

CECROPIA AS A FOOD RESOURCE FOR BATS IN FRENCH GUIANA AND THE SIGNIFICANCE OF FRUIT STRUCTURE IN SEED DISPERSAL AND LONGEVITY¹

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Cecropia (Cecropiaceae) is a Neotropical genus of pioneer plants. A review of bat/plant dispersal interactions revealed that 15 species of *Cecropia* are consumed by 32 species of bats. In French Guiana, bats were captured in primary and secondary forests, yielding 936 fecal samples with diaspores, among which 162 contained fruits of *C. obtusa*, *C. palmata*, and *C. sciadophylla*. A comparative morphological and anatomical study of fruits and seeds taken directly from herbarium specimens, bat feces, and an experimental soil seed bank was made. Contrary to previous reports, the dispersal unit of *Cecropia* is the fruit not the seed. Bats consume the infructescence, digest pulp derived from the enlarged, fleshy perianth, and defecate the fruits. The mucilaginous pericarp of *Cecropia* is described. The external mucilage production of *Cecropia* may facilitate endozoochory. The exocarp and part of the mesocarp may be lost after passage through the digestive tract of bats, but fruits buried for a year in the soil seed bank remain structurally unchanged. Fruit characters were found to be useful for identifying species of bat-dispersed *Cecropia*. Bat dispersal is not necessary for seed germination but it increases seed survival and subsequent germination. Fruit structure plays a significant role in seed longevity.

Key words: bat dispersal; *Cecropia*; French Guiana; fruit anatomy; fruit morphology; mucilage; Neotropical bats; soil seed bank.

Cecropia (Cecropiaceae), a genus of 61 species restricted to the Neotropics (Berg and Franco-Roselli, in press), plays several important ecological roles in tropical forest ecosystems. One of the best studied is the mutualistic interaction among species of *Cecropia* and ants of the genus *Azteca* (Davidson, in press). Nearly 80% of the species of *Cecropia* are myrmecophytes with most of the non-myrmecophytes found at higher elevations and on islands where the ants are absent (Wheeler, 1942; Janzen, 1973; Rickson, 1977). Myrmecophytic species of *Cecropia* possess hollow stems, in which ants nest, and provide an energy source for the ants in the form of glycogen-rich Müllerian bodies found at the base of the petiole on a specialized structure called a trichilium. In return, the ants protect the plant against phytophagous insects and from competition by other plants (Davidson, in press).

Another important ecological role played by species of *Cecropia* is as pioneer plants in disturbed areas. An individual *Cecropia* can yield fruits for 4–5 mo, and some species of the genus produce seeds capable of germinating after 4 or 5 yr of dormancy (Holthuijzen and Boerboom, 1982; Charles-Dominique, 1986; Lescure et al., 1989). An example of the prolific seed-producing capacity is *Cecropia obtusifolia*, an abundant pioneer species found in Mexico, which reliably fruits each

year. This species produces a mean of 80.6 ± 22.8 infructescences per tree per fruiting episode with each infructescence consisting of four rachises and an estimated 2792 seeds per rachis (Estrada et al., 1984a). Estrada et al. (1984a) calculated that a total of 900 141 seeds were produced by each female tree at each fruiting. As a result of this productivity, seeds of *Cecropia* are often the most common in soil seed banks in both primary and secondary forests (Whitmore, 1983). For example, along the Piste de St. Elie in French Guiana, seeds of *C. obtusa* and *C. sciadophylla* may account for 50% of the soil seed bank in primary forest (Prévost, 1982). Because of the abundance of seeds in the soil, as well as the rapid dispersal of them into newly disturbed areas, regeneration of forests in gaps is facilitated by species of *Cecropia* throughout most of the Neotropics.

Trees of *Cecropia* often produce the first shade and litter, which enables later successional species to germinate and establish seedlings in disturbed areas (Maury-Lechon, 1991). Although *Cecropia* species have little economic value (Berg and Franco-Roselli, in press), they appear to play an essential role in initial stages of plant succession after disturbance. At least in French Guiana, *Cecropia* often provide the microhabitat needed for the growth of economically important timber trees such as *Goupia glabra* and *Laetia procera* (Maury-Lechon, 1991).

In all species of *Cecropia*, the fruits are surrounded by a perianth that becomes fleshy and serves as a reward to animal dispersal agents. The infructescences of species of *Cecropia* are exploited by many different species of vertebrates: various birds, bats, monkeys, fish, and others (Holthuijzen, 1979; Goulding, 1980; Charles-Dominique et al., 1981; van Roosmalen, 1985). Hence, the infructescences of species of *Cecropia* are an important source of nutrition for many Neotropical animals.

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In spite of the numerous studies about the dispersal biology of *Cecropia*, there is still confusion in the literature about what is dispersed (i.e., the definition of the diaspore) and what part of the infructescence is consumed by animals. In addition, the morphology and anatomy of the fruits and seeds of *Cecropia* have not yet been adequately described. Therefore, we undertook this study to (1) examine the role that bats play in the dispersal of *Cecropia*, (2) establish what is the dispersal unit (diaspore) of *Cecropia*, (3) determine what part of the infructescence is consumed by animals, (4) provide the first botanical descriptions of the fruit and seed morphology and anatomy of bat-dispersed *Cecropia* species native to French Guiana, (5) ascertain if there are differences in the diaspores of bat-dispersed *Cecropia* species that can be used to identify species from material collected from bat feces, (6) investigate what structural changes occur in the diaspores of *Cecropia* after passing through the digestive tract of bats and after burial in the soil seed bank, and (7) determine the role that fruit structure of *Cecropia* plays in seed longevity in the soil seed bank. Seven species of *Cecropia* are found in French Guiana (*C. distachya* Huber, *C. granvilleana* C. C. Berg, *C. latiloba* Miq., *C. obtusa* Trécul., *C. palmata* Willd., *C. sciadophylla* Mart., and possibly *C. silvae* C. C. Berg) (Berg and Franco-Roselli, in press). It is the bat-dispersed species of *Cecropia* that are the focus of our research.

MATERIALS AND METHODS

To determine what species of bats consume what species of *Cecropia*, we reviewed the literature and constructed a database with the following fields: plant family, plant genus, plant species epithet, bat genus, bat species epithet, and author(s) and year of publication of reference. Each record in the database represents an interaction between a species of *Cecropia* and a species of bat (Mori and Blanchard, 2002).

Fruits and seeds were collected from bat feces on six expeditions to French Guiana (July–August, 1999; August–September, 2000; October–December, 2000; February–May, 2001; April–May, 2001; and July–December, 2001). Bats were captured in primary and secondary forest in ground level mist nets and placed in clean cloth bags until they had defecated. The fruits and seeds from the feces were then air dried in glassine envelopes. A total of 936 fecal samples with fruits/seeds was gathered. The bats carrying the seeds were identified using *Neotropical Rainforest Mammals* (Emmons, 1990) and then released unharmed.

Fruits from herbarium specimens of species of *Cecropia* were compared with fruits from feces of bats. Herbarium vouchers are deposited in the herbaria of The New York Botanical Garden (NY) and the Institut de Recherche pour le Développement (CAY). Fruit/seed collections from bat feces are archived at The New York Botanical Garden and CNRS (Muséum National d'Histoire Naturelle, France).

Fruit morphology and anatomy of the following species were studied (vouchers of herbarium or bat feces collections in parentheses): *Cecropia obtusa* (Smith and Mori 20, herbarium specimen; Peckham 191/1999, Charles-Dominique 662, Charles-Dominique 752, from bat feces); *C. palmata* (Berg 784, herbarium specimen; Charles-Dominique s. n., from bat feces); *C. sciadophylla* (Mori 18749, herbarium specimen; Peckham 209/2000, Peckham 211/2000, from bat feces).

Several fruits of *C. obtusa* collected from bat feces (Charles-Dominique 662, Charles-Dominique 752) were deposited in the seed soil bank at Les Nouragues Research Station in French Guiana. Fruits in nylon mesh bags were buried 3 cm deep at one site with clay soil and at another site with sandy soil. After 1 yr in the soil, the morphology and anatomy of these fruits were compared with fruits that had passed through the digestive tracts of bats.

For morphological studies, dry fruits and seeds, and longitudinal and transverse sections of fruits sputter-coated with gold-palladium were examined with a JEOL 5410LV scanning electron microscope (SEM; Jeol USA, Pea-

body, Massachusetts, USA). For anatomical studies, dry fruits were softened for 7 d in a solution of equal parts distilled water, 96% ethanol, and glycerol. Transverse sections (12 μ m thick) were cut in the middle of the fruits using a freezing microtome. Histochemical reactions were made with Sudan IV, phloroglucinol + HCl, and IKI to determine the presence of lipids, lignin, and starch, respectively (Jensen, 1962). A polarizing filter was used to detect crystals and starch grains. Fruits were placed in tap water and observed for mucilage after 24 h.

RESULTS

Species of *Cecropia* dispersed by bats—After correction for synonymy according to the most recent nomenclature for *Cecropia* (Berg and Franco-Roselli, in press) and for bats (Nowak, 1994), our review of the literature revealed reports of 15 species of *Cecropia* consumed by 32 species of bats (Table 1). In French Guiana, only *C. obtusa* (Foresta et al., 1984; Cooper and Charles-Dominique, 1985; Charles-Dominique, 1986, 1993; Charles-Dominique and Cooper, 1986; Cockle, 1997), *C. palmata* (Charles-Dominique, 1986), and *C. sciadophylla* (Cockle, 1997) have been reported to be bat-dispersed (Table 1). Among the 936 fecal samples we collected with fruits/seeds, 162 contained the fruits of *Cecropia* (Table 2).

