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OBSERVATIONS ON THE LIFE HISTORY OF TRICHODES  
ORNATUS (COLEOPTERA, CLERIDAE), A LARVAL  
PREDATOR IN THE NESTS OF BEES AND WASPS

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*Trichodes ornatus* Say is the commonest and most widely distributed representative of its genus in Western North America. It occurs in nearly every state west of the Rocky Mountains, as well as in British Columbia and Alberta, and ranges from sea level up to ten thousand feet elevation. However, in spite of these facts, little has been recorded of the biology of this (or any other) North American species except that the adults are pollen feeders and have been reared from the cells of bees and wasps. As yet, the present authors are not able to provide the complete biology of *T. ornatus*, but it is believed that at least a general outline of the life cycle has been obtained and a number of significant facts determined which had not been previously recorded for the genus.

HISTORICAL BACKGROUND

Our present knowledge of the habits of *Trichodes* has been largely obtained in Europe. It may be briefly summarized as follows:

Apparently *Trichodes apiarius* (Linn.), sometimes referred to as the hive beetle, was the first species of clerid recorded as living in association with bees. As early as 1737, Swammerdam figured the larva, pupa, and adult from a nest of the mason bee, *Megachile muraria* (Fab.). According to most general treatises on apiculture, the species is also supposed to live at the expense of the honeybee, *Apis mellifera* Linn. Mulsant (1864) credits Herbst (1792) and Sturm (1837) with being the first to express this opinion, while Duncan (1840) attributes the statement to Aristotle. The fact that Linnaeus named the species *apiarius* indicates that the belief was prevalent prior to Herbst and Sturm. In any event, although many entomological textbooks record *apiarius* from bee-hives, we have been unable to find any recent verification of this observation in the literature.

*Trichodes alvearius* (Fab.) was also reared at an early date from the nests of bees. This appears to be the species discussed by Reaumur in 1742, although various authors are in disagreement as to the identity of

the form with which he was concerned. Westwood (1839) and subsequent authors have recorded it from the nests of *Osmia* and *Megachile*, Friese (1923) has added *Xylocopa* and *Anthophora* as well as the wasp *Polistes gallicus* (Linn.), and Carpentier (1883) reared it from the cells of *Odynerus spinipes* (Linn.). In addition, Latreille (1804) has recorded it from *Vespa*, and Goreau (1866) from the hives of *Apis*. However, the most instructive account of the habits of this species is that of Maréchal (1933) who studied it as a predator in the cells of *Chelostoma maxillosum* (Linn.).

A third species which has long been known as a bee predator is *Trichodes octopunctatus* (Fab.). Lichtenstein (1877) reared it from the nest of *Megachile rufescens* (Pérez), and Maréchal (1933) from that of *M. pyrenaica* Lep. The latter author also believed that this was the species frequently referred to by Fabre in his classical studies of the biology of bees.

*Trichodes umbellatarum* Oliv. has been studied in some detail by Cros (1908 *et seq.*). He found it living at the expense of *Megachile muraria* (Fab.), *Anthocopa longispina* (Pérez), *Osmia* spp., *Anthophora talaris* Pérez, *A. albigena* Lep., and *Eumenes* sp.

*Trichodes leucopsideus* (Oliv.) has been recorded by Mayet (1894) from the burrows of *Ceratina*.

In addition to those species associated with bees, several *Trichodes* have been noted as predators of the egg pods of locusts. Kunckel d'Herculais (1890 *et seq.*) and subsequent authors have observed *T. amnios* (Fab.) destroying the eggs of the moroccan locust (*Dociostaurus maroccanus* Thunb.) and according to Jackson (1926) and Cros (1929) eggs of this same species are also preyed upon by *T. laminatus* Chev. and *T. x-litterata* Chev. Jazykov (1931), working in Turkestan, noted two additional species of *Trichodes*, one (?*T. turkestanicus* Kr.) in the egg pods of *Ramburiella turcomana* (Fischer) and *Dociostaurus kraussi* Ingenitskii the other (probably *T. spectabilis* Kr.) in those of *Dociostaurus maroccanus* Thunberg.

