

Biodiversity of Domatia Occupants
(Ants, Wasps, Bees, and Others)
of the Sri Lankan Myrmecophyte
Humboldtia laurifolia Vahl (Fabaceae)

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ABSTRACT

Krombein, Karl V., Beth B. Norden, Melinda M. Rickson, and Fred R. Rickson. Biodiversity of the Domatia Occupants (Ants, Wasps, Bees, and Others) of the Sri Lankan Myrmecophyte *Humboldtia laurifolia* Vahl (Fabaceae). *Smithsonian Contributions to Zoology*, number 603, 34 pages, 70 figures, 1999.—The myrmecophyte *Humboldtia laurifolia* is endemic to Sri Lanka, where it is a common understory tree in lowland rainforests. It attracts a diversity of invertebrate associates and possesses morphology and phenology, including expanded, hollow, self-opening internodes and a variety of extrafloral nectaries that facilitate a relationship with ants.

Fourteen ant taxa were collected on *H. laurifolia*. *Technomyrmex albipes* (F. Smith) was dominant at many sites. Other ant taxa included *Tetraponera* sp., *Cataulacus taprobanae* F. Smith, three species of *Crematogaster*, *Pheidole* sp., *Tetramorium pacificum* Mayr, *Dolichoderus* sp., *Tapinoma* sp., *Anoplolepis gracilipes* (F. Smith), *Camponotus* sp., *Oecophylla smaragdina* (Fabricius), and *Polyrhachis bugnioni* Forel.

Among other invertebrates found on *H. laurifolia* was the internode-nesting crabronine wasp *Krombeinictus nordenae* Leclercq. It is unique among Sphecidae in its attentive maternal care, progressive feeding of pollen to a single larva at a time, and cocoon placement and structure.

Also commonly found nesting in *Humboldtia* was the crabronine *Crossocerus mukalanae* Leclercq. It makes a typical crabronine nest, constructing a linear series of cells from fragments of the dried, collapsed plant pith within the internode. The paralyzed prey provided for the larvae were predominantly Diptera, the majority of them nematocerous species; other less common prey included chalcidoid wasps and Ephemeroptera. Several species of *Perilampus* (Chalcidoidea) are pupal parasites of *C. mukalanae*, and larvae and adults of species of Staphylinidae found in wasp nests are presumed to be brood predators.

A much less common hymenopteran nesting in internodes was an undescribed species of the social xylocopine bee *Braunsapis*. Four nests contained one or two females, an occasional male, and immature brood. A larva of a species of Cleridae, presumably a brood predator, was found in two of the nests.

Several invertebrate associates of *Humboldtia* are clearly ant predators. The fly larva of *Platyteridion edax* Chandler and Matile (Keroplataidae) is primarily predaceous on worker ants. Also recorded were the larvae of *Microdon* sp. (Syrphidae), which feed on ant brood, and the pseudoscorpion *Haplochernes warburgi* (Tullgren), which is predatory on worker ants. The relationship of other associates was less clear. These included spiders (Theridiidae, Hadrotarsinae), the bee *Nomada wickwari* Meade-Waldo (Anthophoridae), the wasps *Carinostigmus costatus* Krombein (Sphecidae) and *Physetopoda fumigata* (Turner) (Mutillidae), and numerous specimens of Psocoptera and Collembola.

Also, clusters of an arboreal annelid, *Perionyx* sp. (Megascolecidae), were found in some internodes, and individuals were noted crawling on stems or leaves during light rains. Adults were observed mating on foliage and were never found on the ground.

The diapausing larva of *Krombeinictus nordenae* is described in an appendix by Howard E. Evans. It is not significantly different from other crabronine larvae of the genera *Crossocerus*, *Crabro*, and *Rhopalum*, even though the larvae were fed pollen rather than paralyzed arthropods.

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Introduction

A number of plants throughout the world have entered into facultative or obligate mutualistic relationships with ants, taking advantage of the insect's ability to protect its territory (the plant) by repelling or killing intruders. The plants have evolved numerous methods to ensure an ant's presence, ranging from offering both a domicile and a constant food supply throughout the year to no domicile and temporal sugar-secreting nectaries only. Either situation improves the chances of having ants present on a plant. The ants present may be obligate and restricted to a single specific plant taxon. A single plant species, however, may attract numerous ant taxa, sometimes as many as fifteen.

Humboldtia laurifolia Vahl (Fabaceae, Caesalpinioideae) is a common understory tree in the lowland rainforest of Sri Lanka. It is a myrmecophyte, but it also attracts a diversity of other animal life. In this contribution we discuss the variety of organisms interacting with and inhabiting this tree.

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The internodes (i.e., domatia) of *Humboldtia* are inflated, hollow cavities that provide nesting sites for ant colonies. In addition to collapse of the central pith against the inner walls of the cavity, a slit-like opening develops at the top of the hollow internode, which allows access to any organism small enough to fit through the opening. The tree also has numerous extrafloral nectaries, which produce sugary secretions where ants and other insects feed. In this mutualistic arrangement, some of the ant species, especially those species nesting in the plant, protect the foliage and flower buds from herbivory.

The internodes not occupied by ants furnish nesting sites for solitary or subsocial wasps and bees, as well as shelter for other invertebrates. Some of the latter are predators or parasites of the ants, bees, and wasps nesting in the same plant.

MATERIALS AND METHODS

We sampled *H. laurifolia* at three distinct and separated locations within Ratnapura District, Sri Lanka (Figure 1). Location A is within 1 km of the road between Ratnapura and Gilimale, in a general area called Induruwa Forest, between kilometer posts 9 and 18, 6°44'N, 80°26'E. Location B includes various sites within Sinharaja Forest Reserve, 6°27'N, 80°26'E. Location C is along two streams 10 km south of Belihul Oya, 6°40'N, 80°45'E. Each location is separated from the others by 20–30 km of straight-line map distance with no obvious populations of *H. laurifolia* visible along roads between the locations. Krombein and Norden collected only at the Gilimale Road location (km posts 9–10) between 18–20 July and 2–3 August 1993, and between 11 March and 5 May 1997, whereas the Ricksons collected repeatedly from all three areas during 1991–1992.

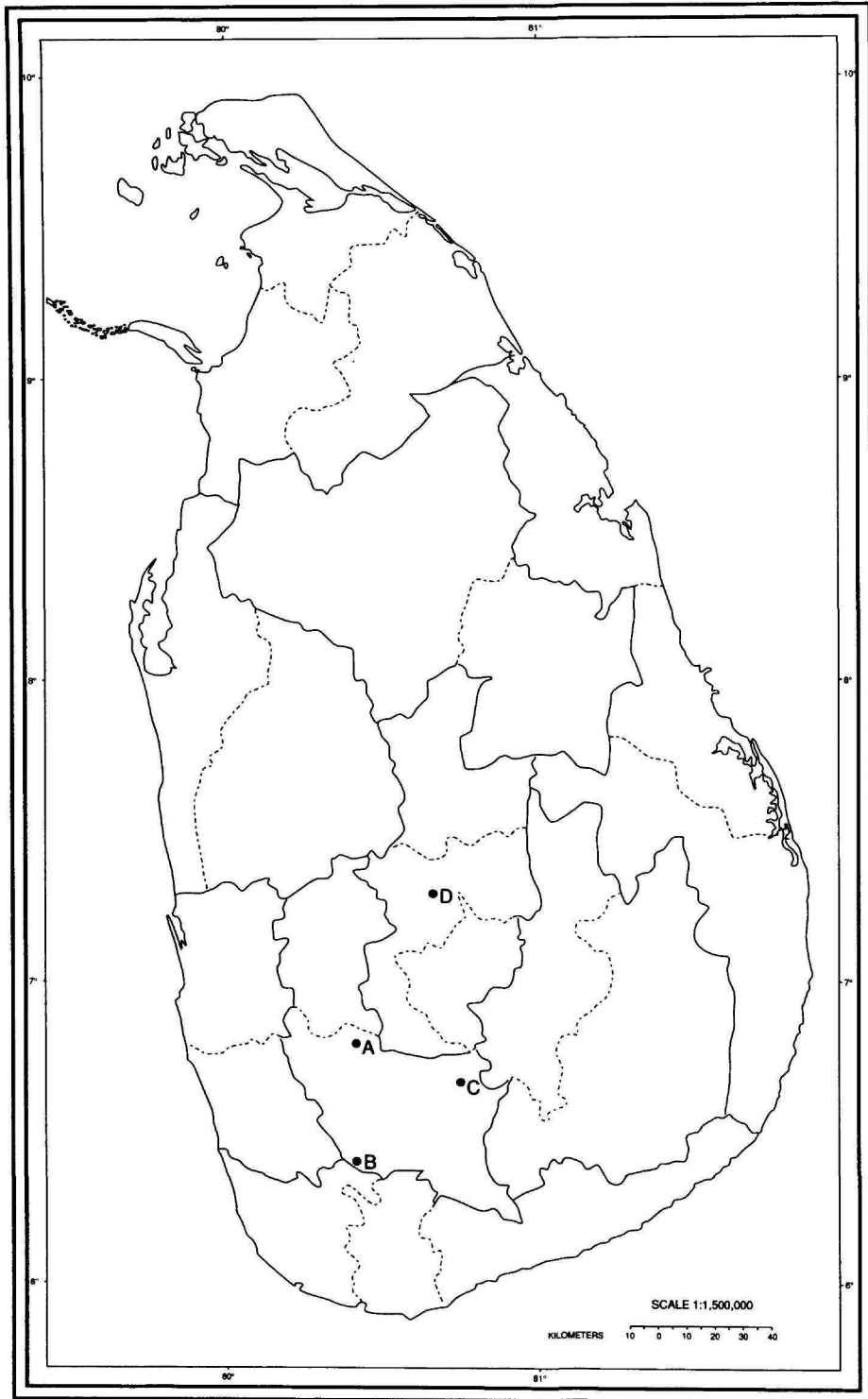


FIGURE 1.—Map of Sri Lanka showing study localities: A, Gilimale; B, Sinharaja Forest Reserve; C, Belihul Oya; and D, Peradeniya. (Solid lines are province boundaries, dashed lines are district boundaries.)

The three sampling locations were vegetationally distinct in total disturbance level, physical access, and rough estimates of plant species composition. The Gilimale Road area was highly disturbed from general fuelwood collection, logging, nearby tea plantations, and the fact that the area is along a hard-surface road providing access to Adams Peak, a sacred pilgrimage site. The area was mostly secondary growth with a sparse canopy of 10–15 m tall trees.

Sinharaja Forest Reserve sites were within unlogged, primary, lowland dipterocarp vegetation. The actual collection locations were near trails approximately 1 km from the nearest forest access road, an area known to the research station staff as the “unlogged 20 ha plot.” More than 500 branches from 118 *H. laurifolia* plants in six separate populations were sampled over a period of 10 months. The sampling was carried out by visual observation, by baiting, and by cutting open individual internodes.

The Belihul Oya site is 12 km south of the town, within an area opened 10 years earlier for access to a nearby dam site. Selective logging had been carried out, and the tree canopy was at 25–30 m. Two populations of more than 100 trees, separated by 1.1 km, were located along small streams. Fifty branch systems were randomly cut within each tree population, and approximately 300 internodes were opened and censused.

In addition to the field locations, there are two very old trees in the Peradeniya Botanical Garden, Peradeniya, which presumably were those studied by F.O. Bower (1887); the ant colonies are still healthy.

At Gilimale, KVK and BBN collected branches from *Humboldtia* trees growing at various heights in both sun and shade, which yielded about 1000 internodes. Pocket knives were used to separate each internode from other stem and leaf material. These inflated chambers were either opened in the field, and their contents were placed in vials of alcohol or Kahle's solution, or they were placed unopened in fine-meshed nylon bags and were put in large jars of alcohol. After returning to the laboratory, each internode was removed, carefully cut open, and the contents recorded. The internodes were opened by making a longitudinal cut from the internode's natural entrance to the stem's base. Care was taken to cut open the hollow internode chamber without cutting into the organisms held within.

Several internodes that were partially opened in the field and found to contain pupal insects also were placed in fine-meshed nylon bags, which in turn were placed between layers of tissue in an insect mailmaster box. The contents were checked every two days, and adults were collected when they emerged. Data from these stems were recorded at each observation and when they were completely opened back in the laboratory.

Observations by KVK and BBN in 1993 were made during an abnormally late southwest monsoon period. The intermittent rain prevented observations of provisioning because the wasps and bees were quite inactive in the internodes. Occasionally a

wasp flew out of the internode, presumably to visit an extrafloral nectary for nectar because prey was not brought to the nest.

The collections by MMR and FRR were handled in two ways. For each population studied, internodes on several small trees were assigned a number, and their positions on the tree or branch were noted. These internodes were opened on site, and the contents were recorded and/or collected in alcohol. After this initial sampling, a series of representative branches was placed in large plastic bags, and the tops were sealed. All internodes were opened that same evening, and the contents were placed in alcohol. Ants from the ground under the trees and on *H. laurifolia* vegetation were baited, using small pieces of canned fish or a honey/fish mixture, and then were aspirated into alcohol. The percentage of inflated and noninflated internodes was calculated by choosing random branches within a single tree and noting the condition of every internode along those branches. Usually, five branches were selected per tree, and five trees were selected within each population. Percent leaf-tissue herbivory was calculated by tracing, on paper, each leaflet of each leaf for three random branches per tree. Tissue missing also was traced. The collection of tracings per tree was weighed, and then the missing tissue was cut from the paper replicas. The resulting tracings were weighed a second time, and the difference was used as a percentage of tissue-removing herbivory. This technique allowed for extensive, nondestructive sampling within the Sinharaja Forest Reserve and other *H. laurifolia* populations.

Final tabulation and analysis of organisms associated with *H. laurifolia* was based on approximately 2500 internodes, 1200 internodes from Gilimale, 1000 internodes from Sinharaja, and 300 internodes from Belihul Oya.

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Humboldtia Vahl

Humboldtia is a genus of five species and one variety of small to medium-size trees of evergreen and semi-evergreen vegetation zones of southwestern India and Sri Lanka (Sanjappa, 1986; Pascal and Ramesh, 1987; Rudd, 1991). Within their habitats in the lowland rainforest, the plants are associated most often with streams or seeps, although they are occasionally found in areas lacking surface water. *Humboldtia laurifolia*, *H. unijuga* Beddome, and *H. brunonis* Wallich are highly gregarious, with groups as small as 10 plants to clusters of hundreds of individuals with only a few other taxa intermixed. Such groups usually are separated by areas completely free of the plant. Broken plants resprout freely, and horizontal branches touching the soil may root. *Humboldtia decurrens* Beddome ex Oliver can be gregarious but often exists as isolated individuals along stream edges. *Humboldtia vahliana* Wight, a medium-size tree to 20 m, with a stem diameter to 60–80 cm, grows as single individuals along streams or rivers.

Humboldtia laurifolia, *H. decurrens*, and *H. brunonis* are consistently associated with a resident ant colony living in hollow, inflated stems and feeding on nectaries found on the leaves, stipules, and flower-bud bracts. The stem cavity is open to the outside by a naturally occurring slit that develops in the uppermost portion of an internode. *Humboldtia unijuga* and *H. vahliana* do not possess inflated, hollow stems or a resident ant colony, but they do attract ants to leaf nectaries.

Sanjappa (1986) listed a sixth species, *H. bourdillonii* Prain, which seems to be a variant of *H. decurrens*, and which has not been collected since a single specimen was found in 1894.

Humboldtia laurifolia Vahl

FIGURES 2–20

Current literature notes only one species of a *Humboldtia* in Sri Lanka, *H. laurifolia* (Sinhalese: gal-karanda, ruan-karanda), and cites this species as also occurring in southern India (Sanjappa, 1986; Pascal and Ramesh, 1987; Rudd, 1991). The original species description by Vahl, as *Batschia laurifolia*, is from Sri Lankan specimens. Vahl, however, discovered the prior usage of *Batschia* for a menispermaceous plant while his book was in press and, in its errata, changed the generic name to *Humboldtia*, thus making *Batschia laurifolia* an invalidly published name. The herbarium specimen referred to as being collected in India is a single sheet of Wight (#846) (Coimbatore, India [MS]) that was probably from a Sri Lankan collection, as the species has not been collected in India since his original citation in the 1830s.

DISTRIBUTION.—FRR has searched the putative location of *H. laurifolia* in Karnataka and Kerala on three occasions without finding any specimens of this very gregarious species. We believe *H. laurifolia* to be endemic to Sri Lanka.

