

## Ampulex Compressa (Fabr.), A Cockroach-Hunting Wasp Introduced from New Caledonia Into Hawaii

BY FRANCIS X. WILLIAMS  
Experiment Station, H.S.P.A.

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In May 1940 the Experiment Station of the Hawaiian Sugar Planters' Association sent the writer to New Caledonia to make a survey of the economic insects—with special reference to those affecting sugar cane—of that large island. With the knowledge thus gained, Hawaii would be forewarned and thus forearmed against entry into the territory—particularly by the swift clipper ships—of injurious forms. Pan American Airways' clippers to and from New Zealand stop at New Caledonia and thus there is danger of bringing in new harmful insects.

In going over a catalogue of insects known to occur in New Caledonia and kindly furnished the Experiment Station by Mr. E. C. Zimmerman, entomologist of the Bernice P. Bishop Museum, Honolulu, the wasp *Ampulex compressa* (Fabricius) is listed by Dr. R. E. Turner <sup>11\*</sup>, as taken in Noumea, New Caledonia, in January and February. Here was a fine opportunity to import this beneficial insect into the Hawaiian Islands.

*Ampulex compressa* is a large, beautiful wasp with a shining, blue-green body and with the femora or thighs of the second and third pairs of legs red. The female is about 22 millimeters or between  $\frac{3}{4}$  of an inch and an inch in length. The male averages smaller and lacks the sting. It is perhaps the most widely distributed species of the large and chiefly tropical genus *Ampulex*, Bingham <sup>1</sup> giving its range as: "Throughout India, Burma, Ceylon"—where it is endemic—"and extending into Africa and to China." It is also known to inhabit St. Helena and some of the islands of the Indian Ocean, as well as New Caledonia in the southwest Pacific.

The known literature referring to the habits of *Ampulex compressa* dates from the year 1742, when Reamur <sup>6</sup> relates the observation of a certain M. Cossigni on this wasp, the "guêpe ichneumon," as noted in Mauritius (Ile de France). H. Lucas <sup>3</sup> in the year 1879 refers to the cocoon of *Ampulex* from New Caledonia, as encased in the remains of *Blatta americana*. In Burma, Bingham <sup>1</sup> states that this wasp frequently enters houses in search of cockroaches. Maxwell-Lefroy <sup>4</sup> has observed *Ampulex compressa*

\* Numbers refer to the list of papers in the Literature.

in Pusa, India, where it is purely arboreal in habit, its chief haunts being the trunks of old "Peepuls" (*Ficus religiosa*), a common banyan or strangling fig, and fig trees which possess numerous holes and chinks—such places being likely to harbor cockroaches. This environment rather than the establishments of man is no doubt its original habitat—insects considerably antedating man—and the adaptable *Ampulex compressa*, where many of its relatives are strictly woodland species, has followed its cockroach prey in and about buildings, walls, etc. And this semi-domiciliary habit may largely account for the wide geographical range of the wasp, and at any rate, adds to its value as an introduction.

Other species of *Ampulex* have much the same habits as *Ampulex compressa*. Sonnerat<sup>10</sup> writes of the habits of *A. sonnerati* Kohl in the suburbs of Manila, Philippine Islands. This insect, "la mouche bleue" stings cockroaches to partial paralysis and stores them in crevices which it stoppers with debris. In West Africa, *Ampulex compressiventris* Guer. (= *A. siberica* Sauss.) enters houses in search of its prey (Perkins, fide Sharp<sup>8</sup>). Hingston<sup>2</sup> gives an excellent account of *Ampulex assimilis* Kohl in the groves of date palms about Bagdad. Its particular cockroach prey is *Shelfordia tartara* Sauss. *Ampulex amoena* Strand (= *A. novarvae* Sauss.) in Formosa stores immature individuals of the two common large cockroaches, *Periplaneta americana* (Linn.) and *P. australasiae* (Fab.) (Sonan<sup>9</sup>). *Ampulex fasciatus* Jurine, a small blackish European species preys upon *Ectobia livida* (Fabr.), a suitably small cockroach<sup>5</sup>. *Ampulex caniculatus* Say, scarcely half an inch long and related to *A. fasciatus* was studied at some length by the writer<sup>12</sup> while stationed one summer at Webster Groves, Missouri. The wasp was successfully bred in a quart jar. Its prey was *Parcoblatta virginica* (Brunner), a common endemic wood roach. The experience gained in rearing this temperate zone *Ampulex* served the writer in good stead while working with *Ampulex compressa*, the well known "cantharide"<sup>†</sup> of New Caledonia.