Description of fruits and seeds: *Cecropia obtusa*—Fruits lanceolate-ellipsoid, ca. 2.9 \times 0.8 \times 0.8 mm, brown, glossy, the end(s) more or less acute; transverse section triangular-rounded or elliptic; surface indistinctly undulate-rugose (Figs. 1–3, 6); mucilage layer ca. 0.1 mm thick exudes after placement of fruits in water. *Pedicel* scar conspicuous, basal, circular (Fig. 2); vascular bundle single, in one lateral side. *Pericarp* (Figs. 5, 6) ca. 160 μ m thick, thicker in lateral sides, thinner in middle of dorsal and ventral sides, with 5–9 layers, differentiated into exocarp, mesocarp, and endocarp (Fig. 9). *Exocarp* single-layered, with two cell types (Fig. 13): first mucilaginous, with wavy, thin, anticlinal walls and thickened outer periclinal walls, some with indeterminate contents at apices, considerably elongated when wet, the cell boundaries usually not destroyed upon wetting, the second cell type non-mucilaginous, with thin walls, filled with brown pigment; mucilaginous cells more abundant and surrounding small groups of non-mucilaginous cells. *Mesocarp* 3–7 layers, differentiated into two (on dorsal and ventral sides) or three (on lateral sides) zones (Fig. 13): outer zone of 2–4 layers of longitudinally elongated cells filled with brown tannins, the cell walls slightly thickened, the outer periclinal walls of first layer thicker; intermediate zone present on lateral sides, of 1–2 layers of sclerified stone cells; inner zone a single layer of cells, each with a large prismatic crystal 11–18 μ m in diameter. *Endocarp* occupying one-half to two-thirds of pericarp, a single layer of radially elongated macrosclereids with very narrow lumens, the lumens broadened and roundish at apex as seen in transverse section, the cell walls considerably thickened, with thin tiny pores, the pores thicker at cell apex (Figs. 9, 13).

Seeds oblong-ovoid, 1.6 \times 0.5 \times 0.5 mm, light brown, glossy, the micropylar end acute (Fig. 7), the transverse section triangular-rounded or elliptic (Fig. 6), the surface indistinctly striate-reticulate (Fig. 8). *Hilum* conspicuous, basal, slightly displaced to one side (Figs. 5, 7). *Seed coat* derived from two integuments, in mature seed reduced to membrane 8–9 μ m thick, of two cell layers (Fig. 13): cells of first layer longitudinally elongated, very small, flat, light brown, thin-walled, the cells of second layer transversally elongated, bigger, thick-

TABLE 1. Species of *Cecropia* reported to be dispersed by bats.

Species of <i>Cecropia</i>	Species of bat	References
<i>Cecropia adenopus</i> Mart. ex Miq. ^a	<i>Sturnira lilium</i>	Marinho-Filho, 1991
<i>Cecropia bureaniana</i> V. A. Richt. ^b	<i>Artibeus jamaicensis</i>	de Carvalho, 1961; Gardner, 1977
<i>Cecropia bureaniana</i> V. A. Richt. ^b	<i>Glossophaga soricina</i>	de Carvalho, 1961; Gardner, 1977
<i>Cecropia concolor</i> Willd.	<i>Artibeus jamaicensis</i>	dos Reis and Gillaumet, 1983; dos Reis and Peracchi, 1987
<i>Cecropia concolor</i> Willd.	<i>Artibeus lituratus</i>	dos Reis and Peracchi, 1987
<i>Cecropia concolor</i> Willd.	<i>Carollia perspicillata</i>	dos Reis and Peracchi, 1987
<i>Cecropia concolor</i> Willd.	<i>Phyllostomus hastatus</i>	dos Reis and Peracchi, 1987
<i>Cecropia concolor</i> Willd.	<i>Vampyrops helleri</i>	dos Reis and Gillaumet, 1983; dos Reis and Peracchi, 1987
<i>Cecropia distachya</i> Huber	<i>Artibeus jamaicensis</i>	Gorchov et al., 1993, 1995
<i>Cecropia distachya</i> Huber	<i>Artibeus lituratus</i>	Gorchov et al., 1993, 1995
<i>Cecropia distachya</i> Huber	<i>Carollia brevicauda</i>	Gorchov et al., 1995
<i>Cecropia distachya</i> Huber	<i>Carollia perspicillata</i>	Ascorra and Wilson, 1992; Gorchov et al., 1995
<i>Cecropia distachya</i> Huber	<i>Phyllostomus hastatus</i>	dos Reis and Peracchi, 1987; Ascorra et al., 1993; Gorchov et al., 1993, 1995
<i>Cecropia distachya</i> Huber	<i>Rhinophylla pumilio</i>	Gorchov et al., 1995
<i>Cecropia distachya</i> Huber	<i>Sturnira lilium</i>	Gorchov et al., 1995
<i>Cecropia exima</i> Cuatrec. ^c	<i>Artibeus phaeotis</i>	Bonaccorso, 1978
<i>Cecropia exima</i> Cuatrec. ^c	<i>Carollia perspicillata</i>	Bonaccorso, 1978
<i>Cecropia exima</i> Cuatrec. ^c	<i>Glossophaga soricina</i>	Bonaccorso, 1978
<i>Cecropia exima</i> Cuatrec. ^c	<i>Phyllostomus discolor</i>	Bonaccorso, 1978
<i>Cecropia ficifolia</i> Snethl.	<i>Artibeus gnomus</i>	Gorchov et al., 1995
<i>Cecropia ficifolia</i> Snethl.	<i>Artibeus jamaicensis</i>	Gorchov et al., 1993, 1995
<i>Cecropia ficifolia</i> Snethl.	<i>Artibeus lituratus</i>	Gorchov et al., 1993, 1995
<i>Cecropia ficifolia</i> Snethl.	<i>Artibeus obscurus</i>	Gorchov et al., 1995
<i>Cecropia ficifolia</i> Snethl.	<i>Artibeus</i> sp.	Uhl et al., 1981
<i>Cecropia ficifolia</i> Snethl.	<i>Carollia brevicauda</i>	Gorchov et al., 1995
<i>Cecropia ficifolia</i> Snethl.	<i>Carollia castanea</i>	Gorchov et al., 1995
<i>Cecropia ficifolia</i> Snethl.	<i>Carollia perspicillata</i>	Ascorra and Wilson, 1992; Gorchov et al., 1995
<i>Cecropia ficifolia</i> Snethl.	<i>Phyllostomus hastatus</i>	Gorchov et al., 1993, 1995
<i>Cecropia ficifolia</i> Snethl.	<i>Platyrrhinus helleri</i>	Ascorra and Wilson, 1992
<i>Cecropia ficifolia</i> Snethl.	<i>Rhinophylla pumilio</i>	Gorchov et al., 1995
<i>Cecropia ficifolia</i> Snethl.	<i>Sturnira lilium</i>	Gorchov et al., 1995
<i>Cecropia ficifolia</i> Snethl.	<i>Sturnira tildae</i>	Uhl et al., 1981
<i>Cecropia ficifolia</i> Snethl.	<i>Uroderma bilobatum</i>	Gorchov et al., 1995
<i>Cecropia ficifolia</i> Snethl.	<i>Vampyrops helleri</i>	Uhl et al., 1981
<i>Cecropia glazioui</i> Snethl. ^d	<i>Artibeus jamaicensis</i>	Zortéa and Chiarello, 1994
<i>Cecropia glazioui</i> Snethl. ^d	<i>Platyrrhinus lineatus</i>	Zortéa, 1993
<i>Cecropia hololeuca</i> Miq.	<i>Artibeus jamaicensis</i>	Zortéa and Chiarello, 1994
<i>Cecropia hololeuca</i> Miq.	<i>Artibeus lituratus</i>	Galetti and Morellato, 1994; Sazima et al., 1994
<i>Cecropia insignis</i> Liebm.	<i>Artibeus phaeotis</i>	Bonaccorso and Humphrey, 1984
<i>Cecropia insignis</i> Liebm.	<i>Carollia castanea</i>	Bonaccorso and Humphrey, 1984
<i>Cecropia membranacea</i> Trécul.	<i>Artibeus jamaicensis</i>	Gorchov et al., 1993
<i>Cecropia membranacea</i> Trécul.	<i>Artibeus lituratus</i>	Gorchov et al., 1993, 1995
<i>Cecropia membranacea</i> Trécul.	<i>Artibeus obscurus</i>	Ascorra and Wilson, 1992
<i>Cecropia membranacea</i> Trécul.	<i>Carollia brevicauda</i>	Gorchov et al., 1995
<i>Cecropia membranacea</i> Trécul.	<i>Carollia castanea</i>	Gorchov et al., 1995
<i>Cecropia membranacea</i> Trécul.	<i>Carollia perspicillata</i>	Gorchov et al., 1995
<i>Cecropia membranacea</i> Trécul.	<i>Glossophaga soricina</i>	Ascorra and Wilson, 1992
<i>Cecropia membranacea</i> Trécul.	<i>Phyllostomus hastatus</i>	Ascorra and Wilson, 1992; Gorchov et al., 1993, 1995
<i>Cecropia membranacea</i> Trécul.	<i>Platyrrhinus helleri</i>	Ascorra and Wilson, 1992
<i>Cecropia obtusa</i> Trécul.	<i>Artibeus concolor</i>	Charles-Dominique, 1986
<i>Cecropia obtusa</i> Trécul.	<i>Artibeus fuliginosus</i>	Charles-Dominique, 1993
<i>Cecropia obtusa</i> Trécul.	<i>Artibeus jamaicensis</i>	Charles-Dominique 1986, 1993
<i>Cecropia obtusa</i> Trécul.	<i>Artibeus lituratus</i>	Foresta et al., 1984; Cooper and Charles-Dominique, 1985; Charles-Dominique, 1986, 1993; Charles-Dominique and Cooper, 1986; Zortéa and Chiarello, 1994; Puig, 2001
<i>Cecropia obtusa</i> Trécul.	<i>Rhinophylla pumilio</i>	Cockle, 1997
<i>Cecropia obtusa</i> Trécul.	<i>Sturnira lilium</i>	Foresta et al., 1984; Charles-Dominique, 1986
<i>Cecropia obtusifolia</i> Bertoloni	bat not reported	Vázquez-Yanes et al., 1975; Galindo-González et al., 2000
<i>Cecropia obtusifolia</i> Bertoloni	<i>Artibeus jamaicensis</i>	Vázquez-Yanes et al., 1975; Gardner, 1977; Morrison, 1978; Prévost, 1981; Orozco-Segovia and Vázquez-Yanes, 1982; Estrada et al., 1984a, b; Herrera-M. et al., 2001
<i>Cecropia obtusifolia</i> Bertoloni	<i>Artibeus lituratus</i>	Palmeirim et al., 1989
<i>Cecropia obtusifolia</i> Bertoloni	<i>Artibeus phaeotis</i>	Palmeirim et al., 1989
<i>Cecropia obtusifolia</i> Bertoloni	<i>Artibeus toltecus</i>	Dinerstein, 1986
<i>Cecropia obtusifolia</i> Bertoloni	<i>Carollia castanea</i>	Palmeirim et al., 1989
<i>Cecropia obtusifolia</i> Bertoloni	<i>Glossophaga soricina</i>	Estrada et al., 1984a
<i>Cecropia obtusifolia</i> Bertoloni	<i>Sturnira lilium</i>	Herrera-M. et al., 2001
<i>Cecropia obtusifolia</i> Bertoloni	<i>Sturnira ludovici</i>	Dinerstein, 1986

TABLE 1. Continued.