It is recorded mainly from lowland localities in the southwestern quadrant of Sri Lanka (Rudd, 1991). The current range is less extensive because much of the lowland rainforest has



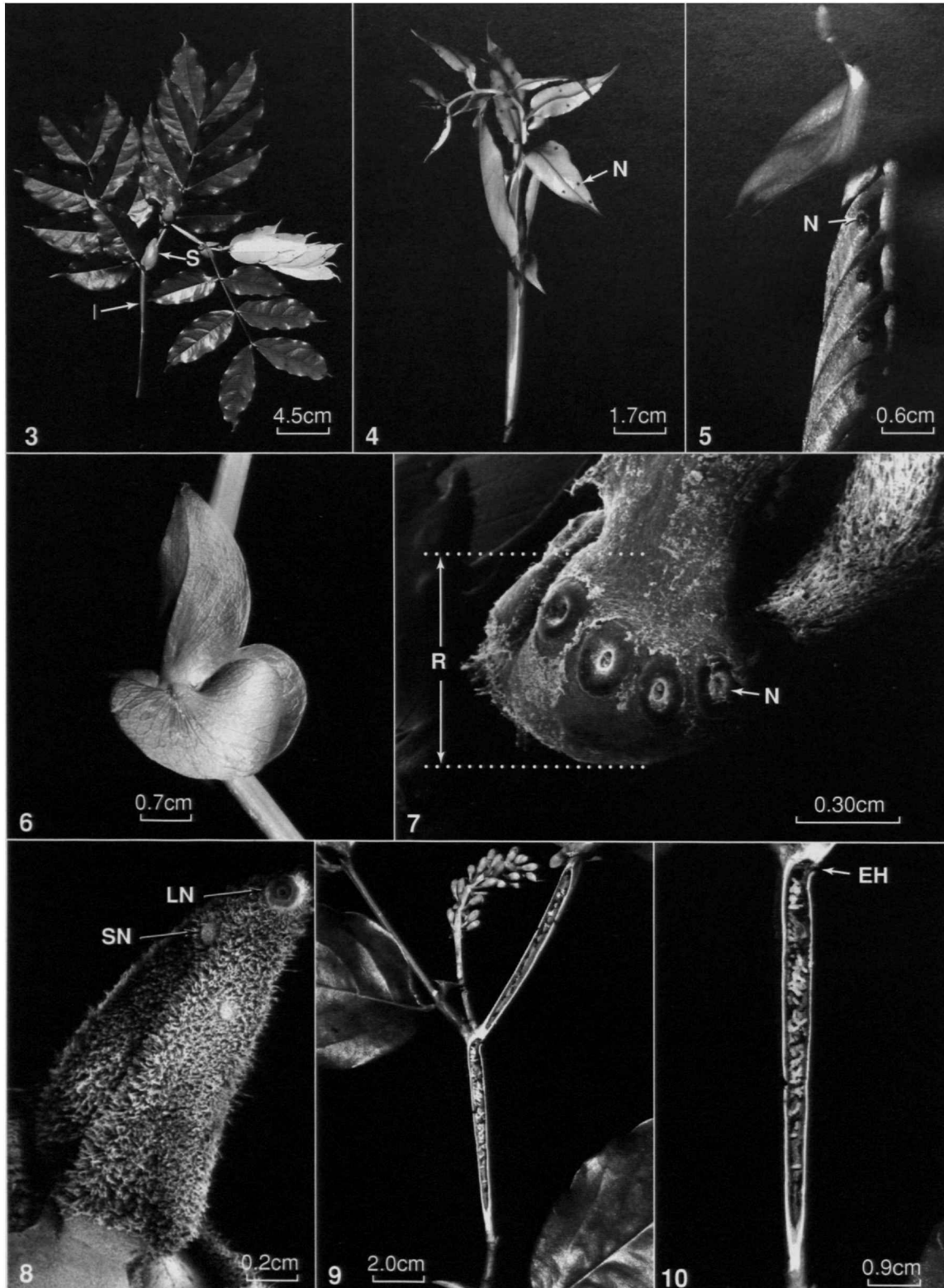
FIGURE 2.—B.B. Norden collecting on *Humboldtia laurifolia* Vahl along road at Gilimale.

been destroyed by lumbering and subsequently converted for agricultural use or for housing for the growing population. Recent surveys (1992–1995) by IUCN/Sri Lanka Forest Department teams (pers. comm., 29 Jul 1995, P.B. Karunaratne) confirmed the presence of *H. laurifolia* in more than 50 forest reserves and state forests in Kegalle, Ratnapura, Kalutara, Galle, Matara, and Hambantota districts. There are no published records of its occurrence in Colombo District, but Karunaratne noted that there are populations of it in the forest surrounding Labugama Reservoir, about 40 km ESE of Colombo, and in the Handapangoda Reserve near Padukka, about 28 km SE of Colombo.

HABIT.—*Humboldtia laurifolia* is a small understory tree (Figure 2). Rudd (1991:94) noted that *H. laurifolia* grows “to about 10 m tall,” and that it has been “introduced elsewhere [i.e., outside of Sri Lanka and India] as an ornamental.” In cultivation, as in the Peradeniya Botanical Garden, the trees are not tall but are wide and spreading. In its native habitat in the rainforest it is probably best characterized as a small tree. The

wood has no commercial uses but is sometimes collected for firewood.

PLANT MORPHOLOGY.—*Leaves:* *Humboldtia laurifolia* possesses pinnately compound leaves and follows a phenology common to legumes in which a period of development produces a flush of four to six new internodes, each with an associated leaf. Each leaf consists of four to six (rarely three) opposite leaflet pairs. A new leaf flush consists of four to six leaf/internode units developing over a period of approximately 60 days. At the completion of a flush, the maturing leaves present a continuum consisting of the oldest leaf (basal on a flush) that is fully expanded, horizontal, and attaining its maximum toughness; a leaf that is still light green, becoming horizontal, and of medium toughness; and the youngest leaf, which is white in color, pendulous, and very delicate (Figure 3). After maturing, that particular branch system remains dormant for nine to 12 months until the process is repeated from the terminal bud and possibly several lateral buds. The greatest new stem/leaf production occurs from September through November, but stem units are produced in small numbers throughout the year. Each



FIGURES 3–10 (opposite).—*Humboldtia laurifolia* Vahl (except 6, *H. vahliana* Wight from India): 3, a flush of four new leaves with the oldest to the left, and the youngest white leaf to the right (L, oldest ant-occupied internode; S, large upright stipule); 4, new leaf in the process of unfolding (note dark, pigmented nectaries, N, on each leaf blade); 5, young folded leaf with four leaflets (note the large, exposed nectary, N, at the base of each leaflet); 6, *H. vahliana* Wight from India illustrating shape, as in *H. laurifolia*, of the upright and horizontal stipules; 7, a very young horizontal stipule possessing functional nectaries (N, note that stipule is little more than a ridge of tissue, R, at the node—the area above R develops into the upright stipule); 8, upright stipule possessing a large nectary (LN) at the tip and two smaller nectaries (SN) below the tip region; 9, two hollow internodes occupied by *Technomyrmex albipes* (F. Smith) (a mature leaf and an inflorescence, both with active nectary systems, illustrate the close proximity of these plant tissues to the resident ant colony); 10, hollow internode occupied by *Technomyrmex albipes* (F. Smith) (note gradually expanding shape, the solid nodal region at base, and the entrance hole (EH) at apex).

leaflet possesses a single abaxial, basal nectary and two abaxial apical nectaries located just below the terminal drip-tip constriction. There may be additional nectaries at various locations on the leaf surface (Figure 4). The basal nectary is positioned so that it is fully exposed and functional even when the developing leaf is small and the leaflets are rolled and imbricate (Figure 5).

Stipules: Each leaf is subtended by a pair of unusually shaped, persistent, two-part stipules (Figure 6). The lower portion of a stipule is reniform in shape, has a pointed portion on the stem side opposite the leaf petiole, and is positioned perpendicular to the stem; this structure is herein referred to as the horizontal stipule. The horizontal stipule has a row of six to nine nectaries set in close proximity to the stem (Figure 7). The second portion of a stipule is triangular in shape and is upright in orientation, with the base inserted just above the horizontal portion (Figure 8). The triangular portion of the stipule has a single (or two) large nectary located just below the apex (Figure 8). The pair of upright stipules remains appressed by their margins, thereby forming an enclosure surrounding the developing distal internode. The most distal, or last-formed, upright stipules on a branch enclose the dormant apical bud for that branch.

The stipules and their numerous nectaries are particularly important in positioning the ant population with respect to tender, young tissues. Development of the horizontal stipules is precocious in that its nectaries enlarge and begin secreting nectar when the stipule is little more than a ridge on the stem surface. Large numbers of ants gather to collect nectar and literally swarm over the adjacent developing leaf and stem system.

Stem: A plant stem consists of nodes, the position of leaf attachment, and internodes corresponding to the stem region between nodes. As noted above, *H. laurifolia* produces a series of four to six internodes/nodes/leaves in succession, and this system then remains dormant for some months. Each internode is usually narrow at the base and enlarged toward the top (Figures 4, 9, 10); however, a small number of “abnormal,” nonexpanded internodes also can be found on any plant. The new leaf is produced in a position that continues the direction of the

internode, whereas the apical bud (for the next internode) is set at an angle to the side and on the opposite side of the stem. The leaf orientation is maintained in the subsequent internode, but the apical bud is shifted 180° on the stem. That is, the apical bud is produced on the opposite side of the stem from that of the lower internode. This alternation of apical bud placement continues through the series of internodes produced, with the final result being a distinctive “zig-zag” branch morphology.

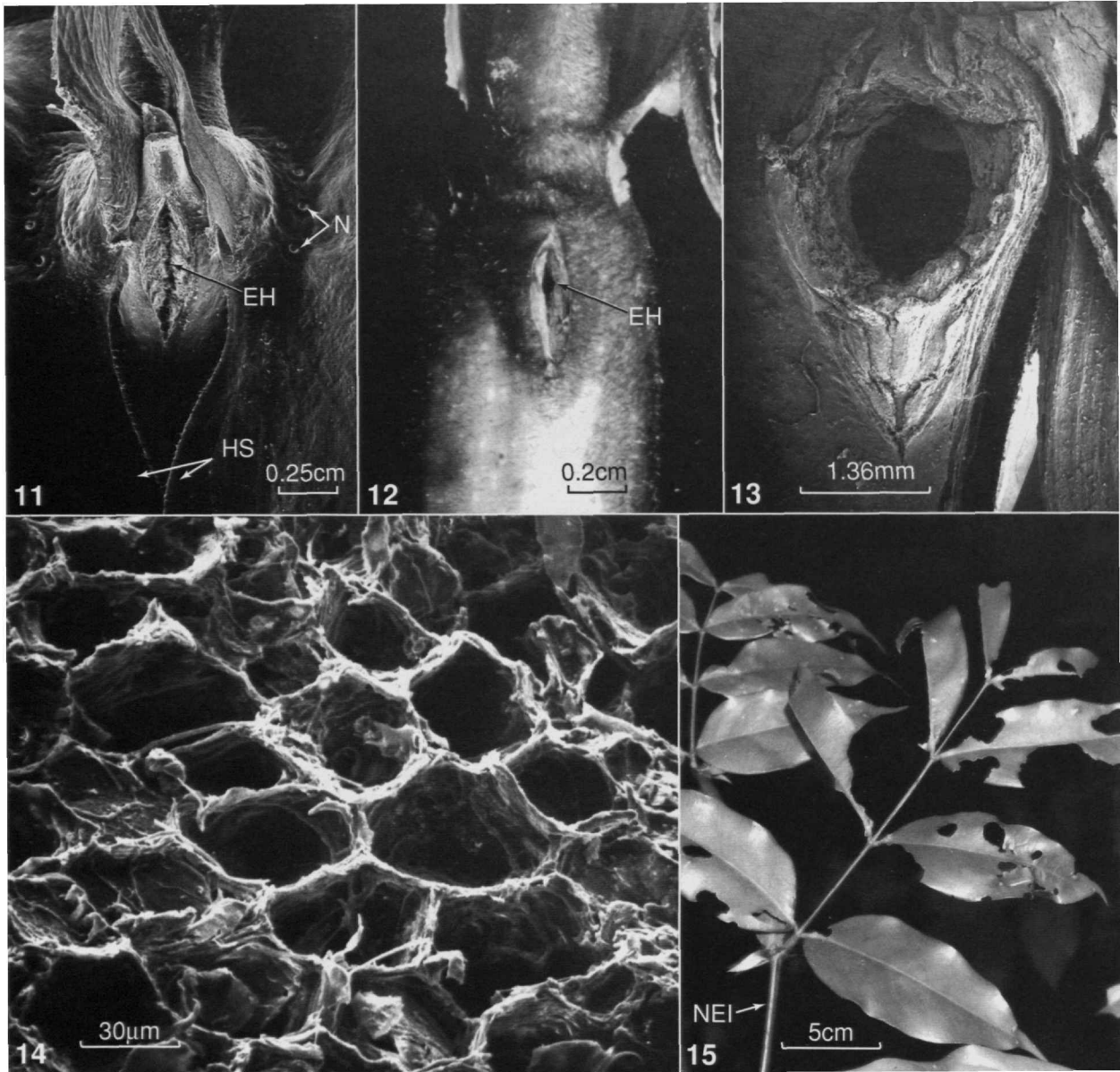
The nodal region and basal portion of an internode are solid, thereby isolating each domatium to a single unit. The inflated upper portion of the internode develops a large central pith. As the internode reaches maturity, the pith breaks down, collapsing against the inner wall, thereby creating a hollow region.

A feature that appears evolutionarily advanced, found in the other ant-associated *Humboldtia* species, as well as several other unrelated ant-associated plants (Maschwitz, Fiala, and Linsenmair, 1994; Maschwitz et al., 1994; Maschwitz and Fiala, 1995), is a site-consistent stem splitting that produces a small, slit-like entrance hole, which allows access to the stem cavity (Figures 11, 12). This “stem opening” event was strongly suggested for *H. laurifolia* by Bower (1887), and we have confirmed its occurrence. Concomitant with the initial splitting, cells lining the opening develop suberized walls, and renewed cell divisions in the area produce a periderm, or “cork,” layer. If the internode is not occupied, this new tissue will close the entrance.

Inhabiting ants enter an internode and clean out the pith remains, creating a smooth-walled domatium. As a result of this series of developmental events and the presence of solid nodal regions, each new internode provides an isolated, completely accessible domicile for any organism that can access the opening. In most cases, new internodes are quickly occupied by the resident ant colony living below the newly formed branch systems. KVK and BBN noted in their study of a more disturbed area that wasps and bees were occupying internodes that were higher up than those occupied by ants.

F.R. Rickson measured mature internode entrances at the stage when the first *Technomyrmex albipes* would be making an exploratory entrance from the ant-occupied internode immediately below the node being measured. The entrances ($n=20$) were 0.9–2.3 mm long (average 1.8) and 0.6–1.1 mm wide (average 0.9). He noted that openings 4–5 internodes below the shoot apex tended to be enlarged by up to 0.3 mm in both length and width. He was unable to determine whether this enlargement was due to continued splitting of the stem or enlargement by the occupying ants.

The entrances of internodes occupied by wasps and bees were more rounded and had a more strongly developed periderm ring (Figure 13). These modifications were apparently due to gnawing around the entrance by the occupant. The smooth inner wall of the internodes from which the wasp *Krombeinicus nordenae* Leclercq and the bee *Braunsapis* sp. removed pith is actually minutely roughened, because the clipping of pith



FIGURES 11–15.—*Humboldtia laurifolia* Vahl: 11, a nodal region at the time of the entrance hole development (the pith can be seen at the entrance hole site (EH), and active nectaries (N) are present on the horizontal stipules (HS)); 12, entrance site at the usual time of occupation by *Technomyrmex albipes* (F. Smith) (the pith has broken down by this stage of development, and the entrance hole (EH) has formed); 13, entrance hole of internode occupied by active nest of *Krombeinictus nordenae* Leclercq (note development of callus surrounding the hole); 14, inner surface of internode from which collapsed pith has been abraded by ants or wasps; 15, typical leaf damage on an unoccupied or poorly occupied branch system (NEI, nonexpanded internode that cannot house an ant colony—compare leaves with those in Figure 3 from a tree possessing a vigorous ant colony).

leaves a small, shallow residue (Figure 14). Norden and Krombein noted that the entrances of internodes occupied by *K. nordenae* and *Crossocerus mukalanae* Leclercq ($n=15$) were 1.0–2.0 mm long (average 1.5) and 0.6–2.0 mm wide (average

1.6). Outer measurements of the periderm callus ($n=14$) were 2.0–4.2 mm long (average 3.2) and 1.0–3.5 mm wide (average 2.4). Measurements were not made of the few *Braunsapis* openings and periderm rings.

The number of nonexpanded internodes on a plant can affect the size of the resident ant population by reducing the total number of potential domiciles. Nonexpanded stems are solid and do not develop an entrance hole. We noted that trees that receive a high level of insolation, such as along streams, trails, roads, or in the Peradeniya Botanical Garden, have the lowest number of solid internodes, have large ant colonies, and show the least amount of herbivore damage. Conversely, tree populations growing within the primary forest, away from trails and streams, where sunlight is minimal, were smaller in both stem height and girth, possessed as much as approximately 60% solid internodes (compared to 5%–8% in open-growing trees), and showed leaf damage to approximately 50% (Figure 15) (as compared to 2%–5% in the most unshaded individuals measured). These findings indicate that the preferred growth habitat is along open streams, but they also show that *H. laurifolia* can exist in low-light conditions in a less healthy condition. Internode expansion seems to be directly related to light availability.

Nectaries: A small leaf and its associated young internode, along with the shoot apex, are found within the tightly joined, upright, triangular portions of a stipule pair. In this resting condition, which can last for more than nine months, the nectaries on this uppermost pair of stipules are active. All leaf and stipule nectaries on the most recent stem flush also are active. Multiplying the average 2.5 nectaries on each of 10 leaflets by the five leaves produced during a growth flush, and adding an average of 20 nectaries on each pair of stipules (horizontal plus upright), gives a possible 225 food sites associated with each active, five-domicile, stem unit. Once growth of this stem is renewed, another complete set of new stems, leaves, and stipules will be formed before the stem again becomes dormant. Ants are constantly swarming around the developing stem system investigating newly opened stem interiors and establishing colony extensions in the new domiciles.

Inflorescence and Flowers: A formal systematic description of the inflorescence and flower can be found in Rudd (1991). In bud, the developing inflorescence is first covered by a single tough scale that has two nectaries on either side of the midrib (Figure 16). The first leaflet-like appendage on the inflorescence stalk, a small prophyll, develops 180° from the initial bud scale, covers the developing inflorescence, and possesses four to six nectaries aligned as pairs on either side of the blade portion of the appendage (Figure 17). In an inflorescence bud just beginning to enlarge, these overlapping structures, with their functional nectaries, attract ants. Each individual developing flower in an inflorescence ($n=58$) is subtended by a bract that possesses a large, centrally placed nectary (Figure 18). The flowers open from base to tip fairly quickly, thus presenting a large number of functioning nectaries that attract feeding ants (Figure 18). Most inflorescences are produced on younger branches, but some also are found on two- and sometimes three-year-old branches as well. Ants may be found feeding on any developing inflorescence irrespective of its location on the

tree. Inflorescences are produced throughout the year but are found in greatest abundance from February to June.

The fine-grained pollen is produced in copious amounts on each of the five stamens (Figures 19, 20). The grains are coated with an oily clumping substance, pollenkit, that facilitates adherence to any insect visiting the flowers.

