Arch. Moll. | 98 | (5/6) | 291—317 | Frankfurt a. M., 20. 12. 1968

New *Tricula* from Thailand.

By

GEORGE M. DAVIS,

406th Medical Laboratory, U.S. Army Medical Command, Japan, APO San Francisco, California 96343.

With 22 figures.

Introduction.

The genus *Tricula* is of interest for several reasons. No anatomical data are available concerning the structures of the reproductive systems, nervous and digestive systems, or head-foot morphology. The genus has been confused with *Oncomelania*, the taxa of which transmit *Schistosoma japonicum* in the Orient. The genus has been associated with the transmission of *Paragonimus* (lung flukes) or schistosomes.

CHUNG & al. (1963) stated that *Tricula* sp. was the first intermediate host of *Paragonimus szechuanensis* in China. HABE & MIYAZAKI (1962) described as *Tricula chiui* the first intermediate host of *Paragonimus iloktsuenensis* on Taiwan (Formosa). DAVIS & CHIU (1964) and DAVIS (1968) found that *"T. chiui"* was actually *Oncomelania hupensis chiui*. *Schistosomaphora minima* BARTSCH (1936) of Japan was referred to *Tricula* by ABBOTT & HUNTER (1949) yet in initial studies on this taxon I have found this snail cannot be considered in the same subfamily as *Tricula*.

Confusion has resulted as an outgrowth of placing Oriental turreted hydrobiid snails smaller than *Oncomelania hupensis formosana* or *O. h. quadrasi*, coming from mountain streams or seepage, and having few gill lamellae — into the genus *Tricula*.

Unfortunately very little is known about the genotype, *Tricula montana* BENSON (1843). This species has not been found again since it was discovered in Bhimtal, India (PRASHAD 1921a, b; RAO 1928). All that is known about the species is summarized by STIMPSON (1865), ANNANDALE (1924), RAO (1928) and THIELE (1928). The data are not sufficient to define the genus or assign the genus to a subfamily.

In 1965 I was notified by members of the Medical Research Laboratory, Southeast Asia Treaty Organization (SEATO), Bangkok, Thailand, that they had located a few populations of *Tricula* in NW-Thailand near the Burma border. In January, 1967, I went to Thailand and collected large numbers of *Tricula* with the SEATO team. The shell material, radula, and habitat agreed very well with what was know of taxa referred to *Tricula* in India, Burma, and China. The glassy or porcelaneous shells were clearly different than those of *Oncomelania* or so-called *Tricula* from Japan.

The purpose of this paper is to 1) describe two new species of *Tricula*, 2) base a generic definition for *Tricula* on the anatomical data presented here, 3) discuss the systematic position of *Tricula* with respect to subfamily position.

Acknoledgements.

I am indebted to the SEATO and the malacological research team associated with the SEATO Medical Research Laboratory for helping me obtain living material of *Tricula*. Special thanks go to Mrs. SETSUKO SUZUKI for her work in sectioning the *Tricula* brought back to the 406th Medical Laboratory. I wish to thank LTC JOSEPH F. METZGER, Commanding Officer, 406th Medical Laboratory for supporting my research efforts in Thailand.

The drawings were made by the author. Photographs of the shells were made by CPT RONNIE J. GARCIA and staff of the 628th Medical Illustration Detachment at the 406th Medical Laboratory.

Materials and methods.

Living material was used for the anatomical studies. All dissections were carried out at magnifications of 40× and 60× using a Nikon (Nippon Kogaku) SM dissecting microscope. Structures of the reproduction system were made clearer by vital staining with aqueous neutral red. Structures of the nervous system were made clear by dissecting under 1/2 strength Bouin's fixative.

Shells were cleaned of black deposits, debris, and periostracum by soaking in commercial Clorox (5·25% sodium hypoclorite). In this way true shell color and micro-sculpture were made clear.

Radulae were prepared and studied as discussed by DAVIS (1966, 1967).

Histological studies involved fixing snails in Bouin's fixative, making serial sections at 8 μ (longitudinal and cross) and staining with standard hematoxylin and eosin.

Drawings were made by measuring all structures with a standard ocular micrometer.

General external morphological features.

The head-foot region of *Tricula bollingi* is shown in Figs. 9 and 12. General features are the same in both species. Of particular interest are the suprapedal fold (Su), omniphoric groove (Om), and morphology at the base of the tentacles.

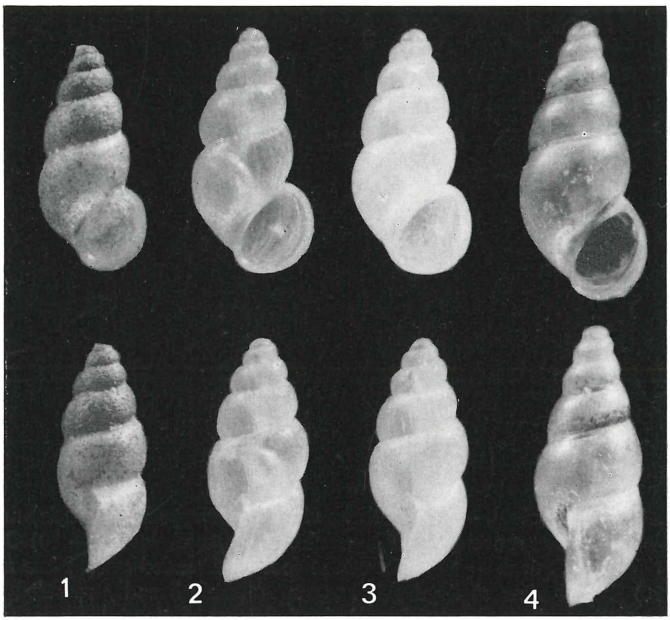
The subfamily Pomatiopsinae is characterized by having a strongly developed suprapedal fold and omniphoric groove (DAVIS 1967) while in the Hydrobiinae the neck region is smooth, tissue extending out to the foot with no inter-

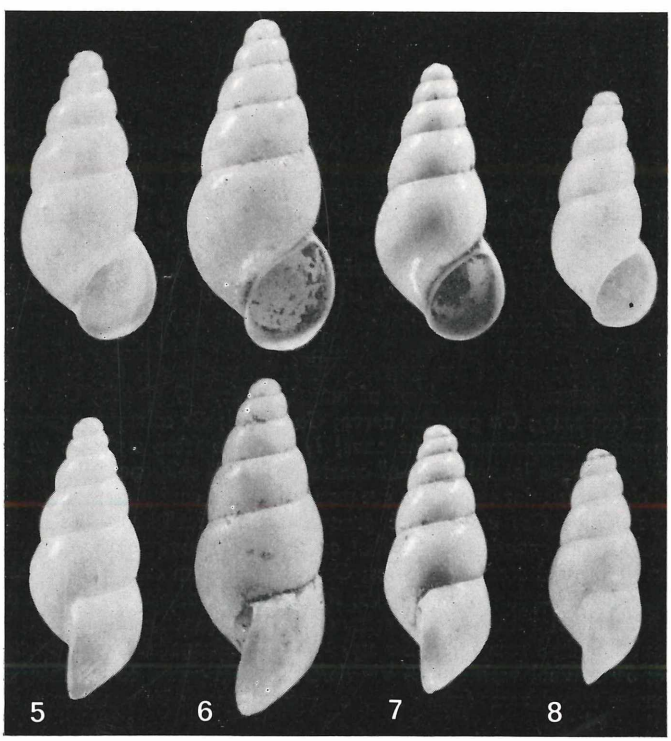
---

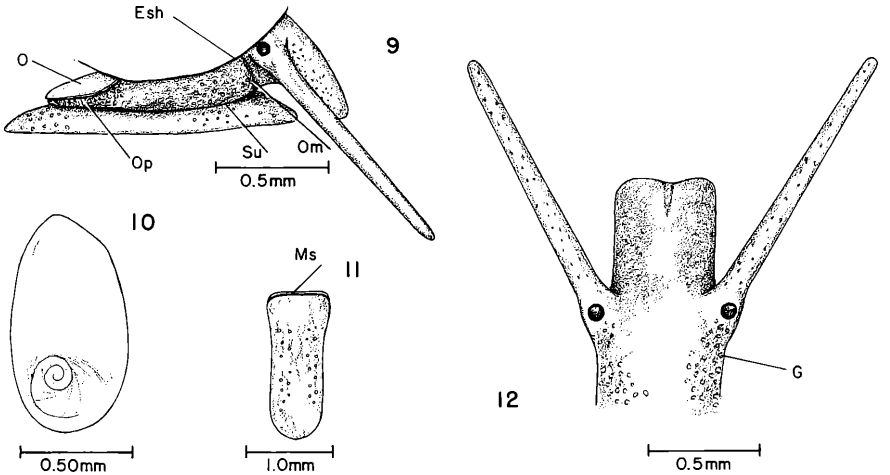
▶

Figs. 1-3. *Tricula burchi.* — 1) Type specimen, see Tab. 1 for measurement. — 2-3) Paratypes which were cleaned with Clorox. All sizes of shells are in proportion to Fig. 1.
Fig. 4. *Tricula bollingi,* type specimen, see Tab. 5 for measurements.

Figs. 5-8. *Tricula bollingi.* — 5) Paratype. — 6) Snail of large class (Tab. 6) from Wat Tamtabtao population. — 7) Intermediate size snail (Tab. 6) from Wat population and similar to the type series of *T. bollingi.* — 8) Snail of small class (Tab. 6) from the Wat population. — Snails in Figs. 6-8 were sub-fossils which were abundant in the sandy river bottom at the Wat area.