A wasp so well known as *Ampulex compressa* could not fail to draw recognition from entomologists as a beneficial insect worthy of introduction into other tropical countries, and I have in mind the report of Mr. H. W. Simmonds<sup>7</sup>. When Mr. Simmonds was in Mauritius in 1939 working on enemies of the rhinoceros beetle (*Oryctes rhinoceros* L.) for importation into Samoa, he observed *Ampulex compressa* there and advised its introduction into Fiji. Unfortunately the advent of the cold season prevented its introduction during his stay in Mauritius. He did observe, however, that, based on a single pair of *Ampulex*, the female wasp was very long

<sup>†</sup> This is a misnomer; the name cantharide properly applies to one or more species of "blister beetles" (Cantharidae) found elsewhere. But both wasp and beetle have in common a metallic blue or green brilliance.

lived, surviving a confinement of 80 days. The male lived but a few days.

When Mrs. Williams and I arrived at Noumea, New Caledonia, on July 3, 1940, it was the cool season of the year, and while insects in general were to be found in plenty, certain species including the large black wasp, *Chlorion fumipennis* (Smith), the mud wasps *Sceliphron hemipterum* (Fabr.), *Rygchium haemorrhoidale*, var. *alecto* Lep., and *Odynerus caledonicus* Sauss., some butterflies and Orthoptera and many beetles of large size and conspicuous habits, were nearly or quite absent. And the "cantharide" or *Ampulex compressa* was nowhere to be found. But it was well known to the inhabitants and appreciated by them as a beautiful and useful insect, and later, Mrs. Williams, who took great interest in this scintillating blue-green insect very aptly named it the "jewel wasp"<sup>13</sup>. On the other hand, large *Periplaneta* cockroaches, the prey of jewel wasp, were abundant.

Slowly, it seemed, the season became more favorable for insect life, and as ever, a sharp lookout was kept for the desired wasp. Kitchen surroundings and gardens in and about Noumea were searched from time to time without success. But finally, on September 29, two female *Ampulex* were observed in the garden of the Hotel du Pacifique in Noumea. I did not succeed in capturing either. But on October 11, immediately following our return from a 10-day trip to the east coast of the island, a third specimen, also a female, was seen on the garden wall of the hotel. By a rather ill-aimed vigorous stroke of the net the prize was captured but in so doing one of its mandibles was broken off, thus rendering the wasp quite useless for dealing with her cockroach prey. On October 15, while we were having lunch in the hotel, a fine large female *Ampulex* appeared at a dining room window. She was hastily grabbed up in a handkerchief and safely placed in a jar in our laboratory.

Up to November 12, when we left New Caledonia by Pan American Airways plane for Honolulu via Canton Island, I was able to secure but 2 additional female *Ampulex*. These, as well as several males, were caught on October 17 and 21, on the trunk of a coconut palm growing in Mr. Lee Johnson's garden in Noumea and where through his kindness I made many collections and observations on insects of economic importance. To facilitate the capture of these wasps, honey was smeared on the palm trunk and this attracted one female and several males. The latter appeared the more frequent and could be seen running up the trunks of palms. It was evident, however, that these insects were only beginning to issue from their cocoons, but everyone said that later on, in the summertime, the "cantharide" would be abundant.