Species of <i>Cecropia</i>	Species of bat	References
<i>Cecropia obtusifolia</i> Bertoloni	<i>Vampyrops helleri</i>	Palmeirim et al., 1989
<i>Cecropia pachystachya</i> Trécul.	<i>Artibeus lituratus</i>	Galetti and Morellato, 1994; Sazima et al., 1994
<i>Cecropia pachystachya</i> Trécul.	<i>Carollia perspicillata</i>	Pedro and Taddei, 1997
<i>Cecropia pachystachya</i> Trécul.	<i>Glossophaga soricina</i>	Pedro and Taddei, 1997
<i>Cecropia pachystachya</i> Trécul.	<i>Platyrrhinus lineatus</i>	Pedro and Taddei, 1997
<i>Cecropia pachystachya</i> Trécul.	<i>Sturnira lilium</i>	Pedro and Taddei, 1997
<i>Cecropia palmata</i> Willd.	<i>Artibeus jamaicensis</i>	dos Reis and Gillaumet, 1983; Charles-Dominique, 1986; dos Reis and Peracchi, 1987
<i>Cecropia palmata</i> Willd.	<i>Artibeus lituratus</i>	dos Reis and Gillaumet, 1983; Charles-Dominique, 1986; dos Reis and Peracchi, 1987
<i>Cecropia palmata</i> Willd.	<i>Carollia perspicillata</i>	dos Reis and Peracchi, 1987
<i>Cecropia palmata</i> Willd.	<i>Uroderma bilobatum</i>	dos Reis and Gillaumet, 1983; dos Reis and Peracchi, 1987
<i>Cecropia palmata</i> Willd.	<i>Uroderma magnirostrum</i>	dos Reis and Peracchi, 1987
<i>Cecropia peltata</i> L.	<i>Artibeus jamaicensis</i>	Ruschi, 1953b; Greenhall, 1957; Goodwin and Greenhall, 1961; Gardner, 1977; Fleming, 1986, 1988
<i>Cecropia peltata</i> L.	<i>Artibeus lituratus</i>	Greenhall, 1957; Fleming et al., 1977; Gardner, 1977; Fleming, 1986, 1988
<i>Cecropia peltata</i> L.	<i>Artibeus phaeotis</i>	Fleming et al., 1977; Fleming, 1986, 1988
<i>Cecropia peltata</i> L.	<i>Artibeus toltecus</i>	Fleming, 1988
<i>Cecropia peltata</i> L.	<i>Carollia perspicillata</i>	Greenhall, 1957; Goodwin and Greenhall, 1961; Fleming, 1982, 1985, 1986, 1987, 1988, 1991; Dobat and Peikert-Holle, 1985; Fleming and Heithaus, 1986; Herbst, 1986; Bonaccorso and Gush, 1987; Fleming and Sosa, 1994
<i>Cecropia peltata</i> L.	<i>Carollia subrufa</i>	Fleming, 1988
<i>Cecropia peltata</i> L.	<i>Glossophaga soricina</i>	Fleming et al., 1977; Gardner, 1977; Fleming, 1986, 1988; Bonaccorso and Gush, 1987
<i>Cecropia peltata</i> L.	<i>Phyllostomus discolor</i>	Fleming, 1982, 1988
<i>Cecropia peltata</i> L.	<i>Phyllostomus hastatus</i>	McCracken and Bradbury, 1981
<i>Cecropia peltata</i> L.	<i>Sturnira lilium</i>	Fleming, 1986, 1988
<i>Cecropia polyphlebia</i> Donn. Sm. ^a	<i>Sturnira ludovici</i>	Dinerstein, 1986
<i>Cecropia schreberiana</i> Miq.	<i>Artibeus jamaicensis</i>	Willig and Gannon, 1996
<i>Cecropia schreberiana</i> Miq.	<i>Stenoderma rufum</i>	Gannon and Willig, 1992; Willig and Gannon, 1996
<i>Cecropia sciadophylla</i> Mart.	<i>Artibeus jamaicensis</i>	Gorchov et al., 1995
<i>Cecropia sciadophylla</i> Mart.	<i>Carollia perspicillata</i>	Cloutier and Thomas, 1992; Gorchov et al., 1995
<i>Cecropia sciadophylla</i> Mart.	<i>Phyllostomus hastatus</i>	Gorchov et al., 1995
<i>Cecropia sciadophylla</i> Mart.	<i>Rhinophylla pumilio</i>	Cockle, 1997
<i>Cecropia</i> sp.	<i>Artibeus jamaicensis</i>	Ruschi, 1953b; Gardner, 1977; Bonaccorso, 1978; Bonaccorso and Humphrey, 1984; Handley et al., 1991; Zortéa and Chiarello, 1994
<i>Cecropia</i> sp.	<i>Artibeus lituratus</i>	Gardner, 1977; Muller and dos Reis, 1992
<i>Cecropia</i> sp.	<i>Artibeus phaeotis</i>	Bonaccorso, 1978; Bonaccorso and Humphrey, 1984; Bonaccorso and Gush, 1987
<i>Cecropia</i> sp.	<i>Artibeus toltecus</i>	Howell and Burch, 1974; Gardner, 1977; Bonaccorso and Gush, 1987
<i>Cecropia</i> sp.	<i>Artibeus watsoni</i>	Howell and Burch, 1974; Gardner, 1977
<i>Cecropia</i> sp.	<i>Carollia perspicillata</i>	Howell and Burch, 1974; Gardner, 1977; Willig et al., 1993
<i>Cecropia</i> sp.	<i>Glossophaga soricina</i>	Gardner, 1977
<i>Cecropia</i> sp.	<i>Micronycteris megalotis</i>	Ruschi, 1953a; Gardner, 1977; Alonso-Mejía and Medellín, 1991
<i>Cecropia</i> sp.	<i>Phyllostomus hastatus</i>	Howell and Burch, 1974; Gardner, 1977
<i>Cecropia</i> sp.	<i>Platyrrhinus helleri</i>	Ferrell and Wilson, 1991
<i>Cecropia</i> sp.	<i>Platyrrhinus lineatus</i>	Muller and dos Reis, 1992
<i>Cecropia</i> sp.	<i>Platyrrhinus recifinus</i>	Pedro and Passos, 1995
<i>Cecropia</i> sp.	<i>Rhinophylla fischeriae</i>	Ascorral et al., 1989
<i>Cecropia</i> sp.	<i>Rhinophylla pumilio</i>	Ascorral et al., 1989
<i>Cecropia</i> sp.	<i>Sturnira lilium</i>	Gardner, 1977; Gannon et al., 1989; Muller and dos Reis, 1992; Willig et al., 1993
<i>Cecropia</i> sp.	<i>Sturnira mordax</i>	Howell and Burch, 1974; Gardner, 1977
<i>Cecropia</i> sp.	<i>Vampyressa pusilla</i>	Gorchov et al., 1995
<i>Cecropia</i> sp.	<i>Vampyrops helleri</i>	Howell and Burch, 1974; Gardner, 1977
<i>Cecropia</i> sp.	<i>Vampyrops vittatus</i>	Howell and Burch, 1974; Gardner, 1977

^a *Cecropia adenopus* Mart. ex Miq. is considered a synonym of *C. pachystachya* Trécul by Berg and Franco-Roselli (Berg and Franco-Roselli, in press).

^b *Cecropia bureaniana* V. A. Richt. is considered a synonym of *C. palmata* Willd. by Berg and Franco-Roselli (Berg and Franco-Roselli, in press).

^c *Cecropia exima* Cuatrec. is considered a synonym of *C. insignis* Liebm. by Berg and Franco-Roselli (Berg and Franco-Roselli, in press).

^d *Cecropia glazioui* Snethl. is spelled as *C. glaziovii* Snethl. by Berg and Franco-Roselli (Berg and Franco-Roselli, in press).

^e *Cecropia polyphlebia* Donn. Sm. is considered a synonym of *C. angustifolia* Trécul. by Berg and Franco-Roselli (Berg and Franco-Roselli, in press).

TABLE 2. *Cecropia* fruits collected from bat feces.