"Movable Feast": The above-described series of extrafloral nectaries, with their special placement and temporal functioning, places *H. laurifolia* in a group of ant plants that present what has been called a "movable feast" (Tilman, 1978) to their resident or visiting ants. The term refers to a food supply (such as the nectaries of *H. laurifolia*) that is temporally active on young leaves and flower buds, the tissues or organs most susceptible to herbivory. The food supply is not present on mature tissues that, presumably, are able to defend themselves through a combination of toughness, hairs, and/or internal chemistry. The term "movable feast" is used most often in association with ant protection, but mites, spiders, wasps, and bees also are drawn to sites of nectar secretion.

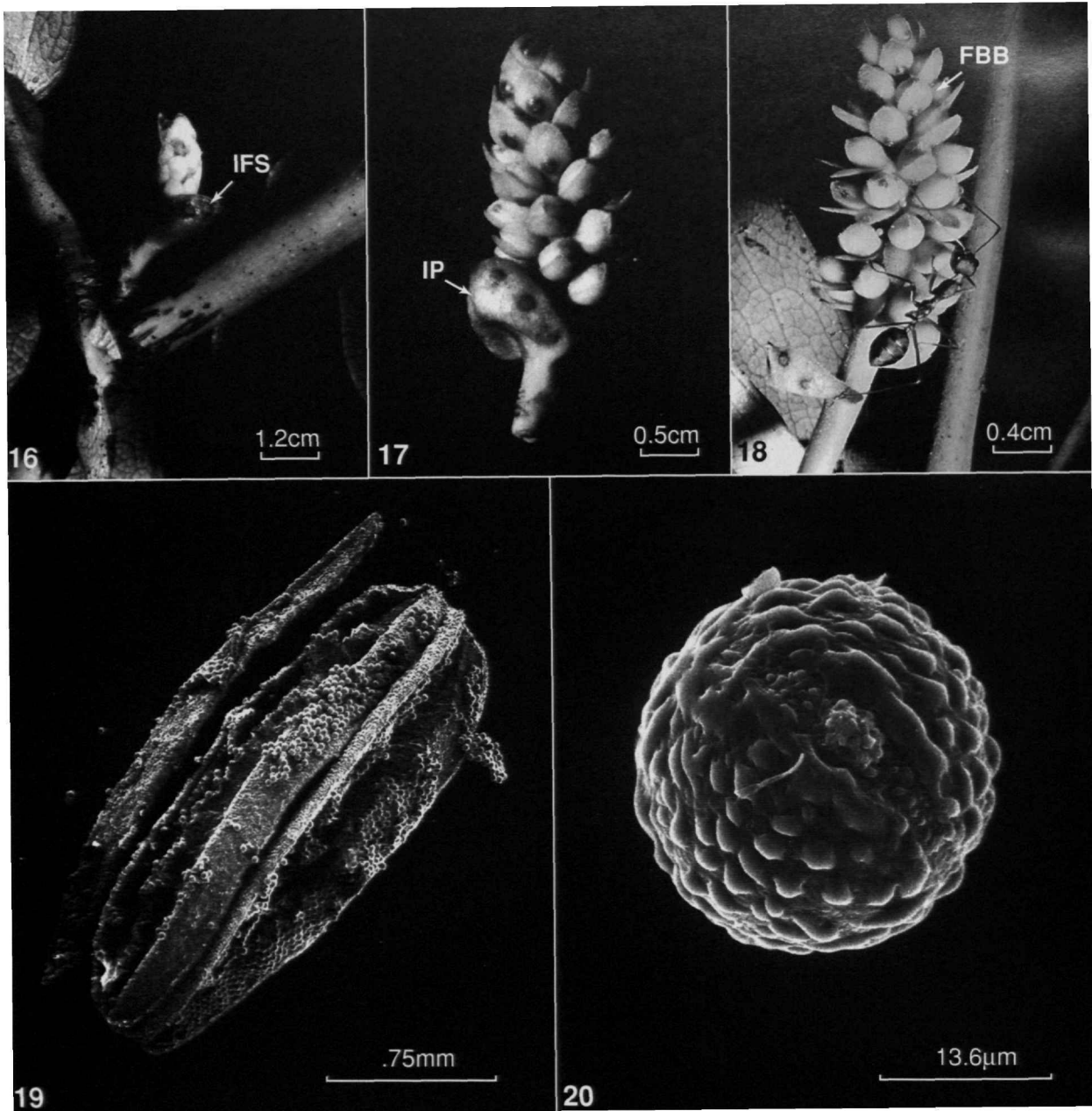
Dominant Invertebrate Associates of *Humboldtia laurifolia*¹

The morphology of the plant, with a solid nodal region separating each hollow internode and with an entrance hole for each cavity, produces a series of nest sites along each stem section. Potential occupants do not need any chewing instincts or special mouth parts to gain access to a cavity. In tropical environments, with their wealth of species and individuals, nest sites can be in short supply, and the internode sections of *H. laurifolia*, especially just after a tree flushes 20 to 30 new branch systems, each with three to five internodes, are attractive to a variety of small organisms capable of finding and accessing the entrance hole. Our collection method of dissecting many individual internodes turned up a surprising variety of stem occupants, in addition to the expected ants. We present below a series of natural history accounts of these diverse invertebrates.

The section on ants is based largely on investigations by MMR and FRR at their three study sites (Figure 1A–C) and is

¹There is evidence of a probable vertebrate predator, found only at Sinharaja Forest Reserve by FRR, which tears open the hollow internodes presumably to feed on the resident ants. The opening looks as if a sharp claw or tooth is inserted at one point and then is pulled downward, breaking open the domicile wall. Two individual entrance attempts can occur on a single internode. Several internodes in succession on a single stem, each treated as an individual unit, will be torn open. The damage was found on only three branches out of the hundreds of trees examined in the course of the study; but in each case there was a systematic opening of several internodes in a row, as if the animal had moved deliberately along the stem, indicating some familiarity with the system. However, the fact that FRR found only three examples of the attack suggests that it is not carried out regularly by some specialized ant predator, at least not one specialized on this system.

F. Rickson (pers. obs., 1982) also found this same method of internode opening in *Macaranga triloba* Muell.-Arg., *M. hypoleuca* Muell.-Arg., and *M. punctulata* Gage (Euphorbiaceae), three species of hollow-stem, ant-occupied trees found in lowland forests of West Malaysia.



FIGURES 16–20.—*Humboldtia laurifolia* Vahl: 16, a very young inflorescence with its bud scale (IFS, note bud scale nectary system); 17, a young inflorescence with a prophyll (IP) subtending the developing flower buds (note row of nectaries on the prophyll); 18, a young inflorescence with each of the floral bud-subtending bracts (FBB) possessing a functional, ant-attracting nectary (ant is *Oecophylla smaragdina* (Fabricius)); 19, stamen from flower bud (note clumping of grains near upper right from oily pollenkitt); 20, individual pollen grain from Figure 19.

supplemented by limited data gathered by KVK and BBN at their study site (A). The succeeding sections on invertebrates

other than ants are based on observations by KVK and BBN and are supplemented by information from MMR and FRR.

Order HYMENOPTERA

Family FORMICIDAE

At locations where MRR and FRR sampled *H. laurifolia* for ants, *Technomyrmex albipes* (F. Smith) was the sole or dominant species recovered from internodes. Where exceptions were found, the secondary ant species often was restricted to a single branch or even a single internode, although two trees were found where *Crematogaster* sp. 1 occupied the entire tree. The two very large, open-growth trees in the Botanical Garden at Peradeniya are shared by *T. albipes* living in the internodes and *Oecophylla smaragdina* (Fabricius), the weaver ant, in its usual nest of bound leaves.

Coccids were not found in internodes occupied by *T. albipes*, and this ant was never observed to leave a tree or even forage near the stem base. It may be that *T. albipes* does forage off the parent tree by using connecting foliage to roam over other vegetation. On one occasion the ant foraged at bait placed on an adjacent shrub by using a foliage bridge for access.

The ants of resident colonies were abundant, and some species were efficient in preventing herbivory and epiphyll glean-ing as most of the foliage was glabrous, shiny, and devoid of injury (Figure 3). Leaves on branches containing no ant nests showed extensive damage, presumably from insect feeding

(Figure 16), and some were encrusted with bryophytes and lichens.

A summary of the ants collected from *H. laurifolia* at the three study sites is presented in Table 1. Detailed notes from each site are given as follows.

Gilimale: As is apparent from Table 1, this location had the largest number of ant species. It is the most disturbed of the three study sites, comprising a narrow strip of rainforest, 1 km wide, bordered on one side by a hard-surface road leading toward Adams Peak and on the other side by the Kalu Ganga (river).

Among the 300 internodes dissected by FRR and MMR, the most common inhabiting ant (80%+) was *Technomyrmex albipes*. Several individual small trees were totally occupied by one of three *Crematogaster* species. These three taxa also were found to share a tree with *T. albipes*. *Cataulacus taprobanae* F. Smith shared trees with *Crematogaster* species and with *T. albipes*. *Anoplolepis gracilipes* (F. Smith) was a visitor at nectaries at three locations but was not found nesting on the host, and *Polyrhachis (Hemioptica) bugnioni* Forel was found foraging on several *H. laurifolia* unoccupied by other ants. The diversity of organisms possible on *H. laurifolia* is exemplified by a single stem with 10 hollow internodes (FRR 91-S-226): the first two chambers below the shoot apex contained a few *T. albipes* workers, most likely from the complete colony in the

TABLE 1.—Ant species nesting in or on *Humboldtia laurifolia* Vahl in Sri Lanka. Species are arranged in the sequence used by Hölldobler and Wilson (1991). Ant nests at our study sites (FRR/MMR and KVK/BBN) are indicated by an X; * denotes a species taken at nectaries but not nesting.

Subfamily/Taxon	Sinharaja Reserve	Gilimale		Belihul Oya	Peradeniya
	FRR/MMR	FRR/MMR	KVK/BBN	FRR/MMR	FRR/MMR
PSEUDOMYRMECINAE					
<i>Tetraoponera</i> sp.			X		
MYRMICINAE					
<i>Cataulacus taprobanae</i> F. Smith		X	X		
<i>Crematogaster</i> sp. 1	X	X	X	X	
<i>Crematogaster</i> sp. 2		X	X	X	
<i>Crematogaster</i> sp. 3		X			
<i>Monomorium</i> sp.†					
<i>Pheidole</i> sp.			X	X	
<i>Tetramorium pacificum</i> Mayr			X		
DOLICHODERINAE					
<i>Dolichoderus</i> sp.	X				
<i>Tapinoma</i> sp.	X		X		
<i>Technomyrmex albipes</i> (F. Smith)	X	X	X	X	X
FORMICINAE					
<i>Anoplolepis gracilipes</i> (F. Smith)	*	*			
<i>Camponotus</i> sp.	X		X		
<i>Oecophylla smaragdina</i> (Fabricius)					X
<i>Polyrhachis bugnioni</i> Forel		*	X		

†Hölldobler and Wilson (1991, table 14-1) listed species of *Crematogaster*, *Monomorium*, *Tapinoma*, and *Technomyrmex* as being residents of *Humboldtia laurifolia*; we did not find *Monomorium* at any of our sites.

third internode; *Cataulacus taprobanae* occupied the fourth and fifth internodes; the sixth was empty; the seventh contained the slender larva of *Platyseridion edax* Chandler and Matile (Diptera: Keroplatidae), a predator of adult ants; the eighth was empty; a female sphecoid wasp, *Krombeinictus nordena* Leclercq, was in the ninth; and the tenth, or most basal, was empty.

An effort was made by KVK and BBN to obtain representatives of each ant species associated with the trees at their site in Gilimale. Nine taxa were nesting in the 29 internodes sampled. It was noted that the ants had removed the dried pith from the inner walls except in one internode. This anomalous nest contained a dealate queen of *Crematogaster* species, with an egg about to hatch, and was in an old nest of the crabronine wasp *Crossocerus mukalanae* Leclercq that still contained particles of pith and fragments of wasp cocoons. A tenth species, a weaver ant, *Polyrhachis bugnioni* Forel, constructed a nest in a pair of upright stipules just above an internode.

As for the 29 ant-containing internodes mentioned above, two species of *Crematogaster* and *Technomyrmex albipes* were in seven internodes each, *Tetramorium pacificum* Mayr occupied five internodes, *Tapinoma* sp. and *Cataulacus taprobanae* F. Smith were in three internodes each, *Camponotus* sp. occurred in two internodes, and *Tetraponera* sp. (queen, naked worker pupa, and a few small larvae) and *Pheidole* sp. were in one internode each. The sampling technique employed was intended to determine species diversity rather than relative abundance.

A colony of a tenth ant, a formicine, *Polyrhachis (Hemioptica) bugnioni*, did not occupy an internode but, instead, made a nest by sealing together the edges of the pair of upright stipules immediately above an internode. The stipules were unusually long, 45 mm, with a maximum width of 16 mm near the base. Their acuminate apices, 7 mm long, were not sealed. The edges below the apices were sealed together with debris and silk spun by the ant larvae. A sizable mass of debris and silk, 1.5 mm thick, sealed off the top of the nest 7 mm from the tips of the stipules. Access to the nest was at the base of the stipules. The inner surface of the stipules was not coated with a sheet of silk. A few small ant larvae were still attached along the edges of the stipules where, apparently, they were being used to strengthen the seal at the time the nest was placed in alcohol. The nest population consisted of the queen, 27 workers, and a number of brood (nine postdefecated larvae and pupae in cocoons, 15 small larvae, and 12 eggs). The coloration of this species (white femora and tibiae contrasting markedly with a black body) is unique among the ant species nesting in *Humboldtia*. Dorow and Kohout (1995) redescribed the species, based in part on our specimens.

Sinharaja Rainforest Reserve: A total of over 500 branches from 118 *H. laurifolia* plants in six separate populations yielded over 1000 internodes for dissection. In general, *Technomyrmex albipes* was the only ant species associated with *H. laurifolia*. Exceptions were four individuals of *Anoplolepis*

gracilipes visiting flower-bud nectaries of a single inflorescence, a colony of *Crematogaster* sp. 1 occupying four internodes in a single branch, a founding queen of *Camponotus* sp., one branch of five internodes containing a colony of *Tapinoma* sp., and one internode containing *Dolichoderus* sp. Three of the six populations possessed only *T. albipes* throughout all plants sampled.

Belihul Oya: Forty branch systems were randomly cut within each of two separate tree populations, and approximately 300 internodes were opened and censused. We found three colonies of *Crematogaster* sp. 1 that occupied all internodes of separate, but adjacent, branch systems; a single internode containing all colony stages of a *Pheidole* sp.; and a single colony of *Crematogaster* sp. 2 occupying two adjacent internodes. The remaining ants, including examples from every tree sampled, were *T. albipes*.

Technomyrmex albipes (F. Smith)

FIGURE 21

Technomyrmex albipes (Figure 21) was the exclusive or strongly predominant ant in all three of the areas sampled. Several subpopulations of *H. laurifolia* in Sinharaja Forest Reserve, including those over one kilometer from the nearest road, have 100% occupation by this ant. Wilson and Taylor (1967:84) noted that *T. albipes* "is the most widespread of all the Indo-Australian *Technomyrmex*, ranging as a dominant ant from India to eastern Australia and throughout the Pacific, including Melanesia and Micronesia." It is a highly successful, vagile species and has colonized many of the Pacific islands as far east as Hawaii and the Marquesas.

The behavioral and colony features of *Technomyrmex albipes* that make it such a successful pest species of humans also make it a strong colonizer of *H. laurifolia*. The species develops very large polydomous colonies containing up to several million adults (Yamauchi et al., 1991). Those authors have

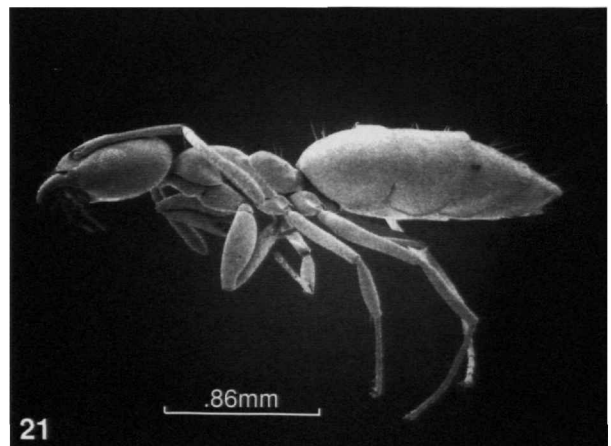


FIGURE 21.—*Technomyrmex albipes* (F. Smith), worker.

shown that new colonies often are established by numerous wingless females that are inseminated by wingless males from the same colony. This method of colony extension, by simply moving up the plant onto new branch systems without the dangers of nuptial flight and host location, works well considering the numerous flushes of new internodes characteristic of leafing in *H. laurifolia*. The horizontal orientation of its branches, which at times droop to form bridges between stems, places large numbers of nesting sites in close physical proximity. In addition, the large, almost monotypic aggregations of closely placed plants provide a good situation for colonization by wingless females.

On *H. laurifolia*, *T. albipes* is very secretive, and on a tree lacking flowers or new leaves, it is difficult to find this ant outside of the internodes. The few patrolling ants must, however, be very efficient at finding nectaries, as a small deposit of honey/fish mixture placed on a leaf surface is usually located by one or two ants within five to 10 minutes, and recruitment of hundreds of individuals occurs within 20 to 30 minutes of bait placement. When an inflorescence or new flush develops, however, ants actively visit each new nectary produced in a diffuse manner so that all new tissues receive an ant guard. This is very different from their mass visiting of a single drop of honey placed on a leaf.

Humboldtia laurifolia contributes to the large ant colonies by a diffuse phenology of leafing and flowering. There are periods of heavy leafing and flowering at regular times during the year, but the constant smaller supply of new nectaries provides the ant colony with a continuous supply of nutrients throughout the year.

In towns, the ant uses pre-existing cracks and crevices as access to building foundations and wall structures for its colonies. In houses, the species is a constant scourge of unattended sweets and meat left lying about. Interestingly, FRR and MMR also have found it nesting in bare soil in a new cashew nut planting. The cashew tree possesses large numbers of leaf and inflorescence nectaries, and *T. albipes* is a regular visitor on this plant (Rickson and Rickson, 1998). The ant also is considered a pest as it regularly tends coccids on various plants, including the important crops cacao, *Theobroma cacao* (L.), and coffee, *Coffea arabica* L.; however, it does not tend coccids on *H. laurifolia*, which can be viewed as a benefit to its host.