The three female wasps, of October 15, 17 and 21 respectively, were placed in separate glass gallon jars. *Ampulex* are quarrelsome creatures. The jars were laid on their sides in the laboratory table by a window and a piece of rough paper spread within on their lower sides. After some experimenting, a tube of corrugated cardboard—the corrugations on the outer periphery—about  $3\frac{3}{4}$  inches long by  $\frac{3}{4}$  inch internal diameter and stoppered at one end, was found suitable as a nest hole for *Ampulex*. Small debris, such as cut up cardboard, and portions of twigs, were strewn on the paper-covered floor of the jar. This debris was to be used by the wasp in stopping up the stored tube. The wasps were fed with honey.

Unlike the small rather unafraid *Ampulex* (*Rhinopsis*) *caniculatus* with which I experimented in Missouri, the more active *Ampulex compressa* was easily frightened and addicted to flying and of thus striking her head against the glass prison. Nevertheless, these large wasps, becoming somewhat tamer, survived their imprisonment in the one—and later the several—gallon jars, normally for several months.

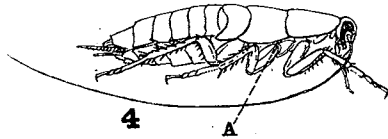
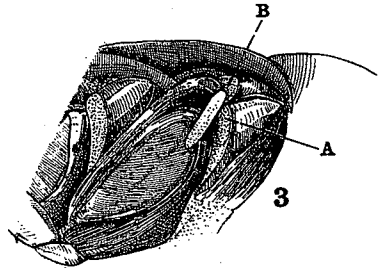
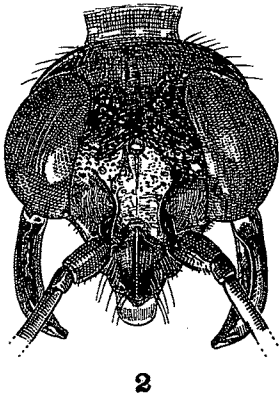
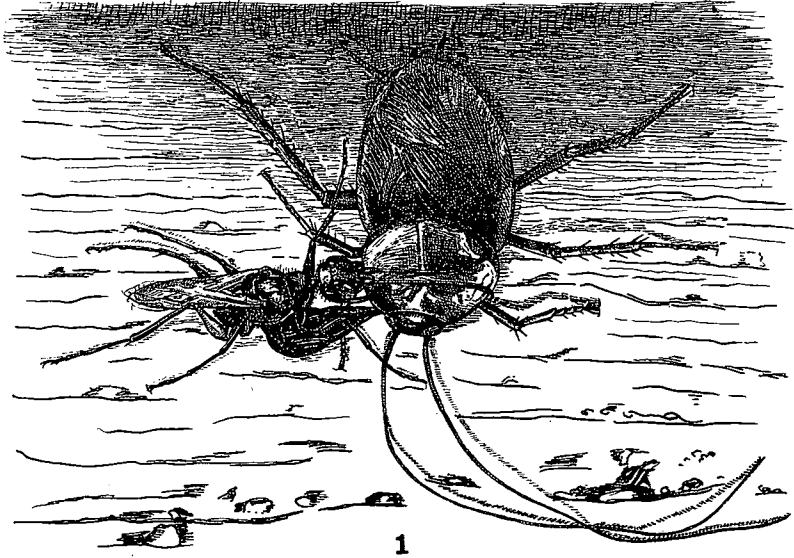
As prey for the wasp a supply of *Periplaneta americana* (Linn.), the ordinary large house (and ship) cockroach of all tropical countries, was soon assured. A goodly number was collected in the tiny lazaret of "Les Trois Amis", a powered ketch moored at the waterfront. Larger quantities were later secured from a hotel kitchen.