Bat	Habitat	<i>Cecropia obtusa</i>	<i>Cecropia palmata</i>	<i>Cecropia sciadophylla</i>
<i>Artibeus cinereus</i>	primary forest			
	secondary forest	1		
<i>Artibeus concolor</i>	primary forest	3		
	secondary forest			
<i>Artibeus gnomus</i>	primary forest	1		
	secondary forest			
<i>Artibeus jamaicensis</i>	primary forest	16		
	secondary forest	24	17	
<i>Artibeus lituratus</i>	primary forest	19		
	secondary forest	1		
<i>Artibeus obscurus</i>	primary forest	35		
	secondary forest	6	3	
<i>Carollia brevicauda</i>	primary forest	1		
	secondary forest			
<i>Carollia perspicillata</i>	primary forest	2		
	secondary forest	2	2	
<i>Chiroderma villosum</i>	primary forest			
	secondary forest	1		
<i>Platyrrhinus brachycephalus</i>	primary forest			
	secondary forest	1		
<i>Platyrrhinus helleri</i>	primary forest	3		
	secondary forest	1	2	
<i>Rhinophylla pumilio</i>	primary forest			2
	secondary forest			1
<i>Sturnira lilium</i>	primary forest			
	secondary forest	2		
<i>Sturnira tildae</i>	primary forest	8		
	secondary forest	8		
Total		135	24	3

walled, filled with tannins. *Endosperm* present in mature seeds (Figs. 5, 6, 9, 13), 2–5 layers of thin-walled cells with protein bodies, small starch grains, and oil. *Embryo* linear, straight, ca. 1.5 × 0.4 mm, the cotyledons large (ca. 1 mm long), planoconvex (Figs. 5, 6, 12).

Fruits of *C. obtusa* were found in 135 samples of feces gathered from bats captured both in primary and secondary vegetation (Table 2). The infructescences are consumed by *Artibeus obscurus* (fruits found in 41 samples), *A. jamaicensis* (40), *A. lituratus* (20), *Sturnira tildae* (16), *Carollia perspicillata* (4), *Platyrrhinus helleri* (4), *Artibeus concolor* (3), *Sturnira lilium* (2), *Artibeus gnomus* (1), *A. cinereus* (1), *Carollia brevicauda* (1), *Chiroderma villosum* (1), and *Platyrrhinus brachycephalus* (1).

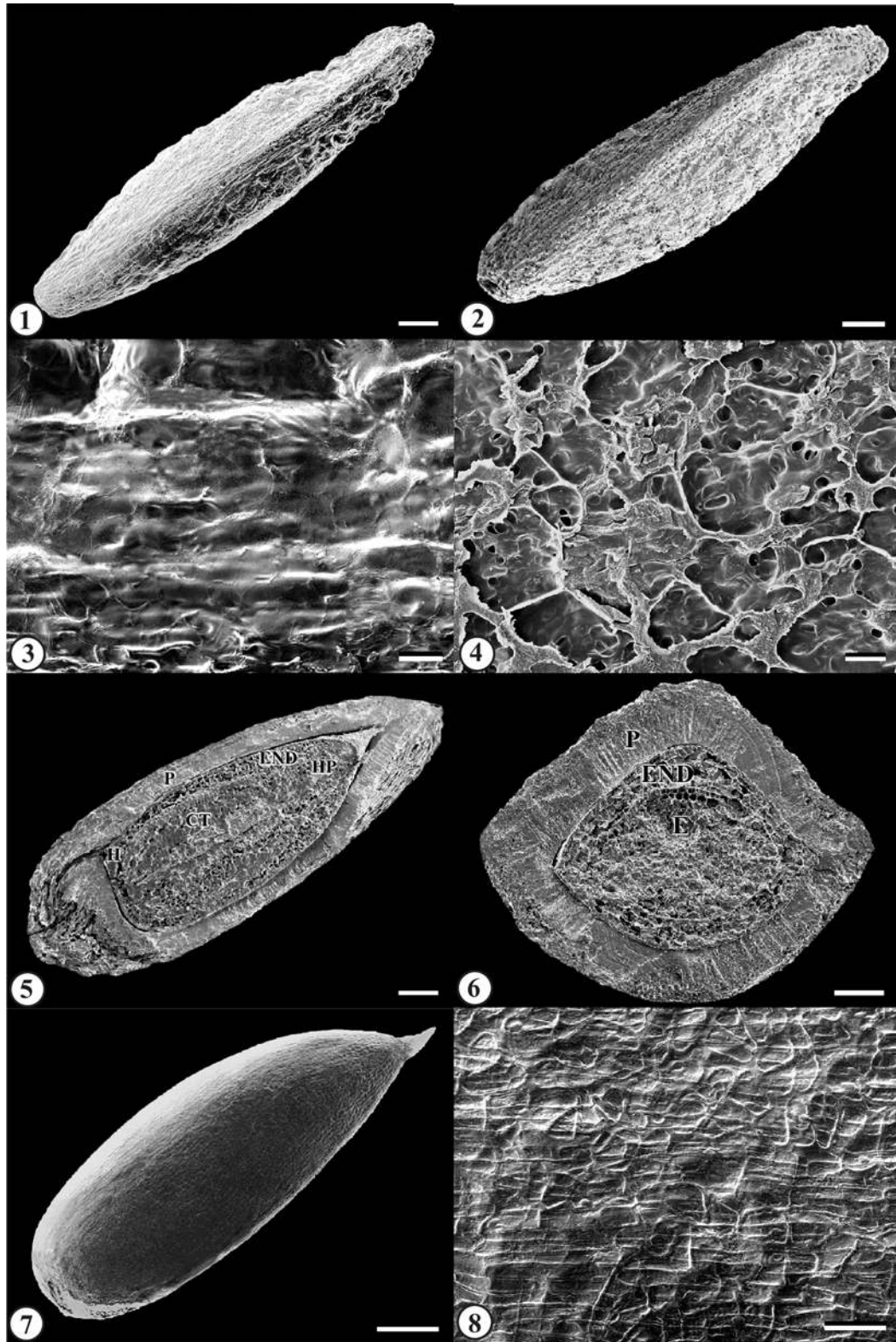
We have observed three intensities of pericarp abrasion in the fruits of *C. obtusa* after passage through the digestive tract of bats (Figs. 2, 4). Most of the fruits lose the mucilaginous cells of the exocarp, some lose only part of the mucilaginous cells with those left maintaining the ability to produce mucilage when placed in water, and others lose the entire exocarp as well as part of the outer mesocarp.

Fruits of *C. obtusa* collected from bat feces and experimentally placed in the soil seed bank had not undergone significant additional structural changes after 1 yr (Figs. 10, 11). The exocarp of all fruits was completely missing as the result of passage through the digestive tract of bats. Fruits buried in clay soil are reddish brown because of the adhesion of clay particles to their surface, while those buried in sandy soil are whitish brown as a result of the loss of tannins from the cells of the outer mesocarp (Fig. 11). The latter color change is probably caused by the higher acidity of sandy soils in comparison to clay soils. Tannins are not dissolved in water, but

are removed by acidic solutions (Johansen, 1940; Schmid, 1977).

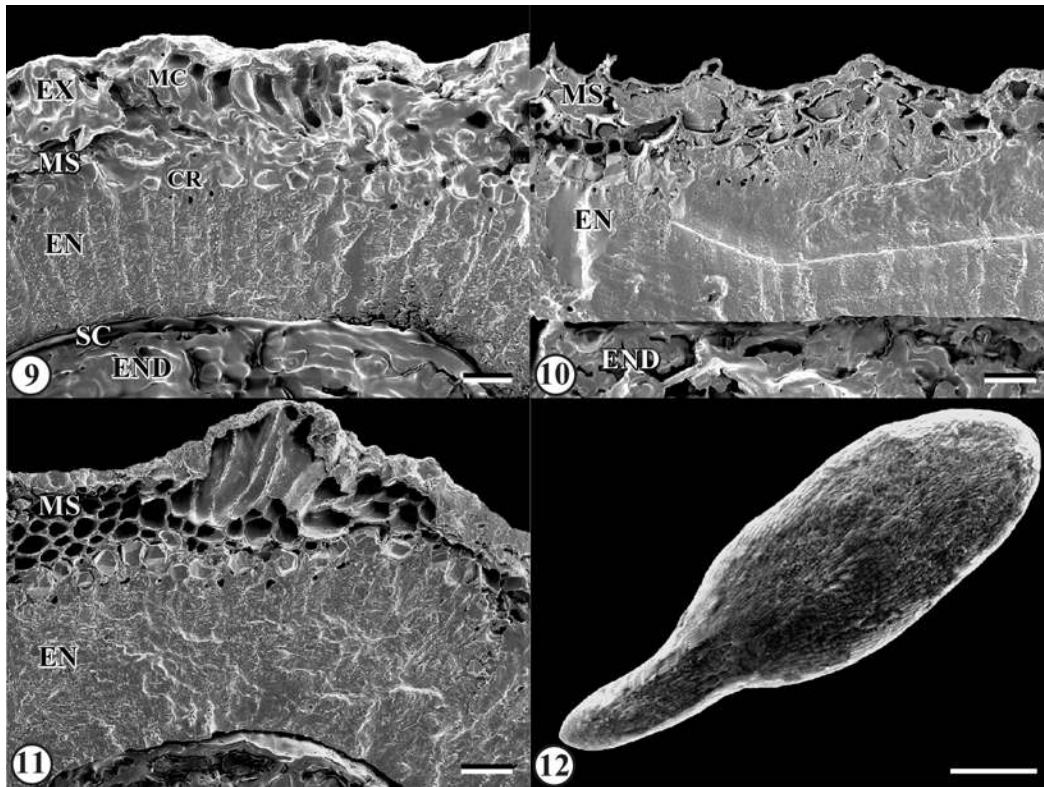
Description of fruits and seeds: *Cecropia palmata*—Fruits obovoid to oblong, ca. 2 × 1.3 × 0.7 mm, whitish-yellow, glossy, the basal end roundish, the apical end more or less flat, obtuse; transverse section triangular-rounded, or elliptic; surface tuberculate (Figs. 16–18, 21), the tubercles small; mucilage layer ca. 0.06 mm thick exudes after placement of fruits in water. *Pedicel scar* conspicuous, basal-lateral, elliptic; vascular bundle single, in one lateral side. *Pericarp* (Figs. 20, 21) ca. 150 μm thick, thicker in lateral sides, thinner in middle of dorsal and ventral sides, with 6–14 layers, differentiated into exocarp, mesocarp, and endocarp (Fig. 22). *Exocarp* single-layered, with two cell types (Fig. 14): first large mucilaginous, with thin anticlinal walls and thickened outer periclinal walls, considerably elongated without destruction of cell boundaries when wet, the second cell type non-mucilaginous, much smaller, with thicker walls, filled with light brown pigment; non-mucilaginous cells rare and situated on top of tubercles. *Mesocarp* 4–12 layers, differentiated into three zones (Figs. 14, 22): outer zone of single layer of small cells with thickened non-lignified walls; intermediate zone of 2–10 (more in lateral sides) layers of longitudinally elongated macrosclereids with lamellar thickened walls; inner zone a single layer of cells, each with a prismatic crystal 6.5–9 μm in diameter. *Endocarp* occupying one-half to two-thirds of pericarp, a single layer of radially elongated macrosclereids, longer in tubercles, the macrosclereids similar to those of pericarp of *C. obtusa* (Figs. 14, 22).