Given the ubiquitous presence of the ant in towns and villages within Sri Lanka, the species seems to have a very narrow habitat range in the field. As part of another effort to census ants in Sinharaja, we baited numerous ground locations, as well as other vegetation in the immediate area of *H. laurifolia* populations, and never attracted *T. albipes*, except to bait placed directly on *H. laurifolia*. Conversely, we never found another ant at bait placed on *H. laurifolia* when *T. albipes* was the resident ant. Ground baiting attracted numerous other ant taxa exhibiting the usual variety of dominance and recruiting abilities. In field habitats, both disturbed and undisturbed, *T. albipes* is not

an apparent ant species, and one would miss it if bait were not placed directly on *H. laurifolia*. *Technomyrmex albipes* is easily attracted, however, to bait in all locations around buildings, yards, and town vegetation in general.

In the artificial setting of the Peradeniya Botanical Garden, 7°17'N, 80°40'E, Figure 1D), *Oecophylla smaragdina* shares *H. laurifolia* with *T. albipes*, but it does not normally forage out of the tree canopy if only leaf nectaries are present. It will, however, descend and intermingle with *T. albipes* to visit lower-placed inflorescences, presumably due to the 60 large nectaries associated with each inflorescence. There is no apparent antagonism when the two taxa meet. *Oecophylla smaragdina* was not found associated with *H. laurifolia* in natural populations. Bower (1887) reported *Technomyrmex* on the same plants over 100 years ago.

Technomyrmex albipes is considered native to Southeast Asia. Because it consistently occupies *H. laurifolia* in both degraded roadside habitats and in the undisturbed, primary rainforest of Sinharaja, completely separated from any access roads, we consider *H. laurifolia* to be its natural habitat. That is, *T. albipes* is probably an arboreal inhabitant of cracks and small spaces, most often in trees or dead wood, and the self-opening, multiple internodes of *H. laurifolia* historically offered such natural nest locations. Over geological time, the ant and its host plant have evolved the tight relationship found in Sri Lanka.

Family SPHECIDAE

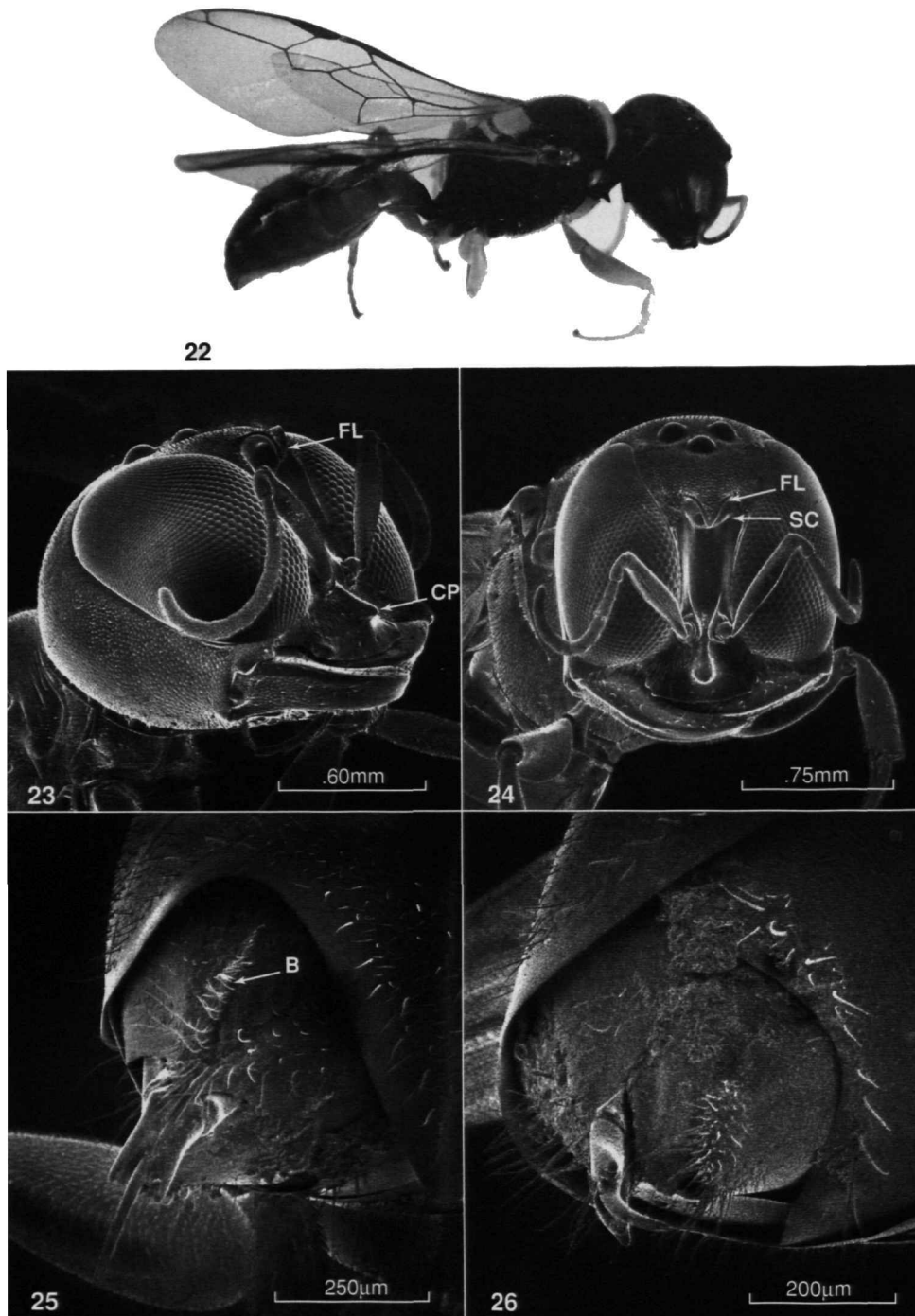
Krombeinictus nordenae Leclercq

FIGURES 22–37

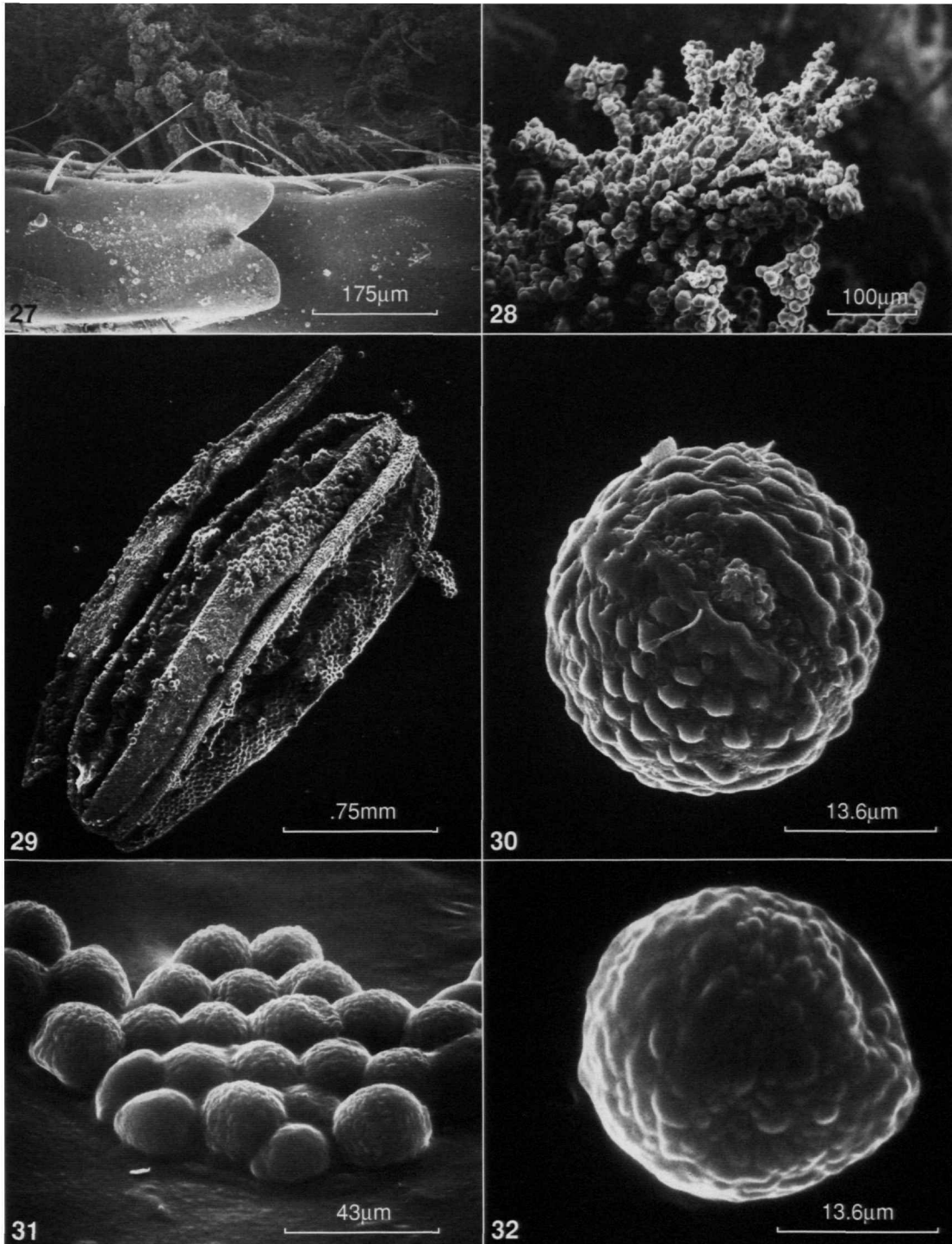
This little crabronine (Figure 22), 5–6 mm long, is one of the most colorful species in the Crabroninae. The black head and thorax provide a striking contrast to the ivory to pale yellow of the mandibles, apex of clypeus, antennae, extreme base and dorsum of the pronotum, scutellum, metanotum, and legs (except for the light red hindfemora and hindtibiae); the abdomen is light red except for small transverse blotches of light brown to black at the base and apex of the first four gastral terga.

Morphologically, *Krombeinictus* Leclercq shares with the Oriental *Vechtia* Leclercq the distinction of being the only crabronine wasps with a downcurved triangular lamella (FL, Figures 23, 24) overhanging the scapal basin in both sexes. The female is unusual among crabronine females in lacking a pygidium delimited by lateral carinae on the convex last abdominal tergite. The latter has scattered setae laterally, and medially there is a narrow strip of two to three rows of close-set setae forming a brush (B, Figure 25).

Most females of *K. nordenae* we collected had a dried secretion on the areas adjacent to and between the medial rows of setae on the last tergite, and some females had it on the last sternite as well (Figure 26). We believe that this secretion may be brushed by the medial rows of setae onto the thickened wall of the internode entrance as small droplets. The droplets may



FIGURES 22–26.—*Krombeinictus nordenae* Leclercq, female: 22, lateral view, 5.5 mm long (from color photograph by L. Penland-Minor); 23, oblique view of head (note frontal lamella (FL) overhanging scapal basin and clypeal projection (CP)); 24, frontal view of head (note frontal lamella (FL) and scapal carina (SC)); 25, dorsal oblique view of last abdominal tergite (note lack of pygidium, and median brush (B) of rows of close-set setae); 26, lateral oblique view of last abdominal segment (note dried secretion on both sternum and tergum and at base of median brush of setae).



FIGURES 27–32.—*Humboldtia laurifolia* Vahl and *Krombeinictus nordenae* Leclercq: 27, pollen grains clumped on hypostomal setae behind apex of mandible of female *Krombeinictus nordenae* Leclercq; 28, pollen grains massed on setae beneath head of female *K. nordenae*; 29, stamen showing massed pollen; 30, individual pollen grain from stamen; 31, pollen grains in meconium of *K. nordenae*; 32, individual pollen grain from meconium of *K. nordenae*.

function as a deterrent to ants or other organisms while the adult wasp is foraging and the nest is vulnerable.

The Oriental *Piyumoides* Leclercq, considered by Leclercq (1996) to be the genus most closely related to *Krombeinictus*, also lacks a pygidium. Females, however, lack the median brush of setae on the last abdominal tergum, and there is no secretion from abdominal glands on this segment in females of three of the four known species in the NMNH collection.

Krombeinictus nordenae is unusual or unique among sphecid wasps in a number of behavioral characteristics. The female manifests extraordinary maternal care, rearing one larva at a time and feeding it progressively. The species also is remarkably different from all other Sphecidae in feeding the larva clumped masses of fine-grained pollen rather than paralyzed arthropods. We found such clumped masses of pollen of *Humboldtia laurifolia* on the hypostomal area of a female (Figures 27, 28) and recovered grains of the same pollen from the exuviae and meconium of postdefecated larvae within cocoons of *K. nordenae* (Figures 31, 32). The cocoon also is unlike that of any other known crabronine (Figures 34, 35); it is discussed at length below (see "Cocoon").

Krombeinictus nordenae is a relatively rare wasp, and only seven females and two males were obtained at Gilimale. We found only 10 nests of *K. nordenae* at this locality compared with about 40 of *Crossocerus mukalanae* Leclercq. Two females and one male were in separate internodes that did not contain evidence of nesting; they were apparently just sheltering there. Another female, mentioned in the section on ants within the discussion of diversity in a single stem (FRR 91-S-226), apparently was about to initiate nesting. The last abdominal tergite was coated copiously with the secretion that we believe may be used as an ant guard (Figure 18), and there was a substantial amount of pollen on the setae of the hypostomal area (Figures 27, 28). A third male was recovered from an internode in the Sinharaja Reserve.

We never found more than one adult female in a nest, and in half the nests there was no female. Our impression is that the females are timid and may take flight if the nest is disturbed.

NEST.—Only ten nests were found, four of them containing a female, presumably the foundress. A fifth nest had been layered dry, rather than immersed in alcohol; a male developed and emerged from the cocoon it contained. The fifth nest also contained five adult males of the crabronine *C. mukalanae*. They apparently were sheltering in the internode as there was no evidence of nesting by *C. mukalanae* within this internode. A sixth nest, also layered, contained two cocoons; one occupant was a mummified postdefecated larva, and the other occupant had emerged prior to the layering. The other four nests were identifiable as *Krombeinictus* by the characteristic cocoon containing either a postdefecated larva or a pupa. The dried pith had been entirely removed from the inner wall of the internode in each of the nests. We presume that the female does this before laying the first egg; however, it also is possible that *K.*

nordenae may take over an internode that has been cleaned out by ants or other occupants and later abandoned.

One nest (Figure 33) provided an insight into some aspects of probable nesting behavior. The internode was 6.3 cm long and up to 4.0 mm wide. The interior cavity was 5 cm long, with a maximum width of 3.4 mm. When this internode was split downward from the opening, we found a small wasp larva, 2 mm long, on the cavity wall just below the entrance hole, a female wasp lower in the cavity, and a cocoon holding a well-colored wasp pupa at the narrowed lower end of the cavity. A second cocoon containing a postdefecated larva was 10 mm above the upper end of the lower cocoon.

It seems probable from these data that the wasp lays her egg on the inner wall of the cavity near the entrance. When the egg hatches, she feeds the larva progressively. The relative developmental stages of the two cocoons suggest that when the first larva is full grown, she carries it lower down in the cavity to spin its cocoon. She then probably deposits another egg near the entrance. When that larva hatches, it is fed until full grown, and is then transported lower in the cavity to spin its cocoon. Then the sequence is begun again.

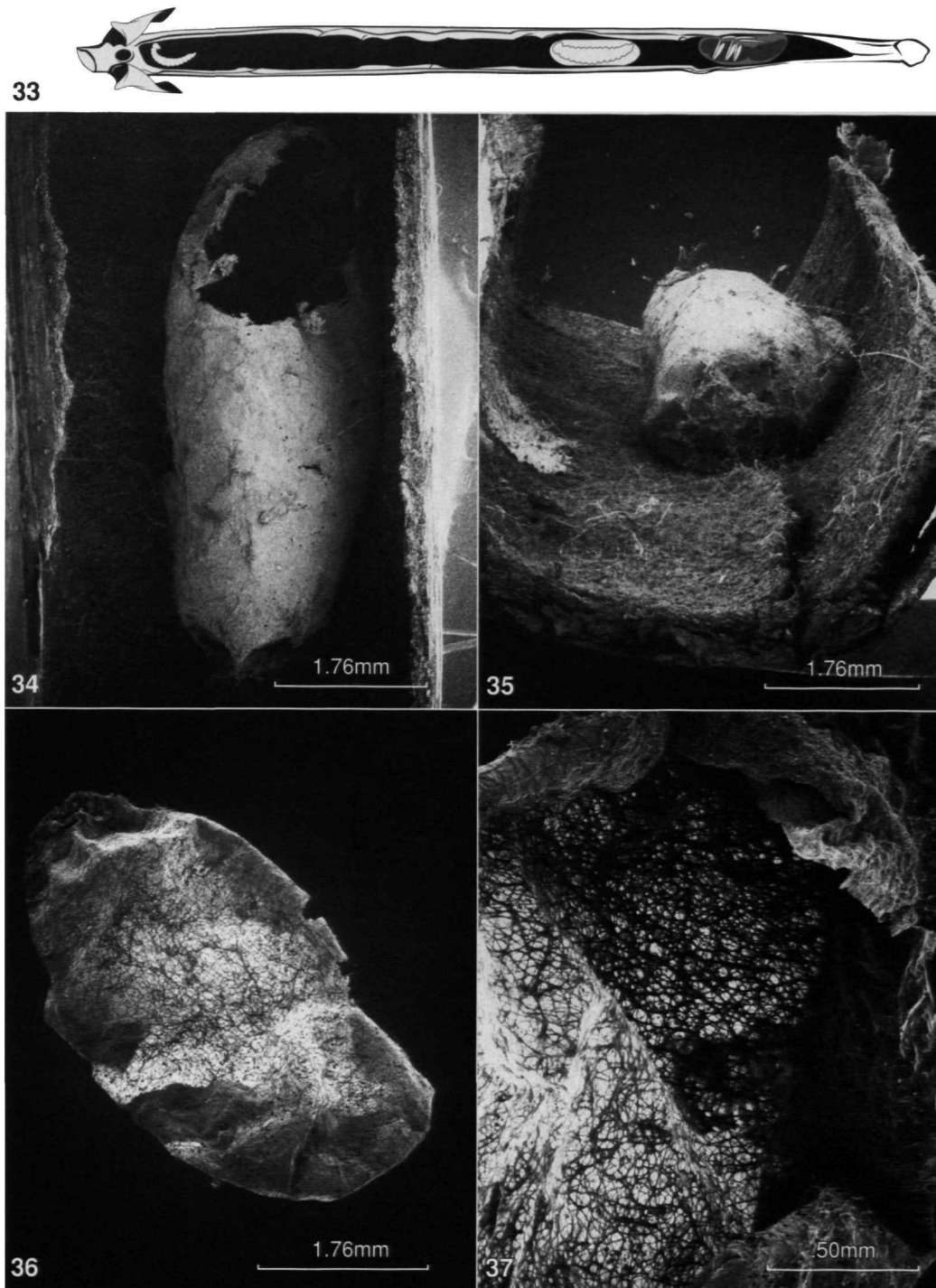
A second nest was in an internode 5.7 cm long, with a maximum width of 5.1 mm. The cavity was 4.7 cm long, with a maximum width of 4.6 mm. The female was not in the nest. A cocoon at the narrowed bottom end of the cavity held a pale female pupa with black eyes. A second cocoon, 23 mm above the first, contained a postdefecated larva.