1
2
3
4


5
6
7
8



Figs. 9-12. *Tricula bollingi.* — 9) Head showing the suprapedal fold (Su) and weakly developed omniphoric groove (Om). No pedal crease was observed. — 10) Operculum; corneous, thin, paucispiral. — 11) Sole of the foot in extended state. Note mucous slit (Ms). — 12) Dorsal view of head and rostrum showing broadly rounded tentacular tips, slight swellings about the eyes, and lack of clusters of glandular units (G) pressed about the medial edge of the eyes.

Glossary of terms: *a* cut wall of the bursa copulatrix; *b* pericardial cavity; *c* posterior mantle cavity; *d* kidney cavity; *e* core of tissue supporting the receptacular duct; *f* point where a group of lobes was removed from the vas efferens; *g* prominent twist where oviduct (Ov) and receptacular duct (Rd) join; *h* point where receptacular duct leaves the pericardium; *Apo* anterior portion of pallial oviduct; *Ast* anterior chamber of the stomach; *B* bursa copulatrix; *Bb* basal bar supporting the basal cusps of the central tooth; *Bp* basal process of the central tooth of the radula; *Ce* cuboidal cells; *Ci* ciliary bands; *Cl* columellar muscle; *Co* columnar cells; *D* digestive gland; *Dob* duct of bursa copulatrix; E_2 external mantle cavity nerve 2; E_3 external mantle cavity nerve 3; *Emc* end of the mantle cavity; Es esophagus; *Esh* edge of the shell; *Fa* face of central tooth; *Fmc* floor of mantle cavity; *G* glands; Gl_2 gland type 2 of the verge (see text); *Gn* gonadal nerve; *Go* gonad; *Gr* calcareous granules; *I* intestine from pellet compressor to the anus; I_1 intestine from style-sac to pellet compressor; *K* kidney; *La* lateral angle of central tooth; *M* thickened edge of the mantle; *Mbg* multilobed testicular units; *Mc* cut ventral mantle cavity epithelium; *Ms* mucous slit; *O* operculum; *Om* omniphoric groove; *Op* operculigerous lobe; *Ov* oviduct (general term; from gonad to the pallial oviduct); Ov_1 oviduct from gonad to point where duct of seminal receptacle arises; Ov_2 oviduct from duct of seminal receptacle to pallial oviduct; *Pn* pericardial nerve; *Ppo* posterior section of pallial oviduct; *Pr* prostate; *Pst* posterior chamber of stomach; *Rd* receptacular duct; *Sbv* subvisceral connective; *Sr* seminal receptacle; *Sts* style-sac; *Su* suprapedal fold; *Suv* supravisceral connective; *Sv* seminal vesicle; Vd_1 vas deferens from gonad to prostate; Vd_2 pallial vas deferens = anterior vas from prostate to tip of verge; *Ve* vas efferens; *Ver* verge; *Vg* visceral ganglion.

ruption by the fold of tissue called the suprapedal fold and there is no omniphoric groove (DAVIS 1966, for *Hydrobia totteni*).

The suprapedal fold is not so strongly developed in *Tricula* and lacks the permanence observed at all times in the Pomatiopsinae. The fold is most evident as an outfolding of the body over the edge of the foot when the animal is moving over the substrate and seems to result from compression of lateral tissue due to the weight of the body. When the shell is held above the substrate and the animal moves out from the shell to stretch the foot towards the substrate, the suprapedal fold is smoothed out, a condition never seen in the Pomatiopsinae.

In *Tricula* there is a very faint or slightly developed omniphoric groove which was seen to appear and disappear depending upon the movements of the animal. The groove in *Tricula* is hard to discern because the animals are small and the area of the groove devoid of dense pigment (no pigment in some cases).

The eyes at the bases of the tentacles are in very pronounced swellings in the Pomatiopsinae. The situation in *Tricula* is the same as that in the Hydrobiinae; the eyes are in slight swellings at the bases of the tentacles.

While masses of glandular units, appearing white or yellow, are found about the medial edge of the eyes in the Pomatiopsinae ("eyebrows" as described by ABBOTT 1948), there is no such concentration in *Tricula* (Fig. 12). Such glandular units are scattered back along the "neck" (G, Fig. 12). RAO (1928), however, stated that in *T. martini* there was "a lunate yellow mark on the inner half ." about the eye which probably corresponds to the "eyebrow" described by ABBOTT (1948).

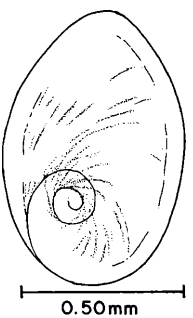


Fig. 13. Operculum of *T burchi*; corneus, thin, paucispiral.

The foot of *Tricula* is agile, elongate, slightly expanded and truncate in front while broadly rounded behind. The mucous slit (MS, Fig. 11) runs across the entire front of the foot. RAO (1928) states for *T. taylori* that the foot was "bell-shaped, broad arcuate anteriorly and rather produced at its antero-lateral angles, and narrower and rounded posteriorly." He says of *T. martini* that the "foot is short, broad, blunt at the lateral angles, and broadly rounded behind."

The operculum of *Tricula* is corneous, thin and paucispiral (Figs. 10, 13).

Description of species.

Tricula burchi n. sp.

Type. — The type is 3481a stored at the SEATO Medical Research Laboratory (SMRL). The uncleaned type is shown in Fig. 1 while two cleaned paratypes are shown in Figs. 2 and 3.

Locality — Chieng Mai Province, Chieng Dao District: Huai Mae Kut at Ban Tham. 23, 26 Jan., 1967.

A road to Chieng Dao Cave turns off the main road from Fang to Chieng Mai 72 km from Chieng Mai. A stream — the Huai Mae Kut — runs along this side road and a point 5 km from the main road is the locality for this species.

The locality is located in Map Series L509, sheet NE 47-2 of the U.S. Army Map Service. It is in section MB, coordinates 495 and 2142. The longitude is about 99° and the latitude is 19° 21′ The stream is part of the Mae Nam Ping River drainage system which flows south.

The water in the stream was cool and clear with a pH of 6·8-7·0. Parts of the stream were choked with aquatic plants and quite shaded by trees and plants along the edge of the stream. The stream flowing from the base of the Chieng Dao Mountain was 4-5 feet wide and 1-3 feet deep at the type locality.

The snails were completely submerged and either on roots and stems of aquatic plants or on leaves and other material of the substrate.

Shell, Type Population. — Shell measurements for the type and 17 of the paratypes are given in Table 1. Females were more numerous than males; the majority of females were 5·5 whorls while the majority of males were 5·0 whorls.

Shells of the type and two paratypes are shown in Figs. 1 to 3. The animal of the type is dried within its shell. Shells of this species are elongate, turreted, and the length of the body whorl is greater than the length of the remaining whorls. The suture is impressed and the whorls are moderately convex. There is no tendency for the formation of a keel. The whorls have an adapical sutural

Table 1: Shell measurements for the type and paratypes of *Tricula burchi*.

shell features measured (mm)	whorls	statistic	shell length	shell width	ratio l/w	aperture length	aperture width	body whorl length
type (female)	5·5	—	2·75	1·25	2·20	1·06	0·88	1·63
paratypes 5 males	5·0	$\bar{X}$	2·50	1·25	2·20	1·04	0·88	1·47
		S	0·07	0·06	—	0·07	0·04	0·13
		Se	0·03	0·03	—	0·03	0·02	0·06
2 males	5·5	$\bar{X}$	2·69	1·28	2·10	1·06	0·88	1·56
10 females	5·5	$\bar{X}$	2·78	1·34	2·07	1·11	0·94	1·64
		S	0·09	0·06	—	0·05	0·04	0·06
		Se	0·04	0·02	—	0·02	0·01	0·02

$\bar{X}$ = mean, S = standard deviation, Se = standard error of the mean, l = length, w = width.

ramp and thus appear slightly shouldered. The suture is slanted and appears crenulated due to the puckering or pleating of the abapical whorl at the suture.

The apex is blunt and the diameter of the apical whorl is 0·29-0·31 mm.

The aperture varies from ovate to subquadrate. In the latter condition the abapical end is expanded. Shells are anomphalous or with a clearly defined umbilical chink or narrow opening. The peristome is complete, the parietal lip is distinct and fused as a callus to the parietal wall. The columellar lip is thick, arched, expanded and reflected either over the umbilical chink or the base of the shell. The outer lip is slightly thickened but does not form a varix; it is sinuate in lateral view.

Shells from living specimens are glassy and transparent; the columella is clearly visible through the shell. Only shells of animals long dead are porcelaneous. Numerous fine orthocline growth lines are crossed by fine spiral lines.

External Morphology. — The head-foot region of this species is devoid of pigment. Behind each eye and back along the "neck" is a strip on each side of scattered yellow granules (= glandular units, G).

The tentacles are elongate, 0·82 ± 0·17 mm long and broadly rounded at their tips. The edges are ciliated; there was no evidence of hypertrophy or sensory bristles (60× magnification).

The animal moves along the substrate in a smooth glide.

There are 21 ± 4 gill leaflets. The structure of the gill is typically hydrobiid. The osphradium is hydrobiid in shape and position.

Male Reproductive System. — The male reproductive system is shown in Figs. 14 and 15. Most of the snail's body is shown uncoiled and in ventral or columellar aspect (Fig. 14). The head-foot region is not shown nor the tip of the digestive gland. The drawing was made to show the relationships of the organs of the reproductive system to the main body regions.

