

**BIOLOGICAL STUDIES ON *TRICENTRUS BUCKTONI*  
(HOMOPTERA: MEMBRACIDAE), WITH NOTES ON  
NYMPHS OF THREE RELATED SPECIES AND  
NYMPHS OF OTHER CENTROTINE SPECIES<sup>1</sup>**

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*Abstract:* The eggs and nymphs of *Tricentrus bucktoni* are described and illustrated. The 5th nymphal instars of *T. nordicornis* and *T. variabilis* are also described and illustrated and compared with those of *T. bucktoni*, *T. fairmairei* and other centrotine species reported earlier. Keys to separate the 5th instars of *T. bucktoni* and the 5th-instar nymphs of the above 3 species are presented.

Capener (1962) stressed the need for study of the morphology of immature membracids and later (1968) emphasized the collection and proper preservation of immature stages, which are usually poorly represented and badly preserved in most collections.

Life histories and immature stages of various species of the Centrotinae Amyot & Serville have been reported by various authors; most of the early works were reviewed by Kopp & Yonke (1973) and Yasmeen & Ahmad (1975). However, biological information on representatives of the Tricentrini Ahmad & Yasmeen is practically non-existent.

In the present studies, eggs and immature stages of *Tricentrus bucktoni* Ahmad & Yasmeen and the 5th-instar nymphs of 2 other species, *T. nordicornis* Yasmeen & Ahmad and *T. variabilis* Ahmad & Yasmeen are described and illustrated. These are compared with the 5th instar of *T. fairmairei* (Stål), described and illustrated by Funkhouser (1919). Keys to separate the 5th instars of *T. bucktoni* and those of the above 3 species are presented.

Immature stages were reared in the laboratory or collected from the field, usually near the roots of the host plants. Rearing was carried out in an air-conditioned laboratory at the Pakistan Medical Research Centre, Lahore. Colonies were maintained at  $27 \pm 1$  °C with any further divergence of temperature noted.

Immature stages and adults of both sexes of *Tricentrus bucktoni* were collected from Lahore (Punjab) on *Withania somnifera* (L.) Dunal. Immatures of *T. nordicornis* and *T. variabilis* were collected from the northern region of Pakistan, i.e., Abbotabad and Balakot, on *Rumex hastatus* D. Don and *Dalbergia sissoo* Roxb., respectively.

Illustrations were made using an ocular grid under Leitz binocular microscope and by suspending the egg and immatures in glycerine on cotton threads. Measurements

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were taken using a micromillimeter slide. Examples of the immature stages of *Tricentrus* species treated are deposited in Bishop Museum (BISHOP).

#### KEY TO NYMPHS OF *Tricentrus bucktoni*

1. Head only slightly wider than long, labium longer, at least reaching abdominal segment III; lateral and costal angles of thorax and abdominal lamellae weakly developed; pronotal process usually not developed but sometimes weakly developed; suprahumeral buds and wing pads not developed ..... 2
- Head much wider than long, labium shorter and never extending beyond abdominal segment II; lateral and costal angles of thorax and abdominal lamellae well developed; suprahumeral buds, pronotal process and wing pads well developed ..... 3
2. Labium always reaching at least abdominal segment IV; posterior pronotal process not apparent ..... 1st instar
- Labium reaching abdominal segment III; pronotum slightly extended medially forming posterior pronotal process ..... 2nd instar
3. Labium reaching abdominal segment II; suprahumeral buds appearing, wing pads usually extending to the lateral borders of the metanotum ..... 3rd instar
- Labium never reaching abdominal segment II; suprahumeral buds well developed, wing pads extending to abdominal segment II ..... 4
4. Labium reaching abdominal segment I; wing pads usually covering the margin of abdominal segment II ..... 4th instar
- Labium never extending beyond posterior coxae; wing pads usually covering  $\frac{1}{2}$  of abdominal segment II ..... 5th instar

#### *Tricentrus bucktoni* Ahmad & Yasmeen      FIG. 1-7

*Egg* (FIG. 1). Elongate, length 0.70–0.97 mm, width 0.21–0.36 mm, slightly rounded at one end but at opposite end somewhat subacute. When freshly laid, appear translucent and whitish; after 2 days turning yellowish, then gradually turning brown, after which a pair of red eye spots appear which turn darker and darker as the egg develops.