## DESCRIPTION

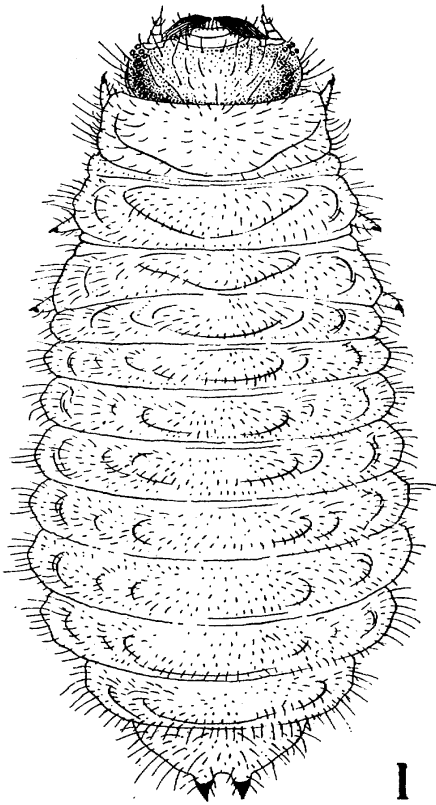
### ADULT

#### Figure 4

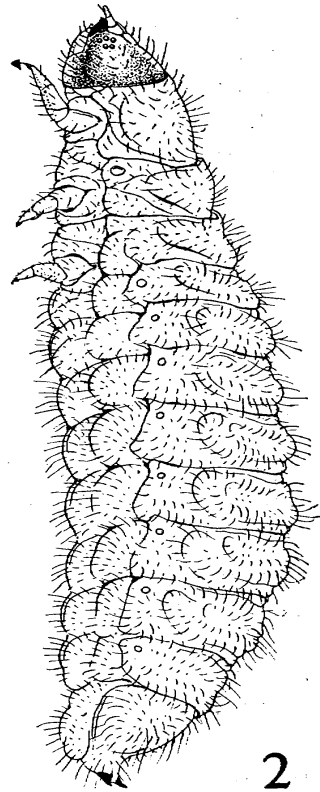
*Male*.—Form elongate, moderately slender, sides of elytra widest behind middle, color shining aeneous green, antennae, mouthparts, and anterior and intermediate tarsi pale brownish, elytra dark blue with yellow markings; pubescence long, erect ochraceous. Head large, as wide as or wider than pronotum; surface moderately coarsely but not closely punctate, the punctures larger on vertex; pubescence sparse, long, erect; eyes moderately prominent, anteriorly emarginate, finely faceted; antennae with club broadly triangular. Pronotum about as long as wide, broadly constricted at base, feebly so at apex; surface moderately coarsely, densely punctate, clothed with long, erect hairs; prosternum transversely rugulose; scutellum small, finely,

## EXPLANATION OF PLATE I

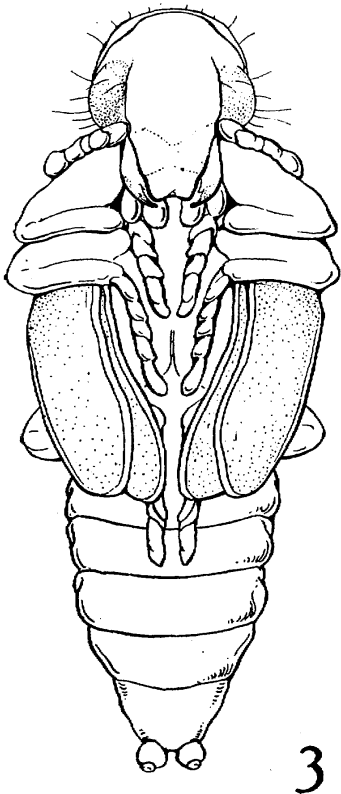
*Trichodes ornatus* Say. Figures 1-2. Fifth instar larva. 3. Pupa. 4. Adult.



