NOTES ON AUSTRALIAN THYNNINAE.

IV. THE MORPHOLOGY OF THYNNOIDES RUFITHORAX TURNER WITH NOTES ON THE PREPUPAL LARVA AND THE COCOON.

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(Twenty-three Text-figures.)

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Synopsis.

The species is taken as a typical example of the tribe Thynnini as represented in Australia. The structure of the larva and adult is described in relation to homology and taxonomic usage. Cocoon structure and function are discussed.

Introduction.

In a recent paper (Salter, 1957) there is an excellent comprehensive account of the history of taxonomic usage of morphological terms and structures in the Thynninae of Australia. This superbly illustrated account is rightly confined to characters which have been taxonomically used, but refers only to the male. The present account covers all external areas of both sexes, the tentorial structures of adult and larva, and details of cocoon structure and function. In this it will be useful in supplementing Salter's account. It also presents new material, particularly in relation to the cocoon, and tentorial homology.

The writer is indebted to Dr A. J. Nicholson, Chief of the Division of Entomology, C.S.I.R.O., Canberra, for communicating this paper for publication, and to Mr E. F. Riek and Dr P. B. Carne, also of the Division of Entomology, for careful and constructive criticism of the typescript.

Morphology.

A. The Prepupal Larva (Figs 1-3).

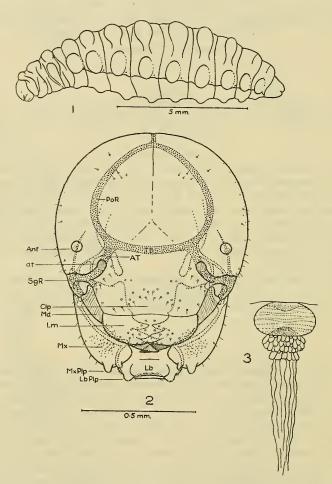
Creamy white in colour, broadly spindle-shaped, head small, dorsal and ventral welts prominent, pleural fold with rather bulbous segmental protrusions on abdominal segments. Integument devoid of hairs or denticles except on the head.

The head (Fig. 2) is not entirely comparable with the normal aculeate larval type. The mandibles (Md) are very large and well developed, tridentate, each with a small pointed tubercle below the basal tooth. The clypeus (Clp) is clearly divided from the labrum (Lm). Maxillae (Mx) are well developed and, apart from the palps (Mx Plp), have smaller papillate structures which appear to arise above glandular organs. The labium (Lb) has a pair of palps (Lb plp), and the opening of the salivary glands is terminal beneath an upper lobe. Vestiture is confined to denticles on the upper surface of the maxillae and lateral margins of the labrum, with small hairs and placoid sensillae on the clypeus, maxillae, labrum, labium and capsule as illustrated. The antennae (Ant) are only slightly raised.

The most interesting features of the head are the tentorium and related structures. The usual larval structures are greatly reduced or missing, the strongest development being in structures homologous with those of the adult. No epistoma or clypeal arch is present, and the hypostoma, labial ring, etc., are reduced. These structures are illustrated in dotted outline but not stippled. The stippled structures are those which are considered to be homologous with the tentorium of the adult or immature stages of more primitive insects. The pleurostoma or subgenal ridge (SgR) is well developed.

leading to the mandibular articulations from well-developed anterior tentorial pits. Anterior tentorial arms (AT), tentorial bridge (TB) and postoccipital ring (Por) are well developed.

The examination of final larval exuvia indicated ecdysis to follow a posterior longitudinal splitting along the longitudinal line of the epicranial suture (which is faintly visible only prior to ecdysis), which does not progress to the level of the tentorial pits.



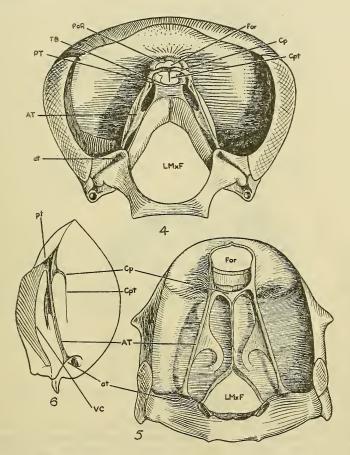
Figs 1-3.—1, Prepupal larva. 2, Larval head, anterior. 3, Larval spiracle.