Copulation or oviposition was not observed in the laboratory, but eggs brought from the field successfully hatched. A few days before hatching, eggs appear somewhat swollen, then the tips of the eggs begin to crack, finally break open at the tip and usually split some distance down the side. The young emerges from the egg head first, quickly followed by the thorax and part of the abdomen; the legs are slowly drawn out in order, beginning with the 1st pair. The insect is now held only by the posterior end of the abdomen, which is finally pulled out, and the young creeps a very short distance away from the egg and rests.

*1st instar* (FIG. 2). General color pale green. Body elongated, arched and widest at head, thoracic and abdominal segment I of about equal width, from which the body tapers posteriorly to subacute tip. Head, thorax and abdominal segments with their lateral lamellae bearing a number of minute scattered tuberculate spines. Head reflexed, extending ventrally to the 1st pair of legs and only slightly wider than long; dorsal ecdysial line in the middle Y-shaped, pointed and reaching to the posterior margin of the metanotum, cranial processes on the dorsal side of head very well developed and blunt; eyes large, lateral and appear reddish, subocular expansion prominent; antennae fine, bristle-like, on ventral side of head between the eyes, 3-jointed, 2 basal segments very short and quadrangular, segment III long with thickened base and gradually becoming slender to almost hair-like; labium 2-segmented, long, reaching abdominal segment IV. Thorax 3-segmented, with all segments of unequal dimensions; pronotum about 2× as wide as long, slightly wider than head but only slightly more than  $\frac{1}{2}$  of head length; mesonotum slightly shorter