At the rate of one, or occasionally two, partly grown to mature cockroaches were offered daily to each wasp. As a rule, *Ampulex* attacks the cockroach soon after the latter's introduction into the jar. The wasp then becoming very alert and with antennae directed towards her intended victim approaches it from the side in front and with a short lightning leap, seizes the edge of the pronotal plate with her beaklike clypeus and labrum above and the curved chisel-like mandibles pressing into the membrane beneath. Immediately directing her flexible abdomen forward and underneath the cockroach's thorax, she extends the point of her abdomen in search of a vital place in which to plunge her sting (Fig. 1). The cockroach now thoroughly frightened, struggles furiously, twisting, straining

## AMPULEX COMPRESSA

### Plate V

1. The wasp stinging the cockroach (*Periplaneta americana*) in the throat. Enlarged.
2. Head of wasp to show the beak formed by the clypeus and labrum, and the chisel-edged mandibles.
3. *Periplaneta americana*, mesopleural region to show coxa bearing the wasp egg at basal end. Dotted areas A and B show membranes through which the wasp grub bites its way into the interior of the cockroach. The membrane at A seems the more frequently used of the two.
4. *Periplaneta americana*, from side, to show wasp's egg at A.

*Ampulex compressa.*

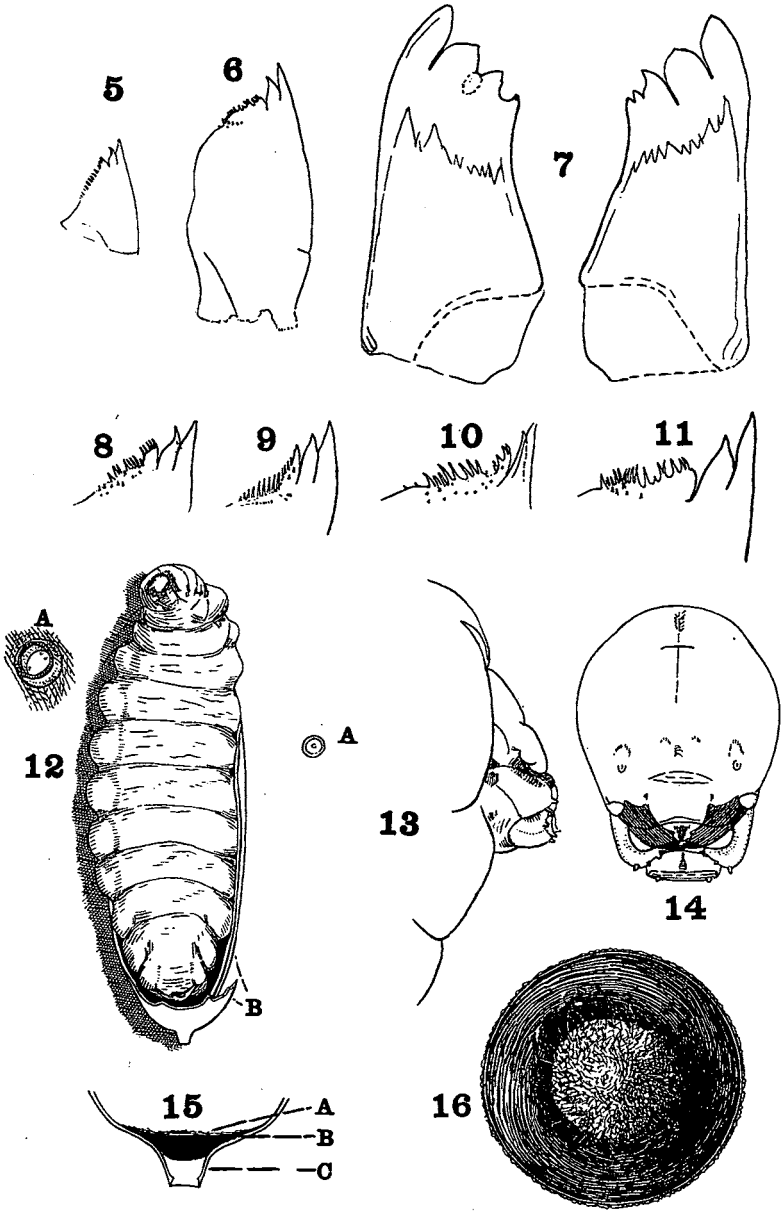
and describing short jerky circles, parrying with its legs, and striving particularly to tuck in its chin so that the tenaciously clinging wasp will not sting its throat. This struggle though often very rough on the aggressor, so often much the smaller of the two, is usually of no avail to the cockroach. It receives a sting in the thorax, its struggles become more feeble, and as *Ampulex* thrusts her sting deep into its throat the head is thereby forced outwards on a membranous neck. After a few moments of injecting the poison the wasp releases her hold and now backs off to view her work alertly. She may even grasp the cockroach and make pretense at dragging it away, but usually leaves it in place—a wretched spectacle, head down and helpless though not immobile and later regaining considerable activity.