The coiled seminal vesicle (Sv) is shown arising from the vas efferens (Ve) in the antero-ventral region of the digestive gland (D). The multilobed testicular units draining into the vas efferens (one such unit arises from f, Fig. 14) were removed so as not to hide the vas efferens or seminal vesicle from view. The tube of the seminal vesicle is thick and the regular coiling pattern is routinely found.

The posterior vas deferens (Vd_1) runs from the seminal vesicle as a straight tube over the esophagus (Es) where the latter enters the stomach, travels along the esophagus a short distance anteriorly, and then turns to the right towards the prostate (Pr). Close to the prostate the tube narrows and enters the prostate with a diameter of 48 μ.

The prostate overlies the end of the mantle cavity (Emc) so that the posterior part is pressed on the anterior end of the style sac (Sts) and the loop of intestine (I) which swings over the ventral tip of the style sac. The prostate is 0·85-0·98 mm long and 0·36-0·40 mm wide. The ventral surface is quite glandular as shown (Fig. 14). The prostatic glands empty into a collecting duct at the left edge of the prostate and just medial enough to be hidden from view when the prostate is studied in ventral aspect. The posterior vas deferens enters this collecting duct 72-80 μ posterior to the point the pallial (anterior) vas deferens (Vd_2) leaves the duct to run obliquely away from the prostate toward the columellar muscle, supported by the ventral wall of the mantle cavity.

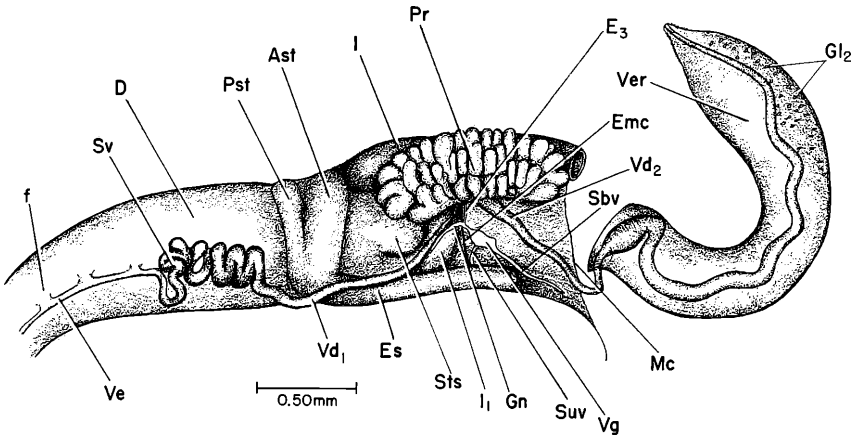


Fig. 14. Male *T. burchi* uncoiled and exposing the ventral or columellar side. The neck and head areas are not shown and only a portion of the digestive gland (D) is illustrated. The lobes of the gonad were removed from the vas efferens at points f in order to enable one to have a clear view of the seminal vesicle (Su). The kidney tissue was removed to expose the style-sac (Sts) and intestine (I, I_1). The intestine at I_1 has just emerged from the left ventro-lateral aspect of the style-sac and coils over the tip of the sac. (see Glossary of terms Figs. 9-12).

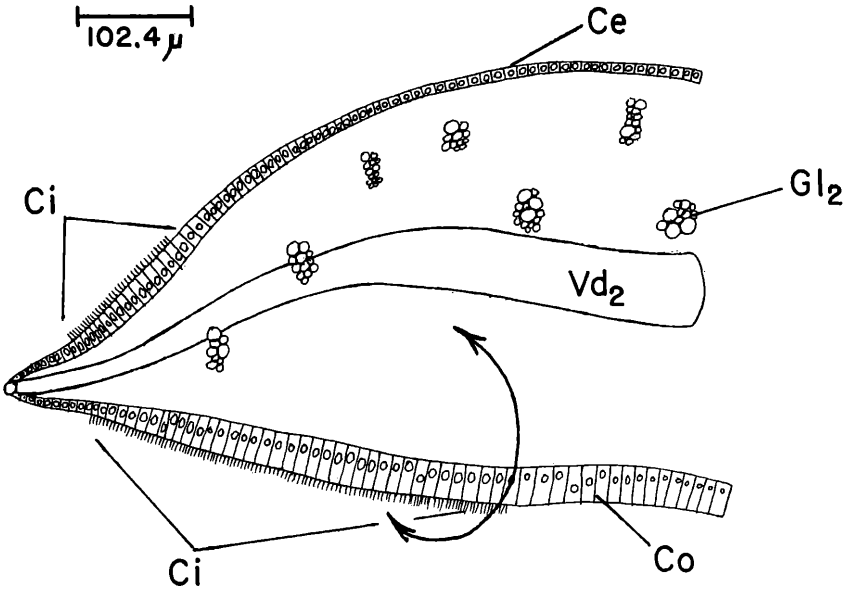


Fig. 15. Schematic enlargement of the tip of the verge showing the characteristic bands of cilia (Ci) and "gland" type (Gl_2). The arrow indicates the extent of the ciliary area over the lateral aspects of the concave section of the verge. (see Glossary of terms Figs. 9-12).

The vas (Vd_2) runs onto the floor of the mantle cavity along the "neck" turns dorsally and enters the "neck" to run into the base of the verge (Ver). In the base of the verge the vas becomes swollen and is wrapped in a thick sheath of circular muscles. This section is the ejaculatory duct. The vas runs the length of the verge in the middle of the verge as a prominent, wide, highly convoluted tube (more convoluted, usually, than shown in Fig. 14). It opens at the tip of the verge as a simple opening without papilla or armature.

The verge is carried coiled counter-clockwise on the "neck". The verge is thick, large, and muscular so that the coil over the neck cannot reach a full 360°. It is "simple" as there are no lobes or appendages; there are no exterior fleshy glands and it has only one duct, the vas deferens.

Scattered under the epithelium, especially along the convex edge, are numerous "glands" (Gl_2, Figs. 14, 15) as discussed by DAVIS (1967) for *Oncomelania* and *Pomatiopsis*. The "glands" are groups of spheroidal units which appear as white dots at magnifications of 40× and 60×. The units observed under the compound microscape appear as shown in Fig. 15.

The verge is ciliated in a distinct manner (Fig. 15). A short strip of cilia is found on the convex side of the verge near the tip. The strip is 115 μ long. On the concave side cilia extend back from the tip of the verge 380-400 μ. On the concave side the cilia are not limited to the edge of the verge but arise from the epithelium along the sides of the verge to a point indicated by the arrow in Fig. 15.

The strips of cilia (long and short strips along the verge) are like those found in *Oncomelania* (DAVIS 1967); in the latter genus the cilia are not found along the sides of the verge. The cilia arise from a pronounced columnar epithelium. On the convex edge of the verge the cells become cuboidal (Ce) with the termination of the cilia; on the concave side the columnar cells remain pronounced to the base of the verge. In the area of the base, columnar cells appear to be quite glandular in function.

Female Reproductive System. — The female reproductive system is shown in Figs. 16 and 17. Eggs pass from the gonad (Go) to the pallial oviduct (Ppo, Apo) via the oviduct (Ov). Near the pallial oviduct the bursa copulatrix (B) and seminal receptacle (Sr) arise from the oviduct. Sperm enter the system at the rear of the mantle cavity and pass to the seminal receptacle along the receptacular duct. No spermathecal duct runs along the pallial oviduct as in the Pomatiopsinae.

The bursa copulatrix (B) is an extremely thin walled sac fused with and inseparable from the posterior section of the pallial oviduct (Ppo). In the living animal, in most cases, one cannot discern where the pallial oviduct ends and the bursa begins. In only a few specimens was there a slight yellow tinge in the bursa thereby readily identifying this organ. The bursa was so thin walled that in gross dissection I could not determine the point of connection of this organ with seminal receptacle, oviduct, or pallial oviduct. The seminal receptacle and interconnections of oviduct, seminal receptacle, and oviduct are medial to the bursa and thus are hidden from view when the bursa is viewed from the ventral aspect (Fig. 16).

The bursa copulatrix varies from 0·41-0·60 mm (average 0·46 mm) in length when measured in gross dissection after vital staining with neutral red. From

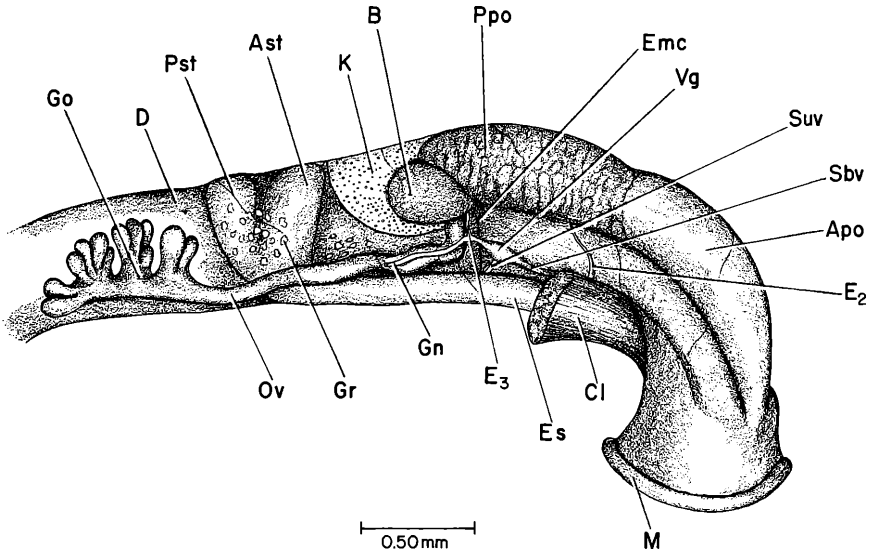


Fig. 16. Female snail *(T. burchi)* uncoiled and exposing the ventral side. Only a part of the digestive gland (D) is illustrated. All structures are shown as observed through the epithelium. The most prominent structures were the pallial oviduct (both sections Ppo and Apo) and whitish kidney tissue (K). (see Glossary of terms Figs. 9-12).

serial sections it was found that the wall separating the bursa and pallial oviduct was 4-5 μ thick. The central core of the bursa was filled with a yellowish fluid packed with unoriented sperm in various stages of disintegration. The cells of the wall of the organ were lightly eosinophilic in contrast with the strongly eosinophilic cells of the posterior pallial oviduct (Ppo). As shown in Fig. 17, reconstruction from serial sections shows that the bursa connects with the duct of the seminal receptacle and receptacular duct with a lumen of 60-65 μ and together they have common access to the oviduct (Ov_2).