The spiracles (Fig. 3) are all similar. The atrium is oblate spheroidal, indented both externally and internally and with rather fine and irregular annulations. Below the atrium is a rather diffuse, apparently cellular mass probably having some valvular function. The trachea leading from this is flaccid, very thin walled and lacking in annular thickening. The diameter of the atrium is 0.06 mm.

B. The Adult (Figs 4-17).

The remarkable aspect of adult morphology is in the extreme dimorphism displayed. In this account, only certain aspects related to homology of larval and adult structures, homology of male and female structures, and systematic usage are discussed. For the most part, the figures will be left to tell their own story.

Figures 4, 5 and 6 illustrate the tentorial development of the male and female, and homology of parts with those of the larva (Fig. 1) is indicated by lettering. The great degree of elongation of the head and reduction in size of the labiomaxillary fossa in relation to assisted feeding of the female (Given, 1954) is indicated by the difference in space between the labiomaxillary fossa (LMxF) and the occipital foramen (For) in the two sexes. This extension is accompanied by the formation of a ventral carina (VC) and elongation and modification of other elements as illustrated. The great degree of reduction of compound eyes and complete lack of ocelli in the female is also a result of male-dependence.



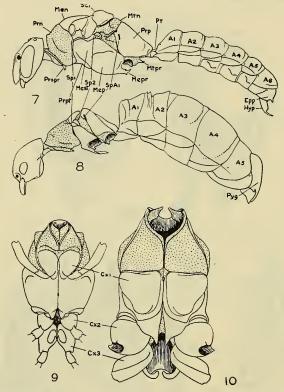
Figs 4-6.—4, Male head, anterior, to show tentorium, etc. 5, Female head, anterior, to show tentorium, etc. 6, Female head, lateral, to show tentorium, etc.

Modification of thoracic elements in the female in accordance with the digging habit as against the flight requirements of the male is striking. This is particularly clearly seen in Figures 9 and 10 which display the relative size of the coxae of the two sexes. It should be noted that these figures are not to scale, the female thorax being drawn more highly magnified than the male. For ease of comparison and interpretation, visible portions of the pro- and metathorax are stippled. In the male, both thoracic spiracles are covered by overlapping plates, whereas in the female only the first spiracle is so covered.

The ultimate abdominal spiracle on the female is illustrated on the fifth segment. Actually it is beneath this plate on the sixth tergite (pygidium). The numbering of abdominal segments is in accordance with systematic rather than comparative morpho-

logical usage, the propodeum or median segment (Prp) being regarded as part of the thoracic structure. The sixth dorsal plate of the female abdomen is termed the pygidium (Pyg) as Turner used this term, and likewise the seventh dorsal plate of the male is termed the epipygium, although these structures are analogous, being the ultimate abdominal coverings for the modified genital segments.

The genital segments proper are illustrated in Figures 11-13 (male) and 16 (female). The male organs vary so greatly in different genera and species that homology is sometimes difficult to interpret. The structures of the female are more



Figs 7-10.—7, Male, lateral. 8, Female, lateral. 9, Male thorax, ventral. 10, Female thorax, ventral.

typical of aculeate hymenoptera as a whole, showing less degree of specialization. The male organs in T. rufithorax are not modified to the degree noted in species of some other genera, and the structure may be readily identified in accordance with the terminology of Snodgrass (1941). The function and manner of coupling for female transportation and copulation has been previously illustrated (Given, 1954).