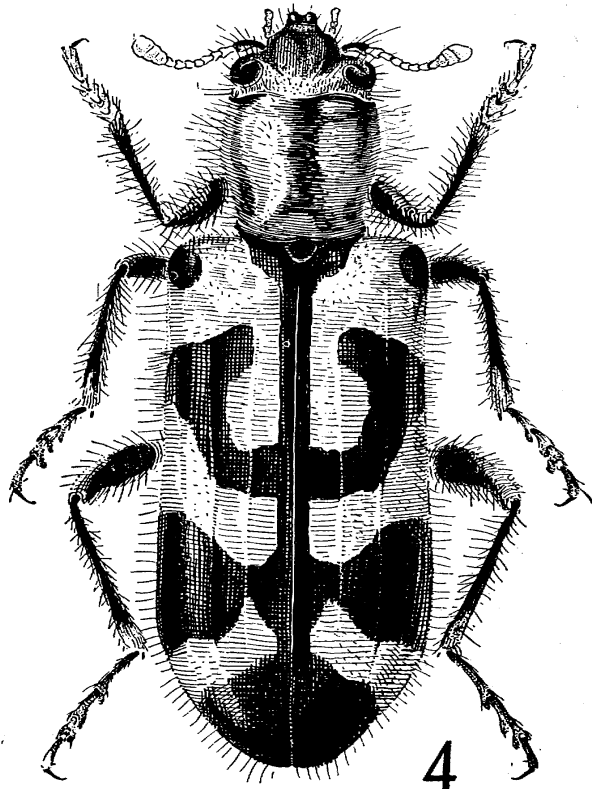
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closely punctate, shining. Elytra more than twice as long as basal width, widest behind middle; surface blue, shining, feebly but closely punctate, clothed with much shorter pubescence than pronotum; yellow pattern consisting of a broad basal band surrounding the humeral umbone and extending back along suture to basal two-fifths where it is dilated and knob-like; an oblique, sinuate median band extending backward from lateral margin to suture; and an oblique subapical band extending backward from the suture; apices rounded. Legs slender, brassy green, at least the anterior and intermediate tarsi pale brownish. Abdomen brassy green, shining; sternites sparsely punctate, very sparsely clothed with suberect pale hairs; fifth sternite broadly emarginate at apex, sixth sternite longer than fifth. Length, 5–11.5 mm.

*Female*.—Form more robust than male; elytra with yellow pattern more extensive; abdomen with sixth sternite shorter than fifth, largely concealed. Length 7–15 mm.

Varieties: Elytra dark blue, blue, or greenish, elytral bands yellow or faintly orange-yellow, very variable in extent, rarely coalescing over basal two-thirds or reduced to an oblique, oval, post median spot.

Subspecies *tenellus* LeConte: Form more slender with a lesser average length; elytra more coarsely, regularly punctate, bands frequently reddish, broad, median band very oblique. Length 5–8 mm. Distribution: arid regions of southwestern United States and northern Mexico.