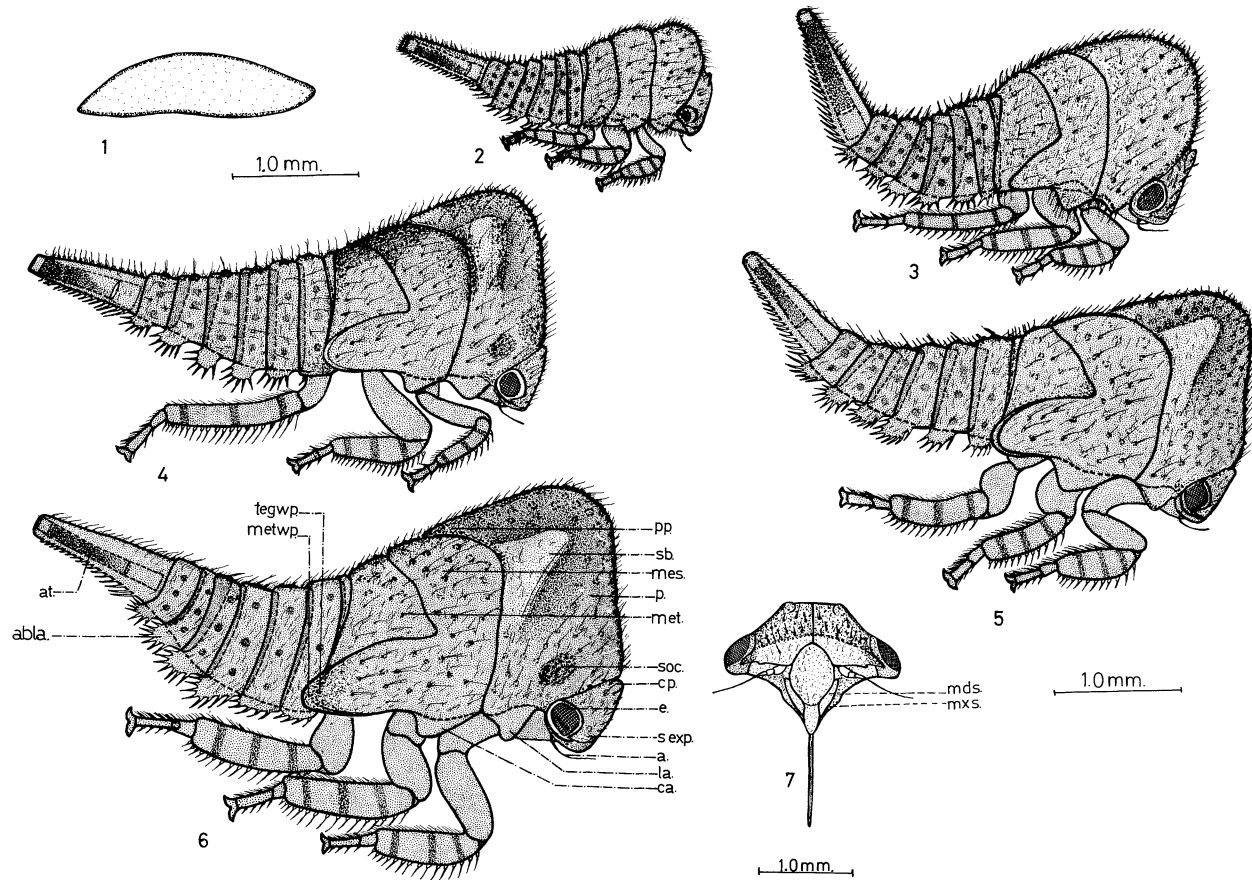


FIG. 1-7. *Tricentrus bucktoni*, egg and nymphs: 1, egg, lateral view; 2, 1st instar, lateral view; 3, 2nd instar, lateral view; 4, 3rd instar, lateral view; 5, 4th instar, lateral view; 6-7, 5th instar: (6) lateral view, (7) head, ventral view. a, antenna; abla, abdominal lamellae; at, anal tube, ca, costal angle, cp, cranial process; e, eye; la, lateral angle; mes, mesonotum; met, metanotum; metwp, metanotal wing pad; p, pronotum; pp, posterior pronotal process; sb, suprahumeral bud; soc, supraocular callosities; sexp, subocular expansions; tegwp, tegminal wing pad; mds, mandibular sclerite; mxs, maxillary sclerite.

and broader than pronotum; metanotum shortest of all with concave posterior margins; lateral and costal angles of meso- and metanotum prominent, extending somewhat posteriorly; metathoracic wing pads not yet developed; legs well developed, stout, tibiae and tarsi bearing minute tuberculate spines, fore tibiae smallest, hind tibiae largest and with 3 dark brown bands, tarsi 2-segmented with basal segment comparatively very small, claws well developed. Abdominal segments II–VII short, broad and of about equal length, widest at segment II and gradually narrowing posteriorly to anal tube; abdominal lamellae on sides of segments II–VII well developed, becoming more pronounced posteriorly; anal tube linear, sides parallel, comprising abdominal segments IX–XI and retractable into the long narrow segment VIII; a circle of fine hairs around the anal orifice; all terga appearing pale greenish and covered with small tuberculate spines, 3 rows of small dark brown spots dorsally on each side, and large tubercles bearing long, rather stout spines on either side of the mid-dorsal line of abdominal segments II–VII; sterna pale. The 1st instar took  $7 \pm 2$  days to complete its development.

*2nd instar* (FIG. 3). Shape and color similar to 1st instar, tubercles and spines practically the same. Head wider dorsally and narrower ventrally, slightly wider than long, labium shorter than in previous instar and reaching abdominal segment III. Pronotum  $\frac{1}{6}$  again as wide as long, slightly more than  $\frac{3}{4}$  again as wide as head width and about  $\frac{1}{2}$  again as long as head; mesonotum slightly extending medially and posteriorly. Abdominal lamellae slightly more developed. Duration of the 2nd instar was  $8 \pm 1$  days.

*3rd instar* (FIG. 4). Shape and color similar to previous instars, body more elongated. Head about  $2\times$  as wide as long, labium reaching abdominal segment II. Pronotum bearing tuberculate spines, slightly less than  $\frac{3}{4}$  again as wide as long,  $\frac{1}{9}$  again as wide as head width and  $\frac{1}{3}$  again as long as head length, pronotum slightly raised in the middle in the form of a crest and extending backward on the median line forming posterior pronotal process, anterior portion of pronotum appearing robust on account of pronounced crest which is largely confined to prothoracic segment and extending medially and posteriorly; dorsal median portion of mesonotum extending posteriorly; wing pads usually extending to the lateral borders of the metanotum. Abdominal lamellae comparatively more developed bearing tuberculate spines. Duration of the 3rd instar was  $10 \pm 2$  days.

*4th instar* (FIG. 5). Shape and color similar to 3rd instar, tubercles relatively large and more complex, body strongly arched, more elongated. Head about  $\frac{3}{4}$  again as wide as long, labium reaching abdominal segment I. Pronotum considerably more developed, slightly less than  $\frac{3}{4}$  again as wide as long, about  $\frac{1}{7}$  again as wide as head width and  $\frac{1}{6}$  again as long as head length; median pronotal process comparatively more developed and extending to the middle of mesonotum; supra-ocular callosities appearing on either side of metopidium; metathoracic wing pads overlapping the mesothoracic wing pads and usually slightly covering abdominal segment II. Abdominal lamellae well developed. The 4th instar lasted  $8 \pm 1$  days.