The seminal receptacle is U-shaped (Sr, Fig. 17). In gross dissection this was always very easily dissected free. The organ was sturdy and easily manipulated; only the duct to the bursa copulatrix and oviduct was too thin-walled to be followed. The distance from the tip of the seminal receptacle to the bend was 0·30 mm (measured in gross dissection). Sperm were packed in the seminal receptacle, their heads oriented together toward the wall. Numerous sperm were free in the lumen.

The receptacular duct (Rd, Fig. 17) was best studied from serial sections although it it was easily studied in gross dissection from the seminal receptacle to the area of the pericardium. The receptacular duct opened along with the duct of the seminal receptacle into a wide tube running immediately into the oviduct (Ov_2). Part of the length of the receptacular duct was bound to the duct of the seminal receptacle. In this section the width of the duct and circular muscle sheath was 32 μ while the lumen was 4-5 μ (from serial sections). 80-

90 μ from the opening, the duct and muscle sheath narrowed to a diameter of 24 μ with a lumen of 3 μ. 90 μ, and beyond the level of the seminal receptacle the duct is in a narrow core of tissue (e, Fig. 17) bounded by three cavities; the pericardial (b), kidney (d) and posterior mantle (c). The duct entrance is at the rear of the mantle cavity. A ciliated groove on the mantle cavity floor leads to the entrance of the receptacular duct; the diameter of the groove was 13-14 μ.

The relationship of the receptacular duct and mantle cavity was studied from 9 snails which were sectioned in cross or longitudinal planes. As the duct became more narrow, it was difficult to discern if the duct was open and functional at the mantle cavity wall. 24 μ from the entrance the circular muscle sheath was 3 μ thick and the lumen of the tube appeared to be 2 μ. In no case did it appear that the duct entered the pericardium.

The gonad was 0·50-0·70 mm long and about 0·27 mm wide when measured in gross dissection. There were 4-5 masses of lobes arising from a very wide collecting duct.

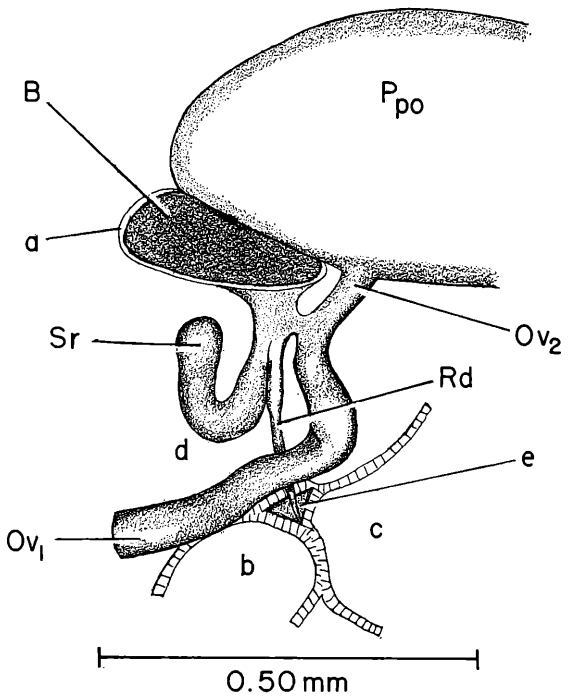


Fig. 17. Female reproductive system of *T. burchi*. A reconstruction from serial section of the way in which the seminal receptacle (Sr), bursa copulatrix (B), receptacular duct (Rd), oviduct (Ov_2) and pallial oviduct (Ppo) interconnect. Only the seminal receptacle and receptacular duct could be easily and clearly dissected free under the dissecting microscop. The bursa and duct connections with the seminal receptacle and oviduct were too thin walled to be dissected free. (see Glossary of terms Figs. 9-12).

The oviduct runs from the gonad, over the stomach covering the point where the esophagus (Es) enters the stomach; it extends along the esophagus and swings toward the bursa copulatrix before reaching the end of the mantle cavity (Emc, Fig. 16). The oviduct appears to disappear beneath the bursa. In gross dissection the oviduct is wide, about 70 μ.

The oviduct from the edge of the bursa as seen in Fig. 16 to its entrance into the pallial oviduct was studied from serial sections. The relationship of the oviduct with the bursa, seminal receptacle, and receptacular duct is shown in Fig. 17. The diameter of Ov_2 was 27-30 μ. The bursa and seminal receptacle connected with the oviduct 85 μ from the point of entry of oviduct (Ov_2) into the pallial oviduct.

The pallial oviduct measured about 1·93 mm long in gross dissection. It was distinctly divided into two sections, a phenomenon easily observed in the whole living animal. The posterior pallial oviduct (Ppo, Fig. 16) appeared highly glandular with flimsy tissue and a greyish appearance while the anterior pallial oviduct (Apo) looked non-glandular, solid with white tissue. The anterior section is longer than the posterior part. The latter overlies the mantle cavity as does the prostate as described for the male. The posterior end of the pallial oviduct and the bursa copulatrix are wrapped in kidney tissue (k, Fig. 16). The opening is into the mantle cavity near the mantle collar.

The two sections of the pallial oviduct are sharply divided histologically; the posterior section staining brightly with eosin while the anterior part stains a very dense blue-purple with hemotoxylin. The lips about the orifice stain lightly with eosin thereby showing their non-glandular nature.

Digestive System. — The salivary glands are "simple", one on each side of the buccal mass. The attachment to the buccal mass is the usual arrangement found in the Hydrobiidae. Each gland is an elongate tube. The stomach is with style sac. The intestine leaves the left ventrolateral side of the style sac, swings across the tip of the style sac and bends dorsally as described for *Pomatiopsis* (Davis 1967).

Fecal pellets are typically rissoacean as discussed by Taylor (1966).

The radula is taenioglassate. Statistics on the length and width of 7 radulae as well as the number of rows of teeth on the radular ribbon are given in Table 2. Rows of teeth were counted as described by Davis (1966). The cusp formula most commonly found for each tooth is given in Table 3 while variation in cusp formula per tooth is documented in Table 4.

Drawings representative of each of the 7 teeth in a row are presented in Fig. 18A. The central tooth morphology is different than that of the Hydrobiinae as discussed by Davis (1966). The basal cusps arise from the face of the tooth, not the lateral angle. In *Tricula* the basal cusps arise from a thickened bar or ridge across the face of the tooth (Bb, basal bar). The basal bar is not present in the Pomatiopsinae. The basal process (Bp) is thin and membranous; it arises from the basal bar. The teeth are shown with cutting edges attached (e. g. left inner marginal) or with cutting edges broken off (e. g. right outer marginal). Denticle counts on the marginals included the tiny supports for cutting edges down along the edges of the tooth (5 such are shown in the right inner marginal, devoid of cutting edges).

Table 2. Statistic on the radulae of 7 specimens of *Tricula burchi*.

radula features measured in μ or counted	statistic $\bar{X}$	S	Se
radular length	464·11	20·86	7·93
radular width	65·21	9·89	3·70
total rows of teeth	69·00	2·27	0·86
No. of rows of teeth in the formative stage	10·00	2·38	0·90

$\bar{X}$ = mean, S = standard deviation, Se = standard error of the mean.

