

Fig. 1. Ultrastructure of the body cuticle of *Atalodera gibbosa*. A: J2, longitudinal section; B: J2, transverse section; C: Young female, longitudinal section; D: J3-J4, transverse section, E, F: Male, transverse section (db = horizontal fibres seen as dense bands; li = lateral incisure). Bar equivalents: A, B, E, F = 0.5 μ m; C, D = 1.0 μ m.

an electron-lucent matrix. Layer B (0.3 μm) is composed of striated fibres in electron-lucent matrix. These fibres are oriented radially and obliquely in transverse and oblique sections, respectively. In the region of the lateral field in J2 and in males (Fig. 1 F), The B layer is forked by one or two electron-dense layers.

Male : (Fig. 1 E, F). Layers A₁ (50 nm), A₂ (0.4 μm), A₃ (0.4 μm) and B (0.5 μm) are shown as in J2.

J3-J4 : (Fig. 1 D). The layer A₁ (80 nm) was viewed as a high electron-dense band. Layers A₂ and A₃ (0.7 μm) consist of electron-dense spots immersed in an electron-lucent matrix. Layer B (0.3 μm) is organized as in J2, but also presents horizontal fibres (electron-dense bands in figure). Layer C (2.5 μm) consists of horizontal filaments in an electron-lucent matrix. Layer D (2.5 μm) has a felt-work texture.

Young female : (Fig. 1 C). Layer A₁ (90 nm) is divided into two zones: electron-lucent and electron-dense. Layer A₂ (0.8 μm) and layer A₃ (0.4 μm) are similar to those of J2. Layer B (0.4 μm) consists of groups of horizontal fibres separated by radial ones (as in mature females, Fig. 2 C, D), whereas layer C (3.0 μm) is organized as in J3-J4. Layer D (4.0 μm) consists of fibers embedded in an electron-lucent matrix, presenting circular and irregular patterns at longitudinal and transverse sections, respectively.

Mature female : (Fig. 2). Layers A₁ (0.1 μm) and B (0.5 μm) are similar to those of young females, and so are layers A₂ and A₃ (0.8 μm each) to J2, layer C (3.0 μm) to J3-J4, and layer D₁ (3.5 μm) to D layer of young females. There were electron-dense deposits in layer D₁ in some mature females (Fig. 2 A). The layer D₂ (0.9 μm) consists of parabolic-form fibres in two lamellae in longitudinal and an irregular pattern in transverse section (Fig. 2 A, B and E). There were "islands" of horizontal fibres disposed in different directions to longitudinal axis in layers A₂ and C (Fig. 2 C).

Discussion

Layers A₁, A₂ and A₃ of *A. gibbosa* are similar to those of J2, females and males of other heteroderids (Shepherd *et al.*, 1972; Baldwin & Hirschmann, 1975; Johnson & Graham, 1976; Johnson, 1981; Baldwin, 1983; Cliff & Baldwin, 1985). Layer A₄ in J2 of *A. gibbosa* has not been reported previously. Layer B in J2 is also similar to those of other heteroderids, but in females it is characterized by groups of horizontal fibres separated by radial ones. This pattern has not been reported in other species. The D layer in young females (as D₁ in mature ones) of *A. gibbosa* is similar to those of *A. lonicerae*, *A. ucrici*, *A. gracililancea* and *Cactodera* sp. (Baldwin, 1983; Cliff & Baldwin, 1985). In *A. gibbosa* layer D₁ is distinguished from D₂ by the parabolic pattern with two lamellae in the latter, and by larger diameter of fibres (50 nm *vs* 30 nm). The layer D₂ is different from the layer E in *A. ucrici* and layers E₁-E₂ of *Heterodera schachtii*

and *Bellodera utahensis* (Cliff & Baldwin, 1985; Cordero & Baldwin, 1990; Baldwin & Eddleman, 1992).

Cuticular modifications of female with age have been described in *Heterodera* spp., *Globodera* spp., and *B. utahensis* (Shepherd *et al.*, 1972; Cordero & Baldwin, 1990; Baldwin & Eddleman, 1992). In *A. gibbosa* the changes in layer D from J3-J4 to mature female may be attributed to collagen crystallization, as mentioned by Shepherd *et al.* (1972). Furthermore, layer D₂, the electron-dense deposits in layer D₁, and the "islands" of fibres in A₂ and C were observed only in mature females.