*5th instar* (FIG. 6–7). Color similar to previous instars, body very strongly arched, rather more elongated, tuberculate spines on head, thorax and abdomen more numerous and pronounced. Head distinctly at least  $\frac{3}{4}$  to about  $2\times$  as wide as long, cranial processes less developed, labium short and reaching posterior coxae. Pronotum greatly developed, more elongated, about  $2\times$  as wide as long, about same width as that of head but slightly shorter in length than head; supra-ocular callosities darker and more developed; suprahumeral buds comparatively more developed, with median portion darker in color and bearing more tuberculate spines; margins of pronotal crest brown, median pronotal process comparatively more developed, extending to more than  $\frac{1}{2}$  of mesonotum, broad and abruptly tapering to subacute tip; mesonotum extending somewhat posteriorly and medially, meso- and metanotum medially brown; wing pads much more developed and usually extending to  $\frac{1}{2}$  of abdominal segment II; minute spines appearing on trochanters of hind legs. Abdomen arched, with numerous tuberculate spines, lateral lamellae more pronounced; in ♂ subgenital plate makes its appearance with a broad base, which gradually tapers to subacute apex. This instar completed development in  $13 \pm 2$  days.

*Ecdysis.* The splitting of the integument first appears on the dorsal part of the head. It then continues down the median dorsal line but seldom extends farther than abdominal segment VI. The head is released slowly, the thorax quickly follows, and the abdomen is removed slowly. The process is a comparatively rapid one, usually taking about 12 min. The newly emerged adults are pale green and the whole body

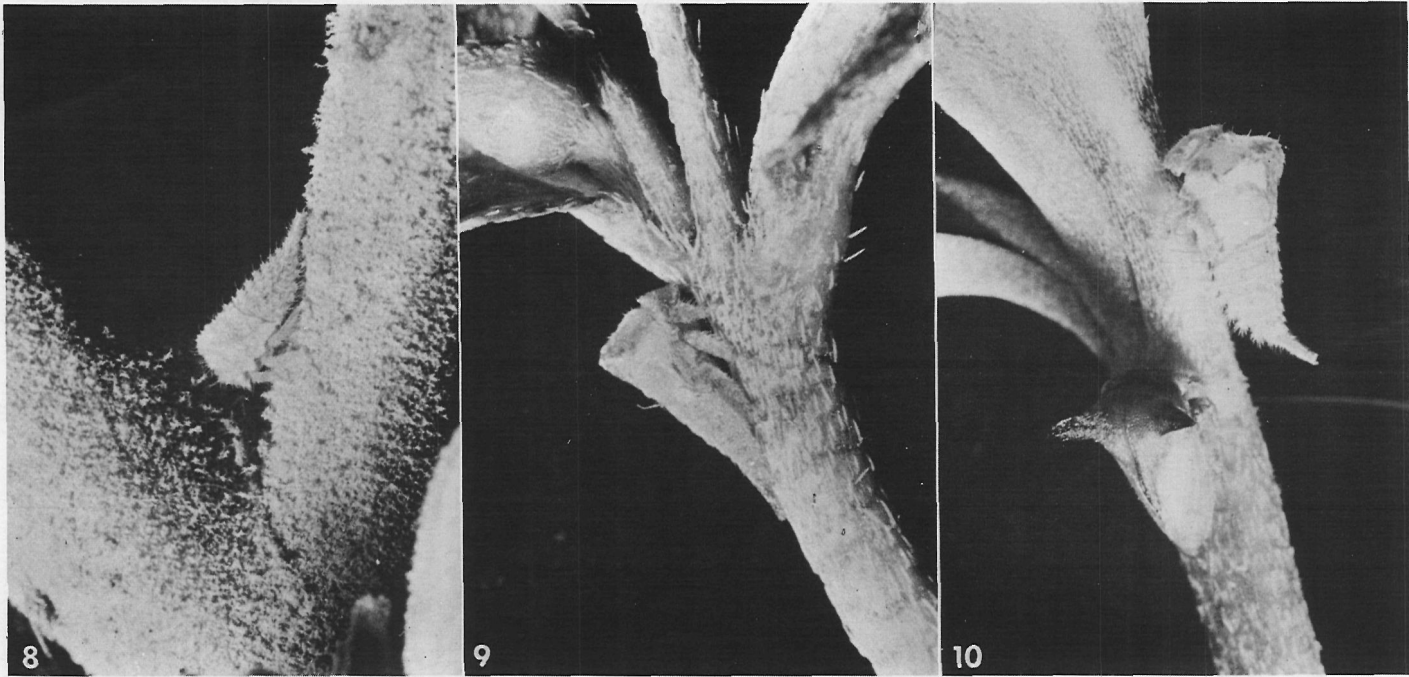


FIG. 8-10. *Tricentrus bucktoni*, nymphs and adult photographed on *Withania somnifera* and *Phyla nodiflora*: 8, 3rd instar; 9, 5th instar; 10, newly emerged adult with molted skin.

appears very soft. The thorax hardens rapidly and the normal color is completely apparent usually after 6 h.