Table 3. A general formula for the most common cusp arrangement found in *Tricula burchi* (from 8 radulae).

tooth	cusp formula	snails where the arrangement was commonly found on each tooth (%)
central	$\frac{2—1—2}{2—2}$	100
lateral	3—1—3 (4)	100
inner marginal	12 (13)	100
outer marginal	10 (11)	100

Table 4. The various types of cusp arrangement for the different teeth in 8 radula of *Tricula burchi* and the percentage of radulae showing that arrangement at least once.

central		lateral		inner marginal		outer marginal	
arrangement of cusps	%	arrangement of cusps	%	number of cusps	%	number of cusps	%
$\frac{2—1—2}{2—2}$	100	3—1—3	88	13	100	11	88
$\frac{2—1—2}{3—3}$	38	3—1—4	88	12	63	10	75
$\frac{2—1—3}{2—2}$	13	4—1—4	25	11	25		
		2—1—4	13	14	25	12	25
		2—1—3	13	15	13	9	13

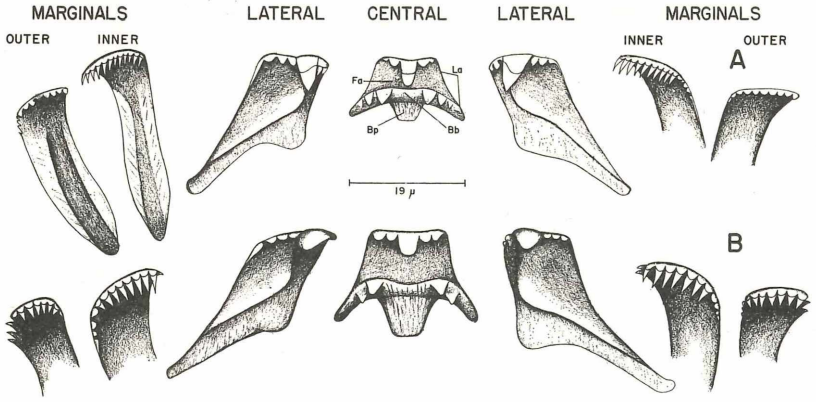


Fig. 18. A row of teeth from *Tricula burchi* (A) and *T. bollingi* (B). In the central tooth basal cusps arise from a thickened ridge (basal bar, Bb) which arises from the face of the tooth.

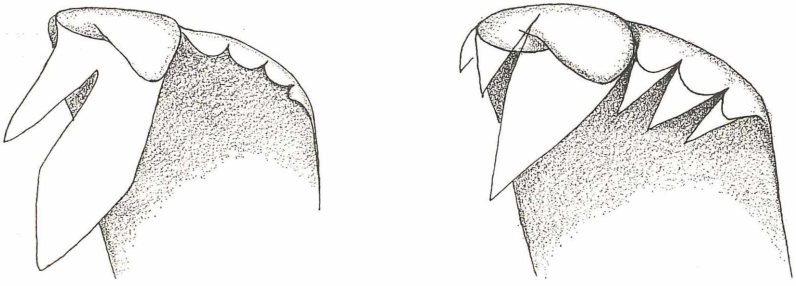


Fig. 19. Two lateral teeth of *T. bollingi* showing variation in the cutting edges of the prominent cusps.

Tricula bollingi n. sp.

Type. — The type is SMRL 3487a. The uncleaned type is shown in Fig. 4; a cleaned paratype is shown in Fig. 5.

Locality — Chieng Mai Province, Fang District, Pang Makham Pom Village, 24 Jan. 1967.

One leaves the main road from Chieng Mai to Fang 38 km from Fang and follows the course of a small shallow stream up to its source, a swamp about 2 km from the road. The swamp is at the base of a rocky cliff in the base of which is a shallow cave.

Snails were abundant , living on leaves under water at the margin of the stream where the stream left the swamp. The stream was 3-4 feet wide and about 1 foot deep. It flowed gently and had clear, cool clean water. The bottom was of soft black mud.

The locality can be located in map series L509 of the U.S. Army Map Service, sheet NE 47-3, edition 1-AMS. It was in the NB section with coordinates 217 and 512. The longitude was 99° 5′ and the latitude 19° 36′. The stream is part of the Huai Mae Fang River drainage which flows north.

Another population considered to be the same species was found in Chieng Mai Province, Fang District, at Wat Tamtabtao 1·7 km from the main road between Chieng Mai and Fang. The road to the Wat turns off the main road 32 km from Fang. This population is considered apart from the type population.

This second population is at 700-800 meters in the Doi Hin Mox (mountain range) and is located in the same map sheet described above at coordinates 514 and 2174. The longitude is 99° 7′ and latitude 19° 38′.

Etiology: This species is dedicated to Dr. WERNER BOLLING, Bamberg, who has contributed to our knowledge of Hydrobiidae.

Shell, Type Population. — Shell measurements for the type and paratypes are given in Table 5. Females were more numerous than males in the population. Females of 6·0 whorls were prevalent while males of 5·5 whorls were more common. There was no apparent sexual dimorphism in shell characteristics.

Shells are elongate, turreted, with the length of the body whorl greater than the length of the remaining whorls. The suture is slightly impressed; the whorls are evenly yet slightly convex. There is no tendency to form a keel. The whorls are not shouldered nor is there a sutural ramp. The suture is slanted and without crenulations. The apex is blunt and the diameter of the apical whorl is 0·29-0·31 mm.

The aperture varies from ovate to subquadrate; in the latter the abapical end is expanded. The peristome is complete. The parietal lip is thick and fused to the parietal wall. The columellar lip is somewhat expanded and reflected; it is straight to slightly arched and in many shells is sharp. The outer lip is thickened from within the aperture; it is without varix, and is straight or faintly sinuate in lateral view. Shells are anomphalous, with umbilical chink, or narrowly omphalous.

Shells from living specimens are glassy and transparent. The columella is clearly visible through the shell. Only the shells of those animals long dead are porcelaneous. The sculpture consists of fine orthocline growth lines.

Table 5: Shell measurements for the type and paratypes of *Tricula bollingi*.

shell features measured (mm)	whorls	statistic	shell length	shell width	ratio l/w	aperture length	aperture width	body whorl length
type	6	—	3·37	1·50	2·24	1·25	1·00	2·00
paratypes								
3 males	6	$\bar{X}$	3·43	1·56	2·20	1·21	0·96	1·98
5 males	5·5	$\bar{X}$	3·16	1·49	2·12	1·18	0·93	1·93
		S	0·16	0·08	—	0·07	0·07	0·13
		Se	0·07	0·04	—	0·03	0·03	0·06
9 females	6	$\bar{X}$	3·52	1·60	2·20	*1·24	0·98	2·06
		S	0·14	0·04	—	0·05	0·01	0·10
		Se	0·05	0·01	—	0·02	0·04	0·03
3 females	5·5	$\bar{X}$	3·23	1·54	2·10	1·23	0·97	2·04

$\bar{X}$ = mean, S = standard deviation, Se = standard error of mean, *N = 8, l = length, w = width.

Shell, Wat Tamtabtao Population. — Three size classes of shell were found in this population. Shell measurements for arbitrary categories large (Fig. 6), intermediate (Fig. 7), and small (Fig. 8) are given in Table 6. There were no intermediate forms between the small and larger size classes. The large class appears to be a slightly more elongate and stout form of the intermediate class.

Snail shells in the intermediate size class corresponded to the type series. While there was no sexual dimorphism in the type series, this was not the case in the Wat population. All the intermediate and large snails were females while 70% of the small snails were males (Tables 6 and 7). It is most important to note that the morphology of the snails of the 3 size classes of Wat snails and the type population was the same.

Table 6. Shell measurements (mm) for 3 size classes of snails from the Wat Tamtabtao Population.

size class	No. snails	whorls	statistics	shell length	shell width	ratio l/w	aperture length	aperture width	body whorl length
small	5 females	5·5	$\bar{X}$	2·96	1·36	2·18	1·08	0·88	*1·81
			S	0·14	0·05	—	0·05	0·04	0·05
			Se	0·06	0·02	—	0·02	0·02	0·03
	10 males	5·5	$\bar{X}$	2·84	1·28	2·22	1·00	0·78	1·68
			S	0·15	0·07	—	0·08	0·06	0·11
			Se	0·05	0·02	—	0·03	0·02	0·03
	2 males	6·0	$\bar{X}$	3·03	1·31	2·31	1·06	0·81	1·78
inter-mediate	10 females	5·5	$\bar{X}$	3·25	1·46	2·23	1·21	0·95	2·00
			S	0·07	0·04	—	0·04	0·04	0·06
			Se	0·02	0·01	—	0·01	0·01	0·02
	7 females	6·0	$\bar{X}$	3·63	1·61	2·25	1·29	1·00	2·12
			S	0·22	0·11	—	0·10	0·06	0·11
			Se	0·08	0·04	—	0·04	0·02	0·04
	2 females	6·5	$\bar{X}$	4·06	1·66	2·45	1·28	1·03	2·22
large	7 females	5·5	$\bar{X}$	3·53	1·63	2·17	1·31	1·03	2·15
			S	0·08	0·10	—	0·05	0·07	0·06
			Se	0·03	0·04	—	0·02	0·03	0·02
	1 female	6·0	$\bar{X}$	3·75	1·75	2·14	1·31	1·06	2·19

*N = 4, $\bar{X}$ = mean, S = standard deviation, Se = standard error of the mean, l = length, w = width.

Table 7: The number of snails of each sex found for the 3 size classes of *Tricula bollingi*. The 44 snails were from the Wat Tamtabtao Population.

sex	small	intermediate	large
males	12	0	0
females	5	19	8

External Morphology. — The head was uniformly dusted with a dark melanin pigment in 60-70% of the specimens observed. In other animals the rostrum was white scattered flecks of pigment. The sides of the head to the weakly developed suprapedal fold were lightly dusted with pigment giving the area a greyish appearance. The tentacles were devoid of pigment in some specimens, flecked with pigment spots in others (latter case, Fig. 12). The mantle over the verge was densly pigmented in males; in females the mantle over the ctenidium was densly pigmented. A light diffuse pigment was present in the epithelial sheets covering the pericardium. A broad band of diffuse pigment ran over the dorsal surface of the digestive gland to the tip of the apex; this band was often 72-97 μ wide.

The tentacles were elongate and broadly rounded at their tips. They averaged 1·16 ± 0·10 mm in length and 0·13 ± 0·10 mm in width at the base in living animals. The edges of the tentacles were strongly ciliated and several minute sensory hairs were noticed (with difficulty) near the tip of each tentacle.