The structure of the body wall cuticle has been used in studies on taxonomy and phylogeny of Heteroderinae (Baldwin, 1983; Cliff & Baldwin, 1985; Baldwin & Bell, 1985; Luc *et al.*, 1988; Baldwin & Schouest, 1990; Baldwin & Eddleman, 1992). However, five of nine non-cyst forming genera are monospecific, suggesting fewer intrageneric variations. Similarly, only two of seven *Meloidodera* species and one of two *Verutus* species were studied (Baldwin, 1983; Cliff & Baldwin, 1985). In *Cryphodera* with four species, only limited optical microscope studies were done (Baldwin & Schouest, 1990). *Atalodera* sensu Souza and Huang (1994), with nine species, is the most widely studied genus. Thus, *A. gracililancea* has C and D layers, *A. lonicerae* presents C₁, C₂ and D, *A. gibbosa* has C, D₁ and D₂, and *A. ucrici* shows C₁, C₂, D and E (Baldwin, 1983; Cliff & Baldwin, 1985; this article). Because of this great intrageneric variability in C and D layers, and the absence of diagnostic characters in A₁, A₂, A₃ and B ones, only the presence *vs* absence of D-layer in mature females, as used by Luc *et al.* (1988), is suggested as differentiated character.

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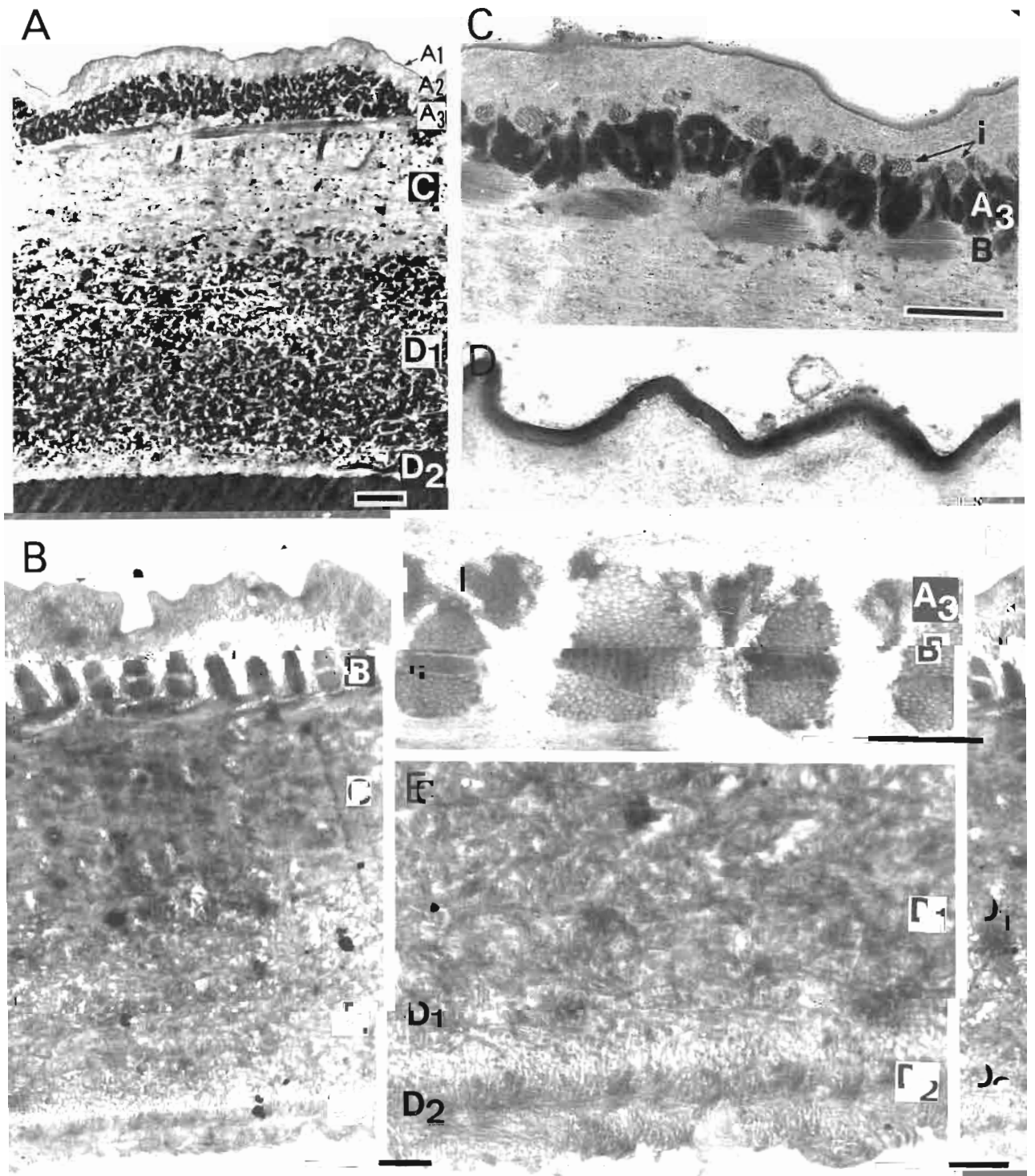