The wasp now cleanses herself after the battle with the malodorous giant, and we note that the latter also grooms itself, passing its antennae through the mouth parts and reaching down to lick its legs.

Nesting operations proceed slowly. *Ampulex* discovers the cardboard tube and she enters and explores it. Then after a while she approaches her somewhat dazed victim and, grasping one of its antennae close to the base, in the tip of her mandibles, draws it through them to perhaps a little less than its middle length when, with a marked effort, characterized by a downbent head and often a quivering body, she severs or attempts to sever it. The other antenna is likewise dealt with. Several attempts may be necessary for this amputation. Frequently the wasp draws the cockroach's antennae through her jaws for their entire length. Where many cockroaches have been operated on by the wasp, the portions of their antennae conspicuously strew the paper-laid floor. More delay follows. Finally, after an hour or so, *Ampulex*, having assured her-

#### Plate VI

5. Mandible, 1st stage larva.
6. Mandible, 4th stage larva.
7. Mandible, pair, 5th or last stage, from larva in cocoon. Figs. 5, 6 and 7 all to same scale.
- 8-11. Mandibles—to show their toothed extremity. 1st to 4th stage. All are to same scale, but the magnification is higher than Figs. 5, 6 and 7. The 3rd stage (Fig. 10) shows mandible with the large teeth somewhat out of plane.
12. Full-fed resting larva, dissected from cocoon cask. A, spiracle detached and greatly enlarged. B, remnant of cask.
13. Full-fed larva, head and part of prothorax, side view. A, first spiracle.
14. Full-fed larva, head, front view.
15. Cocoon, inner cask divested of silken envelope; anterior end, from side, to show, edge on; A, the interior silken mat; B, the hard leathery layer; C, the nipple-like tube to exterior.
16. Same as 15, looking towards anterior end, from within. The central silken mat is conspicuous.



*Ampulex compressa*

self of the suitability of the corrugated tube as a storage receptacle for her prey, approaches the latter, and, grasping it by the very sensitive base of one antenna, and, in several starts and stops, at last backs into the tube dragging the cockroach in after her.

She remains in the tube for a short time to glue a delicate white egg about two millimeters in length along one of the cockroach's mid-coxal plates, as illustrated. In this position the egg can hardly be dislodged by any leg movement. The thicker extremity of the egg touches, or at least extends very near one of the two delicate membranous areas that help hinge the leg to the thorax (Fig. 3, A and B).