Total time to complete the life cycle from 1st instar to adult is  $46 \pm 8$  days.

KEY TO THE 5TH INSTARS OF 4 *Tricentrus* SPECIES

1. Generally yellow marked with black, thorax and abdomen black above and bright yellow on sides and behind spines, but metanotum bright yellow above and jet black at sides; legs and under-surface of body shining luteus, smooth, not punctate; head much broader than long; pronotum with 3 strong spines and mesonotum with a strong median spine at posterior margin; wing pads extending backward as far as the lateral spine of the abdominal segment I . . . . . **T. fairmairei**  
 Pale greenish or brown marked with brownish black spots and patches, covered with minute tuberculate spines; head not much broader than long; spines of pronotum and mesonotum absent; wing pads extending to at least abdominal segment II . . . . . 2
2. Comparatively large, dark brown and marked with brownish black patches; cranial processes prominent and subacute, labium comparatively long and reaching abdominal segment I; suprahumeral buds remarkably developed, prominent and projecting upward; wing pads entirely covering abdominal segment II; 2 distinct, large median black spots on ventral sides of abdominal segments VI and VII present . . . . . **T. nordicornis**  
 Comparatively small, pale green or ferruginous brown marked with dark brown patches; cranial processes blunt, labium comparatively shorter, reaching to or only slightly beyond posterior coxae; suprahumeral buds not so remarkably developed or directed upward; wing pads not extending beyond 1/2 of abdominal segment II; median black spots on ventral sides of abdominal segments VI and VII absent . . . . . 3
3. Pale green with light brown patches; labium reaching to posterior coxae; posterior pronotal process comparatively long, broad and abruptly tapering to subacute tip, posterior margin of mesonotum substraight . . . . . **T. bucktoni**  
 Ferruginous brown marked with brownish black pigmentation; labium extending slightly beyond posterior coxae; posterior pronotal process comparatively short, narrow and gradually tapering to subacute tip; posterior margin of mesonotum distinctly concave; tubercles, on either side of mid-dorsal line of abdominal segments II and III darker in color . . . . . **T. variabilis**

**Tricentrus nordicornis** Yasmeen & Ahmad      FIG. 11–12

*5th instar.* General color dull brown mottled with brownish black, body elongated. Head (FIG. 12) reflexed and distinctly 1/3 again as wide as long, cranial processes subacute, a median tuberculate spine near upper margin of vertex present, eyes large and appear dark brown, subocular expansions prominent and well developed; antennae 3-jointed; labium comparatively long, reaching abdominal segment I, posterior portion of mandibular sclerite dark brown. Pronotum about 1/2 again as wide as long, only slightly wider than head but of the same length, lateral and costal angles of thorax prominent and well developed, suprahumeral buds dark brown, remarkably developed and directed upward in the form of projections and bearing tuberculate spines; median pronotal process well developed, strongly elevated bearing numerous tuberculate spines, median carina and portion behind middle dark brown, gradually narrowing toward apex, with tip acute and lighter in color, metathoracic wing pads dark brown anteriorly and entirely covering abdominal segment II; sides of thorax dark brown, legs ochraceous brown. Abdomen with 2 prominent large black median spots on ventral sides of segments VI and VII.

**Tricentrus variabilis** Ahmad & Yasmeen      FIG. 13–14

*5th instar.* *T. variabilis* shows similarities in many features with those of *T. bucktoni* and *T. nordicornis*, but differs in the following characters.

General color ferruginous brown mottled with brownish black, body widest at thorax and rather abruptly narrowed posteriorly. Head (FIG. 14) about 1/2 again as wide as long, cranial processes of the head weakly developed and blunt, eyes appearing reddish; labium passing slightly beyond posterior coxae, outer mar-

TABLE 1. Measurements in mm of nymphs of 3 species of *Tricentrus*.

