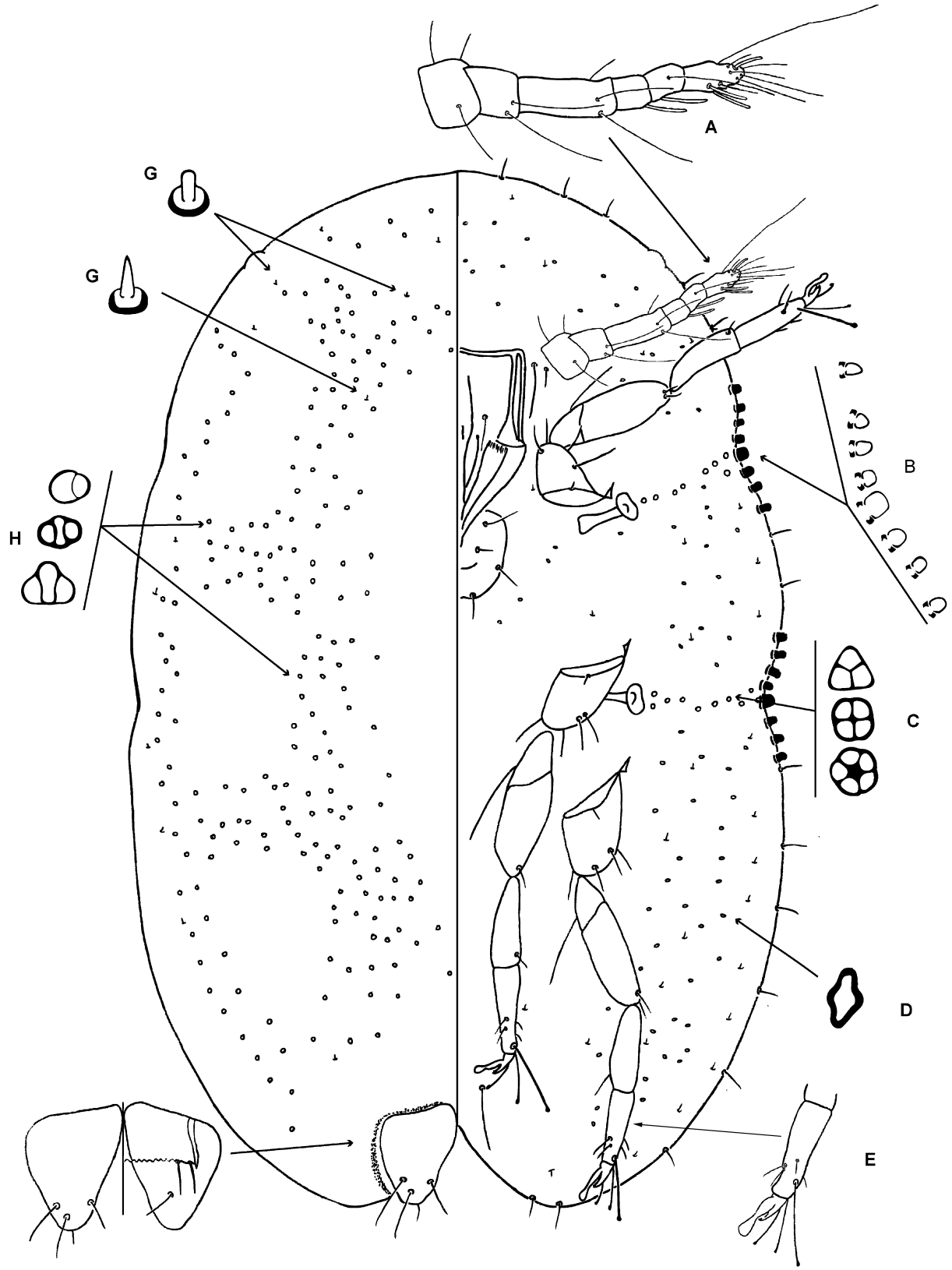

FIGURE 35. *Ceroplastes formosus* Hempel. Third-instar nymph.