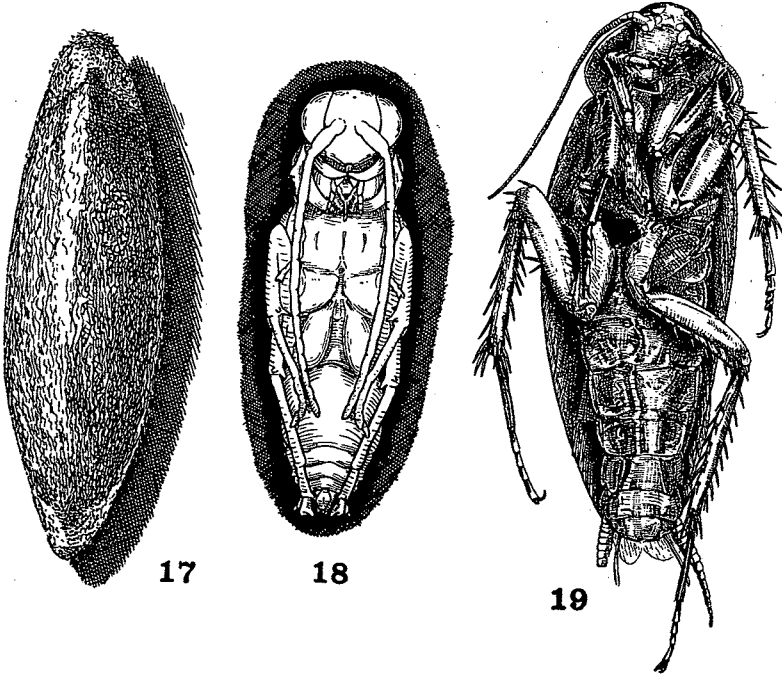
Issuing alertly from her stored tube, *Ampulex* soon avails herself of the small bits of debris lying about. She grasps a piece in her jaws and walking into the tube lodges it against or near the imprisoned cockroach. This performance is briskly repeated again and again. *Ampulex* often emits a little squeak as she securely packs in the debris that quickly fills up the tube and thereby imprisons her fairly active victim. Rarely such a victim succeeds in breaking through this barrier, although if properly parasitized, the young wasp may successfully develop on its host at large. If for some reason the wasp's egg fails to hatch, or the grub dies very young, the cockroach may survive for weeks.

There are variations in all these nesting activities, although their sequence remains the same. Sometimes the wasp attacks the cockroach when the latter is quiet; or she may, by digs of her mandibles first spur it into activity. Very frequently she pursues her intended victim, even flying after it. The fact that some sort of pause seems necessary to allow the wasp to get in the proper sidewise position to seize the cockroach, gives the latter some advantage in its flight. Sometimes *Ampulex* may grasp her prey too far forward, or especially too far to the rear to effectively use her sting; in such cases the wasp may release her hold for a better grip. As a rule the wasp will not attack a cockroach that is struggling on its back. But on one occasion a very old female (127 days) attacked one such—a not too vigorous cockroach that she had vainly and wearily pursued. Here she gripped her prey somewhere at the end of the clypeus and then length to length of the prostrate insect set about stinging it.

#### Plate VII

17. Wasp cocoon. Through the outer covering of silk may be faintly seen the nipple-like ends of the interior cask. Length 26 mm. Large specimen.
18. Wasp pupa; freshly formed. Length 16.2 mm.
19. The dead and dried cockroach, *Periplaneta americana*, that contains a hatched *Ampulex* cocoon. Perforation indicates where the wasp has issued. Length 37 mm.
20. Female wasp, in a characteristic pose. From photograph from life by W. Twigg-Smith.

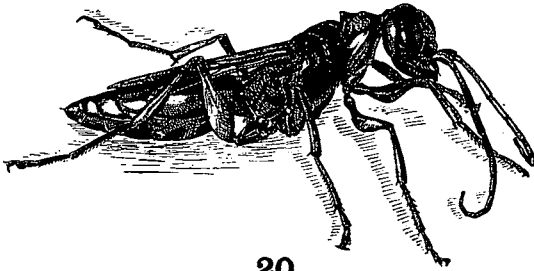




17

18

19



20

*Ampulex compressa*

Soon however *Ampulex* shifted her grip to the middle of the front margin of the pronotum directly behind the head and effectively stung her prey. An old or incautious wasp attacking a vigorous and aggressive roach may be badly bitten in the abdomen, the roach's jaws even breaking a tough sclerite so that the wasp succumbs in a few days. Thus, it was advisable to give the smaller *Ampulex* females a correspondingly small cockroach. In such a case, *Periplaneta australasiae* (Fabr.) was most suitable. Another cockroach readily accepted by *Ampulex* is the large wingless or rather strikingly marked *Neostylopyga rhombifolia* (Stoll). The very common scuttling gray *Nauphoeta cinerea* (Oliv.) drew little or no notice. On one occasion *Ampulex* effectively stung *Diploptera dytiscoides* (Serv.), the beetle-roach, but there the episode ended. Further experiments here would be of interest.