MEASUREMENTS TAKEN	<i>T. bucktoni</i> NYMPHAL INSTARS					<i>T.</i> <i>nordi-</i> <i>cornis</i> 5th	<i>T.</i> <i>vari-</i> <i>abilis</i> 5th
	1	2	3	4	5	INSTAR	INSTAR
Total length	2.3-2.7	3.2-3.4	3.9-4.1	4.5-4.7	5.0-5.1	5.2	4.5-5.1
width	0.86-0.87	0.94-1.05	1.4-1.63	1.62-1.75	1.6-2.1	2.4	1.9-2.1
Head length	0.78-0.80	0.59-0.62	0.50-0.77	0.78-0.90	0.90-1.2	1.5	1.3
width (including eyes)	0.81-0.83	0.62-0.65	1.20-1.47	1.42-1.55	1.7-2.1	2.0	1.85
Pronotum length	0.44-0.47	0.80-0.90	0.47-1.0	0.95-1.07	0.80-1.1	1.5	1.4
width	0.85-0.87	0.94-1.05	1.35-1.63	1.62-1.75	1.6-2.1	2.2	2.1

gins of maxillary and mandibular sclerites brownish black. Pronotum distinctly  $\frac{1}{2}$  again as wide as long, slightly longer than width of head; suprahumeral buds ferruginous, developed in the form of prominent ridges at right angles to median pronotal process and covered with dark brown tubercles bearing sharp spines; median pronotal process with median and lateral carinae brownish black, gradually tapering with tip subacute and pale; metathoracic wing pads with internal margins darker in color and extending to  $\frac{1}{2}$  of abdominal segment II; legs brown. Abdomen without black median spots on ventral side of segments VI and VII, segment VIII black behind middle except for apex.

## DISCUSSION

Types of oviposition of membracoid species, with reference to both the location of the eggs and the mechanics of the process, are discussed by Funkhouser (1917). In *Tricentrus* Stål, *Gargara* Amyot & Serville and *Otinotus* Buckton, eggs are most commonly deposited on or under the bases of younger twigs. However, a number of species oviposit in buds, on leaves, or in leaf axils.

There appears to be no egg burster, micropyle or cap in the eggs of the species of the above genera studied from Pakistan, but Funkhouser (1917) reported a large cap on the eggs of most of the membracid species of Caygua Lake Basin. Capener (1962) regarded characters of the immatures useful at the tribal level but underrated their importance at the species level, stating that features varied from one instar to another and intergraded between species so that differences could be of no more than subsidiary use in separating species. However, the immature characters have proven to be excellent tools for the separation of not only previously confused genera, but also to delimit closely related species groups and species.

Within the Centrotinae, the late instars (i.e., 3-5) show marked differences and have proven helpful in separating tribes and genera. The following characters are particularly useful.

1. *Presence or absence of cranial processes in head.* The cranial processes are entirely absent in the Gargarini but are usually well developed in other tribes, particularly in early instars. As development proceeds, these are gradually reduced in size and may become inconspicuous; e.g., in *Sextius virescens* Fairmaire (Centrotypini Haupt) the cranial processes are in the form of 2 anterodorsally directed blunt projections on