Seeds obovoid, 1.6 × 1.2 × 0.5 mm, light yellow, glossy, the micropylar end acute (Fig. 23), the transverse section tri-

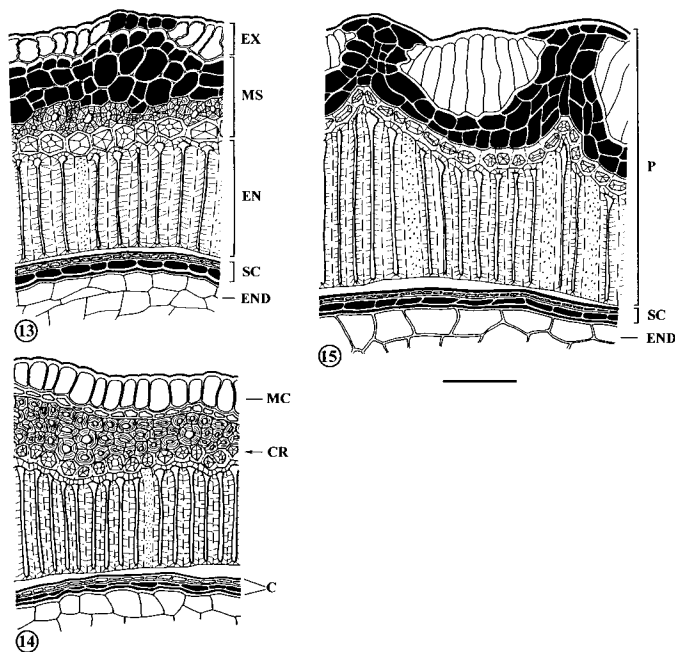


Figs. 1–8. *Cecropia obtusa* (SEM). 1. Fruit. 2. Fruit from feces. 3. Surface of fruit (1). 4. Surface of fruit from feces (2). 5. Longitudinal section of fruit. 6. Transverse section of fruit. 7. Seed. 8. Surface of seed. Scale bars = 200 μm in Figs. 1, 2, 5, and 7; 20 μm in Figs. 3, 4, and 8; 100 μm in Fig. 6.

Figure Abbreviations: C, cuticle; CR, crystal; CT, cotyledons; E, embryo; EN, endocarp; END, endosperm; EX, exocarp; H, hilum; HP, hypocotyl; MC, mucilaginous cells; MS, mesocarp; P, pericarp; SC, seed coat.



Figs. 9–12. *Cecropia obtusa* (SEM). 9. Fragment of pericarp in transverse section. 10. Fragment of pericarp in transverse section of fruit from soil seed bank (clay soil). 11. Fragment of pericarp in transverse section of fruit from soil seed bank (sandy soil). 12. Embryo. Scale bars = 20 μm in Figs. 9–11; 200 μm in Fig. 12.



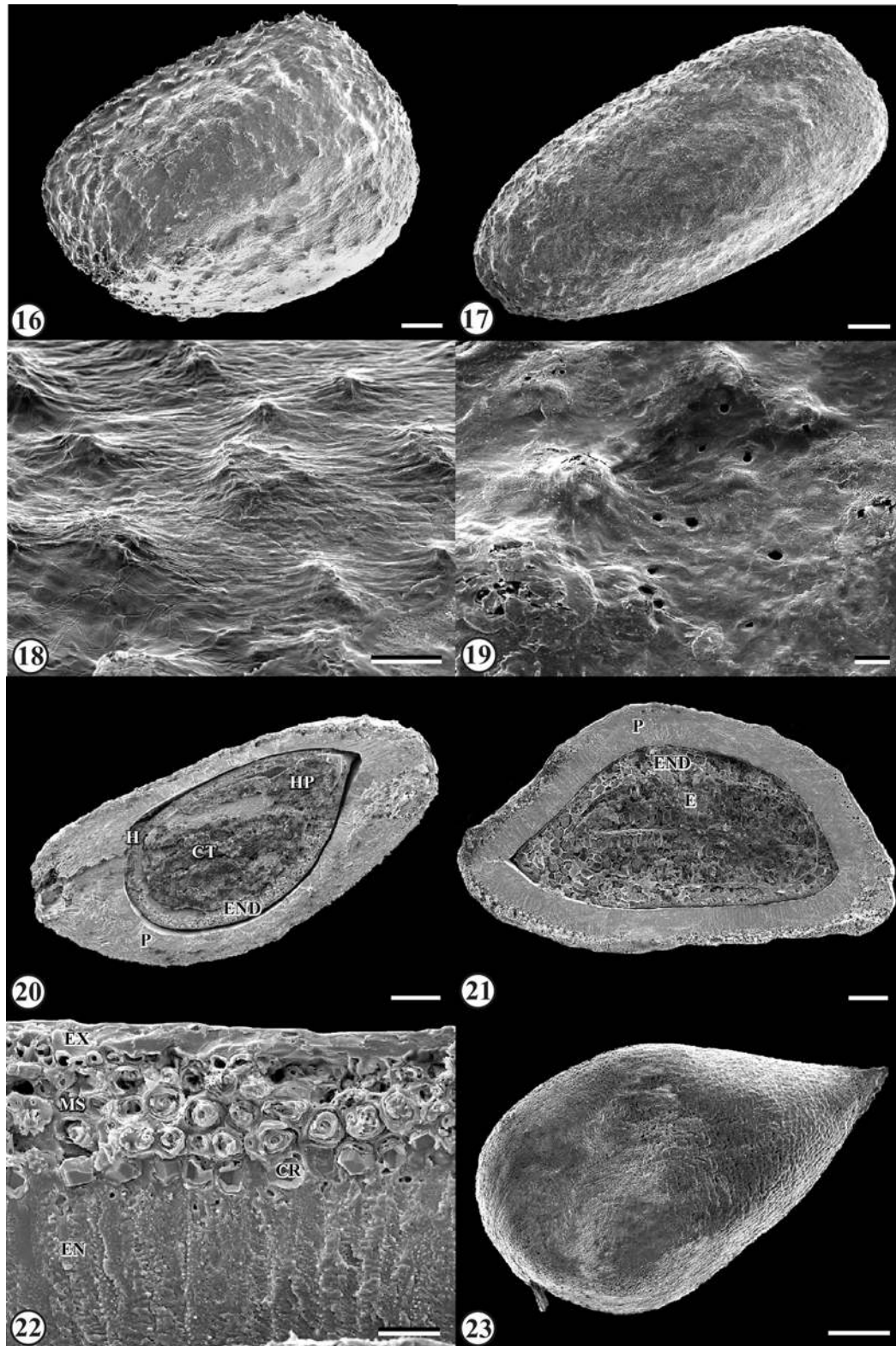
Figs. 13–15. Structure of pericarp, seed coat, and endosperm in transverse sections of *Cecropia* species. 13. *C. obtusa*. 14. *C. palmata*. 15. *C. sciadophylla*. Black filling indicates presence of tannins in cells. Scale bar = 50 μm .

angular-rounded or elliptic (Fig. 21), the surface indistinctly striate-reticulate (Fig. 24). *Hilum* conspicuous, basal, slightly displaced to one side (Figs. 20, 23). *Seed coat* reduced to membrane 8–9 μm thick, of two cell layers (Fig. 14): cells of first layer longitudinally elongated, very small on sections, flat, thin-walled, the larger cells of second layer transversal elongated, thicker-walled, filled with tannins. *Endosperm* of 2–6 layers of thin-walled cells (Figs. 14, 20, 21) with protein bodies, starch grains, and oil. *Embryo* linear, straight, ca. 1.1 \times 0.6 mm, the cotyledons large (ca. 0.7 mm long), plano-convex (Figs. 20, 21, 25).

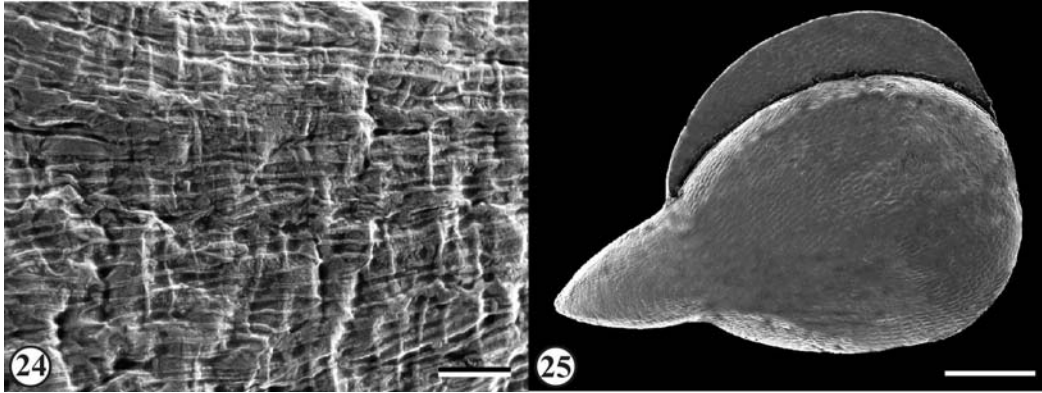
Fruits of *C. palmata* have been found in 24 samples of feces gathered from bats captured in secondary forest (Table 2). The infructescences are consumed by *Artibeus jamaicensis* (fruits found in 17 samples), *A. obscurus* (3), *Carollia perspicillata* (2), and *Platyrrhinus helleri* (2).