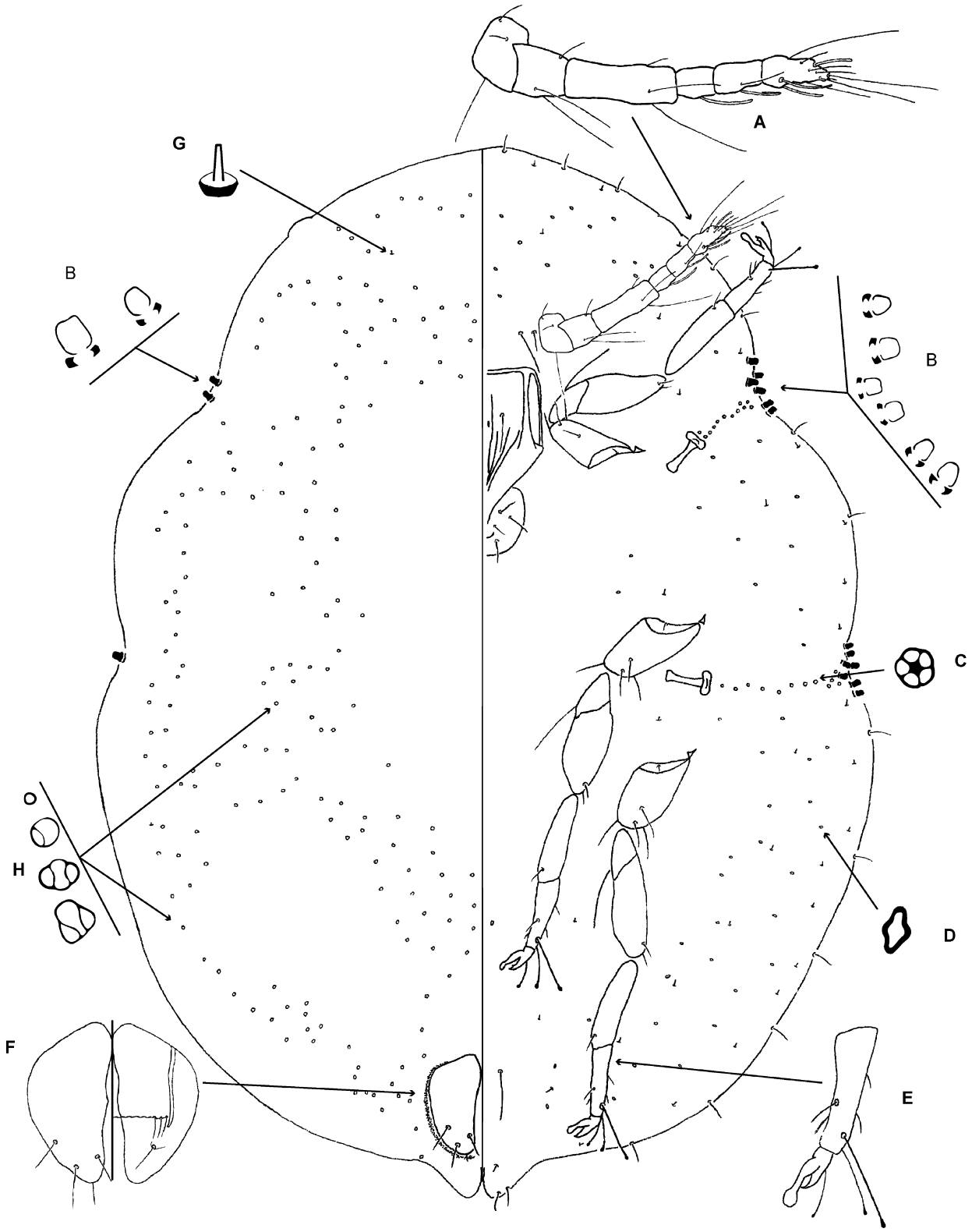

FIGURE 36. *Ceroplastes lucidus* Hempel. Third-instar nymph.