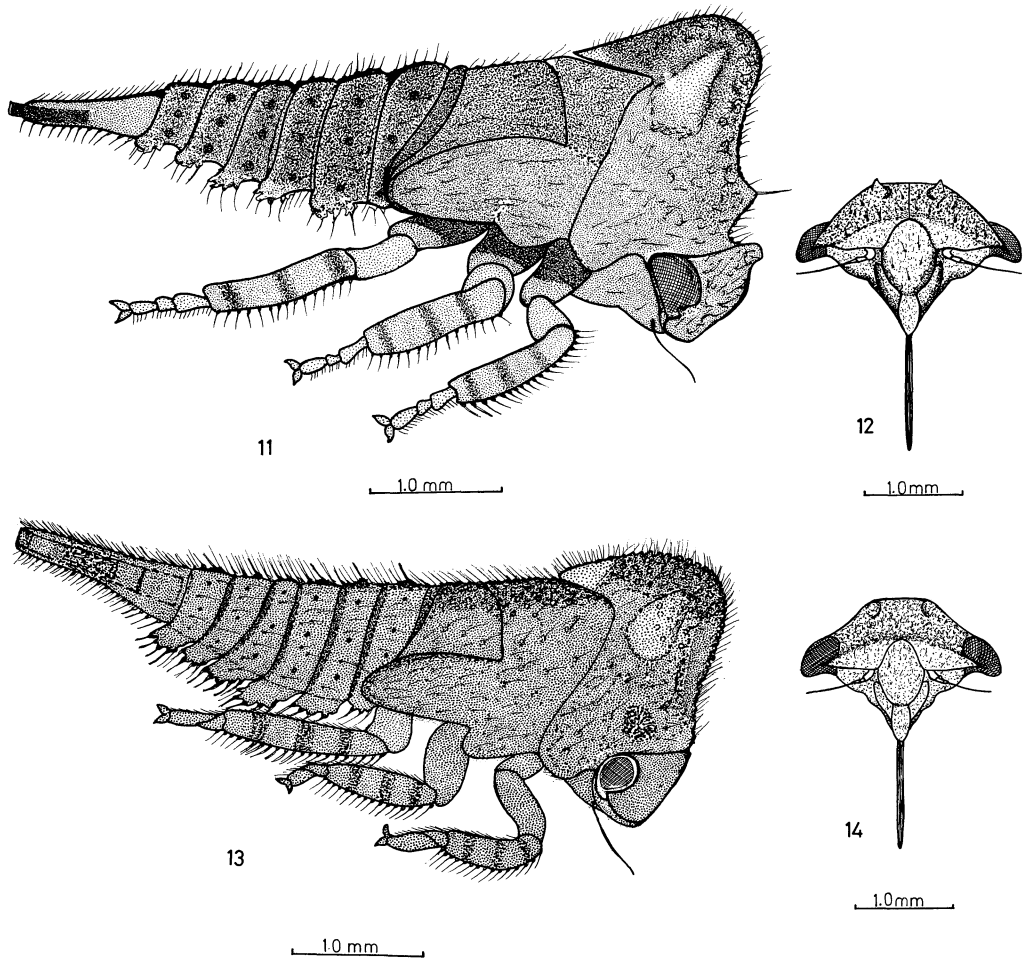


FIG. 11-14. 11-12. *Tricentrus nordicornis*, 5th instar: 11, lateral view; 12, head, ventral view. 13-14. *Tricentrus variabilis*, 5th instar: 13, lateral view; 14, head, ventral view.

each side of mid-line, but in the 4th instar these are vestiges only and in the 5th instar these are completely lost. The cranial processes are well developed in the last instars of the Tricentrini Ahmad & Yasmeen, and in *T. nordicornis* these are well developed and blunt. In the Leptocentrini Dist., the cranial processes are prominent although blunt in all instars.

2. *Shape of pronotum and its dorsal crest, presence or absence of suprahumeral buds and shape and length of posterior pronotal processes.* The pronotum with its appendages, particularly the suprahumeral buds and posterior process, shows a remarkable degree of variation in the different tribes. Within the Tricentrini, the pronotum is usually hammer-shaped with high pronotal crest, prominent suprahumeral buds and pos-



terior process usually extending to  $\frac{1}{2}$  the length of mesonotum. In the closely related tribe Gargarini, the pronotum is smoothly sloping with low pronotal crest, without any appearance of suprahumeral buds and with posterior process extending to about  $\frac{1}{2}$  the length of mesonotum. On the other hand, Capener (1968) noted that in the Centrotini and Leptocentrini the pronotum differs in shape in different genera. In Centrotini, the pronotum sometimes possesses an erect thorn-like process or is subconically directed forward and upward. The pronotal crest may be moderately curved or raised high and strongly rounded, with vertical or rather concave metopidium, with small or developed suprahumeral buds and with posterior process usually extending to about  $\frac{1}{2}$  the length of mesonotum. In the Leptocentrini, the pronotum appears elevated in an upright thorn-like process having a cleft at the tip or with receding metopidium which then curves forward into the pronotal crest, shaped something like a phrygian cap. The pronotal crest may be low and weakly arcuate or high and strongly elevated, with posterior process variable in length and extending to about  $\frac{2}{3}$  of mesonotum, sometimes covering the metanotum, usually with prominent suprahumeral buds. However, Capener (1968), while describing the last instar of African Centrotinae, noted a moderately high but somewhat truncated pronotal crest in the Xiphopoeini Capener.

In the last instars of the Centrotypini, the pronotum is usually dominant, comprising about  $\frac{1}{2}$  the thorax when viewed externally, with "dorsal hump" (pronotal crest) extending back in the form of a posterior process covering the entire length of the mesonotum and with well developed suprahumeral buds. Kitching & Filshie (1974) discussed in detail the progressive distortion of the thorax with immature stages of *Sextius virescens* and noted that this distortion reaches a maximum in the 5th instar and does not appear to increase upon ecdysis to the adult. Most of the development which occurs at the time of the transformation from 5th instar to adult involves the increase in size and length of lateral pronotal projections, which are comparatively less developed in the last instar.