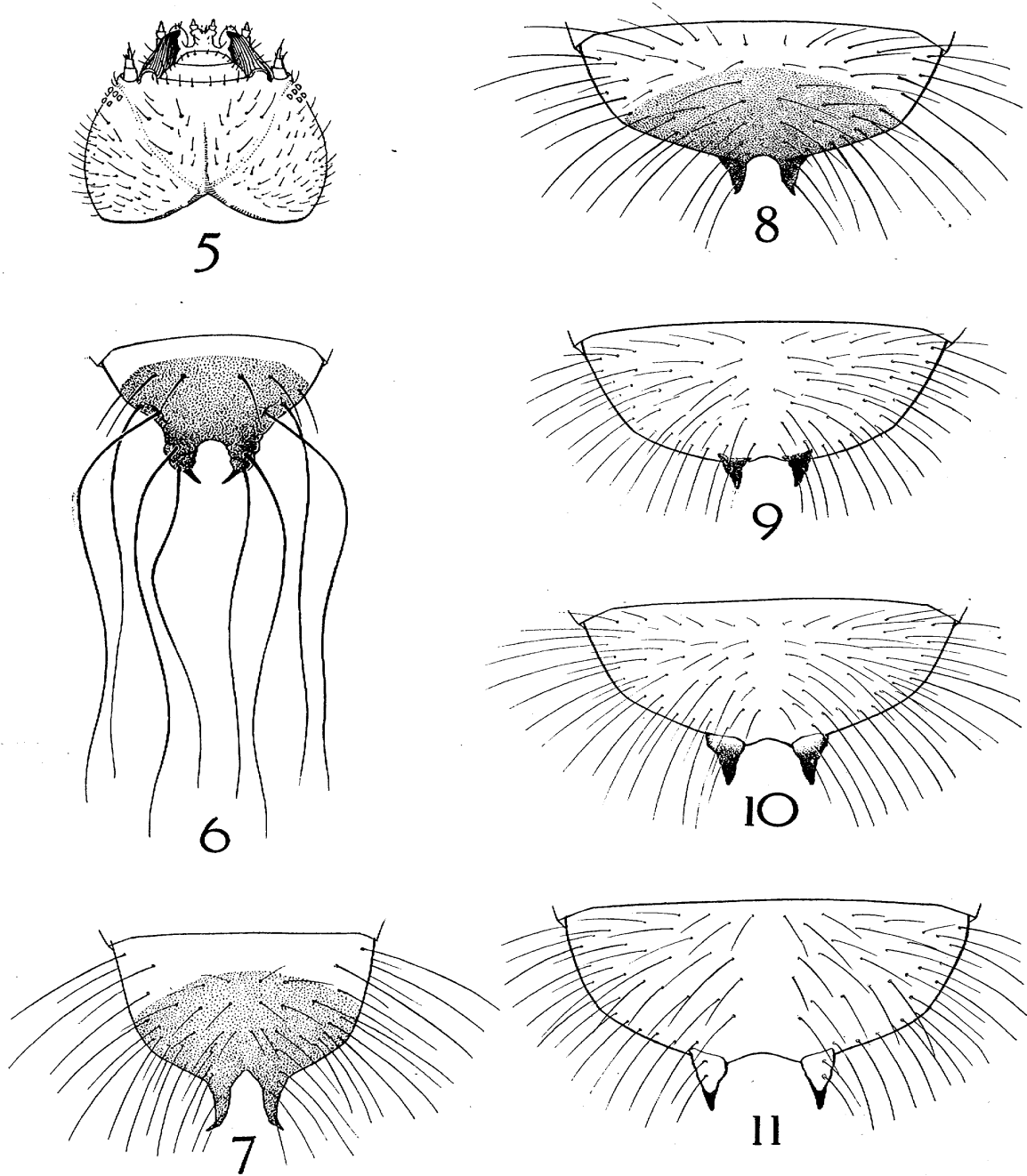
#### EGG

Form elongate, slender, slightly curved, tapering at each end, broadest at middle, a little wider at one end than at the other; color of contents pale orange, becoming bright orange with development, narrow end colorless; chorion smooth, shining, transparent, without ornamentation. Length 1.73 mm.; median breadth 0.46 mm.

#### LARVA

Böving and Champlain (1920) have characterized the mature larva (probably fifth instar) of *T. ornatus* as follows:

“Total length of body, 13 mm.; extreme width, 3 mm.; extreme thickness,  $2\frac{3}{4}$  mm.; anterior width of prothorax,  $2\frac{1}{2}$  mm. Mandibles, epistoma, tip of cerci dark brown; remainder of head capsule, prothoracic shield and other delicately chitinized parts pale cadmium yellow; membranous parts salmon red. Setae thin, long, yellowish. Frons hardly sculptured. Labrum more than twice as wide as long. Mandible from apex to attachment of retractor tendon about two-thirds the length of frons; length to width as 9 to 8; apex does not project over inner corner of mandibular basis; distance between retinaculum and apex of mandible one-third the length of mandibular inner margin; elevation of inner margin between retinaculum and apex slightly convex; at least seven fine mandibular setae. Basal plate of cerci poorly developed. Cerci upright, pointed, conical, slightly curved, from end to attachment less than half as long as frons.”



EXPLANATION OF PLATE II

*Trichodes ornatus* Say. Figure 5. Head capsule of fifth instar larva.  
6. Caudal plate of first instar larva. 7. Same, second instar. 8. Same, third instar. 9. Same, fourth instar. 10. Same, fifth instar. 11. Same, sixth instar.  
(All drawings to different scales.)

The remaining larval instars have not, however, been differentiated. They may be recognized as follows:

*First Instar* (fig. 6).—Length 2 mm. Form elongate, very slender; color cream to pale salmon pink. Head with longer lateral setae about twice head length; mandibles acute at apex. Caudal plate covering most of ninth abdominal tergite except for a narrow band at base; caudal processes very robust, wrinkled, with a stout spine at apex, setae very long, coarse, about three times as long as caudal plate.