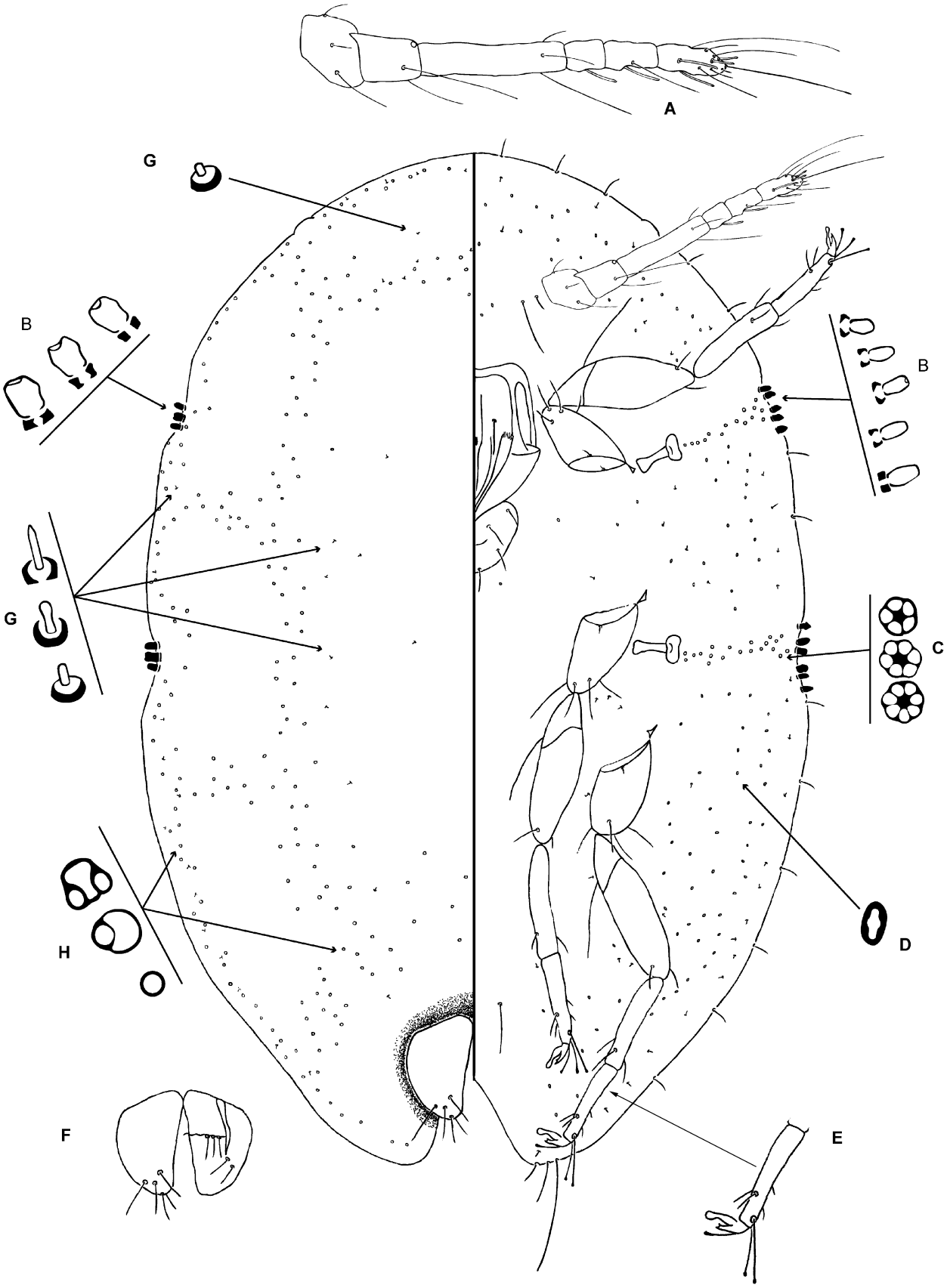

FIGURE 37. *Ceroplastes diospyros* Hempel. Third-instar nymph.