In the attack upon her ill-smelling prey, *Ampulex* avoids touching it more than appears necessary. Thus, one or more of her legs are elevated in air (Fig. 1) while the remainder are employed in bracing herself against the cockroach's struggles. Sometimes *Ampulex* attempts to grasp a lively unstung roach by the base of the antenna. And rarely we find a carton devoid of prey, but nevertheless well stoppered by the wasp! Occasionally we find "wasters" among these wasps. Such a one may sting a cockroach and trim its antennae but proceed no further. Perhaps the wasp's body contained no egg ready for deposition.

The egg of the jewel wasp hatches in about three days, the larva breaking through the blunter end. Excepting for its larger size and a somewhat segmented body, it does not at first differ much from the egg. The larva feeds at or near the spot where it has hatched. It thus lives externally on the coxal plate of its victim for four or five days and during this period overgrows the collapsed egg shell and casts its skin four times, these thin semi-transparent skin membranes accumulating as a flattened pad beneath its body. Thus, during its life as a grub or larva it has used five pairs of mandibles, as illustrated (Figs. 5-11). The first four of these are delicately spine-tipped and are probably employed in puncturing the host's body. The last pair of jaws are large and stout-toothed and it is with these that the larva immediately bites through the cockroach's body to enter it and feed within. This entrance is effected at the junction of the mid-coxa and body; more commonly the upper or mesepimeral, rather than the lower or mesepisternal membrane being chosen (Fig. 3). The larva now feeds ravenously within its weakening host, hollowing out its body even to the base of the legs. The cockroach soon perishes—having provided the wasp during its life as a grub with a continuous supply of fresh meat. The larva, now full fed, white and apparently hairless, commences the formation of a cocoon within the stiffening body of its host. A more loosely woven

outermost envelope of golden brown silk is formed, then follows a fine thin layer of silk which closely envelops the smooth deep brown rather brittle cask that is drawn out funnel or nipple-like at either end. Tough brown leather-like material plugs up the base of each funnel, and this material is superposed by a mat of silk (Figs. 15 and 16). The entire cask is smooth, strong, tight and varnished within and seems impervious to air. The larva may shed its skin to become a pupa within perhaps two weeks, in the warm summer time, or may rest for weeks or even months without pupating, in the cooler or drier season. Such a resting larval stage is common to most or at least to a great many stinging wasps. The pupa is delicate and whitish with a down-bent head. I do not believe that this stage endures more than two or three weeks. Laboratory records here show a minimum of egg plus larva plus cocoon stage of 34 days and a maximum of 140 days. In the laboratory it was found that the insect often died in the resting larval and in the pupal stages.

The pupa gradually acquires the coloration of the adult insect that in due time frees itself of the delicate envelope. It usually issues from the cocoon in the morning when vigorous squeaky buzzes within the dried cockroach announces the wasp's readiness to gain the outer world. Soon one jaw and then the pair may be seen biting through the tough skin and then a scintillating *Ampulex* wasp works its way out bit by bit. It has bitten off a rough cap from the slightly blunter end of the cocoon, which more frequently lies toward the anterior end of the cockroach, and then chewed its way through the latter (Fig. 19).

The wasps mated readily in large jars. Upon discovering an unmated female, the male becoming quite excited faces her, his antennae brought close together forward, his body rapidly shaking from side to side. The female is often annoyed at his attentions and then chases him away. At an opportune moment he succeeds in mating, the process lasting perhaps a minute. But one mating seems necessary; a female once fertilized may successfully parasitize dozens of cockroaches.