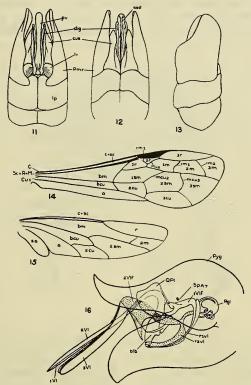
The wing venation illustrated in Figures 14 and 15 is interpreted according to Tillyard's "New System" (1926) and the "Jurinian" naming of veins and cells as used by Turner is given in the key to lettering of wings at the end of this paper. To date these are the only systems used in the systematics of the Thynninae.

It is of interest that the alimentary tract of the male (Fig. 17) is remarkably similar to that of the worker honey-bee (Snodgrass, 1925, p. 154). This is to be expected as both are nectar gatherers which regurgitate from a "honey-stomach" (HS).

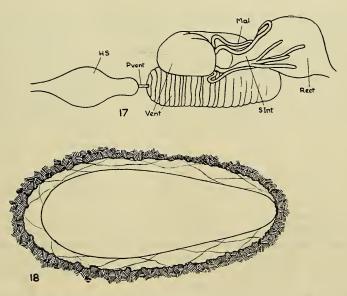
The Cocoon (Figs 18-23).

As has been previously recorded (Given, 1957), there is reason to believe that the relationship between soil-water and adult emergence is a close one. This infers

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Figs 11-16.—11, Male genitalia, dorsal. 12, Male genitalia, ventral. 13, Male genitalia, lateral. 14, Fore-wing. 15, Hind-wing. 16, Female genitalia, lateral.



Figs 17-18.-17, Male, alimentary tract. 18, Cocoon in earth cell, longitudinal section.

a sensitivity of the prepupa within the cocoon to water outside the cocoon, which in turn infers nice physical properties of water conduction in the cocoon structure.

Figure 18 illustrates in diagrammatice section, the cocoon within its earth cell. It will be noted that loose silken fibres suspend the cocoon so that it is out of contact with the soil except at its small end, which will be referred to as the posterior end.

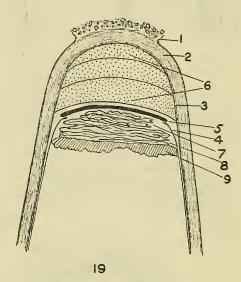


Fig. 19.—Posterior end of cocoon, longitudinal section.

This suspension within the earth cell indicates that the interior moisture conditioning of the cocoon is through the posterior end. Examination discloses that at this end the outer layer of the cocoon turns outward, exposing inner layers to soil contact. The inner layers have loose fibres at this point, which incorporate soil particles in the cocoon structure (Fig. 19).

Table 1.

Layers Separated from Hemithynnus Cocoon. (Layers numbered from inside to outside.)

Layer.	Fibre Type.	Layer Thickness.	Mesh Sealed or Unsealed.
1	Fig. 23.	Medium.	Partly sealed.
2	Finer than 23.	Thin.	Completely sealed.
3	Fig. 21.	Very thin.	Completely sealed.
4	Finer than 23.	Thin.	Completely sealed.
5	Finer than 23.	Thick.	Completely sealed.
6	Fig. 21.	Medium.	Partly sealed.
7	Fig. 21.	Thin.	Unsealed.
8	Fig. 20.	Medium.	Unsealed.
9	Fig. 20.	Very thin.	Unsealed.
10	Fig. 20.	Very thin.	Unsealed.
11	Fig. 20.	Thin.	Unsealed.
12	Fig. 20.	Thin.	Unsealed.
13	Fig. 23.	Medium.	Completely sealed.

Careful examination of a sectioned cocoon wall shows the presence of a number of layers, and to facilitate examination of these layers, a cocoon of a larger species (*Hemithynnus* sp.) was carefully dissected after first examining the two different ones in order to ensure that there were no obvious differences in structure. The layers determined may be classified as in Table 1.

Condensing Table 1 to simpler terms, the general characteristics of the cocoon wall can be readily seen (Table 2).