The ctenidium consisted of 26 ± 6 gill leaflets of the usual hydrobiid type. The osphradium was typically hydrobiid; it was 0·31 ± 0·02 mm long and about 0·09 mm wide. The osphradial ganglion was observed through the white and swollen tissue covering the osphradium. The anterior end of the osphradium was 0·29-0·30 mm from the mantle edge where the latter fused with the "neck"

The mode of progression of this species was observed both in a large volume of water in a Petri dish and in a drop of water on a glass slide. The animal moved in a glide attributed to ciliary activity. The glide was not smooth but halting — the halt coordinated with contraction of the columellar muscle which pulls the shell forward. Often the anterior 1/3 of the foot glided forward fol-

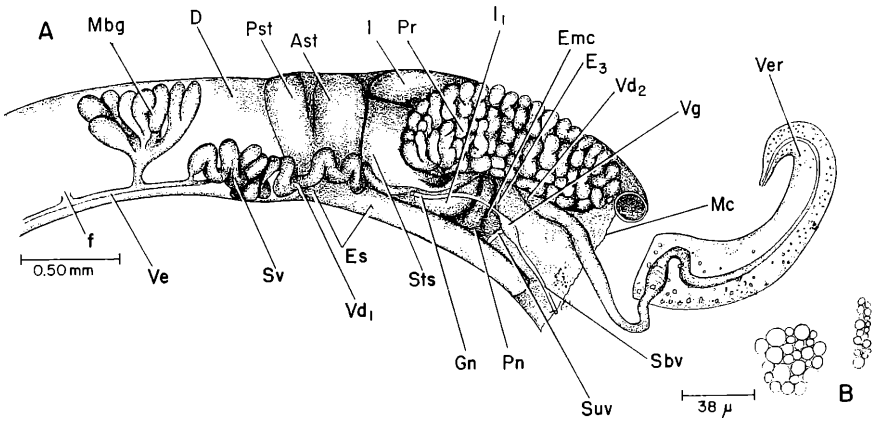


Fig. 20. A. Male *Tricula bollingi* uncoiled and exposing the ventral side. The neck and head areas are not shown and only a portion of the digestive gland (D) is illustrated. The epithelium was removed as was the kidney tissue which covers the style-sac (Sts). Only a portion of the male gonad is shown (Mbg).
B. Two clusters of spherical "glandular units" which are seen scattered under the epithelium of the verge, especially along the convex curvature towards the tip. These are the same Gl_2 illustrated for *T burchi*, Fig. 15. (see Glossary of terms Fig. 9-12).

lowed by a pulling up of the posterior $^2/_3$. This was in sharp contrast with the rapid smooth glide I have seen in *Hydrobia* (DAVIS 1966). The extension of the anterior $^1/_3$ of the foot and the halting movement gave the impression that this is the first phase in developing the step-like manner of progression in the Pomatiopsinae (STIMPSON 1865; DAVIS 1967).

Male Reproductive System. — This system is illustrated in Fig. 20A and B. The ventral aspect is shown with external epithelium removed and kidney tissue stripped away from the latter's usual position covering the style sac (Sts).

The system in gross aspect is the same described for *T. burchi*. The seminal vesicle (Sv) is characteristically knotted and the posterior vas deferens (Vd_1) is convoluted over the stomach. The prostate is kidney-shaped and overlies the end of the mantle cavity (Emc) with $^1/_2$-$^2/_3$ of the organ posterior to the mantle cavity. The pallial vas deferens (Vd_2) runs a short distance anteriorly along the prostate before turning to an oblique course towards the columellar muscle. In the base of the verge the vas becomes the swollen ejaculatory duct, wrapped in thick layers of circular muscle. After the characteristic bend beyond the ejaculatory duct the vas runs in the middle of the verge to the latter's tip. The vas is not convoluted and only weakly undulating in few specimens.

The verge is quite slender and not very muscular in contrast with that of *T. burchi*. Measurements on the verge (and prostate) are given in Table 8. It is carried on the neck, coiled counter-clockwise and is thin enough to circle more than 360°. There are no cilia at the tip and the epithelium near the tip is of cuboidal cells. The height of these cells is about 10 μ in the living animal. At the base of the verge on the concave side the epithelial cells were 13-14 μ high and appeared glandular. Patches of cilia were found at the base of the verge. The cells along the convex curvature were 7-8 μ high. The opening of this organ was simple, no papilla or armature.

Table 8. Dimensions of male and female reproductive organs measured from animals of *Tricula bollingi* in gross dissections or serial sections.

sex	organ	length (mm)	width (mm)
male (living)	prostate	0·80—1·18	0·41—0·56 (posterior thicker end)
	verge	1·46—1·92	0·33—0·36 (base of verge)
female (living)	bursa	0·31—0·43	0·18—0·19
	seminal receptacle	0·12—0·17	0·06—0·07
	pallial oviduct	1·57—2·66	0·45—0·49 (posterior thicker end)
(measured from sections)	bursa	0·10—0·15	0·10—0·12
	seminal receptacle	0·05—0·09	0·04—0·06

The "glandular units, Gl_2" described for *T. burchi* were scattered along the convex curvature of the verge and near the tip (Fig. 20, B). Calcareous granules were scattered at the base of the verge.

Female Reproductive System. — This system is illustrated in Figs. 21 and 22. The two species have similar systems only in the gonadal structure, two-sectioned pallial oviduct, lack of spermathecal duct, and a receptacular duct opening at the rear of the mantle cavity. Differences involve the structure and relationships of the bursa copulatrix, seminal receptacle, and receptacular duct.

The bursa copulatrix (B) was easily discerned in gross dissection and readily separated from the posterior pallial oviduct (Ppo). It was thick-walled and not fused with the tissue of the pallial oviduct. Measurements for this organ taken from gross dissection and serial section are given in Table 8. It is evident that structures measured from fixed and sectioned specimens are smaller (shrunken) than those measured from gross dissection.

When the bursa was lifted up and folded forward, the point where the receptacular duct (Rd) and posterior oviduct (Ov) appeared to join was revealed as well as the position where the duct of the seminal receptacle entered the oviduct (Fig. 22). The duct from the bursa leaves the right antero-lateral surface of the bursa and runs out to the oviduct (Ov_2) to enter the latter a short distance before Ov_2 enters the pallial oviduct (Ppo).

In sections, the bursa appeared fluid-filled and with numerous unoriented sperm in various stages of decomposition.

The seminal receptacle (Sr) was pressed between the bursa copulatrix and the posterior pallial oviduct in every specimen examined. With the animal positioned as in Figs. 16 or 21 the seminal receptacle was hidden as well as the duct from the receptacle to the oviduct (also Fig. 22A drawn from extrapolation

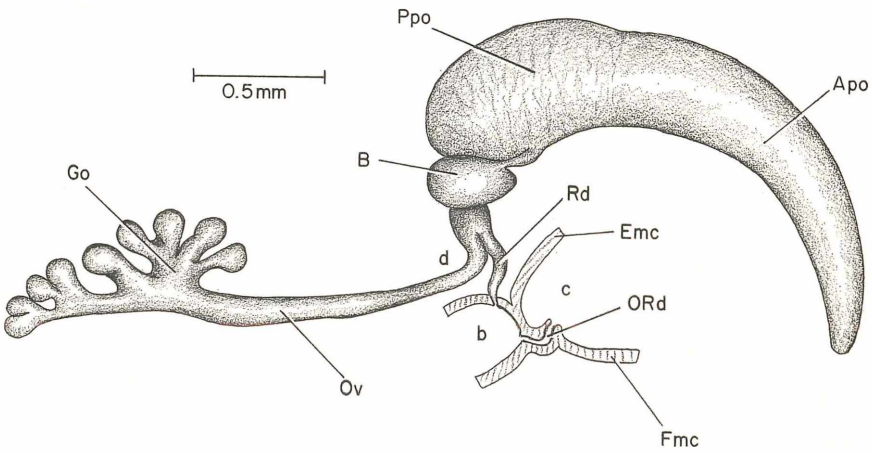


Fig. 21. Female reproductive system of *T. bollingi* shown in the same orientation as that of *T. burchi* in Fig. 16. The space of the end of the mantle cavity (c), pericardium (b) and kidney (d) are shown schematically. Ord is the opening from the mantle cavity to the pericardium. (see Glossary of terms Figs. 9-12).

from serial sections). As shown in Fig. 22B, a more medial plane of observation revealed the oval or spherical seminal receptacle pressed against the bursa copulatrix; also shown was the duct running into the oviduct (hidden by anterior bursa tip in Fig. 22A). Sperm were packed in the seminal receptacle and oriented with heads pointed to the wall.