*Ampulex compressa* in its transference from the South Pacific to the Hawaiian Islands north of the equator, immediately conformed to the changed seasons. It is thus most active in all its stages here during our summer time although the wasps did parasitize cockroaches throughout the year in an outdoor laboratory. The warm moist season in New Caledonia is about from November to April, at which time the wasp is active there.

These wasps are long-lived. Several males lived to be two months old and one reached 85 days. It is probable that their life may be a good deal in excess of this figure. Cool weather, rendering the wasps somewhat inactive, seems to increase their longevity.

The following table shows the longevity of females and the number of cockroaches stored by some of these:

| Captured in<br>New Caledonia | Died              | Days<br>Longevity | No. Cockroaches<br>Stored |
|------------------------------|-------------------|-------------------|---------------------------|
| October 15, 1940             | November 4, 1940  | 20                | Not recorded              |
| " 17, "                      | December 30, 1940 | 74                | About 65                  |
| " 31, "                      | February 10, 1941 | 102               | About 78                  |
| Hatched in Honolulu          |                   |                   |                           |
| January 6, 1941              | May 11, 1941      | 125               | 85                        |
| " 23, "                      | " 12, "           | 109               | 88                        |
| May 12, "                    | June 12, "        | 31                | 20                        |
| " 15, "                      | " 20, "           | 36                | 25                        |
| " 15, "                      | Sept. 11, "       | 119               | 65                        |
| " 25, "                      | " 9, "            | 107               | 55 <sup>a</sup>           |
| June 9, "                    | October 10, "     | 123               | 49 <sup>a</sup>           |
| " 20, "                      | " 9, "            | 111               | 41 <sup>a</sup>           |
| Sept. 15, "                  | December 16, "    | 92                | 33 <sup>a</sup>           |
| October 6, "                 | February 12, 1942 | 129               | 46 <sup>a</sup>           |
| " 6, "                       | " 17, "           | 134               | 43 <sup>a</sup>           |
| " 13, "                      | March 12, "       | 150               | 39 <sup>a</sup>           |
| " 24, "                      | April 1, "        | 159               | 57 <sup>a</sup>           |

<sup>a</sup> These wasps were not supplied with a cockroach per day, throughout. Towards the end of their life wasps were often too feeble, stiff and short-winded to successfully cope with a cockroach.

*Ampulex compressa* was not reared in large numbers, from two to six females each in her large jar being used at one time. This breeding work is now entering its second year. Up to March 31, 1942, two hundred and two mated females and a somewhat smaller number of males have been liberated. Most of these liberations were made in several parts of Honolulu. Two small consignments were released on the Island of Maui and one on Kauai. Already the wasp seems firmly established here, for it has been seen in one locality about the buildings of a chicken farm in Honolulu, for the better part of a year, and is being reported from different parts of the city. In another place where it has been liberated, one to several males may be seen, months afterwards, running up the trunks of certain trees and then taking off for an inspection elsewhere.

The jewel wasp puts up a wonderful exhibition of boldness, skill and strength in the attack on her often huge prey, once to the effect that a French scientist upon witnessing such a battle in our hotel room laboratory in New Caledonia, much impressed, exclaimed: "C'est formidable!" Many have witnessed the wasp's bold exploits in New Caledonia. On our Pan American Airways voyage from Noumea to Honolulu, we stopped for a day and a half at the equatorial atoll of Canton. Here the two *Ampulex* jars were brought out of their travel bags, a large cockroach was given each of the wasps, and airplane passengers, the airplane and the ground crews were treated to an exciting rough and tumble performance. Here

in Honolulu, a large number of the staff of the Hawaiian Sugar Planters' Experiment Station and others have viewed the wasps at work in their outdoor laboratory. In busy downtown Honolulu two of our *Ampulex* wasps formed part of a New Caledonian Exhibit, prepared by Mrs. Williams, in the show window of Pan-American Airways. This exhibition lasted for nearly two weeks and attracted many people. It was found that in addition to working in the day time the wasps would carry on during the night as well in their warm brilliantly illuminated quarters.

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