Another nest contained a well-colored pupa in a cocoon 14 mm from the inner end of the cavity. An empty cocoon, from which an adult had emerged, was 15 mm above the lower cocoon. At the bottom of the cavity was a female that had moved head inward to escape the alcohol. It is unlikely that this female is the foundress. Had the foundress still been active, there should have been a nearly full-grown larva near the entrance. It is more likely that this female emerged from the empty cocoon.

Another nest was layered in the field and was examined later in Washington, D.C. It appeared that at one time it contained four cocoons, but only two cocoons remained from which adults had already emerged. There was also a small, mummified, yellow larva of *K. nordenae*. The other nests contained only a single cocoon with either a postdefecated larva or a pupa; the yellowish color of fresh larvae was reminiscent of that of bee larvae. A final nest is discussed below (see "Associates").

IMMATURE STAGES.—We obtained no information on duration of the immature stages nor on the size of the egg. Three post-defecated larvae from cocoons were 5.0, 5.5, and 6.0 mm long. Four pupae were 4.5 and 5.0 mm long, two of each length.

LARVAL FOOD.—The larva is fed fine-grained *Humboldtia* pollen that clumps together from an oily substance, pollenkitt, secreted on the pollen grains (Figures 29, 30). The female gathers the pollen in clumps on the hypostomal setae behind the



FIGURES 33–37.—*Krombeinictus nordenae* Leclercq: 33, diagram of nest, young larva near internode entrance at apex, pupa in cocoon at base, and postdefecated larva in cocoon to left of pupa; 34, cocoon from which adult emerged in internode; 35, cocoon in section of internode, oblique view (note ample space for passage of foundress or emerging adults); 36, cocoon, base toward upper left; 37, cocoon, higher magnification to show splotch of meconium at posterior end (darker mesh, upper right).

mandibles (Figures 27, 28). We found *Humboldtia* pollen only on the hypostomal area of one female and voided with the exuviae and meconium of final instar larvae (Figures 31, 32) within cocoons of *K. nordenae*. The mechanics of transfer of food to the larva is unknown. Inasmuch as the larva is positioned on the inner internode wall just below the entrance, the female could just insert her head to feed the larva. However, because of the danger of predation by birds or lizards, the female perhaps is more likely to enter the internode to transfer food.

All females were part of the short type series. We did not sacrifice any to ascertain whether pollen also might be carried in the crop.

COCOON.—The cocoon is totally unlike that spun by any other crabronine. The normal crabronine cocoon is more or less ovoid, with the posterior end tapering rather narrowly, and the cocoon is circular in cross section. In contrast, the *Krombeinictus nordenae* cocoon (Figures 34–36) is broadly ovoid and tapers very slightly posteriorly. The exposed upper surface is gently convex so that, in cross section, the cocoon is more curved on the side appressed against the inner wall of the cavity and rather slightly curved on the surface not in contact with the wall. Cocoon dimensions ($n=9$) are 6–9 mm long, 2.6–3.4 mm wide, and about 2.0–2.1 mm high. The diaphanous cocoon wall is an irregular mesh of silken strands overlying a delicate semitransparent film (Figure 36). The meconium is plastered as one or two black splotches at the posterior end of the cocoon (Figure 37).

The cocoon is somewhat flattened, so that there is a space at least 2 mm high between its upper surface and the inner wall of the cavity (Figure 35). This permits the mother to crawl over a cocoon, if necessary, to carry a larva toward the lower end of the cavity, or to allow a newly emerged adult from a cocoon lower in the cavity to reach the entrance. Postdefecated larvae and pupae in cocoons were oriented with the head facing the entrance, except that one pupa in a cocoon 3 mm below the entrance (the only cocoon so close to the entrance) was oriented with the head away from the entrance. Had this misoriented occupant enclosed, it would have had no difficulty turning around in the cavity to make an exit. The unusual location of this cocoon so close to the entrance suggests that something happened to the nesting female at about the time the larva reached maturity. Otherwise, the larva probably would have been moved lower into the cavity.

ASSOCIATES.—One nest, not discussed above, had two unexpected occupants. The female *Krombeinictus nordenae* was not in the internode, but her slender, immature larva, about 5 mm long, was near the entrance, and there was a pale male pupa, 4.5 mm long, in a cocoon near the inner end of the cavity. In addition, there were in the internode a male parasitic anthophorid bee, *Nomada wickwari* Meade-Waldo, 6.4 mm long, and a female mutillid wasp, *Physetopoda fumigata* (Turner), 5.0 mm long. The former was certainly a chance visitor seeking shelter. The female mutillid, however, is possibly a parasitoid of *K. nordenae*.

We found no evidence that larvae of the keroplastid *Platycedion edax* Chandler and Matile are predators in nests of *K.*

nordenae, although they attack *C. mukalanae*, the other crabronine nesting in internodes. If secretions are placed around the entrance as an ant guard by female *Krombeinictus nordenae*, that also might inhibit oviposition within the nest entrance by a keroplastid female.

DISCUSSION.—The data reported above provide tantalizing glimpses of a crabronine behaving in an extraordinary manner. The foundress and several brood in varying stages of development form a subsocial group. Additional observations are extremely desirable to ascertain whether this subsocial group reaches the level of social behavior by having a daughter join the foundress in caring for later brood.

The practice of moving brood within the nest also is found in the eusocial xylocopine bee *Braunsapis hewitti* (Cameron) (Maeta et al., 1992). The nature of brood movement, however, is different because the eggs are laid at the inner end of the nest, and successively larger larvae are moved toward the nest entrance. Moving the brood occurs when there is an extension of the burrow, feeding of the larvae, or grooming of the brood. Our observations indicate that *Krombeinictus nordenae* has only one larva at a time, and that it is not moved from its position near the entrance hole until it is fully mature. At that time it is carried toward the lower end of the cavity to spin its cocoon.

It is tempting to speculate that *Krombeinictus nordenae* is so coadapted to *Humboldtia* that the wasp nests only in the plant's internodes, where nearby there is a plenitude of extrafloral nectaries and pollen when the plant is in bloom. In support of this speculation, it should be noted that *K. nordenae* was never collected during the dozen years, 1968–1980, of the Ceylon Insect Project (Krombein, 1981). None of us collected on *Humboldtia*, but several specialists, including KVK during a dozen trips, collected at emergence holes in dead wood both in the rainforest and in the Dry Zone, and in tunnels in wood. If this coadaptation is a fact, we wonder if *K. nordenae* or another species of *Krombeinictus* may be associated in southern India with *H. decurrens* and *H. brunonis*.

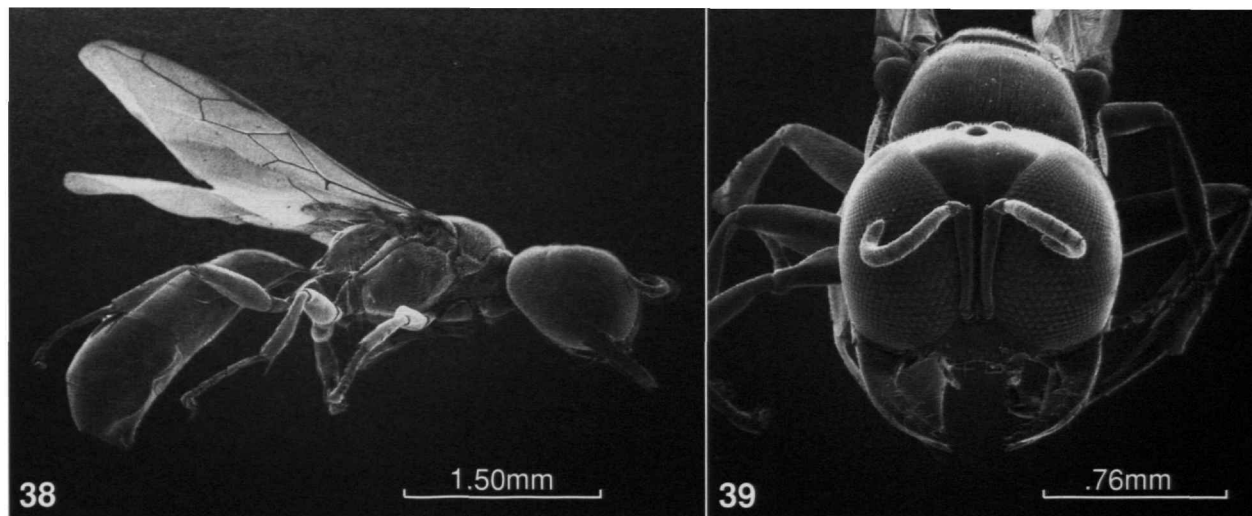
Krombein and Norden (1997a, 1997b) published abbreviated accounts of the nesting behavior of *K. nordenae*.

Crossocerus (Ablepharipus) mukalanae Leclercq

FIGURES 38, 39

This solitary wasp (Figures 38, 39), 4.0–4.5 mm long, is the most common aculeate, other than ants, nesting in *Humboldtia*. Forty of the internodes placed in alcohol were occupied by *C. mukalanae*. The evidence from these internodes suggests that the wasp selects a mature, unused internode with collapsed pith in which to construct her nest. Using her mandibles, she rasps tiny, irregularly shaped particles, 0.1–0.2 mm wide, from the pith to form the initial and closing plugs and the partitions between the individual cells in the linear series.

NEST.—It was difficult to obtain details of the nest architecture because the contents of many nests were disarranged by brood that had transformed to adults during the delayed monsoon season. During sunny periods between rains, some of



FIGURES 38, 39.—*Crossocerus (Ablepharipus) mukalanae* Leclercq, female: 38, lateral view; 39, frontal view, head.

these adults left the nests temporarily and then returned when the rain resumed. This movement of newly emerged adults within the nests broke down the fragile partitions between many of the cells and also disarranged the closing plugs at the nest entrances.

Initially the foundress constructs a firmly packed plug of pith at or near the inner end of the cavity. This plug was 4 to 30 mm thick ($n=7$) and at the inner end of the cavity, except in one nest that had an empty space of 5 mm before the plug. One nest lacked an initial plug.

The foundress then constructs a series of cells in a linear sequence. She oviposits on the first prey that she brings into the cell, stocks the cell with more prey, and then makes a closing plug of closely packed particles of pith. Partitions capping the cells were 1.0–3.0 mm thick. Seven cells with partitions in four nests were 5.0–8.0 mm long. Normally, in crabronine wasps nesting in cavities (Krombein, 1964) there is an empty vestibular cell above the outermost provisioned cell and then a closure of firmly packed pith to the nest entrance. We obtained measurements from only one nest where the occupants had not disturbed the arrangement by their frequent egress and ingress. The vestibular cell and the closing plug were each 15 mm long.

A nest in an internode with an inner cavity 5.0 cm long had a plug of pith particles 4 mm thick at the inner end. There were five enclosed adults (2♀, 3♂) in the nest. Three cells toward the outer end of the cavity contained pupae (1♀, 2♂) in cocoons. The first two of these cells, including the pith partitions capping them, were 8 mm long (1♀) and 5 mm long (1♂); the partition of the third cell had been destroyed by movements of the enclosed adults.

The nest with the largest number of occupants had an inner cavity 8.3 cm long. It contained nine enclosed adults (4♀, 5♂), a female pupa in a cocoon ready to eclose, a larger larva about 4 mm long, and a recently hatched larva, 1.8 mm long, in a cell with prey.

IMMATURE STAGES.—The eggs ($n=2$) are sausage-shaped, slightly curved, 1.2–1.3 mm long, and 0.3–0.4 mm wide. We found one nest with the foundress and a single, stocky acalyptrate fly, 1.8 mm long, bearing the egg. The cephalic end of the egg was attached to the thoracic venter of the fly just behind the head.

We obtained no information on duration of the immature stages, but such data on another crabronine wasp, *Ectemnius paucimaculatus* (Packard), may be helpful (Krombein, 1964). In the Washington, D.C., area, where high heat and humidity characterize many summer days, this wasp burrows into the central pith of *Hibiscus militaris* Cavanilles, and, like *C. mukalanae*, constructs a linear series of cells sealed by partitions of pith particles. The summer generation of *E. paucimaculatus* requires 24 to 31 days from egg to adult, the larva completes feeding seven to eight days after the egg is laid, the prepupal stage lasts five to 10 days, and 10 to 11 days elapse between pupation and adult emergence.

COCOON.—The cocoon of *C. mukalanae* is always rather densely covered with tiny particles of pith that the larva obtains from the partitions enclosing it in the cell. The cocoons are normally ovoid, with the posterior end somewhat narrowed although not so markedly as in the normal crabronine cocoon. Six postdefecated larvae from cocoons were 3.5–4.5 mm long. Fourteen female pupae were 4.2–4.6 mm long, and their cocoons ($n=12$) were 4.6–5.5 mm long and 1.8–2.2 mm wide. Five male pupae were 3.7–4.2 mm long.

PREY.—Whole prey or remains thereof were found in 31 nests. The prey from these nests consisted of 183 specimens of Diptera, 10 of Chalcidoidea, and three of Ephemeroptera. Unquestionably, Diptera are the preferred prey, and only Diptera were found in 23 of 31 nests. Five nests contained predominantly Diptera, but there were also a few Chalcidoidea. Two nests had one or two Ephemeroptera and five to 12 dipterons, and one nest contained only a single ephemeropteron.

The dipterous prey were 0.7–2.2 mm long, except for one tipulid that had a body length of 4.5 mm. Many of the prey specimens were slender, midge-like Nematocera, but there were occasional Phoridae and small, bulky acalyptrate dipterons. A cell that had a small, recently hatched wasp larva contained 17 prey, probably a full prey complement considering the size of the small larva; there were three Cecidomyiidae, one Mycetophilidae, three Sciaridae, five Phoridae, an acalyptrate dipteran, three unidentified dipterons, and one chalcidoid, a species of Encyrtidae. Twenty-eight prey from several cells in another nest consisted of 20 Ceratopogonidae and eight unidentified dipterons. Fifteen prey from a third nest included one Cecidomyiidae, three Sciaridae, three Phoridae, one acalyptrate dipteran, and seven unidentified dipterons.

The 10 chalcidoid prey from five nests were 1.1–2.2 mm long and consisted of one Pteromalidae species, six Encyrtidae species, two Eulophidae species, and one Eupelmidae species.

The four Ephemeroptera were identified as a species of Baetidae. The body length was 2.8–2.9 mm, and the forewings were 3.0–3.8 mm long, 1.2–1.4 mm wide. The abdomen of one had been eaten by the wasp larva, and the other specimens were entire.

Examination by scanning electron microscope of particles of pith from nests that contained adult brood revealed some ant fragments. We presume that such fragments might be the remains of an ant that entered the internode and was made into prey by the nesting female *C. mukalanae*.

One nest from Sinharaja contained a small larva and two pale pupae of *C. mukalanae* and one prey of each of the following dipterous families: Ceratopogonidae, Cecidomyiidae, Phoridae, and Agromyzidae. A second nest from this locality had three females and a male of *C. mukalanae* and one specimen each of the following dipterous and hymenopterous families: Chironomidae, Sciaridae, Phoridae, and Eulophidae.

Reviewing the prey records, we note that many of the specimens could have been attracted to the sweet secretions of the abundant extrafloral nectaries of *Humboldtia*. Some of these nectaries are near the internode entrances and would thus provide a convenient hunting ground for wasps nesting in the internodes.

ASSOCIATES.—We found a number of invertebrate species other than prey in nests of *C. mukalanae*. These included parasites, predators, and visitors that may have entered the nests for shelter or to feed on dead pith.

One specimen of a chalcidoid pupal parasite, *Perilampus* spp. (Pteromalidae), was found in each of five nests of *C. mukalanae*.

Another possible chalcidoid parasite of the *C. mukalanae* brood is the torymid *Diomorus* species. See that entry in Hymenoptera section of "Other Invertebrates."

Two nests of *C. mukalanae* in the Sinharaja were destroyed by a larva of the keroplastid fly *Platyseridion edax* Chandler and Matile. Each internode contained disarticulated exoskeletons of the wasp and of the ant *Technomyrmex albipes*.

A staphylinid larva, a species of the paederine subtribe Astenina, was found in each of two nests of *C. mukalanae*. One was

in a nest containing a small wasp larva and several prey specimens. The other was in a nest containing two newly emerged wasps, a wasp pupa in a cocoon, a wasp larva, and a couple of prey. These beetle larvae are presumed to be predators of the wasp. An adult staphylinid, possibly *Stilicopsis* sp., was found in each of two other nests of *C. mukalanae*; they also are presumed to be predators and may represent the adult stage of the larvae mentioned above.

An accidental predator was a moth larva, probably a species of Yponomeutidae, that was found as a pupa in a *C. mukalanae* nest. As a larva it fed on two newly eclosed *C. mukalanae* adults that were in their cocoons. The lepidopterous larva is presumed to feed normally on the pith in a *Humboldtia* internode.