Layer 1 (Fig. 19, 4) is incomplete and loosely attached to the more compact and complete cocoon structure. It plays no obvious part in moisture conduction, but may serve to separate the pupa or prepupa from layer 2 when this is wet, or it may be laid down as part of the excretory process in the final elimination of unwanted body products. This layer is usually a dark brown in colour, as also is the pad (Fig. 19, 5) separating the larval excrement (6) from the exuvia (7, 8) and the meconial excrement (9). This pad, like layer 1, is rapidly permeable to water.

Table 2.

Grouped Characteristics of Cocoon Layers of Hemithynnus sp.

Layer.	Fibre Type.	Sealed or Unsealed.	Water Resistance.
$\begin{bmatrix} 1 \\ 2 \end{bmatrix}$	Fine.	Partly sealed.	Rapidly permeable.
3	Medium.	Sealed.	Permeable.
$\left.\begin{array}{c}4\\5\end{array}\right\}$	Fine.		
$\binom{6}{7}$	Medium.	Partly scaled.	Porous.
8 9 10 11 12	Coarse.	Unsealed.	Porous.
13	Medium.	Sealed.	Almost impermeable.

The outermost layer is a light amber colour and very tough. Intermediate coarse layers (7, 12) are red-brown in colour and form a very porous layer highly reminiscent of rubberized horsehair mattress filling. Layer 6 is intermediate, and layers 2 to 5 are reddish-gold and have the consistency of tough paper glazed on the inner surface.

The outermost layer (layer 13) is difficult to moisten, and does not become completely saturated in less than 24 hours' contact with water. Through the posterior end of the cocoon which has direct soil contact, water is almost immediately conducted on contact, and penetration of all internal layers to number 2 is complete within 10 minutes. However, although layer 2 becomes saturated, no free water collects within the cocoon after 48 hours of partial immersion.

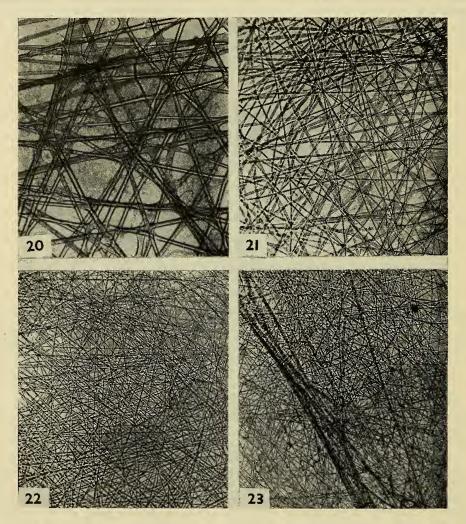
The faecal layers (Fig. 19, 6) rapidly absorb moisture, and to a less extent the pad (Fig. 19, 5) is also absorptive. This may assist in prolonging and regulating the high humidity within the cocoon, and this entire hydrostatic structure may even serve a gas exchange function in relation to carbon dioxide/oxygen balance within the cocoon.

An examination of the faecal material (Fig. 19, 6) discloses the presence of chitin fragments, bristles, soil particles and coarse silk fibres in a dark brown amorphous matrix. This indicates that in the final stages of feeding on the host, the gut, its contents, and the host integument are ingested. The final meconial excrement (Fig. 19. 9) is a pure white, amorphous mass.

TECHNIQUE.

The larva was described from a single specimen removed from a cocoon, fixed in Kahle's fluid and preserved in 70% ethyl alcohol. The head was first treated with hot 5% caustic potash solution, washed in water and temporarily mounted in Berlese's

fluid. Detail was drawn during progressive clearing in this medium, after which the head was removed from the mountant, washed, overstained in acid fuchsin, destained in acid alcohol, completely dehydrated in absolute alcohol and permanently mounted in euparal. From this permanent mount, final details were drawn. The spiracle was drawn from the unstained larval skin mounted in euparal after caustic treatment.



Figs 20-23.—20, Cocoon fibres, coarse, porous layer. 21, Cocoon fibres, intermediate layer. 22, Cocoon fibres, fine, fixed inner layer. 23, Cocoon fibres, fine, free inner layer. \times 70.