*Second Instar* (fig. 7).—Length 5 mm. Form elongate, moderately slender; color salmon pink to reddish. Head with longer lateral setae about one-fourth head length; mandibles less acute at apex. Caudal plate covering most of ninth abdominal tergite except for a relatively broad, curved band at base; caudal processes long, slender, curved, tapering to an acute tip, longer setae a little more than twice as long as caudal processes.

*Third Instar* (fig. 8).—Length 11–12 mm. Form elongate, moderately robust; color salmon pink to scarlet. Head with longer lateral setae about one-half head length; mandibles moderately obtuse at apex. Caudal plate covering most of ninth abdominal tergite except for a broad, curved band at base; caudal processes long, moderately slender, apex curved, with a very short tooth, longer setae a little more than twice as long as caudal processes.

*Fourth Instar* (fig. 9).—Length 13–14 mm. Form elongate, moderately robust; color salmon pink to scarlet. Head with longer lateral setae about one-half head length; mandibles moderately obtuse at apex. Caudal plate reduced to caudal processes; caudal processes heavily sclerotized, short, obtuse, moderately robust, longer setae less than twice as long as caudal processes.

*Fifth Instar* (figs. 1, 2, 5, 10).—Length 12–13 mm. Form elongate, moderately robust; color salmon pink to scarlet. Head with longer lateral setae about one-third head length; mandibles obtuse at apex. Caudal plate reduced to caudal processes; caudal processes sclerotized nearly to base, short, stout, separated by at least twice basal width, apex moderately acute, longer setae more than twice as long as caudal processes.

*Sixth Instar* (fig. 11).—Length 12–13 mm. Form elongate, moderately slender; color salmon pink to scarlet. Head with longer lateral setae about one-third head length; mandibles obtuse at apex. Caudal plate reduced to caudal processes; caudal processes sclerotized at apex only, short, stout, separated by more than twice basal width, apex moderately acute, longer setae more than twice as long as caudal processes.

## LIFE HISTORY OBSERVATIONS

### ADULTS

The adults of *Trichodes ornatus* (fig. 4) have been taken from March to September and in any one given locality may be found over a period of about two months. After emergence they seek a wide variety of flowers, particularly *Achillea millifolium*, *Asclepias* spp., and various

yellow Compositae. Böving and Champlain (1920) state that the adults are not predaceous but feed solely on pollen. Although pollen is undoubtedly a major item of food, the present writers have observed adults to completely dismember and feed on other living insects (mostly small Coleoptera) and the female to consume the male after copulation. These observations were made in the field and were duplicated in the laboratory. (See also Linsley, 1942.)

Similar observations have been made by de Gaule (1874) who observed *Trichodes alvearius* plunging its mandibles into the abdomen of a hymenopteron; Cros, who recorded attacks by *T. umbellatarum* on beetles and bees; and Portchinsky (1914), who watched a *Trichodes* devour a specimen of *Mylabris*.

Mating takes place upon flowers and the pairs copulate for several minutes, during which time feeding and other activities are discontinued. Females which have previously copulated attempt to dislodge subsequent males by rapid lateral vibrations of the body. Mating is not preceded by preliminary courtship and upon its completion the female may devour the male.

Oviposition occurs on the flower heads frequented by the beetles. The act of oviposition has been observed in the field on *Achillea*, with the female assuming a position on the underside of the floral head and forcing the tip of the abdomen among the flowers to oviposit. The eggs are laid singly, depending for support upon a mucilaginous coating. Sometimes they are deeply imbedded in a single flower. The incubation period of eggs under laboratory conditions (20°–23° C.) varied from 18 to 20 days.