The shape and position of the seminal receptacle are quite different compared with *T. burchi* (Fig. 17). In *Tricula burchi* the organ was not pressed between the bursa copulatrix and pallial oviduct but was found pressed against the

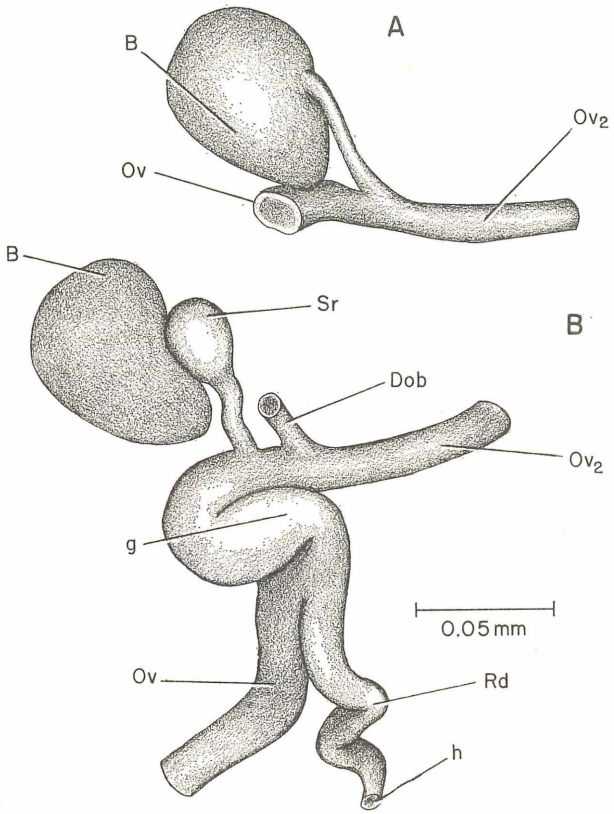


Fig. 22. Drawing of structures of female *T. bollingi*, as extrapolated from serial sections, are shown to demonstrate the interconnection of tubes associated with oviduct, bursa copulatrix (B) and seminal receptacle (Sr). A. More ventral view in which the seminal receptacle is hidden behind the bursa copulatrix. B. Further medial sections reveal the seminal receptacle tightly pressed against the bursa. The seminal receptacle is pressed between the bursa and the posterior section of the pallial oviduct. The oviduct (Ov) and receptacular duct (Rd) run in a common sheath and together are twisted in a characteristic manner (g) before joining as a common large tube. The twist places the track of the receptacular duct at the opening of the seminal receptacle. (see Glossary of terms Figs. 9-12).

medial surface of the bursa wrapped in kidney epithelium, a position similar to that found in *Oncomelania* and *Pomatiopsis* in the Pomatiopsinae. In this position the seminal receptacle was clearly appart from the pallial oviduct. The U-shaped arrangement of the organ and the duct were in contrast with that of *T. bollingi.* A comparison of Figs. 17 and 22 points up the differences between species in the duct connections between seminal receptacle, bursa copulatrix, receptacular duct, and oviduct.

The receptacular duct (Rd) as shown in Fig. 22 was easily observed in gross dissection when vital staining with neutral red was used. Only the relationships between the receptacular duct, pericardium, and mantle cavity were too vague and serial sections were needed (Fig. 21, schematic portion).

The oviduct and receptacular duct seem to join as a broad tube (Figs. 21, 22). Actually each entered a common sheath and traveled to the right, closely bound together (100 μ diameter for common sheath as measured from serial section). The tubes made a pronounced twist medial to the bursa and hidden from view in Fig. 21. The 2 ducts join in common duct just prior to or within the twist (g, Fig. 22). It appeared that as a result of the twist the channel of the receptacular duct was oriented towards the opening of the seminal receptacle.

The connection of the receptacular duct to the pericardium was distinct in at least 2 of the 5 sets of serial sections suitable enough for the study of this area (b, Fig. 21). The duct became a channel along the inner wall of the pericardium and then became unidentifiable for 8-12 sections. In subsequent sections a distinctly ciliated channel at the rear of the mantle cavity (ORd, Fig. 21) was observed leading into a coiled tube which narrowed to a tiny opening into the pericardium. Packets of sperm were noted in one series of sections from the seminal receptacle to the pericardium.

The ciliated channel along the floor of the mantle cavity ran to Ord, Fig. 21. The external diameter of the tube at the opening was 24-28 μ (average 38). Just before the pericardium the tube narrowed to 24-36 μ (average 32) while the actual entrance to the pericardium was 4-5 μ. A distance of 105-130 μ between the entrance to the pericardium and the duct leaving the pericardium was indicated by the number of sections cut through this region. The diameter of the lumen of the receptacular duct leaving the pericardium was 5 μ while the outside diameter of the tube was 19-29 (average 24) μ. The diameter of the tube 1/3 the distance from pericardium to juncture with the oviduct was 27-36 μ (lumen 14-15).

The pericardium was bizarre in being greatly pronounced, by bulging out into the mantle cavity more than usual, and by being thick walled with internal glandular tissue — conditions not seen in the males.

The pallial oviduct was similar to that described for *T. burchi.* Dimensions for this organ are given in Table 8.

Digestive System. — Aspects of the digestive system described for *T. burchi* exclusive of the radula pertain to this species.

Statistics on the radular length and width are given in Table 9 along with the number of rows of teeth along the length of the radula. The cusp formula per tooth most commonly encountered is given in Table 10 while total variation in cusp arrangement per tooth is given in Table 11.

Table 9. Statistics on the radulae of 10 specimens of *Tricula bollingi*.

radula features measured in μ or counted	statistic		
	$\bar{X}$	S	Se
radular length	586·9	38·7	12·2
radular width	78·3	8·6	2·7
total rows teeth	75	4·4	1·4
No. rows teeth in the formative stage	11	3·5	1·1

$\bar{X}$ = mean, S = standard deviation, Se = standard error of the mean.

Table 10. A general formula for the most common cusp arrangement found in *Tricula bollingi* (from 10 or 11 radulae).

tooth	cusp formula	snails where the arrangement was commonly found on each tooth (%)
central	$\frac{3—1—3}{3—3}$	70
lateral	3—1—3 (4)	91
inner marginal	12—14	90
outer marginal	9—12	90

Table 11. The various types of cusp arrangement for the different teeth in 10 or 11 radulae of *Tricula bollingi* and the percentage of radulae showing that arrangement at least once.

central		lateral		inner marginal		outer marginal	
arrangement of cusps	%	arrangement of cusps	%	No. cusps	%	No. cusps	%
$\frac{3—1—3}{3—3}$	73	3—1—3	73	12	70	10	60
$\frac{3—1—3}{2—2}$	45	3—1—4	64	13	70	11	50
$\frac{2—1—2}{3—3}$	18	4—1—4	45	14	60	12	40
$\frac{2—1—2}{2—2}$	18	4—1—3	18	11	40	13	40
$\frac{3—1—2}{3—3}$	9	3—1—2	9	10	20	9	20
$\frac{3—1—2}{2—2}$	9	4—1—5	9	15	10	15	10
		2—1—3	9	16	10	16	10
						17	10

The structures of the central and other teeth are the same in both species. Representative teeth are illustrated from *T. bollingi* in Figs. 18 and 19. Data in Tab. 9 and 11 were derived from both populations. The type population had a central formula of

$$\frac{2—1—2}{3—3}$$

for the 2 radulae studied from that population. *T. bollingi* has a longer and wider radula than *T. burchi* (significant at 0·02 level with small t test). *T. bollingi* has more rows of teeth (very significant difference at 0·01 level). The teeth of *T. bollingi* are distinctly larger.

Nervous System. — It is not the intent of this paper to describe in detail the structure of the nervous system. I have made note of several structures felt to have importance in discussing family, subfamily, and generic categories in a comparative manner.

1. Although the animals are tiny, there is a relatively elongate pleuro-subesophageal connective. While the left pleural and subesophageal ganglia were 96-120 μ long, the connective varied from 72-120 μ in length. The mid-columellar nerve (Mcv, DAVIS 1967) arose from the connective but was displaced towards the left pleural ganglion.

Nerves Mn_1, Mn_3, and Sbv were found as described for *Pomatiopsis* and *Oncomelania* (DAVIS 1967).

2. The pleuro-supraesophageal connective was elongate (218 μ) with the supraesophageal ganglion 121 μ long. Only a 70-120 μ space exists between the supraesophageal ganglion tip and the wall of the "neck" The supravisceral connective and osphradio-mantle nerve leave the tip of the ganglion.

3. The cerebral ganglion is 169-190 μ long. The tentacular nerve leaves from the dorso-anterior tip of the ganglion with a pronounced swelling at the origin of the nerve.

4. The visceral ganglion is single and about 165-170 μ long.

Discussion.

Subfamily Category.

The lack of data on numerous genera considered hydrobiid makes a discussion on placement of taxa within a subfamily most difficult. As TAYLOR (1966) pointed out for the Hydrobiinae, "In the present state of knowledge the Hydrobiinae consist of (a) genera similar to *Hydrobia*, and (b) those left over when obviously distinct groups have been separated." He continues "... the group will surely be refined as knowledge increases."

To TAYLOR's definition of the Hydrobiinae should be added the facts that the prostate should overlie the end of the mantle cavity and that in females there is a discrete seminal receptacle, bursa copulatrix, pallial oviduct, but no spermathecal or receptacular ducts (see FRETTER & GRAHAM [1962] for *Hydrobia ulvae*). There is no opening of the female reproductive system at the rear of the mantle cavity.

Presently the subfamilies are organized on structure of verge, radula, operculum, shell, eye-tentacle morphology, pigmentation, and mode of progression (TAYLOR 1966). In assessing subfamily characters I place emphasis on the following characters ranked in order of importance: 1) structure of the female reproductive organs, 2) structure of male reproductive organs, 3) head-foot morphology coupled with mode of progression, 4) operculum, 5) radula, 6) shell.

As so few hydrobiid genera are known in terms of all 6 of the above, it is apparent that new subfamilies will be defined, genera will be shifted about, and some subfamilies will prove too artificial to be useful. Therefore, systematic inflation should be avoided for some time, i. e. the elevation of subfamilies to family until numerous little-know genera are studied and current subfamilies re-evaluated.