Examination of adult heads was based mainly on material cleaned by boiling in 10% caustic potash, washed, acidulated with dilute hydrochloric acid, bleached in chlorine water and mounted in euparal. Prior to treatment, one male head from a dried specimen was mounted on a wooden match-stick and the vertex ground away on a very fine scalpel hone. The final mount after cleaning and bleaching proved to be highly satisfactory for examination of internal structures. Adult thorax and abdomen examinations were from dried specimens and from slide mounts of material treated in caustic potash and chlorine water.

Cocoon layer examinations were from permanent mounts in euparal of separated layer samples.

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Key to lettering of figures (except wings).

A1-A6, Abdominal segments; aed, Aedeagus; Ant, Antenna; AT, Anterior tentorial arm; at, Anterior tentorial pit; blb, Bulbous swelling of ovipositor shaft; Clp, Clypeus; Cp, Corporotentorium; Cpt, Corpotendon; cus, Cuspis or distivolsella; Cx1-Cx3, Coxae; dig, Digitus; Epp, Epipygium; For, Foramen magnum or occipital foramen; HS, Honey stomach or crop; Hyp, Hypopygium; Lb, Labium; LbPlp, Labial palp; Lm, Labrum; LMxF, Labiomaxillary fossa; Ip, Parameral plate or basiparamere; Iv, Volsellar plate or basivolsella; Mal, Malpighian tubules: Md, Mandible; Men, Mesonotum or mesoscutum; Mep, Mesepimeron; Mepr, Mesosternal intercoxal process: Mest, Mesepisternum; Mtn, Metanotum; Mtpr, Metasternal intercoxal process; Mx, Maxilla; MxPlp, Maxillary palp; Pgl, Poison gland; Pmr, Paramere; PoR, Postoccipital ring; Prn, Pronotum; Prp, Propodeum or median segment; Prspr, Prosternal intercoxal process; PT, Posterior tentorial arm; Pt, Petiole or pedicel; pt, Posterior tentorial pit; Pv, Penis valve or lamina aedeagalis; Pvent, Proventriculus; Pyg, Pygidium; QPl, Quadrate plate; Rect, Rectum; r1vl, r2vl, Rami of valvulae; Scl, Mesoscutellum or scutellum; SInt, Small intestine; SgR, Subgenal ridge or pleurostoma; Sp1, Sp2, Thoracic spiracles; SpA1, Propodeal spiracle; TB, Tentorial bridge; VC, Ventral carina; Vent, Ventriculus; 1VL, 2VL, 3VL, Valvulae; 1VLF, 2VLF, Valvifers.

Notation.	Lettering of "New System" (Tillyard, 19	-			
	Cells.				
a	Anal	Anal			
bcu	Basicubital	Median			
h m	Basimedian	Subcostal			
c + sc	Costal plus first subcosta	al Costal			
2cu	Second cubital				
3cu	Third cubital	Second posterior			
1m	First median	Second cubital			
2m	Second median	Third cubital			
3m	Third median	Fourth cubital			
r	Radial	Cubital			
1r	First radial	First cubital			
2r	Second radial	First radial			
3r	Third radial	Second radial			
sa	Subanal				
1sm	First submedian	First discoidal			
2sm	Second submedian	Second discoidal			
3sm	Third submedian	First posterior			
Veins and cross-veins.					
C	Costa	Costa			
Cu1	Cubitus, first branch	Median			
im1	First inter-median	Second transverse cubital			
im2	Second inter-median	Third transverse cubital			
M1 + 2	Media, basal piece	First transverse cubital			
mcu2	Second medio-cubital	First recurrent			
mcu3	Third medio-cubital	Second recurrent			
Sc + R + M	Principal vein	Subcostal			
Numbering of Figure 19.					
1.	Termination of outer layer.	6. Larval faeces.			
2.	Porous layer.	7. Larval exuvium.			

Sealed inner layer.
 Loose inner layer.

5. Silk pad.

8. Pupal exuvium.

9. Meconial excrement.