After passing through the digestive tract of a bat, the fruits of *C. palmata* lose some of the mucilaginous cells of the exocarp (Figs. 17, 19). The remaining cells retained their ability to produce mucilage when placed in water.

Description of fruits and seeds: *Cecropia sciadophylla*—Fruits ellipsoid, ca. 2.9 \times 1.2 \times 0.9 mm, dark brown, glossy, the end(s) acute; transverse section triangular-rounded or elliptic; surface tuberculate, the tubercles smaller or absent on ends (Figs. 26–28, 31); mucilage layer ca. 0.1 mm thick exudes after placement of fruits in water. *Pedicle scar* conspicuous, basal, circular; vascular bundle single, in one lateral side. *Pericarp* (Figs. 30, 31) ca. 160–200 μm thick, thicker in lateral sides, thinner in middle of dorsal and ventral sides, with



Figs. 16–23. *Cecropia palmata* (SEM). 16. Fruit. 17. Fruit from feces. 18. Surface of fruit (16). 19. Surface of fruit from feces (17). 20. Longitudinal section of fruit. 21. Transverse section of fruit. 22. Fragment of pericarp in transverse section. 23. Seed. Scale bars = 200 μm in Figs. 16, 17, 20, and 23; 50 μm in Figs. 18 and 19; 100 μm in Fig. 21; 20 μm in Fig. 22.



Figs. 24–25. *Cecropia palmata* (SEM). 24. Surface of seed. 25. Embryo. Scale bars = 20 μm in Fig. 24; 200 μm in Fig. 25.

5–8 layers, differentiated into exocarp, mesocarp, and endocarp (Fig. 32). *Exocarp* single-layered, with two cell types (Figs. 15, 32): first large mucilaginous, with thin anticlinal walls and thickened outer periclinal walls, considerably elongated without destruction of cell boundaries when wet, the second cell type non-mucilaginous, much smaller, with thicker walls, filled with brown pigment; non-mucilaginous cells situated on tubercles, the mucilaginous cells between them. *Mesocarp* 3–6 layers, differentiated into two zones (Figs. 15, 32): outer zone 2–5 (more in tubercles) layers of longitudinally elongated tanniferous cells, the walls slightly thickened, the outer periclinal walls of first layer thicker; inner zone a single layer of cells, each with a prismatic crystal 6.5–13 μm in diameter. *Endocarp* occupying one-half to two-thirds of pericarp, a single layer of radially elongated macrosclereids, longer in tubercles, the macrosclereids similar to those of pericarp of *C. obtusa* (Figs. 15, 32).

Seeds oblong-ovoid, 1.9 \times 0.9 \times 0.6 mm, light brown, glossy, the micropylar end acute (Fig. 33), the transverse section triangular-rounded or elliptic (Fig. 31), the surface indistinctly striate-reticulate (Fig. 34). *Hilum* conspicuous, basal, slightly displaced to one side (Figs. 30, 33). *Seed coat* reduced to membrane 8–11 μm thick, of two cell layers (Fig. 15): cells of first layer longitudinally elongated, very small, flat, light brown, thin-walled, the cells of second layer transversal elongated, bigger, thick-walled, filled with tannins. *Endosperm* of 2–5 layers of thin-walled cells (Figs. 15, 30–32) with protein bodies, small starch grains, and oil. *Embryo* linear, straight, ca. 1.5 \times 0.6 mm, the cotyledons large (ca. 1 mm long), plano-convex (Figs. 30, 31, 35).

Fruits of *C. sciadophylla* have only been found in three samples of feces gathered from *Rhinophylla pumilio* captured in both primary and secondary vegetation (Table 2).

After passing through the digestive tract of a bat, the fruits of *C. sciadophylla* lose all or part of their exocarp (Figs. 27, 29). The remaining mucilaginous cells retained their ability to produce mucilage when placed in water.

DISCUSSION

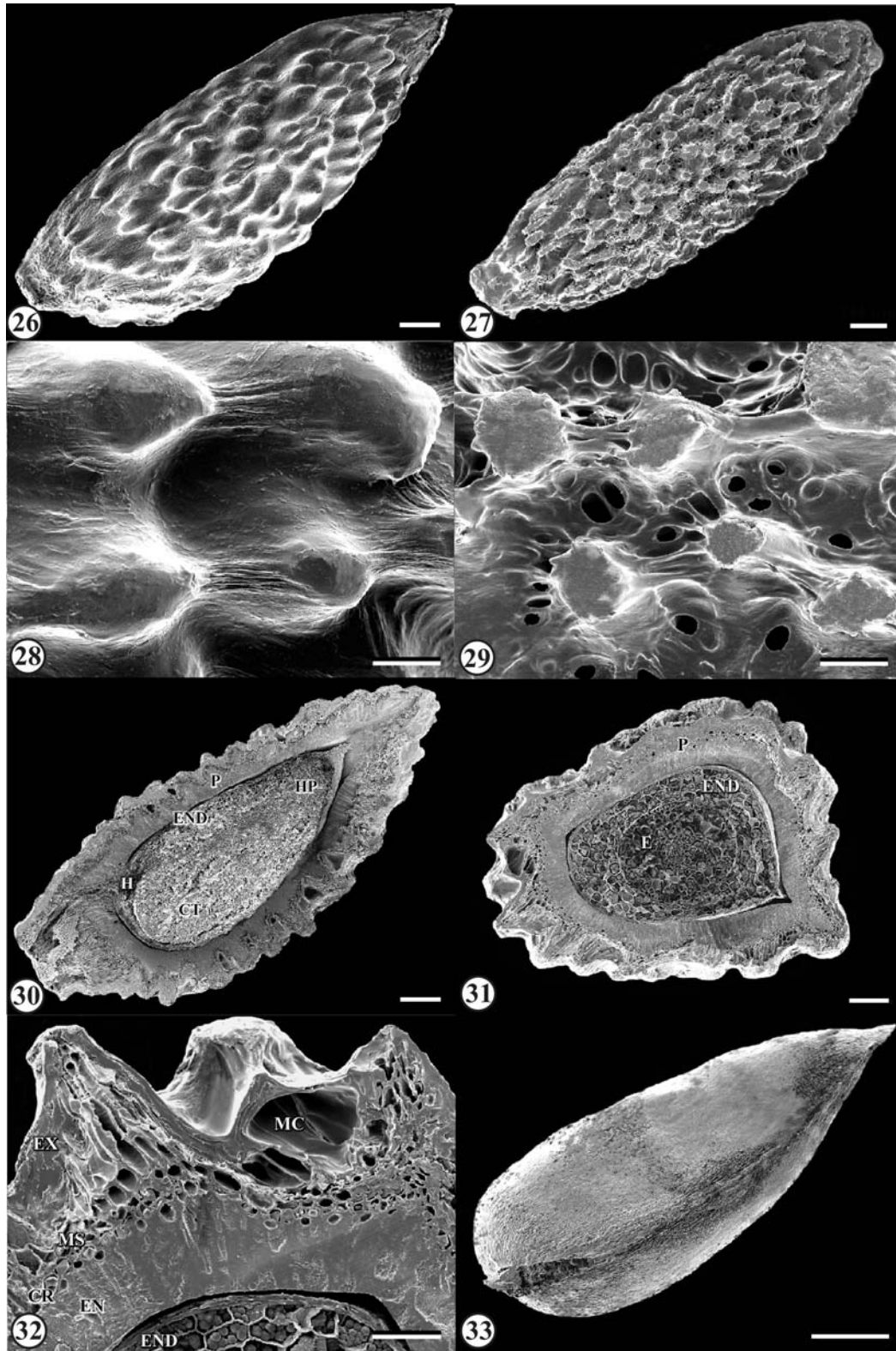
Role of bats in the dispersal of *Cecropia*—Review of the literature (Table 1) and our own collections (Table 2) confirm that bats throughout the Neotropics as well as in French Guiana frequently disperse species of *Cecropia*. Species of 12 genera of bats have been recorded in the literature as eating the infructescences of *Cecropia*, and, of the 32 species, nine

belong to *Artibeus* (Table 1). Our collections demonstrate that *Artibeus obscurus* (41 feces samples containing *Cecropia*) and *A. jamaicensis* (40) commonly feed on *C. obtusa*, and that *A. jamaicensis* (17) also commonly feeds on *C. palmata* (Table 2). Thus, species of *Artibeus* seem to be especially important in dispersing *Cecropia*.

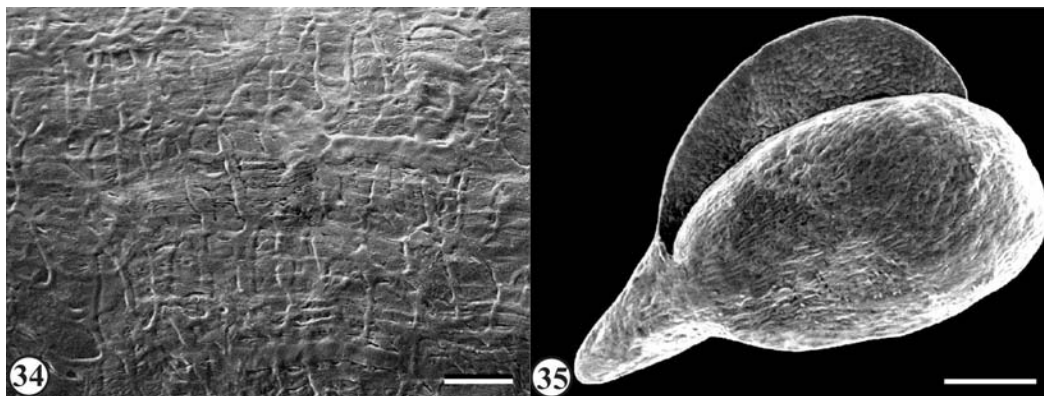
Artibeus lituratus, the largest South American frugivorous bat, has been calculated to eat 144 g, nearly double its body mass (Charles-Dominique et al., 2001), of *C. obtusa* per night. Because *A. lituratus* does not eat large quantities of insects, most of its nutrients come from fruits. The dry mature infructescences of *C. obtusa* in French Guiana contain approximately 50% fruits, 25% non-hydrosoluble fibers, and a 25% hydrosoluble fraction consisting mostly of C6 and C12 sugars and 0.4–0.6% nitrogen, represented by 21 free amino acids (Charles-Dominique, 1986). The infructescences of *C. obtusa* contains 2.2 mg/g dry pulp (derived from the perianth) of free amino acids (0.22%) and 45.5 mg/g dry pulp of soluble sugars (4.55%). The infructescences of *C. sciadophylla* have a similar composition of amino acids and sugars. The relatively low nutrient content is compensated for by the fact that bats eat a lot of infructescences (Charles-Dominique, 1986).