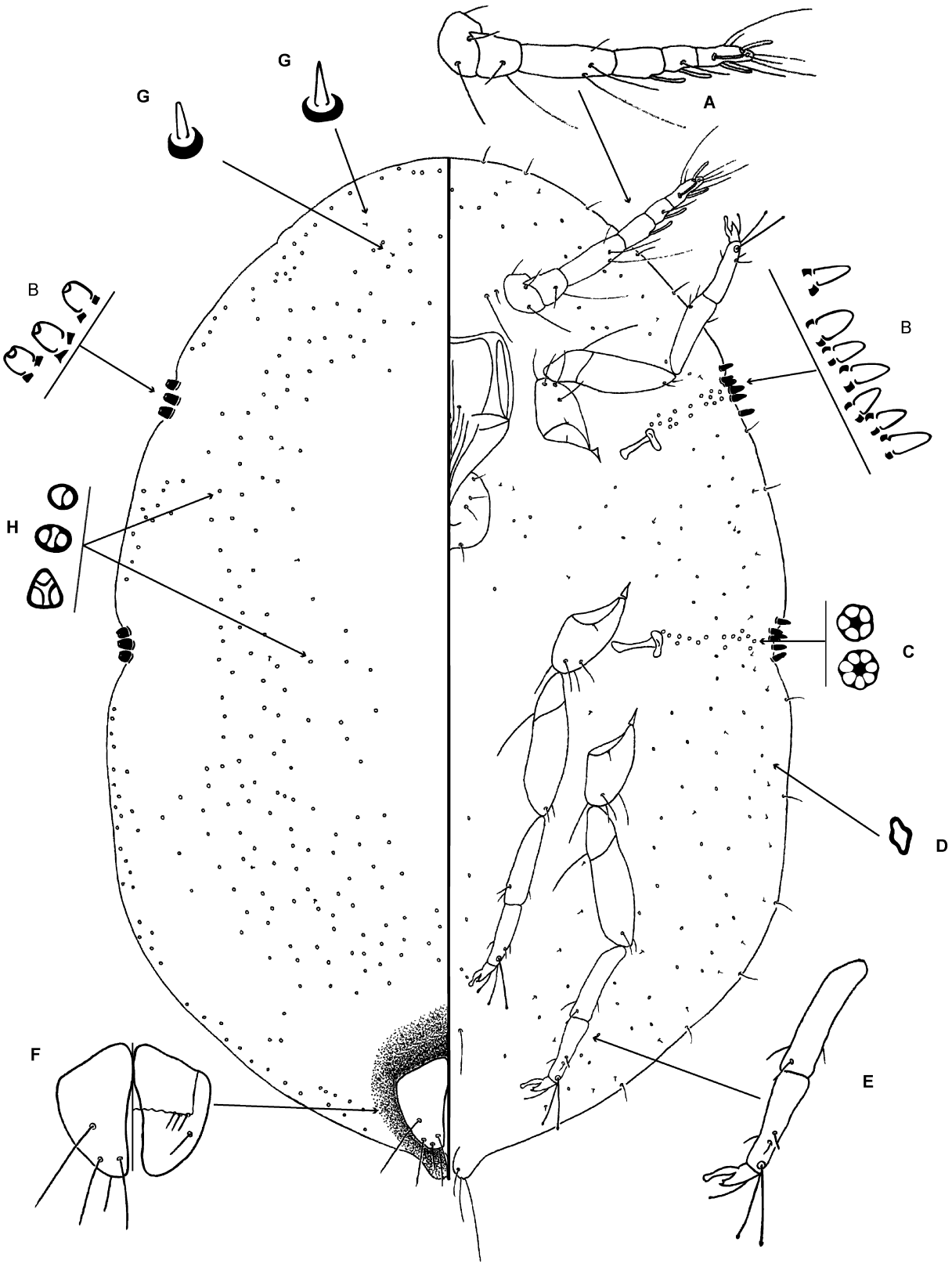

FIGURE 38. *Ceroplastes flosculoides* Matile-Ferrero. Third-instar nymph.