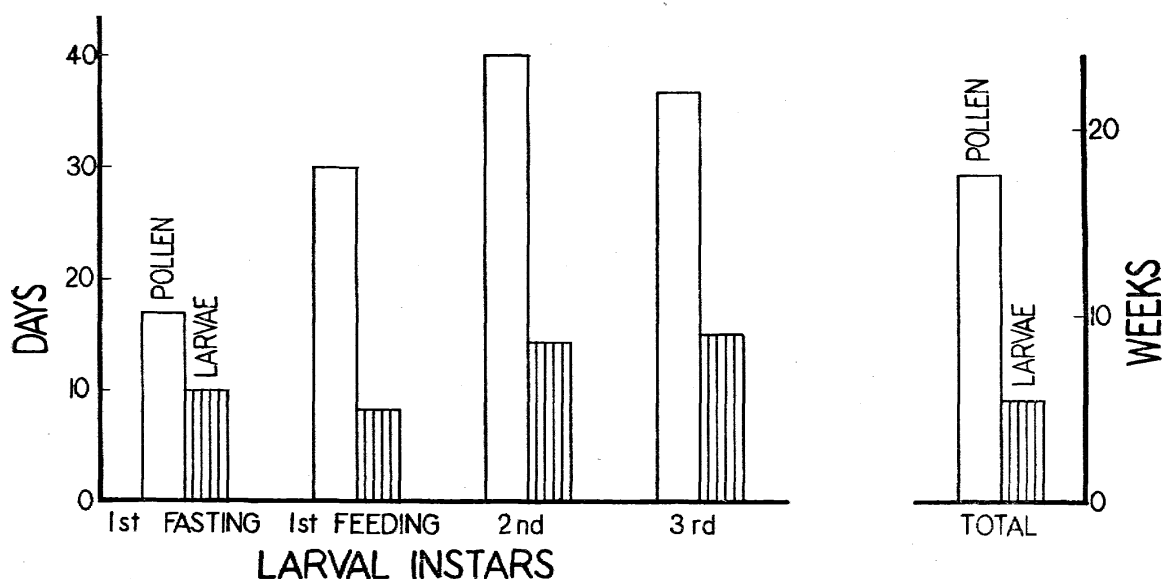
#### LARVAE

The means of access to the cell of the host bee or wasp was not definitely determined but in any event, having entered the cell, the primary larvae remain for a considerable period of time without feeding. Usually this period is sufficiently long to allow the host to attain the prepupal state. In the laboratory, in the presence of prepupal larvae, this period of fasting varied from 9 to 12 days (mean, 10 days). When ready to begin feeding, each larva makes a small puncture in the body of the host and feeds upon the liquids which exude. In the first instar, from two to five such punctures may be made. During this period growth is rapid but the time from the moment feeding begins until the first molt occurs may vary from 5 to 18 days (mean, 6 days).

In order to study some of the gross reactions of the first instar larvae, eggs were obtained in the field and laboratory and the resultant larvae subjected to various conditions of food and moisture. One group was supplied with a solution of one part honey to one part water mixed with dry pollen and placed in relative humidities of 50 and 75 per cent at temperatures of 20°–23° C. A second group was provided with prepupal larvae of *Anthophora linsleyi* Timb., a species selected because its larva has a relatively tough integument. These series were likewise placed under the same conditions of temperature and humidity. A third group was established with prepupal larvae of *Odynerus blandinus* Sauss., selected because of its soft, thin, flaccid integument. The larvae which were supplied with pollen alone were slow to begin

feeding and subsequent growth and development was greatly retarded (text fig. 1); those provided with *Anthophora* larvae encountered difficulty because the first puncture resulted in almost immediate deterioration of the host through bacterial infection; but those offered larvae of *Odynerus*, apparently found satisfactory food conditions (text fig. 1). However, in all cases, the better results were obtained in a relative humidity of 75 per cent at temperatures of 20°–23° C.

The second instar larva of *Trichodes* continues feeding by a series of punctures and it is during this period that the host larva usually dies. The length of time spent in the second instar varied from 13 to 15 days (mean, 14 days). The third instar is the last larval feeding stage and during this period the larva obtains its maximum growth (this instar required from 12 to 16 days, with a mean of 15 days). When feeding has been completed, the larva attempts to leave the cell in which it has



TEXT FIGURE 1. Comparison of the duration of the three larval feeding instars of *Trichodes ornatus* when reared on pollen and on larvae of *Odynerus blandinus*.

been reared. Thus larvae which have fed on bees nesting in banks excavate pupal cells about a half inch away from the burrows of their host; in twigs they normally construct an elliptical cell apart from the main tunnel of the bee or wasp; and in the hard cells of *Odynerus* and *Dianthidium* they cut their way out and pupate elsewhere or die later as unemerged adults within the cell. In the laboratory, the larvae readily burrow into corks and construct pupal chambers. Shortly after entering the cork, they transform to the fourth instar. In this instar the pupal cell is completed and any cracks are sealed with a dark brown oral secretion. In addition a burrow is made nearly to the surface of the cork, leaving only a thin partition to be broken through by the emerging adult. The winter is passed as a fourth instar larva within this pupal cell and transformation to the fifth instar occurs in spring or early summer. Occasionally an additional (sixth) instar may occur. In such



cases the sixth instar may follow the fifth within a few weeks or in the summer of the second or third year. Pupation requires about twenty days under laboratory conditions.