In search of fruit, *Artibeus lituratus* makes approximately 40 feeding flights per night; and, as in many species of frugivorous bats, fruit passage through the gut is as short as 5 min when the bat is actively foraging (Charles-Dominique and Cooper, 1986). Examination of 212 fecal samples from *Artibeus lituratus*, *Sturnira lilium*, and *Carollia perspicillata* by Charles-Dominique and Cooper (1986) revealed the presence of fruits of *C. obtusa* in 10 of 19 samples, 1 of 41 samples, and 0 of 152 samples from each species of bat, respectively. *Artibeus lituratus*, therefore, preferentially feeds on *C. obtusa*, but documentation of this is difficult to obtain because this bat flies relatively high in the canopy, i.e., above the level that most nets are set (Charles-Dominique, 1986).

Bats play an important role in moving the diaspores of secondary forest species into primary forest (Table 2) and in transporting the larger seeds of primary forest into secondary forest. *Artibeus lituratus*, for example, consumes the seeds of the secondary forest species *Cecropia obtusa* (Tables 1, 2), as well as the fruits of the primary forest species *Symphonia globulifera*, *Licania* spp., *Parinari* spp., *Caryocar glabrum*, *Dipteryx odorata*, *Bocoa prouacensis*, and *Swartzia panacoco* (Foresta et al., 1984; Charles-Dominique and Cooper, 1986). The seeds of these species are relatively large, but this bat is



Figs. 26–33. *Cecropia sciadophylla* (SEM). 26. Fruit. 27. Fruit from feces. 28. Surface of fruit (26). 29. Surface of fruit from feces (27). 30. Longitudinal section of fruit. 31. Transverse section of fruit. 32. Fragment of pericarp in transverse section. 33. Seed. Scale bars = 200 μm in Figs. 26, 27, 30, and 33; 50 μm in Figs. 28, 29, and 32; 100 μm in Fig. 31.



Figs. 34–35. *Cecropia sciadophylla* (SEM). 34. Surface of seed. 35. Embryo. Scale bars = 20 μm in Fig. 34; 200 μm in Fig. 35.

capable of transporting fruits and seeds almost as large as itself (Foresta et al., 1984).

Radio tracking of *Artibeus lituratus* in French Guiana (Foresta et al., 1984) has demonstrated that this species feeds in fruiting trees within a radius of 200–400 m and that it changes feeding patches 2–3 times a night. The patches may be 1–2 km apart from one another. Moreover, this bat can have its day roosts in primary forest as well as in or close to secondary forest. Consequently, *Artibeus lituratus* plays a role in the movement of at least one secondary forest species, *Cecropia obtusa*, into primary forest and can potentially transport the seeds of a number of primary forest species into secondary forest. In a study of bat dispersal of *C. obtusa*, Charles-Dominique (1986) found that bats visiting this species sometimes arrived with the fruits of primary forest species such as *Licania* sp. and *Symphonia globulifera*. In Mexico, Vásquez-Yanes et al. (1975) found that *Artibeus jamaicensis* also transported seeds between primary and secondary vegetation. Measurement of the seed rain in primary forest in French Guiana using eight 1-m² plots yielded a total of 2864 fruits and seeds during the course of a year. Among the propagules were 1111 fruits of *C. obtusa* (139 fruits \cdot m⁻² \cdot yr⁻¹) and 25 fruits of *C. sciadophylla* (3.1 fruits \cdot m⁻² \cdot yr⁻¹) (P. Charles-Dominique, unpublished data).

Although bats commonly consume the infructescences of species of *Cecropia*, many other animals exploit this abundant resource. The murine mouse opossum, *Marmosa murina*, has been photographed eating a fragment of an infructescence of *Cecropia* sp. and fruits of *C. palmata* have been found in its digestive tract (Charles-Dominique et al., 1981). The primate *Alouatta palliata* consumes the fruits of *C. obtusifolia* in the area of Los Tuxtlas, Mexico (Estrada et al., 1984b) and the fruits of *C. peltata* in Costa Rica (Fleming and Williams, 1990). But this howler monkey feeds on unripe infructescences and therefore should be considered a seed predator as well as potential seed disperser (Fleming and Williams, 1990). Estrada et al., (1984a) observed 48 different species of animals consuming the infructescences of *C. obtusifolia*. Kinkajous and marsupials seek the infructescences of *C. obtusa* in French Guiana (Charles-Dominique, 1986; Julien-Laferrière, 2001). Charles-Dominique (1986) observed that the tiny arboreal rodent *Oecomys bicolor* consumes the unripe fruits of *C. obtusa* and *C. sciadophylla*, and, hence, it is a seed predator rather than a seed disperser. Additionally, at least 76 species of birds in 19 families are known to feed on *Cecropia* (Holthuijzen, 1979). Fleming and Williams (1990) documented that in a

Costa Rican tropical dry forest diurnal and nocturnal animals consume similar amounts of *C. peltata* fruits and suggested that the digestive systems of birds and bats treat *Cecropia* fruits more gently than do monkeys.

Earlier work on *C. obtusa* and *C. sciadophylla* has suggested that some species of *Cecropia* are adapted for dispersal primarily by birds and others primarily by bats (Charles-Dominique, 1986; Charles-Dominique and Cooper, 1986). Although fruit of *C. obtusa* is mostly dispersed by bats, birds (e.g., *Thraupis* spp., *Ramphocelus carbo*, and *Pteroglossus* spp.) remove 17% of the fruits during the day (Charles-Dominique, 1986). In contrast, the fruits of *C. sciadophylla* are usually dispersed by birds (Charles-Dominique et al., 1981; Foresta et al., 1984; Charles-Dominique, 1986, 1993; Charles-Dominique and Cooper, 1986). Nevertheless, Cloutier and Thomas (1992), Gorchoy et al. (1995), and Cockle (1997) have identified fruits of *C. sciadophylla* in the feces of species of *Artibeus*, *Carollia*, *Phyllostomus*, and *Rhinophylla* (Table 1).

In our study, fruits of *C. sciadophylla* were obtained only from *Rhinophylla pumilio* on three occasions (Table 2), supporting Cockle's (1997) findings that *R. pumilio* at least occasionally consumes the infructescences of *C. sciadophylla* in French Guiana. Our collections are the first documentation of the consumption of the infructescences of *C. obtusa* by *Artibeus obscurus*, *A. gnomus*, *A. cinereus*, *Carollia perspicillata*, *C. brevicauda*, *Chiroderma villosum*, *Platyrrhinus helleri*, *P. brachycephalus*, *Sturnira tildae* and the infructescences of *C. palmata* by *A. obscurus* and *P. helleri*.

Diaspores of *Cecropia*—In all species of *Cecropia*, the fruits are achenes surrounded by enlarged perianths aggregated into digitate infructescences (Berg and Franco-Roselli, in press). We do not consider the fruit to be a sorosus (compound fruit) in the sense of Spjut (1994) because the fruit is not fleshy; moreover, there are no fusions among adjacent perianths or between the perianth and the fruit. Fruits of *C. obtusa*, *C. palmata*, and *C. sciadophylla* are easily removed from the perianth when fresh or dry. During germination, the pericarp splits along the lateral sides into two equal parts to expose the seed (T. Lobova, unpublished data). Because the fruits are small, indehiscent, and one-seeded, they are referred to as seeds in most of the bat/plant literature. However, the diaspores of species of *Cecropia* are technically fruits, so bats (as well as other animals) disperse fruits and the soil seed bank contains fruits. Bats consume the ripe parts of an infructes-

TABLE 3. Difference in fruit morphology of *Cecropia* species.

Species	Size (mm)	Color	Shape	Surface
<i>C. obtusa</i>	2.9 × 0.8 × 0.8	brown	lanceolate-ellipsoid	indistinctly undulate-rugose
<i>C. palmata</i>	2 × 1.3 × 0.7	whitish yellow	obovoid to oblongoid	tuberculate, with small tubercles
<i>C. sciadophylla</i>	2.9 × 1.2 × 0.9	dark brown	ellipsoid	tuberculate

cence, digest the pulp derived from the enlarged, fleshy perianth and defecate the fruits.

We assume, therefore, that the “fruit nutritional content” of *Cecropia* reported in the literature refers to the nutritional content of the persistent perianth. Because dispersal agents digest no part of the fruit, fruits should be removed from the perianth, and only the nutritional composition of the perianth should be assayed in future studies.

Comparison of fruit structure—The fruits of *C. obtusa*, *C. palmata*, and *C. sciadophylla* all produce mucilage when placed in water and are morphologically and anatomically similar. In these three species, the pericarp is thick, the exocarp contains both mucilaginous and non-mucilaginous cells, the mesocarp has a crystal-bearing inner layer, and the endocarp consists of large macrosclerids (Figs. 13–15). The same general pericarp structure was described by Kravtsova (1995) for *C. distachya* Huber, *C. membranacea* Trécul., *C. obtusifolia* Bertoloni, *C. pachystachya* Trécul., *C. peltata* L., and *C. schreberiana* Miq. Species-specific pericarp characters for *C. obtusa* are the rugose surface and presence of an intermediate stone cells zone in the mesocarp, for *C. palmata* the small tubercles, the presence of an outer cell layer with non-lignified walls and macrosclerids in the mesocarp, and the lack of tannins in the pericarp, and for *C. sciadophylla* the large tubercles and absence of sclerids in the mesocarp. Size, color, shape, and surface provide other characters that can be used to identify these species based on material collected from bat feces (Table 3). We conclude that the fruits of these and some other species (Kravtsova, 1995) of *Cecropia* possess the interspecific variation needed for identifying fruits in plant/animal studies. Moreover, we suggest that morphological and anatomical characters of fruit may be useful in the species taxonomy of *Cecropia*.