Tricula is placed in the subfamily Triculinae, a subfamily first described by ANNANDALE (1924). ANNANDALE's description is no longer adequate because it did not consider complete reproductive anatomy. He had placed *Oncomelania* in the Triculinae when the genus is allied with *Pomatiopsis* and *Blanfordia* in the Pomatiopsinae (STIMPSON 1865; DAVIS 1967; TAYLOR 1966).

The Triculinae consist of snails where the female reproductive organs have discrete seminal receptacle, bursa copulatrix, 2-sectioned pallial oviduct, and a receptacular duct opening at the rear of the mantle cavity. In the male the prostate overlies the end of the mantle cavity, the verge is "simple" and only 1 duct runs through the verge. There are slightly developed suprapedal fold and omniphoric groove, the eyes are in slight swellings at the bases of the tentacles, and progression is by ciliary glide which may be jerky as described in this paper. The operculum is corneous and paucispiral. The basal cusps of the central tooth of the radula arise from the face of the tooth, not from the lateral angle. The shell is small (3-6 mm), glassy or porcelaneous, turreted with 5-7 whorls, without varix.

Generic Definition.

Tricula is a genus of aquatic snails. The shell is glassy in the living animal. The basal cusps arise from a basal bar on the face of the tooth. The tentacles are elongate and broadly rounded at the ends. The medial edge of the eye is devoid of an "eyebrow". The seminal receptacle and bursa copulatrix are large discrete organs. The receptacular duct is elongate as described.

In general the subfamily diagnosis is based on the genus. Little more can be said until the other named species of *Tricula* are studied.

Species Differences.

Tricula burchi and *T. bollingi* are distinct species and numerous differences serve to characterize them. The most noticable differences are given in Table 12. Especially of importance are the differences in reproductive organs.

The shell polymorphism in *T. bollingi* from the Wat population is confusing. The differences in size per whorl did not correspond to any qualitative anatomical difference. This phenomenon deserves intensive study. It is evident that because such polymorphism exists in a species one cannot simply match

Table 12. Listing species specific differences between *Tricula burchi* and *T. bollingi*.

Species	*burchi*	*bollingi*
Shell		
1. average length (mm) for snails 5·5 whorls		
a) males	2·69	3·16
b) females	2·78	3·23
2. maximum No. whorls	5·5	6·5
3. maximum average size	3·52	4·06
4. crenulated suture	+	—
5. whorls with shoulder	+	—
6. spiral microlines	+	—
Animal		
1. head-foot pigmented	—	+
2. verge thick and relatively large	+	—
3. verge ciliated at tip	+	—
4. vas deferens undulating in verge	+	—
5. seminal vesicle knotted	—	+
6. bursa copulatrix fused to pallial oviduct	+	—
7. seminal receptacle U-shaped and apart from pallial oviduct	+	—
8. duct of seminal receptacle connected directly with the bursa copulatrix	+	—
9. receptacular duct pronounced, thick	—	+
10. receptacular duct involved with the pericardium	—	+
11. percentage of radula with central formula of: $\frac{2—1—2}{2—2}$	100	18
12. total rows of teeth on the radula	69	75
13. length of radula in μ	464	587
14. relative size of teeth	smaller	larger

+ = yes, — = no.

Table 13. Radular formula for species of *Tricula* given in the literature.

species	tooth formula	author	figure
minutoides	$\frac{2—1—2}{2—2}$, 2—1—2, ?, ?	Thiele 1928	text fig. 18
montana	$\frac{1—1—1}{2—2}$, 5, 5, 5	Annandale 1924	text fig. 4A
taylori	$\frac{2—1—2}{(3)2—2(3)}$, 2—1—?, ?, ?	Rao 1928	none
martini	$\frac{1—1—1}{(2)1—1(2)}$, 2—1—?, ?, ?	Rao 1928	none
humida	$\frac{1—1—1}{3—3}$, ?, ?, ?	fide Annandale 1924	none

? = not given by the author.

shells against illustrations of previously described shells in making species identifications. The distinction between species must be made on more definitive data.

The structure of the teeth is important. THIELE (1928) presented an outline drawing of the central and lateral teeth of *Tricula minutoides* in which one cannot discern if a basal bar (Bb, Fig. 18) is present as it is in the species described here, or absent as in genera of the Pomatiopsinae. The drawing of ANNANDALE (1924, Textfig. 4A) is too confusing and inadequate to be used.

More than 1 or 2 radulae must be studied to understand variation in cusp number. The cusp formulae for various teeth of *Tricula* spp. as found in the literature are given in Table 13. These should be compared with variation documented for *burchi* and *bollingi* (Tables 4 and 11, respectively).

Until more is known, *Tricula humida, martini,* and *montana* are different than the other species in having a central tooth with only one small cusp flanking either side of the large medial cusp on the anterior edge.

The relationships between the species described here cannot be discussed in more than superficial terms with other species as little or nothing is known of the anatomy of other species. Comparisons were particularly made with *Tricula* from the near by Shan States of Burma.

Tricula horae and *taylori* have flat-sided whorls and keelation on the body whorl not known for the species here described. RAO (1928) described *T. martini* as an animal with chocolate brown color, short-tapering tentacles, and lunate yellow marks about the medial edge of the eyes. *T. gregoriana, g. expansa,* and *horae* are too large to be the species described here. *T. montana* and *gravelyi* from India have shell size and shape differences from the species described here.

YEN (1939) presents photographs of *Tricula m. minutoides* (GREDLER), *m. fuchsi* (GREDLER), *cristella* (GREDLER), *utaiensis* (GREDLER), *humida* (HEUDE). The shell of *T. bollingi* has a resemblance to the shell of *T. cristella* from China.

Literature cited.

ABBOTT, R. T. (1948): Handbook of medically important mollusks of the Orient and Western Pacific. — Bull. Mus. comp. Zool., Harvard, **100** (3): 246-328.

ABBOTT, R. T. & HUNTER, G. W. (1949): Studies on potential snail hosts of *Schistosoma japonicum*. 1. Notes on the amnicolid snails. — Helminth. Soc. Wash., 16 (1): 73-84.

ANNANDALE, N. (1924): The molluscan hosts of the Human Blood Fluke in China and Japan, and species liable to be confused with them. — Amer. J. Hygiene, (Monogr. Ser.) **3**: 215-294.

BARTSCH, P. (1936): Molluscan intermediate hosts of the Asiatic Blood Fluke, *Schistosoma japonicum,* and species confused with them. — Smiths. misc. Coll., **95** (5): 1-59, 8 pls.

BENSON, W. H. (1843): Description of *Camptoceras,* a new genus of the Lymnaeadae, allied to *Ancylus,* and of *Tricula,* a new type of form allied to *Melania*. — Calcutta J. nat. Hist., **3** (12): 465-468.

CHUNG, H. L., HO, L. Y., TS'AO, W. C., HSING, O. H., TUNG, Y. C. & MU, S. H. (1963): The discovery of a minute freshwater snail, *Tricula* sp. as the first intermediate host of *Paragonismus szechuanensis*. — Chinese med. J., **82** (11): 712-717.

DAVIS, G. M. (1966): Notes on *Hydrobia totteni*. — Venus, Jap. J. Malac., **25** (1): 27-42.

— — — (1967): The systematic relationship of *Pomatiopsis lapidaria* and *Oncomelania hupensis formosana* (Prosobranchia: Hydrobiidae). — Malacologia, **6** (1-2): 1-143.

— — — (1968): A systematic study of *Oncomelania hupensis chiui* (Gastropoda: Hydrobiidae). — Malacologia, in press.

DAVIS, G. M. & CHIU, J. K. (1964): Anatomy of *Oncomelania chiui*. — Ann. Rep. to Comm. Parasitic Diseases, U.S. Armed Forces Epidem. Bord — from Univ. Michig.: 14.

FRETTER, V. & GRAHAM, A. (1962): British prosobranch mollusks. — London (Ray Society), 755 p.

HABE, T. & MIYAZAKI, I. (1962): *Tricula chiui* sp. nov., a new snail host for the Lung Fluke *Paragonimus iloktsuenensis* CHEN in Formosa. — Kyushu J. med. Sci., **13** (1): 47-49.

PRASHAD, B. (1921a): Reports on the freshwater gastropod mollusks of Lower Mesopotamia. III. — The families Neritidae, Hydrobiidae, and Melaniidae. — Rec. Ind. Mus., **18**: 215-227.

— — — (1921b): The Indian species of the genus *Tricula*, BENSON. — Rec. Ind. Mus., **22** (2, 9): 67,69.

RAO, H. S. (1928): The aquatic and amphibious mollusks of the Northern Shan States, Burma. — Rec. Ind. Mus., **30** (4): 399-468, 3 pls.

STIMPSON, W. (1865): Researches upon the Hydrobiinae and allied forms. — Smiths. Misc. Coll., **201**: i-iii, 1-59.

TAYLOR, D. W. (1966): A remarkable snail fauna from Coahuila, Mexico. — Veliger, **9** (2): 152-228.

THIELE, J. (1928): Revision des Systems der Hydrobiiden und Melaniiden. — Zool. Jb. (Syst.), **55**: 351-402, 8 Taf.

YEN, T.-CH. (1939): Die chinesischen Land- und Süßwasser-Gastropoden des Natur-Museums Senckenberg. — Abh. senckenb. naturf. Ges., **444**: 1-235, Taf. 1-16. Frankfurt a. M. (V. KLOSTERMANN).