*Trichodes* larvae can be reared solely on pollen. However, such larvae take about three times as long to complete their growth (text fig. 1) as those fed on bee or wasp larvae under the same conditions of temperature (20°-23° C.) and relative humidity (75%).

#### HOSTS

*Trichodes ornatus* has been taken by the writers from the following aculeate Hymenopterous hosts. Two published records have also been included in order to make the list as complete as possible.

#### Family Megachilidae

*Callanthidium illustre* (Cresson). Mt. Diablo, Contra Costa Co., Calif., December 8, 1940, nesting in sandstone cliff. *Trichodes* larva, having destroyed contents of terminal bee cell, had burrowed into bank for several mm. and constructed its pupal cell.

*Dianthidium consimile* (Ashmead). Palm Springs, Riverside Co., Calif. Two dead adults and two living larvae found in unopened cells two years after they were collected in the field (Davidson, 1896: 25).

*Dianthidium pudicum provancheri* Titus Antioch, Contra Costa Co., Calif., June, 1938, nesting on dry plant stem. One dead adult found in unopened cell eighteen months after it had been brought into the laboratory. Coarsegold, Madera Co., Calif., May 12, 1942. One unemerged adult found in 1941 cell series (Linsley, 1942).

*Dianthidium macswaini* Timberlake. Mt. Diablo, Contra Costa Co., Calif., May 9, 1939, nesting on surface of sandstone boulders. One dead adult and one living fifth instar larva found in unbroken cells of different nests. June 1, 1941, a second instar larva found consuming prepupal bee in same locality.

*Dianthidium* sp. Strawberry, Eldorado Co., Calif., October 31, 1931. *Trichodes* larva left cell and bored into cork of vial; pupa observed Nov. 16, 1933, adult emerged Nov. 26, 1933 (Essig, 1934: 724).

*Megachile brevis onobrychidis* Cockerell. Davis, California, October 10, 1940, nesting in twig of elderberry (*Sambucus*). One fourth or fifth instar larva in cell series of 1940 season (G. E. Bohart).

*Hoplitis productus* (Cresson). Mineralking, Tulare Co., Calif., August 10, 1939, nesting in twigs of elderberry (*Sambucus*). One fifth instar larva found in bee cell. This larva subsequently refused all food and was still alive in May, 1941.

*Hoplitis sambuci* (Titus). Mineralking, Tulare Co., Calif., August 10, 1939, nesting in twigs of elderberry (*Sambucus*). One fifth instar larva in resting cell.

*Hoplitis biscutellae* (Cockerell). Twenty miles east of Indio, Riverside Co., Calif., April 1, 1941, nesting in bank. One immature larva found in a cell provisioned during the 1941 season.

*Anthocopa xerophila* (Cockerell). Ten miles south of Little Lake, Inyo Co., Calif., April 3, 1941, nesting in low bank and utilizing old burrows of *Anthophora linsleyi* Timb. One sixth instar larva found in closed cell. Larva pupated on April 7, 1941, and transformed to adult on April 26, 1941.

*Osmia* (*Nothosmia*) *clarescens* Cockerell. Twenty miles east of Indio, Riverside Co., Calif., April 1, 1941, nesting in bank in old burrows of *Anthophora* n. sp. One fifth instar larva and one freshly transformed pupa.

*Ashmeadiella* n. sp. Mt. Diablo, Contra Costa Co., Calif., December 8, 1940, nesting in old cells of *Odynerus* sp. One dead adult found in unopened cell.

#### Family Ceratinidae

*Ceratina acantha submaritima* Cockerell. Kyburz, Eldorado Co., Calif., July 26, 1941, nesting in stems of elderberry (*Sambucus*). One dead adult in cell series.