Fig. 2. Ultrastructure of the body cuticle of mature female of *Atalodera gibbosa*. A, C : Transverse section; B, D, E : Longitudinal section. (Fig. E enlarged from B; i = "islands" of fibres). Bar equivalents : A-C = 1.0 μm ; D, E = 0.5 μm .

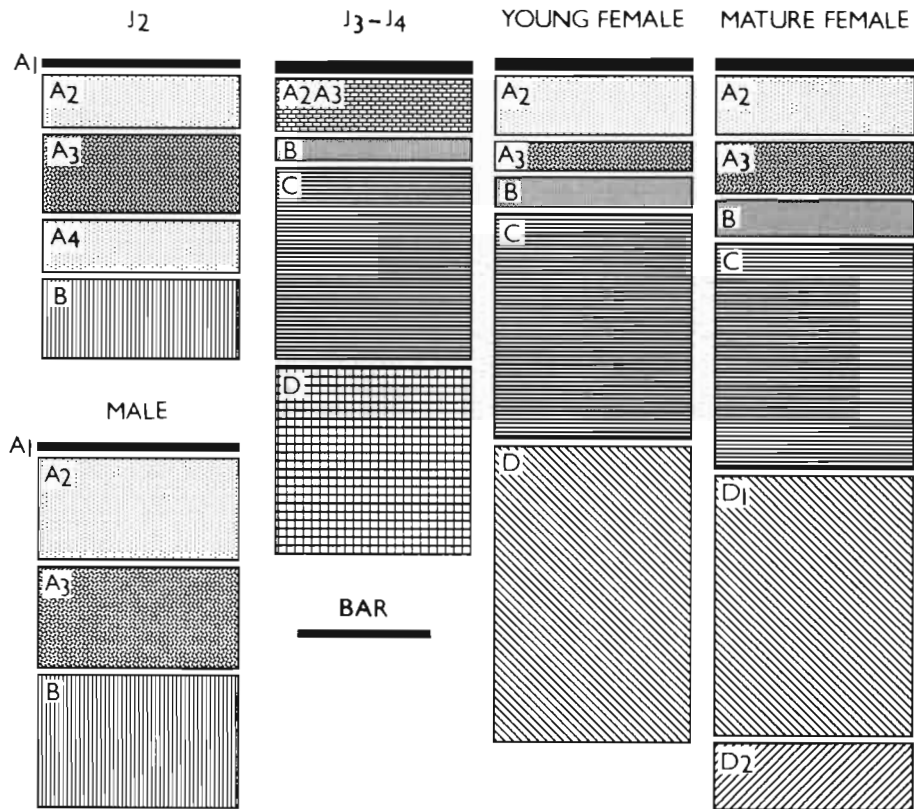


Fig. 3. Schematic drawing of the body cuticle of J2, J3-J4, young females, mature females and males of *Atalodera gibbosa*. Similar patterns correspond to same organization of layers. (Bars equivalents : J2 and male = 1 μm ; J3-J4 and females = 1.8 μm .)

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