In contrast, the seeds, which are not easily detached from the indehiscent fruits, are similar in morphology and anatomy and variation in their features is not useful for identifying species. The seed coat, reduced to two layers of nonlignified cells, is very thin, as is often the case in indehiscent fruits. Thus, the pericarp, rather than the seed coat, assumes the function of protecting the seed. Furthermore, we point out that seeds of *Cecropia* possess a conspicuous endosperm, a feature that has been mistakenly recorded as absent (Engler, 1889; Hutchinson, 1967).

Significance of external mucilage production—The ecological functions of the external production of mucilage in fruits and seeds has been hypothesized to (1) aid in water retention during germination; (2) fix the diaspore to the soil or other substrates; (3) lubricate the radicle as it penetrates the soil; (4) increase diffusion of water from the substrate into the seed; (5) facilitate hydrochory; (6) enhance epizoochory by increasing the ability of diaspores to adhere to animals; (7) build an additional protective barrier by promoting adhesion of soil particles to the diaspore; and (8) prevent the germina-

tion of seeds under water-logged conditions by hindering oxygen uptake (Haberlandt, 1914; Murbeck, 1919; Gill, 1935; Harper and Benton, 1966; Gutterman et al., 1967, 1973; Kuijt, 1969; Witzum et al., 1969; Fahn and Werker, 1972; Grubert, 1974; Werker, 1997). The significance of mucilage to endozoochorously dispersed diaspores has not been broadly discussed in the literature.

The fruits of *C. obtusa*, *C. palmata*, and *C. sciadophylla* partly or entirely lose the mucilaginous part of the exocarp while passing through the digestive tracts of bats (Figs. 4, 19, 29). We consider this to be the result of moisture absorption by the fruits combined with mechanical and/or chemical abrasion during passage. Fruits that have been placed in water followed by air drying display almost the same fruit surface pattern as those that have passed through the digestive tracts of bats. Species-specific differences in the original size and extent of mucilaginous cells play a role in the degree of change the fruit surface displays. Thus, *C. obtusa* and *C. sciadophylla*, which produce a mucilage layer 0.1 mm thick, undergo considerably more exocarp destruction (Figs. 4, 29) than *C. palmata*, with a mucilage layer only 0.06 mm thick (Fig. 19). However, because infructescences are consumed in pieces, the fruits are differentially protected depending on their position in relation to the remaining parts of the infructescence as they pass through the digestive tracts of bats. These differences may account for the variable amount of change seen in pericarp of fruits from feces within each species.

Kravtsova (1995) noted the presence of a mucilaginous exocarp in the fruits of *Cecropia distachya*, *C. membranacea*, *C. obtusifolia*, *C. pachystachya*, *C. peltata*, and *C. schreberiana*. All these species are also reported to be dispersed by bats (Table 1).

It seems unlikely that mucilage is nutritionally important to bats because the fruits of *Cecropia* produce an insignificant amount of it. Moreover, the mucilaginous cells are often intact after passing through the bat's intestines, whereas the perianth surrounding the fruit is completely digested. Nevertheless, the nutritional content of the mucilage of *Cecropia* has not been determined. We suggest that mucilage covering the fruit of *Cecropia* provides lubrication and thereby promotes fruit passage through the digestive tracts of animals.

Influence of bats on dispersal and seed germination—Diaspores pass through the digestive tracts of bats within 5–20 min (Fleming and Heithaus, 1981; Charles-Dominique, 1986). This short passage time lessens the amount of mechanically and chemically induced changes suffered by the diaspores. The passage removes the perianth and all or part of the mucilaginous layer surrounding the fruit of *Cecropia*, thereby reducing the adhesion of fruits with one another. Because bats defecate in flight, the fruits from a single defecation are spread over a surface of about 2–3 m long and 0.5–1 m wide (P. Charles-Dominique, unpublished data). Therefore, bat dispersal of *Cecropia* provides efficient dissemination into large gaps and primary forest.

Endozoochorous dispersal may increase the germination of many seeds owing to the removal of an impermeable layer of the seed coat and/or a soluble germination inhibitor (van der Pijl, 1972; Traveset and Verdú, 2002). Estrada with coauthors (Estrada et al., 1984a; Estrada and Coates-Estrada, 1986) observed that fruits of *Cecropia obtusifolia* after passage through the digestive tracts of animals have greater germination than fruits not consumed by animals. Fleming (1988) found similar results for *C. peltata*. In contrast, Vázquez-Yanes and Orozco-Segovia (1986), in their study of *C. obtusifolia*, concluded that passage through the digestive tracts of bats did not influence seed germination.

In our germination experiments with *C. obtusa* (T. Lobova, unpublished data), we obtained 100% seed germination after 10–15 d from fruits taken from 2-yr-old herbarium specimens and 100% germination after 30–35 d from fruits taken from a 2-yr-old bat fecal sample (fruits kept in tap water at room temperature under ambient office light). These observations support the findings (Vázquez-Yanes and Orozco-Segovia, 1986) that passage of the fruits of *Cecropia* through the digestive tracts of bats is not necessary for seed germination. In addition, these findings suggest that external mucilage production does not play a significant role in the germination of *Cecropia* seeds as they germinate with or without mucilage in nature or in the laboratory.

We consider, however, that removal of tissue surrounding the diaspore, whether it is the result of passing through the digestive tract of a bat or because of a controlled experiment, is probably essential for optimum seed germination. Estrada et al., (1984a) reported that whole infructescences of *C. obtusifolia* fallen on to the forest floor were rapidly attacked by fungi, and the seeds did not germinate. Under these circumstances, the intact perianth may have prevented the penetration of the light needed for germination. Also, under excessively moist conditions, the fleshy perianth and the mucilaginous layers of the diaspores can serve as a substrate for bacterial growth, which results in seed rot (Gutterman et al., 1973). We conclude that fruit passage through a bat's digestive tract increases seed survival and enhances germination by removing the perianth and some of the mucilaginous tissue from the fruits.

Role of fruit structure in seed longevity—As mentioned previously, the fruits of *C. obtusa* and *C. sciadophylla* are among the most common in the soil seed bank (Prévost, 1982). At two sites in French Guiana, one in primary forest and another in primary forest close to secondary forest, fruits of *C. obtusa* were found at densities of 50 fruits/m² and 70 fruits/m² and fruits of *C. sciadophylla* at densities of 28 fruits/m² and 32 fruits/m² to a depth of 3 cm, respectively (P. Charles-Dominique, unpublished data). Seeds of *Cecropia* can germinate after 4, 5 (Holthuijzen and Boerboom, 1982; Charles-Dominique, 1986; Lescure et al., 1989) or even up to 9 yr after dispersal (P. Charles-Dominique, unpublished data).

Ecological longevity of seeds in tropical rain forest is among the shortest of any plant community because seeds tend to germinate soon after dispersal (Foster, 1986; Garwood, 1989; Vázquez-Yanes and Orozco-Segovia, 1993). Delayed germination, a feature of species found in soil seed banks, exposes diaspores to the diverse population of year-round predators and parasites common to environments with high soil moisture and temperature (Foster, 1986; Vázquez-Yanes and Orozco-Segovia, 1993). Factors that independently, or in

combination, may extend the longevity of seeds in forest soil are (1) the presence of a dormancy mechanism that prevents rapid germination; (2) the presence of a hard and/or impermeable coat that prevents rehydration and diminishes predation; and (3) the presence of strong chemical defenses against parasitism and predation (Janzen et al., 1982; Hopkins and Graham, 1987; Alvarez-Buylla and Martinez-Ramos, 1990; Vázquez-Yanes and Orozco-Segovia, 1993; Baskin and Baskin, 1998). The diaspores of *Cecropia* meet these requirements. First, they possess an efficient dormancy mechanism, requiring light for germination (Holthuijzen and Boerboom, 1982; Vázquez-Yanes and Orozco-Segovia, 1986; Souza and Válio, 2001). In addition, our study of the fruit anatomy of *C. obtusa*, *C. palmata*, and *C. sciadophylla* reveals a number of features that may enhance seed longevity in the soil seed bank. These species have a hard and somewhat impermeable pericarp consisting of a very thick inner sclerified layer, support from a crystal-bearing layer, and additional sclereids in the mesocarp of *C. obtusa* and *C. palmata*. Furthermore, the pericarps of *C. obtusa* and *C. sciadophylla* have a layer of tanniferous cells. Tannins protect seeds from attack by herbivores, fungi, bacteria, and viruses (Roth, 1987) and may also make the cell layers containing them harder and impermeable to water (Rangaswamy and Nandakumar, 1985). Nevertheless, the fruits of *Cecropia* are not completely impermeable because the vascular bundle penetrates the pericarp at the pedicel scar. Evidence of the efficacy of these structures is that fruits of *C. obtusa* that have been in the soil seed bank for a year have not changed from those collected from the feces of bats. An exception, however, is the disappearance of tannins from the pericarps of fruits that are taken from the seed banks of sandy, presumably more acidic, soils.

We conclude that the fruits of *Cecropia* have evolved features that allow them to remain dormant in the soil seed bank until conditions become favorable for seed germination. These features make it possible for species of *Cecropia* to play an essential role in forest regeneration after disturbance. The occurrence of stands of *Cecropia* in many large and small gaps throughout the Neotropics reflects the fruit adaptations of this ecologically successful pioneer species.

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