Visitors in *C. mukalanae* nests included eight specimens of a small species of Collembola, 0.7–1.1 mm long. There were 29 specimens of a dozen or more species of Psocoptera, 0.8–3.0 mm long, all of them winged except one species. The Collembola and Psocoptera were not damaged, so apparently they were not stored as prey; we presume that they had entered the nests to feed on particles of dead pith used in nest construction or on other organic debris. One or more Collembola and/or Psocoptera were found in 13 nests.

There were a few casual visitors that apparently entered the nests just to shelter from the weather. A female pemphredonine wasp, *Carinostigmus costatus* Krombein, was in a nest that contained nine newly eclosed *C. mukalanae* adults. Two small spiders, a species of Hadrotarsinae (Theridiidae), 1.3–1.8 mm long, were found in two *C. mukalanae* nests containing female wasps and brood.

DISCUSSION.—We suspect that *C. mukalanae* may nest only in *Humboldtia* internodes. Other than our extensive series from internodes, the species is known only from the type series: two females collected by Krombein et al. in the mid-1970s, one near Weddagala, the other at Kitulgala, both localities where *Humboldtia* is abundant. See also "Discussion" under the preceding species, *Krombeinictus nordenae* Leclercq.

Tsuneki (1960) reported on the biology of *Crossocerus* (*Ablepharipus*) *fukuiensis* Tsuneki (misidentified as *C. (A.) congener* (Dahlbom)). It is the only other Oriental member of the subgenus whose biology is known. Tsuneki found it nesting in the thatched roof of a barn in Japan. It constructed a linear series of five to 12 cells in the canes and provisioned them with 14–23 flies, mostly Mycetophilidae but sometimes including Empididae. The partitions between the cells were made of pith particles gnawed off the inner wall of the cane. The egg was usually placed on the innermost fly.

Family ANTHOPHORIDAE

Braunsapis sp.

FIGURE 40

There were four nests of an undescribed species of *Braunsapis* (Figure 40), each in an internode from which the pith had been removed. One nest contained two female bees, 5.7 mm long, a female pupa, 3.7 mm long, and three curved bee larvae,

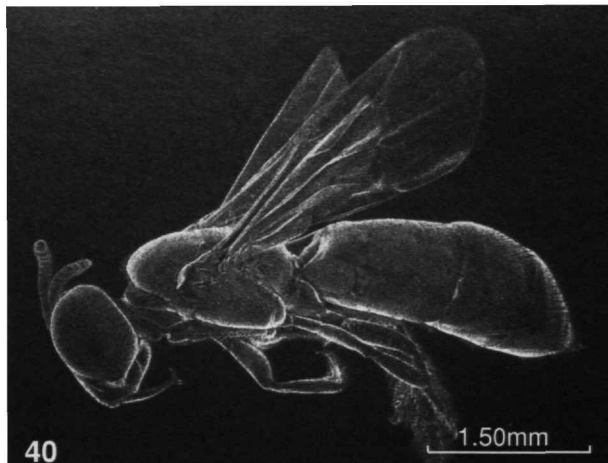


FIGURE 40.—*Braunsapis* species, female, lateral view.

respectively 5.1, 4.8, and 3.0 mm long. The second nest contained a female bee, 4.2 mm long, a male bee, 4.5 mm long, a female pupa, 4.7 mm long, two curved larvae, 5.2 and 4.5 mm long, and an egg, 1.8 mm long and 0.4 mm wide. The third held two females, 5.2 mm long, a damaged, colored male pupa, a small curled larva, and two eggs, one damaged, the other 1.5 mm long. The last nest contained two females, 5.1 and 5.3 mm long, a colored female pupa, 4.6 mm long, two curved larvae, 3.9 mm long, one more robust, the other more slender.

There also was a predaceous beetle larva, a species of *Calilimerus* (Cleridae) in each of the first two nests, that in the first nest, 6.3 mm long, and that in the second, 9.7 mm long.

A possible chalcidoid parasite of the *Braunsapis* brood is the torymid *Diomorus* sp. See that entry in "Hymenoptera," below.

Other Invertebrate Associates of *Humboldtia laurifolia*

We place here accounts of the species other than nesting aculeate Hymenoptera (ants, wasps, and bees) that we found in internodes. Some of them are known to be or thought to be parasites or predators of the foregoing aculeate Hymenoptera. Others undoubtedly were visiting the internodes to feed on the collapsed pith or just to seek shelter in the internodes.

Order HYMENOPTERA

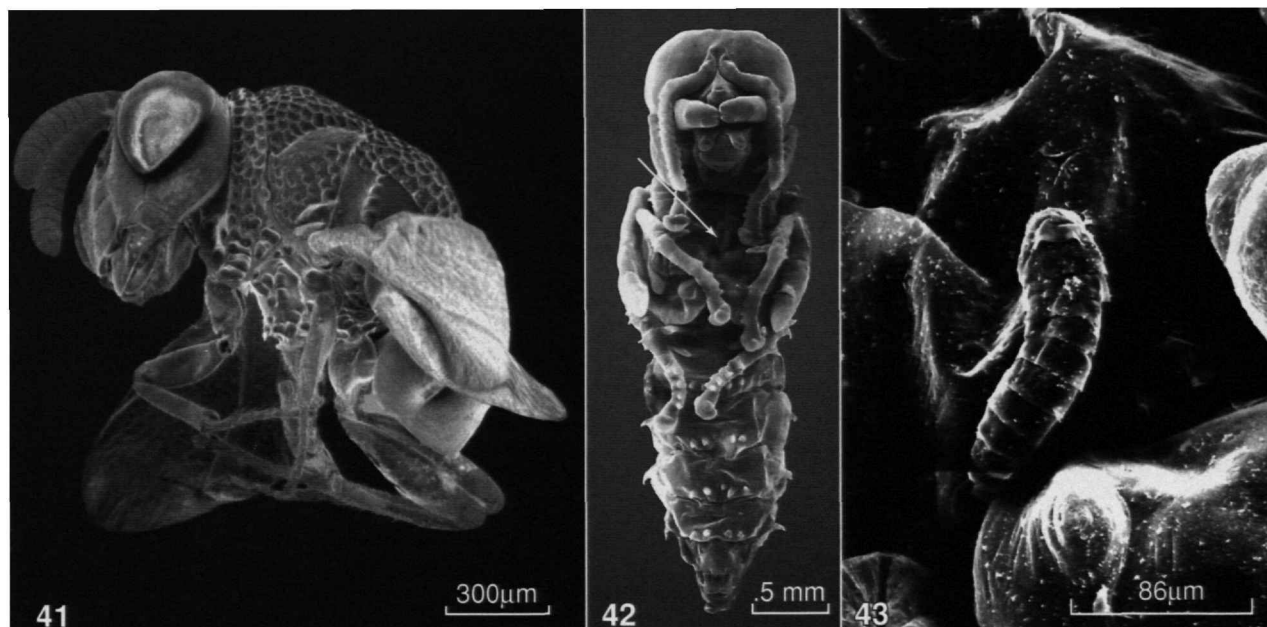
Family PERILAMPIDAE

Perilampus species

FIGURES 41–43

The earliest stage of this pupal parasite that we obtained was a first instar planidium, 0.16 mm long (Figure 43). It was attached to the mesosternum (Figure 42) of a pink-eyed pupa of *Crossocerus mukalanae* Leclercq within the host cocoon.

We found *Perilampus* spp. in four other nests of *C. mukalanae*. One was a pupa, 2.2 mm long, beginning to color within the host cocoon, 4.5 mm long. Another was a fully colored *Perilampus* adult (Figure 41), 2.5 mm long, within a host



FIGURES 41–43.—*Perilampus* species: 41, male, lateral view; 42, pupa of *Crossocerus mukalanae* Leclercq bearing on thoracic sternum a first instar planidium (arrow) of *Perilampus* species; 43, first instar planidium of *Perilampus* species.

cocoon in another nest; the nest also contained specimens of *C. mukalanae*, an adult female and a female pupa in a cocoon. The last two *Perilampus* adults were in two nests of *C. mukalanae* whose occupants had emerged from their cocoons and were sheltering in the nests. One nest contained two females and one male of the host wasp and a *Perilampus*, 2.6 mm long; the other contained four pairs of the host wasp and a *Perilampus*, 1.5 mm long.

D.C. Darling identified the three adult *Perilampus* as two males and a female; the two males are not conspecific, and he was unable to decide whether the female was the opposite sex of one of the males or if it was a third species. Darling (pers. comm., 2 Oct 1996) believes that the planidia of the *Perilampus* spp. gain access to the nest on bodies of the prey brought into the nest by the wasps. The host wasps are probably incidental or fortuitous hosts, a belief that is consistent with the low parasitism rate.

Family TORYMIDAE

Diomorus species

We found a small mature larva in a vial that contained the pooled contents from several internodes. The vial also contained adults of *Braunsapis* sp. and *Crossocerus mukalanae*; brood of either might have been the host. E.E. Grissell identified the larva and reported that known hosts of *Diomorus* include several genera of twig-nesting sphecid wasps and the bee genera *Osmia* and *Ceratina*.

Family MUTILLIDAE

Physetopoda fumigata (Turner)

FIGURES 44–46

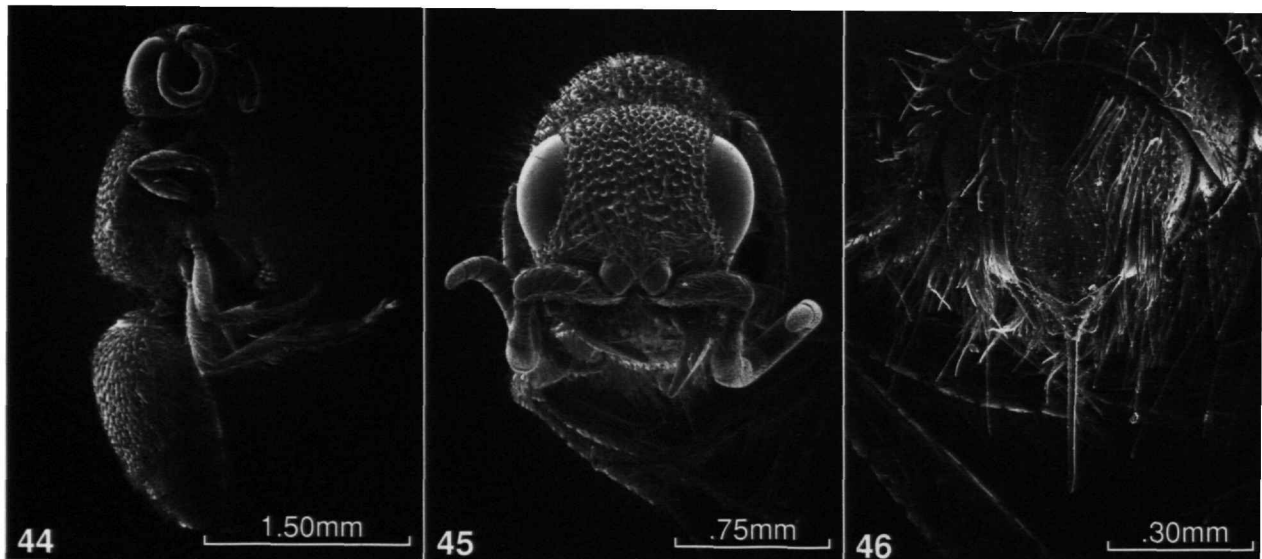
We recovered a female of this species, 5.0 mm long, in a nest of *Krombeinictus nordenae* Leclercq. Mutillids normally attack the resting stage of the host, i.e., the pupa or postdefecated larva. If the host is in a cocoon, the mutillid chews a hole in the cocoon, stings the host, and deposits an egg on it. The *K. nordenae* cocoon was undamaged, and neither the pupa nor the immature larva bore a wasp egg. The mutillid may have entered the internode just prior to our preservation of the latter in alcohol, thus lacking the time needed for oviposition. Perhaps, it too was just seeking shelter; it may have climbed into the *Humboldtia* to visit the extrafloral nectaries, some of which were just above the internode entrance. However, females of *Physetopoda* have a weak pygidial area covered anterolaterally by setae (Figure 46). This type of pygidium is characteristic of Mutillidae that are parasitoids of species that do not nest in the ground. So it is quite possible that this female *P. fumigata* entered the internode to parasitize the *K. nordenae* rather than to take shelter.

Family PEMPHREDONIDAE

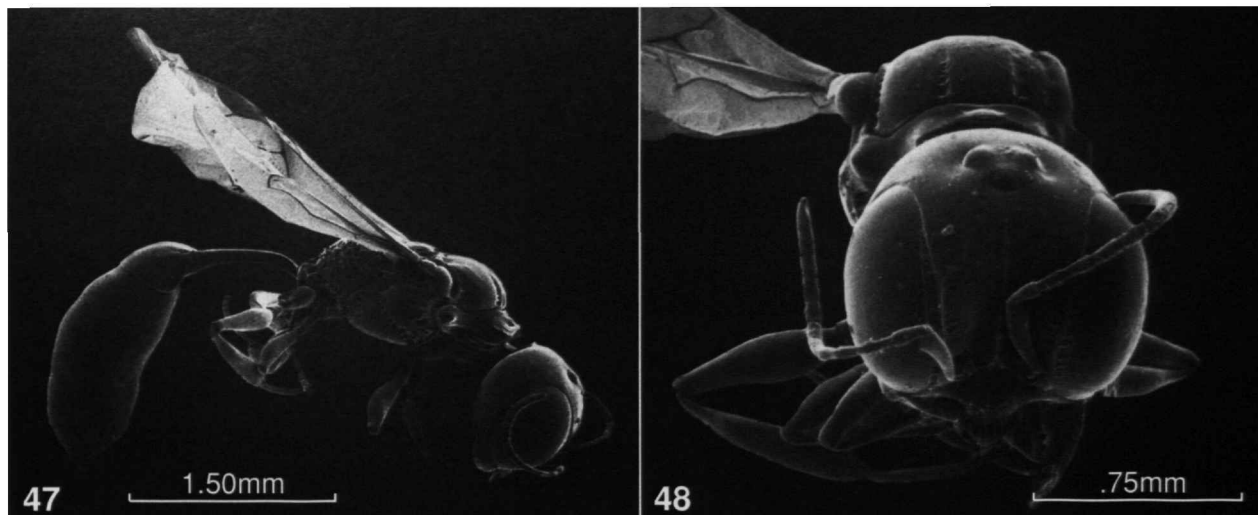
Carinostigmus costatus Krombein

FIGURES 47, 48

A female of this pemphredonine wasp, 5.1 mm long, was a visitor in a nest that contained nine newly eclosed adults of *Crossocerus mukalanae*. At least one other species of Cey-



FIGURES 44–46.—*Physetopoda fumigata* (Turner), female: 44, lateral view; 45, head, frontal view; 46, pygidium, dorsal view.



FIGURES 47, 48.—*Carinostigmus costatus* Krombein, female: 47, body, lateral view; 48, head, frontal view.

lonese *Carinostigmus* is known to make a linear series of cells in soft pith, which it provisions with aphids (Krombein, 1984). *Carinostigmus costatus* may nest in *Humboldtia* internodes, but this specimen apparently was there for shelter only.

Family ANTHOPHORIDAE

Nomada wickwari Meade-Waldo

FIGURE 49

We found a male of this anthophorid bee, 6.4 mm long, also sheltering in the *K. nordenae* nest discussed above under *Physetopoda fumigata*. It was obviously there for shelter only.

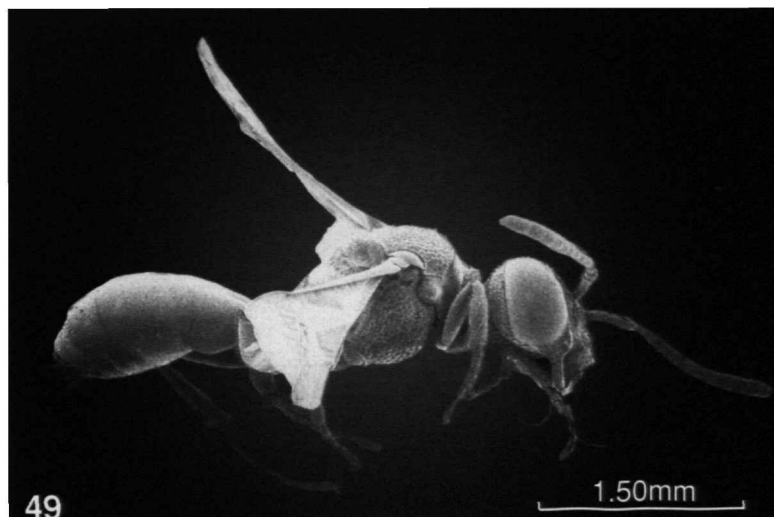


FIGURE 49.—*Nomada wickwari* Meade-Waldo, female, lateral view.