3. *Presence or absence of spinules on hind trochanters.* The spinules on hind trochanters appear only in the Tricentrini. This character also serves to separate the adults from those of other closely related tribes, such as the Gargarini and Centrotini.

4. *Presence or absence of abdominal lamellae.* The lateral lamellae on either side of the abdominal segments are usually developed in most instars of most tribes; however, sometimes they are entirely absent. Within the Tricentrini, Gargarini and Leptocentrini, the lamellae are usually well developed; in the Leptocentrini, they are either long, flattened and apically rounded or spine-like, but they are entirely absent in *Otinotus*. In the Xiphopoeini and Centrotini, the abdominal lamellae are comparatively short, and in the latter these are either broad and fringed with hairs or appear rounded. In the Centrotypini, the lamellae appear in the late stages and usually have serrated edges.

5. *Shape of subgenital plate in the ♂.* The subgenital plate does not make its appearance until the 5th instar. The shape of this plate may be used to separate members

of closely related genera, such as *Gargara* and *Tricentrus*; in *Gargara* it has a much broader base and gradually narrows to an acute apex, whereas in *Tricentrus*, it appears narrower and stub-like, with a subacute or rounded apex.

The following characters were found to be important in distinguishing the 5th instars of the different *Tricentrus* species discussed.

1. *Color*. The last instar of *T. fairmairei* is usually lighter in color than that of all other species studied. The immatures of all species are marked with definite spots and pigmentation on thorax, legs, wing pads and abdomen and are easily distinguished by their color pattern, e.g., immatures of *T. nordicornis* are characterized by the presence of 2 large median black spots on abdominal sterna VI and VII.

2. *Size of the head*. The head is distinctly more than  $2\times$  wider than long in *T. fairmairei*, comparatively less wide but about  $2\times$  as wide as long in *T. bucktoni* and about  $\frac{1}{2}$  again as wide as long in *T. variabilis*; in *T. nordicornis* it is distinctly  $\frac{1}{3}$  again as wide as long.

3. *Shape and size of the cranial processes*. The cranial processes also differ in shape and size. These are well developed and rather subacute in *T. nordicornis*, weakly developed and rounded in *T. bucktoni* and *T. variabilis* and almost inconspicuous in immatures of *T. fairmairei*.

4. *Length of labium*. The labium is usually very long in immatures of *T. nordicornis* extending to abdominal segment I, comparatively short in *T. variabilis* where it extends slightly beyond the posterior coxae, and very short in *T. bucktoni*, just reaching the posterior coxae. There is no mention of length of labium in the description of the 5th instar of *T. fairmairei* given by Funkhouser (1919).

5. *Presence of tubercles and spines on body*. Funkhouser (1919) reported for last instar of *T. fairmairei* 3 strong spines on the pronotum, including a median dorsal spine and 2 lateral spines, 1 on each side above humeral angles, a median dorsal spine on mesonotum and a strong lateral spine on each abdominal segment. In *T. nordicornis*, a median tubercle on the head near upper margin of the vertex bearing a spine is present.

6. *Shape of suprahumeral buds*. The suprahumeral buds, which appear as lateral projections on the pronotum, are usually well developed in immatures of all *Tricentrus* species. The suprahumeral buds in immatures of *T. nordicornis* are remarkably developed and directed upward, recalling the long and well-developed suprahumeral horns of the adult.

7. *Shape of posterior pronotal process*. The median projection of the pronotum extends backward in the form of a posterior process and differs in shape and size in immatures of different *Tricentrus* species. The posterior process in *bucktoni* appears longest among all of the studied species and abruptly tapers to a subacute apex. It is similar to the long posterior process of the adult, which usually extends far beyond internal angles of the tegmina.

8. *Length of wing pads*. The length of the wing pads also varies in the immatures of different species, but comparatively less so. The wing pads are usually short, reaching

to abdominal segment I in instars of *T. fairmairei*, slightly longer in *T. bucktoni* and *T. variabilis* where they reach to ½ of abdominal segment II and much longer in *T. nordicornis*, entirely covering abdominal segment II.

In summary the characters of the immatures of *Tricentrus* go hand-in-hand with the adult characters and are important in differentiating closely related species and species groups.

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