Family **Eumenidae**

*Odynerus blandinus* Cresson. Mt. Diablo, Contra Costa Co., Calif., December 8, 1940, nesting in mud cells plastered on rocks. One fourth instar larva found in an unopened cell which had contained a prepupal larva of *Odynerus* (as evidenced by the silken lining of the cell); larval skins found in a cell from which *Trichodes* had emerged. December 24, 1940, same locality, two dead adults and one fifth instar larva found in unbroken cells of different series.

Family **Massaridae**

*Pseudomassaris coquilletti* Rohwer. Mt. Diablo, Contra Costa Co., Calif., December 8, 1940, nesting in mud cells plastered on rock. Third instar larva found opening an escape hole to the surface.

## DISCUSSION

The method by which the larvae of *Trichodes* gain access to the cell of the host bee or wasp was not determined. However, in view of the fact that the eggs are laid on flowers, only two alternative methods suggest themselves. Either the larvae find and enter the cell under their own locomotion or are carried there by the hosts. The former method seems highly improbable because of the relatively few eggs laid by *Trichodes*, the fact that most of the infested nests encountered were widely separated from flowers, and the scattered and secretive nesting habits of many of the commoner hosts. Infested nests were found in dead logs, twigs of living trees and shrubs, hollow stems of annual plants, burrows in the flat ground and in banks, and in cells on the surface of rocks. The only evident common denominator was the fact that the nests were those of bees or wasps. Furthermore, it is apparently necessary for the *Trichodes* larva to gain access to the host cell in that brief interval when it is being provisioned. This is emphasized by the facts that the primary larvae are incapable of boring into a closed cell and that all of the hosts with which *Trichodes* has been found provision their cells during the period when the adult clerids are active.

Variation in the number of larval instars in *Trichodes* parallels similar variation in certain other species of predaceous beetles. Ingram and Douglas (1932) and Horsfall (1941) record five feeding larval instars in two species of *Epicauta*; yet, under certain conditions, two additional non-feeding instars occur. Struble (1941) found that there may be either five or seven larval instars in the ostomatid *Temnochila virescens* (Fab.). However, this same author found only three larval instars, all feeding stages, in *Enoclerus sphaeus* (Fab.). Apparently, this represents the normal number of feeding instars in the family Cleridae and the supernumerary instars serve to carry the species over unfavorable conditions.

Plasticity and adaptability in the food habits of *Trichodes* is indicated by the fact that newly hatched larvae deprived of insect food can complete their development on pollen alone. In our experiments such larvae fasted twice as long as those offered prepupae of wasps and when feeding began they required about three times as many days for each larval instar. However, the fact that they can live on pollen is another survival factor in their favor, since the host bee or wasp may die in the egg or as a very young larva. It also probably indicates that there is a close relationship between the nutritive value of pollen and that of insect eggs and of larvae fed on pollen, since many insects may live on either.

## CONCLUSIONS

- (1) *Trichodes ornatus* is normally predaceous in both the adult and larval stages.
- (2) Larval food is normally restricted to the immature stages, especially the prepupae of aculeate Hymenoptera, in particular the bee family Megachilidae. However, in the absence of insect food the larvae can complete their development on pollen.
- (3) Larval development includes three feeding and two non-feeding instars. Under certain conditions a sixth instar may occur.
- (4) The life cycle varies from a single year to three or more years.

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THE INTERNAL ANATOMY OF DERMACENTOR ANDERSONI STILES, by J. R. DOUGLAS, 1943. University of California Publications in Entomology 7(10): 207-272, pls. 8-26, and 7 text figs. UNIVERSITY OF CALIFORNIA PRESS, Berkeley and Los Angeles. Paper bound. Price \$1.25.

For years we have needed studies of the internal anatomy of mites and ticks. Few outside the larger Ixoidae are easily studied. Our experience has been that the average student on opening a mite or tick and after seeing the complexity of branching and convoluted parts gives up and works on some insect with relatively simple internal parts. One has to admit he shows judgment as far as easy success is concerned.

Douglas has stuck it out and has given us some good figures of internal anatomy in a Dermacentor, one of the larger forms. His drawings are more satisfying than his plates of photomicrographs. Perhaps his venture will lead the way for others in this important group of Arthropods. The students of parasitology should learn what is inside a tick.—C. H. K.