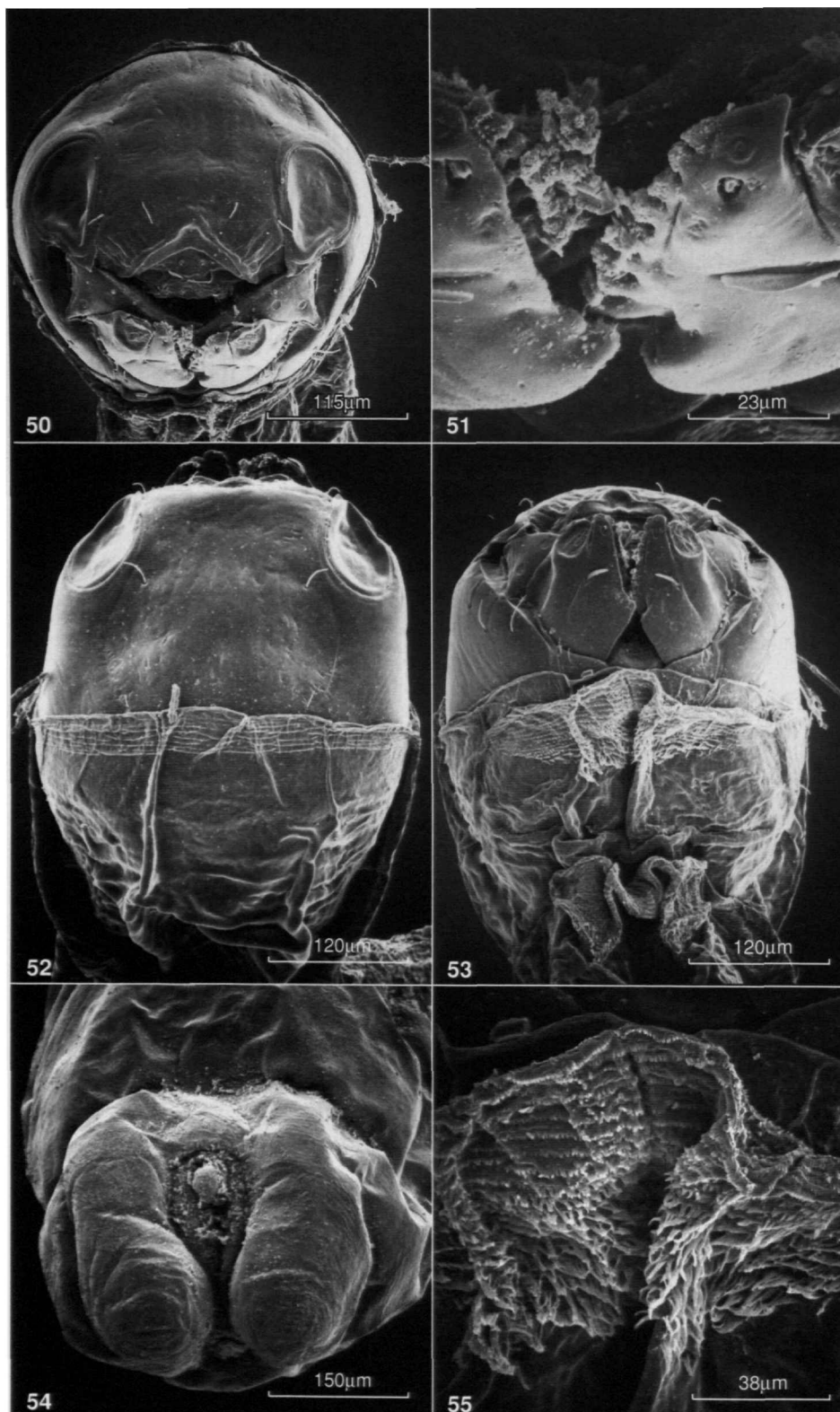
Order DIPTERA

Family KEROPLATIDAE

Platyceridion edax Chandler and Matile

FIGURES 50–61

Other than ants, the most common predaceous insects in the *Humboldtia* internodes are larvae of *Platyceridion edax* Chandler and Matile (Keroplastidae, formerly considered a subfamily of Mycetophilidae). We recovered 42 larvae, only one per internode, and two recently emerged, teneral female adults still within the internodes. One adult was 5 mm long, and the wing was 4.5 mm long. Many of the lower ends of the internodes



FIGURES 50–55 (opposite).—*Platyceridion edax* Chandler and Matile, larva: 50, head, frontal view (eyes collapsed during drying); 51, apices of jaws (note asymmetry, probable prey-grasping modification below, and probable crushing modification along upper, thickened, ridged area); 52, head, dorsal view (note anterior part of first thoracic segment covering posterior part of head); 53, head, ventral surface (note retraction of head within first thoracic segment, and modified median area on the latter); 54, anal papillae; 55, modified median area on venter of first thoracic segment.

contained fragments of exoskeletons of ants, principally emptied head capsules and legs. The identifiable fragments were those of species of *Crematogaster* and *Technomyrmex albipes*. Two internodes from the Sinharaja Reserve contained, respectively, a larva and a pupa of *P. edax*. Parts of the exoskeleton of a female of *Crossocerus mukalanae* Leclercq also were found in each of these two internodes, as well as many fragments of ant exoskeletons.

Our findings strongly suggest that the *Platyceridion* larva is primarily a predator of the ants that occupy so many of the internodes. In one internode we counted head capsules of 50 ants and three chalcidoids, an uneaten worker of *T. albipes*, 2.1 mm long, together with the *Platyceridion* larva, 15 mm long and 1 mm wide. Prey remains were always found at the bottom of the internode, suggesting that the prey is dragged to the bottom immediately after capture and is consumed there.

We noted in the field that the *Platyceridion* larva was on a strand of mucus extending downward from the entrance to the lower part of the internode. We also noted that the larva slid up and down on the strand quite rapidly. We saw one larva grasp an ant at the entrance and drag it into the internode. Presumably the larva lies in wait at the entrance, perhaps with its head out (Figure 50), and grasps with its jaws (Figure 51) any ant or other small insect crawling nearby. It then slides rapidly down the mucus strand to the bottom of the internode where the prey is consumed.

The stout jaws are asymmetrical and exquisitely adapted to capture and then crush the prey. The apex below one side ends in a stout tooth that fits into a slot at the lower apex of the opposing side; we presume that the prey is grasped with this apparatus. The upper part of the jaw is thickened and has close-set transverse ridges that are presumably adapted to crushing the prey.

The posterior part of the head is retracted within the anterior end of the first thoracic segment (Figures 52, 53, dorsal and ventral views, respectively). The prominent, facetless eyes, collapsed in Figures 50 and 52, have a convex surface in specimens preserved in fluid.

The larva has a pair of anal papillae (Figure 54) that may be characteristic of keroplastid larvae. Mansbridge (1933) suggested that in the English species of *Platyura* the papillae might be used as feelers when the larva moves backward along the mucus strand. Those in *Platyceridion* are quite large and are capable of being partially retracted apically. We wonder if they might be used to help the larva lunge forward to grasp a prey.

The anterior ventral surface of the first body segment has an area of about 20 transverse, narrow strips of minutely serrulate, lightly chitinized membrane (Figures 53, 55). This modified area possibly enables the larva to glide rapidly up or down the mucus thread within the internode.

The action of the larva in sliding the anterior end of the body in and out of the entrance hole results in the deposit of a substantial amount of mucus (Figures 56, 57). This coating is quite marked in a comparison of highly magnified entrance holes of internodes occupied by and free of larvae (Figures 58, 59).

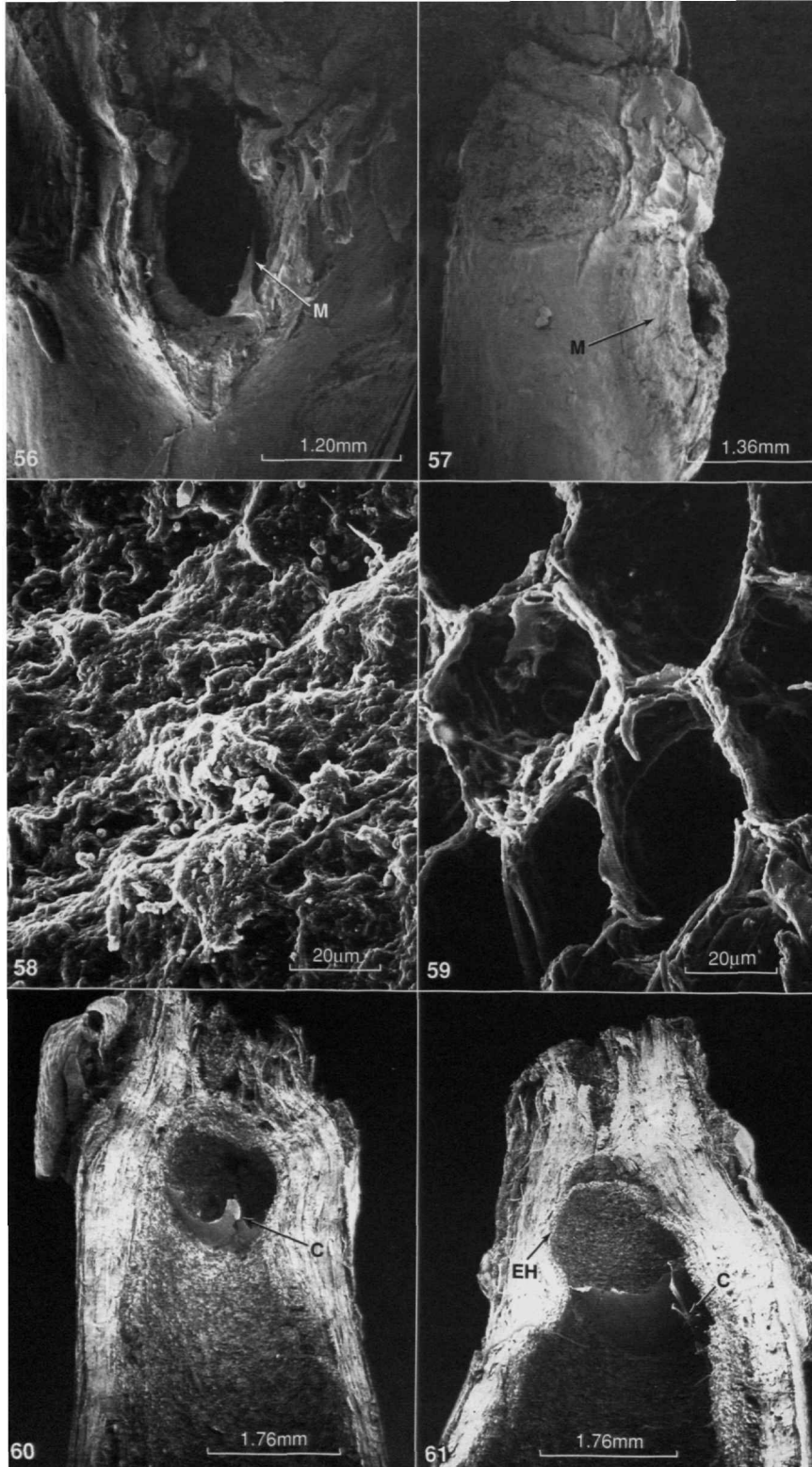
When the larva is fully grown and ready to pupate, it secretes a transverse, delicate cap (Figures 60, 61) just below the entrance, thereby sealing off most of the internode. It pupates near the cap, remaining attached to the mucus strand. A pupa about 6 mm long was found in a nest of *C. mukalanae* from the Sinharaja Reserve.

DISCUSSION.—The adult and larva of *Platyceridion edax* were described from our specimens (Chandler and Matile, 1999). It is the third species with primarily myrmecophagous larvae to be described in the keroplastid tribe Orfeliini since 1997.

Mansbridge (1933) made detailed observations on three species of the keroplastid *Platyura* in England. He found that the larva spun a web, frequently beneath the loose bark of a large log that had started to rot, and sometimes beneath the log. The web occupied an area of 3 to 4 square inches when it was built on a plane surface. Most of the web consisted of fine threads in which droplets of clear fluid were suspended. A coarser thread ran through the middle of the web along which the larva could move rapidly and get to any part of its web. He noted (1933: 78) that the larva was “apparently in the center of the thread along which it moves, so that it is always enclosed in a fine layer of the thread-mucus.” Pupation also occurred within the tube-like structure of the main thread. Mansbridge found that in the field the larvae fed on dipterous larvae, Collembola, Myriapoda, and Oligochaeta.

Aiello and Jolivet (1997) published an account of the Panamanian keroplastid *Proceroplatus belluus* Matile. They found seven slender larvae, 1.5–2 cm long and about 1 mm in diameter, each in an inflated vesicle near the base of the leaf blade of the ant-plant *Besleria formicaria* Nowicke (Gesneriaceae). The larva of *P. belluus* glided along a silk thread in a bed of clear slime within the vesicle. Some other vesicles were occupied by a species of the ant *Pheidole* with brood. Aiello and Jolivet reared one adult fly and an endoparasitic ichneumonid wasp, *Megastylus panamensis* Wahl, from two dipterous larvae that had been fed freshly crushed *Pheidole* workers, a live mosquito, and a variety of small invertebrates that occurred on leaves of *Besleria*. We believe that the larvae of *Proceroplatus belluus* probably prey upon ants in a manner similar to what we found in *Platyceridion edax*, namely lying in wait at the vesicle entrance and grasping an ant as it crawls across the leaf base.

Kovac, working in Malaysia, found that larvae of *Truplaya ferox* Kovac and Matile (1997) occurred individually in upright



FIGURES 56–61 (opposite).—*Humboldtia laurifolia* Vahl internodes occupied by larva of *Platyceridion edax* Chandler and Matile: 56, internode opening (note dried shred of mucus (M)); 57, internode opening, lateral view (note buildup of mucus (M) on callus surrounding opening); 58, greatly enlarged area of edge of opening (note mucus deposit obscuring basic mesh of surface, cf. Figure 59); 59, greatly enlarged basic mesh of internode edge not occupied by *Platyceridion*; 60, 61, opposite halves of apex of internode showing cap (C) of mucus secreted by larva across internode just beneath entrance hole (EH) prior to pupation.

bamboo culms. The larva occupied the upper part of a culm partially filled with water whose walls had been pierced by wood-boring organisms. The larva secreted a slimy web above the water adjacent to an opening. It extended the anterior part of its body out of the opening, grasped a passing prey, and dragged it onto the web, just as we noted in *Platyceridion edax*. It was noted that a larva may have remained for hours with the anterior part of the body hanging downward from the opening while it waited for prey. Sometimes the larva closed the opening with layers of secretion and preyed upon adults, especially mosquitos emerging from aquatic immatures. Ants, however, constituted 80.7% of the prey items, and remains of as many as 15 ants were found at one time in a web. Kovac drilled circular holes of three diameters (10, 5, and 1.2 mm) and a slit-shaped hole (20 × 8 mm) in bamboo culms at intervals several months apart. One female *T. ferox* was noted hovering in turn in front of several artificial 3 mm holes. Her abdomen was bent forward as she hovered, and it was thought that she was ovipositing, “shooting” an egg into the opening. The first *Truplaya* larva was found seven weeks after the first hole was drilled. The extent of the larval period was not ascertained, but in one case it was less than six months. The larva was reported to construct a cocoon suspended in the web for pupation. After eclosion the

adult stayed in the web for several days before emerging from the culm.

Platyceridion adults were not collected during the dozen years, 1970–1981, of the Smithsonian's Ceylon Insect Project (Krombein, 1981), although our teams made collections by Malaise and blacklight traps in areas of the rainforest. It is possible that adults may be very short-lived. L. Matile noted (pers. comm., 2 Nov 1995) that adults of the European *Keroplatus tipuloides* Bosc live only about a week, as compared to several months for the larvae, and are crepuscular to nocturnal. Only three adults have been collected since Bosc collected the unique type in 1793.

Family SYRPHIDAE

Microdon sp.

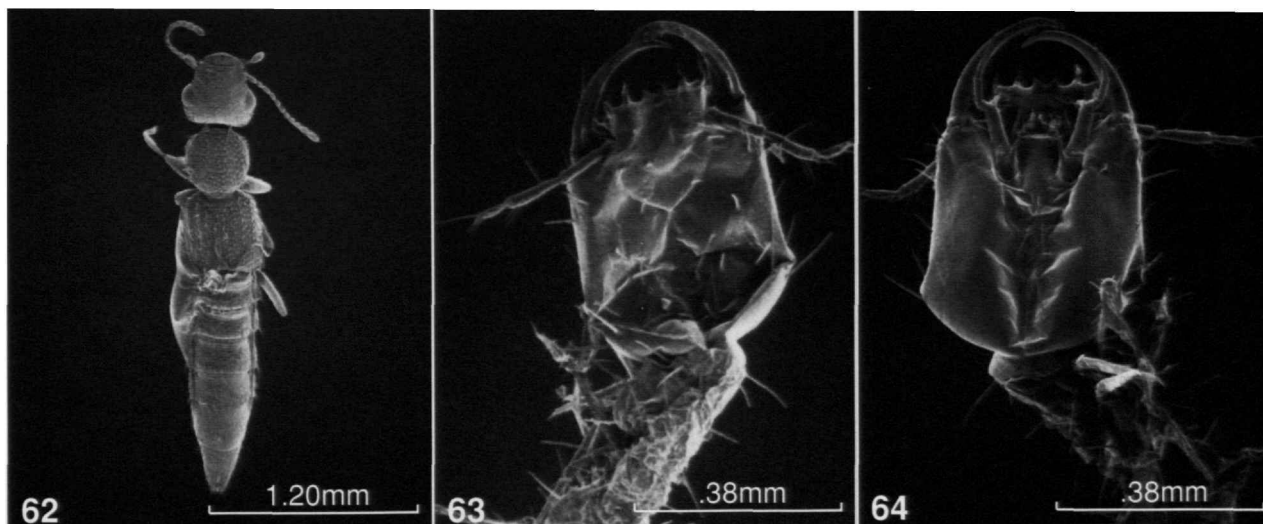
Four internodes at Gilimale and one in Sinharaja each contained a single, light blue *Microdon* larva. Members of this genus are all obligate temporary inquilines of social insects. Strong colonies of *T. albipes* were present in all cases, and *Microdon* is a well-known predator of larvae within ant nests (Akre and Paulson, 1993), primarily species of *Camponotus* and *Formica*.

Order COLEOPTERA

Family STAPHYLINIDAE

FIGURES 62–64

We recovered two adult females and two larvae from internodes. The adults were identified as cf. *Stilicopsis* sp. (Figure 62), and the larvae (Figures 63, 64) were identified as belong-



FIGURES 62–64.—Staphylinidae species: 62, cf. *Stilicopsis* species, adult, dorsal view; 63, Paederini larva, subtribe Astenina, possible larval stage of Figure 62, dorsal view (note thorax and abdomen shriveled from critical point drying); 64, same as Figure 63 but ventral view.

ing to the paederine subtribe *Astenina* and are very likely the same species as the adults. A.F. Newton, Jr., noted (pers. comm., 7 Dec 1994) that both stages are presumed to be predators. The two larvae were recovered from nests of *Crossocerus mukalanae* Leclercq. One larva, 1.8 mm long, of which 1.0 mm was the head, was in a nest with a very small wasp larva and four dipterous prey. The other larva, 3.8 mm long, head length 0.7 mm, was in a nest with two female wasps, a pupa in a cocoon, a larva, and one dipterous and one chalcidoid prey. One adult was in an otherwise empty internode, and the other was among internode contents pooled in the field.