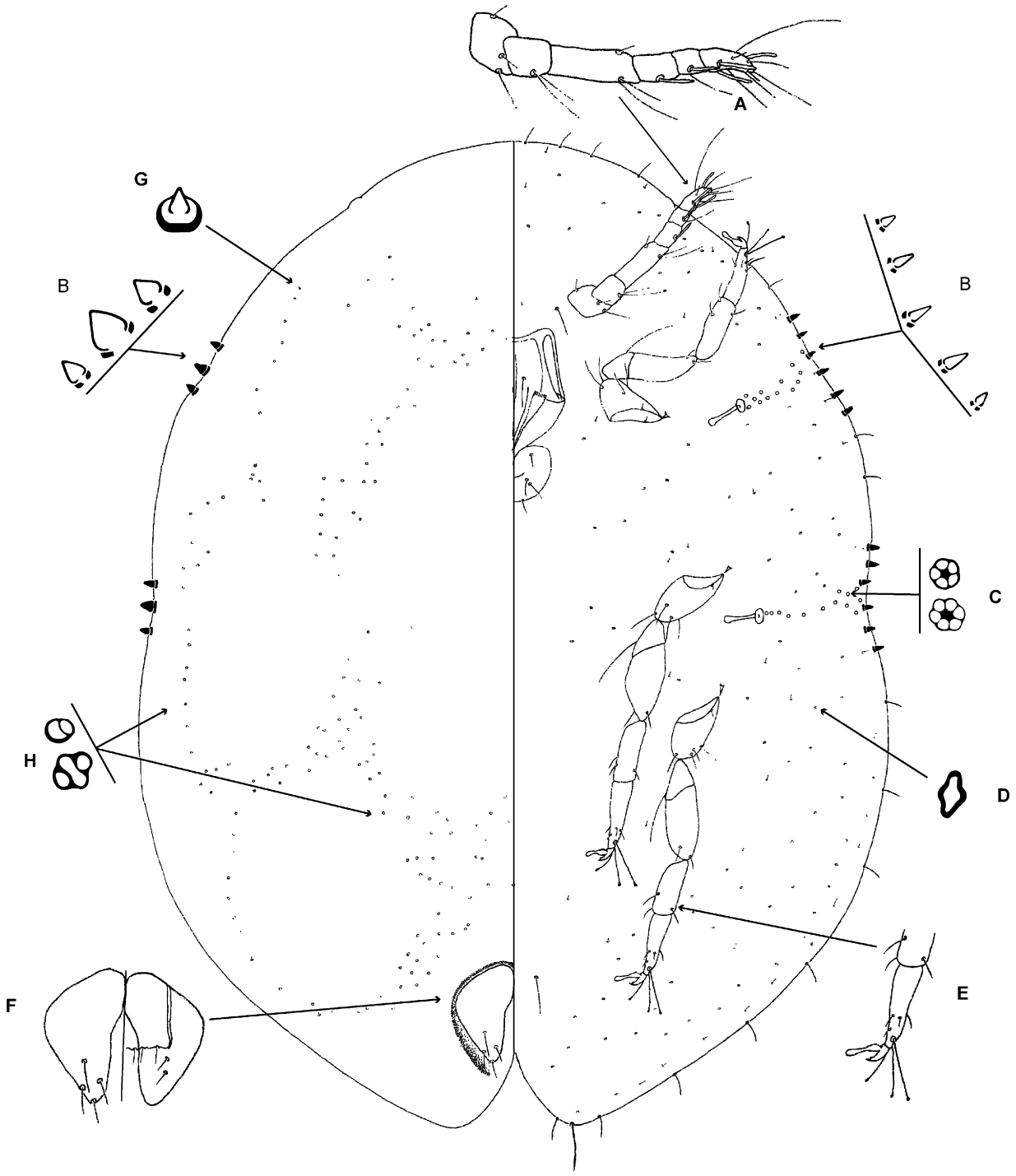

FIGURE 39. *Ceroplastes iheringi* Cockrell. Third-instar nymph.