Family CLERIDAE

We found a slender larva of a *Callimerus* species (Cleridae) in each of two nests of the bee *Braunsapis* sp. One beetle larva, 9.7 mm long, was in a nest that contained a pair of the *Braunsapis* and brood, a female pupa, two larvae, and an egg. The other larva, 6.3 mm long, was in a nest with two female *Braunsapis* and brood, a female pupa, and three larvae. Four more *Callimerus* larvae, 6.0–8.0 mm long and belonging to two or three species, were found among internode contents that were pooled in the field or in empty internodes with unidentifiable fragments of chitin.

Gardner (1937:40) found a larva of Phyllobaeninae (reported as Hydnocerinae) "in company with pupae of a small species of Apidae in a slender soft-pithed stem." We presume this to be the nest of a species of Xylocopinae, probably *Braunsapis*.

Order LEPIDOPTERA

One internode had a lepidopterous cocoon 3 mm below the entrance. The internode also contained some pith particles, remnants of two wasp cocoons, and two fully colored, disarticulated adults of *Crossocerus mukalanae* Leclercq. The lepidopterous larva is presumed to have fed on the soft parts of the adult wasps. R.W. Hodges identified the pupa as probably belonging to the Yponomeutidae. Hodges thought that the larva probably was not predaceous, but he noted that many larvae feeding internally on plant tissue will kill and eat other insects they encounter within the site. We presume that the larva of this moth most likely feeds on the pith of the *Humboldtia* internode.

Orders PSOCOPTERA and COLLEMBOLA

These two insect orders, commonly called booklice and springtails, respectively, are conveniently considered together. Individuals of each were found only in nests of *Crossocerus mukalanae* Leclercq that contained a number of adult wasps. The wasps had eclosed during the delayed monsoon season and were flying in and out of the nests.

Psocopterans and collembolans feed on detritus of various kinds. We presume that the individuals we recovered had entered the nests to feed on the small fragments of pith the wasps had used in constructing their nests. The specimens were

not damaged, and we do not believe that they had been brought in as prey by the nest foundress.

One to eight specimens of Psocoptera and/or Collembola were found in 13 of the 39 internodes in which *C. mukalanae* nested. Eight specimens of several species of Collembola were 0.7–1.1 mm long. Twenty-nine specimens of a number of species of Psocoptera were 0.8–3.0 mm long; all were winged except one specimen.

ORDER PSEUDOSCORPIONIDA

Family CHERNETIDAE

Haplochernes warburgi (Tullgren)

FIGURES 65, 66

We found the pseudoscorpion *Haplochernes warburgi* (Tullgren) (Figure 65) in numerous empty internodes. One stem internode contained three adults (2♂, 1♀), 2.5–3.5 mm long, whereas another internode contained nine specimens, 1.8–4.2 mm long, three adults (1♂, 2♀) and six nymphs. Often a single internode on a branch containing several ant colonies would house one or a pair of *H. warburgi*. This arthropod is a predator of ants, as ants were found clinging to the entrance hole while being held by the claw-like pedipalps (Figure 66) of the pseudoscorpion, and ant heads and other body parts were found in the lower portion of an internode occupied by *H. warburgi*.

Order ARANEIDA

Family THERIDIIDAE

We found two spiders, a species of the subfamily Hadrotarsinae, each in an otherwise empty internode. One was a female, 1.8 mm long, the other a juvenile, probably of the same species, 1.3 mm long.

Forster et al. (1990:111) noted that the four genera placed in the Hadrotarsidae, as well as some genera of Theridiidae, "seem to be specialist feeders on ants." Carico (1978) noted that one of these theridiids, the North American *Euryopsis funebris* (Hentz), about 4.5 mm long, preys upon ants foraging in trees. It immobilizes an ant by throwing adhesive-laden silk with its posterior pair of legs, thus fastening the ant to the tree. Perhaps the Sri Lankan species noted above may exhibit somewhat similar behavior.

Order OLIGOCHAETA

Family MEGASCOLECIDAE

Perionyx sp.

FIGURES 67, 68

A number of internodes contained one to a dozen *Perionyx* sp. The worms formed a tight cluster at the upper end of the internode opposite the entrance. During an early morning rain we observed the worms crawling on top of leaves and branches. They exhibited a leech-like motion, with the anterior part of the body



FIGURES 65, 66.—*Haplochernes warburgi* (Tullgren): 65, dorsal aspect; 66, claw-like pedipalp, lateral view.

raised and waving around as if searching, and the posterior end remaining attached. The body is concave ventrally, more deeply so on the posterior one-third (Figure 67). This section probably functions as a suction cup while the anterior part (Figure 68) is probing the surroundings. The worms remained in the internodes during diurnally sunny periods.

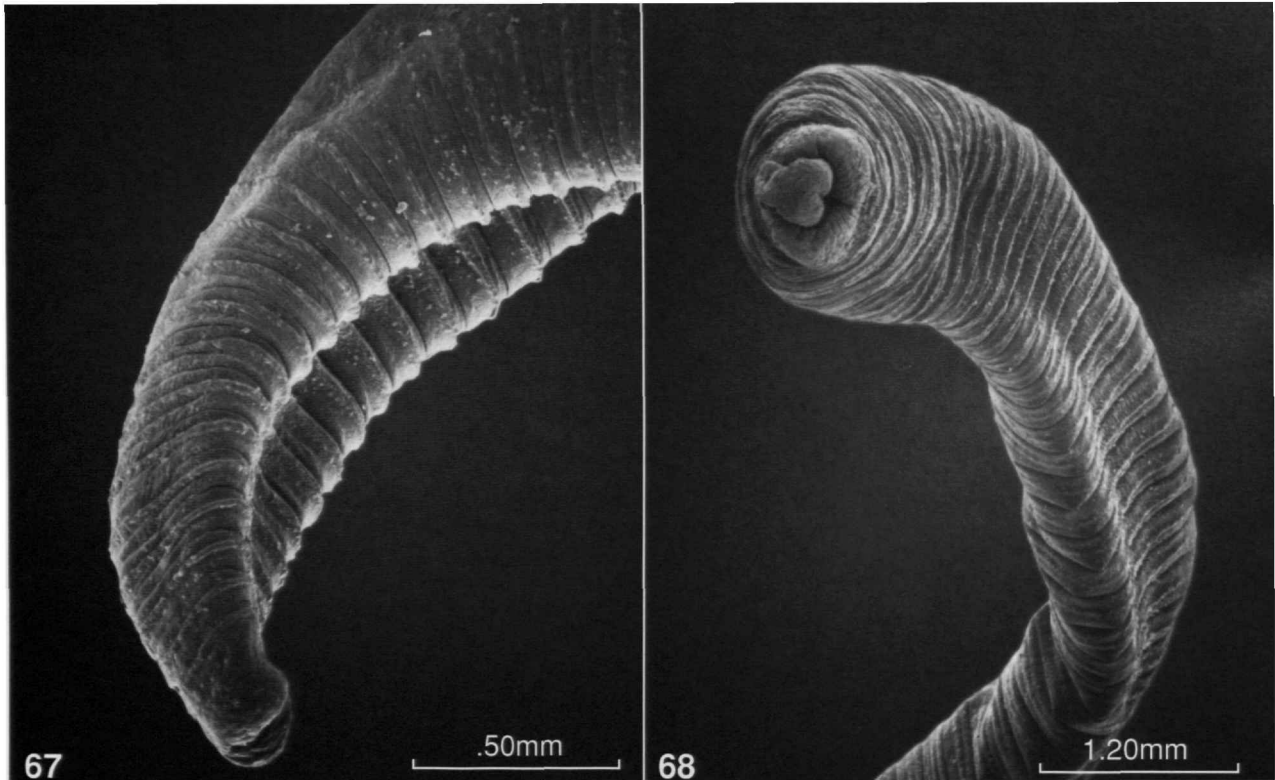
All worms that we collected were immatures. The late P.B. Karunaratne and F. Naggs, The Natural History Museum, London, collected adult worms at Ratnapura on 30 April 1996. They observed several specimens mating on stems and foliage of *Humboldtia laurifolia* and collected two pairs in copula; they did not find any worms on the ground.

Conclusion

Humboldtia laurifolia, by virtue of its naturally hollow, individual internodes, each with a self-opening entrance hole, provides available domiciles for a number of organisms able to pass through or enlarge the entrance. In addition to the domiciles, the tree possesses a number of extrafloral nectaries situated in the immediate vicinity of the hollow internodes. This collection of potential domiciles and adjacent food supplies existing on a common, gregarious, tropical tree within species-rich, humid, evergreen ecosystems represents a magnet for a myriad of organisms.

The self-opening stem entrance hole with stem occupation by ants is not unique to *H. laurifolia*, as it has been reported from other unrelated plant taxa: *Hydnophytum* and *Myrmecodia* (Rubiaceae) (Huxley, 1978; Rickson, 1979); *Neonauclea* spp. (Rubiaceae) (Maschwitz and Fiala, 1995); *Clerodendrum fistulosum* (Verbenaceae) (Maschwitz, Fiala, and Linsenmair, 1994); and *Ficus obscura* var. *borneensis* (Moraceae) (Maschwitz et al., 1994). None of these plants has been surveyed for domicile residents to the extent of the present study, but Huxley (1978) listed "dipteran larvae" and "brenthid beetles" as being found within *Hydnophytum* and *Myrmecodia* plants at Hombrom Bluff, Papua New Guinea. No doubt these other plants would reveal a rich assortment of inhabitants if surveyed in depth.

Ants are the dominant occupants of *H. laurifolia* internodes, and the abundance of Formicidae and their ability to find resources leads to their occupation of most available internodes of this tree species. In our study, the ant *Technomyrmex albipes* dominates trees in both pristine and lightly disturbed habitats within Sinharaja Forest Reserve and Belihul Oya, but it is only one of 11 ant species in residence in the highly disturbed Gilimale area. *Technomyrmex albipes* can occupy all internodes in tree populations comprising hundreds of individuals and thousands of individual domiciles. We see *H. laurifolia* as being a historically natural colony location for this ubiquitous ant species.



FIGURES 67, 68.—*Perionyx* species: 67, posterior segments of venter, oblique ventral view (note strong, narrow concavity of this region enabling worm to cling tightly to stem and edge of leaf); 68, anterior section of venter (note lack of concavity on segments immediately behind head and much slighter concavity of following segments).

In reviewing the social biology of ants, Bourke and Franks (1995:193) regarded *T. albipes* as having an “unusual social system” more like termites than ants. This species, in addition to the usual winged males and females that engage in nuptial flights, produces large numbers of wingless sexuals that mate within the colony; the females subsequently establish numerous nearby colony extensions without utilizing a dangerous flight phase. This concession to strong inbreeding as part of rapid colony extension and size (1–3 million individuals) is suggested to have evolved as an adaptation to life within a bamboo grove with its innumerable hollow stem internodes (Yamauchi et al., 1991; Tsuji and Yamauchi, 1994). The similarity in number of potential colony sites between a bamboo grove and a population of *H. laurifolia*, with its numerous hollow internodes and predictable burst of yearly domicile formation, is striking. This life cycle also fits the observation that a single colony of *T. albipes* may occupy a complete building foundation and walls and may overwhelm discovered food sources, thereby excluding most other ant species.

Where different ant species occupy neighboring trees, or even adjacent internodes along a single branch, the closely juxtaposed mix of species is an example of spatial tolerance not

often reported with ants. The ant literature is rich in examples of colony or nest dispersion based on interspecific negative reaction. However, here we have numerous examples of complete nests (colonies) of *T. albipes*, *Crematogaster* sp., *Catantopus taprobanae*, or *Pheidole* sp. occupying internodes only centimeters apart along a single branch. We have no information on such interesting questions as to how the various taxa come to occupy their positions, spatially and temporally, along a branch system. These questions, however, are very approachable considering the thousands of new domiciles that are produced each year following a defined direction and with specific timing.

A self-opening, hollow structure would seem advantageous, given that ants could be expected to be the most consistent occupier of the system, and this insect group has a well-established reputation for providing guard systems against plant herbivory. Indeed, we always find that trees well occupied by ants have a consistently clean and healthy leaf system. Conversely, those trees lacking ants show elevated levels of herbivory. *Humboldtia laurifolia*, however, illustrates one drawback to such a “free-access” system in the number of ant predators and other visitors (e.g., *Platyseridion edax* and *Haplochernes war-*

burgi) that also gain access to the domicile system and then prey on mature ants as they explore open internodes or that exist as parasites by consuming colony larvae (*Microdon*). The numerous ant remains found within predator-occupied internodes attest to intruder success.

Although we obtained data on the identity of a diversity of invertebrates occupying *H. laurifolia* internodes, untimely rains prevented direct observation of nesting behavior. We feel certain that additional occupants of the internodes still await discovery, and that complex behaviors between the inhabitants are yet to be recorded. For example, although we found several species of the chalcidoid *Perilampus* (Pteromalidae) to be parasitic on *Crossocerus mukalanae*, we did not find members of other chalcidoid families that are common parasites of bees and wasps, such as *Leucospis* Fabricius (Leucospidae), or of ants, such as *Stilbula* Spinola (Eucharitidae).

We also are convinced that some occupants are so coadapted to life in *Humboldtia* internodes that they do not utilize other plants as domiciles. Examples of such probable coadaptees are three species of small wasps and bees, *Krombeinictus nordenae*, *Crossocerus mukalanae*, and an undescribed species of

Braunsapis. Neither *K. nordenae* nor the species of *Braunsapis* was collected during 12 periods of field work in the Sri Lankan rainforests by KVK, who did not investigate *H. laurifolia* during those visits but searched for wasps and bees nesting in tunnels in wood. Only two females of *C. mukalanae* were known previously, both were collected in the rainforest in two localities where *H. laurifolia* is common. It also is likely that a dipteran ant predator, the larva of *Platyceridion edax*, and an arboreal annelid *Perionyx* sp., are to be found only in association with *H. laurifolia*.

Finally, we must emphasize the desirability of a thorough survey of the invertebrate fauna associated with internodes of the two endemic Indian myrmecophytes *Humboldtia brunonis* and *H. decurrens*. If, as we suggest above, some of the Ceylonese invertebrates are coadapted to *H. laurifolia* and domicile only in that plant, then a similarly interesting evolutionary situation could exist in India between the two species of Indian *Humboldtia* and congeners of these Ceylonese invertebrates. Habitat destruction throughout this region of Asia dictates the urgency of further study of *Humboldtia* and its associated invertebrates.

Appendix

Description of the Larva of *Krombeinictus nordenae* Leclercq

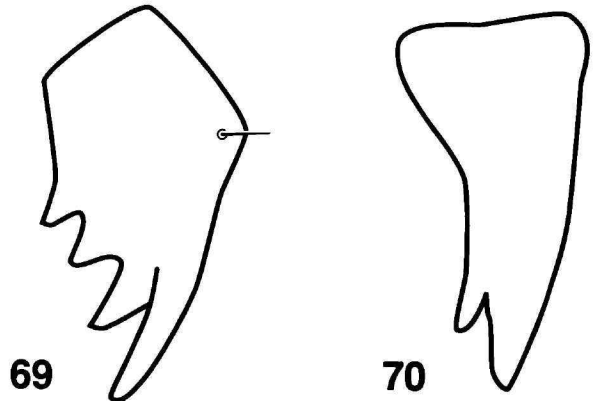
Howard E. Evans

Because of the unusual biological features of *Krombeinictus nordenae*, it seemed desirable to ask whether the larvae differ from those of other Crabroninae, perhaps having mandibular cusps, concavities, or small teeth similar to those of bee larvae.

DESCRIPTION.—Based on three postdefecated larvae from Sri Lanka: Rat[napura] Dist[RICT], Induruwa Jungle, Gilimale, 18–20 July and 2–3 August 1993. Collectors: K.V. Krombein, P.B. Karunaratne, A.W. Norden, and B.B. Norden.

More slender and cylindrical than in groundnesting Crabroninae, with length 6.5 mm; maximum width (midabdominal segments) 1.4 mm. Pleural lobes prominent; anus located ventrally on a rounded terminal segment. Body setae or spinules not detected. Head about 0.6 mm wide, less than one-half maximum body width; head capsule (exclusive of labrum and other mouthparts) 1.14 times as wide as high. Parietal bands and antennal papilla absent. Sides and top of head with several strong setae; clypeus with six such setae in transverse row. Labrum truncate, about twice as wide as high, bearing 14 setae; apical margin bristly but without sensory cones; epipharynx covered with small spinules. Mandibles lightly pigmented, 0.32 mm long and 0.16 mm wide at base, bearing a single basal seta and four strong, sharp teeth along inner margin (Figure 69), the apical two slightly offset, so that mandibles appear bifid in full lateral view (Figure 70). Maxillae prominent, rounded apically, with several lateral setae; lacinial area spinulose; palpi about three times as long as their basal width, galeae similar but smaller in both dimensions. Labium with two patches of strong spinules. Spinnerets long and slender, extending well beyond the palpi, which approximate the galeae in size.

Howard E. Evans, Professor Emeritus, Colorado State University, Department of Entomology, Fort Collins, Colorado 80523.



FIGURES 69, 70.—*Krombeinictus nordenae* Leclercq, mandible of postdefecated larva: 69, frontal view; 70, full lateral view.

DISCUSSION.—The larvae are typical of those of Crabroninae, as defined by Evans (1959); in his key to genera they will run to *Crossocerus*. Indeed, the description of the larva of *C. fergusonii* Pate provided by Evans (1957) will do almost equally well for *Krombeinictus nordenae* except that I was unable to find integumental setae or spinules on the latter. Clearly larval characters are very conservative despite differences in diet. Larvae of *Crabro* and *Rhopalum* (= *Euplilis*) are also doubtfully separable from those of *Crossocerus*. It is perhaps noteworthy that species of *Crossocerus* and *Rhopalum*, although predators, utilize insects of several different orders. Crabronine larval mouthparts are evidently “multipurpose.” Generalizations concerning generic differences are difficult because larvae of relatively few species have been described, and many of these descriptions are incomplete.

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