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by Alan Solem

I KOMMISSION HOS E. MUNKSGAARD

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BY

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KØBENHAVN
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INTRODUCTION

The molluscan fauna of India and Burma is comparatively well known through the studies of STOLICZKA, BENSON, BLANFORD and GODWIN-AUSTEN, with an admirable summary in the "Fauna of British India". There are many scattered publications on the non-marine mollusks of the areas included in former French Indo-China by MORLET, FISCHER, BAVAY and DAUTZENBERG, but comparatively little is known concerning the mollusks of Thailand.

Early papers by HAINES (1858), MARTENS (1867), MORLET (1891) and MOELLENDORFF (1894 and 1902) are fragmentary. Very little has been published since then. Faunistic reports by BLANFORD (1903), TOMLIN (1929 and 1932), and HAAS (1952) are supplemented by scattered descriptions (BLANFORD 1902, TOMLIN 1931, BARTSCH 1932, SALISBURY 1949). GUDE (1903) presented a check-list of the helicoid species, ANNANDALE (1920) a semi-popular account of the Pilidae, and SUVATTI (1938) summarized previously published papers in a Thai-English check-list. Other data is widely scattered in systematic monographs.

Through the courtesy of Dr. JORGEN KNUDSEN, Universitetets Zoologiske Museum, København, it was possible to study a miscellaneous collection of some 156 sets of Thailand non-marine mollusks, mostly collected by Mrs. BIRGIT DEGERBØL HANSEN pH.D. in northeast Thailand near Doi Sutep and Chieng Dao while employed on the 1st. Thai-Danish Expeditions to Thailand 1958–1959. Also included were several sets from southeast and southwest Thailand collected by PALLE JOHNSEN Ph.D. for the Natural History Museum, Aarhus, a few sets collected by Dr. KNUDSEN in Laos and South Vietnam, and some material taken by subsequent Danish field trips to Thailand.

The collections were taxonomically diverse, with 54 species from Thailand and four from the neighbouring countries. Two of the Thailand species were too young for identification and others could not be referred to specific names because of imprecise descriptions in previous literature. Eight species were unquestionably new to science, and two new genera are proposed – *Teraia* and *Muangnua* – both in the Helicarionidae. Despite the limited material, this is the largest single collection of non-marine mollusks yet reported from Thailand and adds considerably to our knowledge of that country's molluscan fauna.

ACKNOWLEDGEMENTS

For the privilege of studying this material, I am deeply indebted to Dr. JORGEN KNUDSEN, Universitetets Zoologiske Museum, København and to Mrs. W. S. S. VAN BENTHEM JUTTING VAN DER FEEN, who had sorted and identified many of the species showing Malayan affinities. Her efforts made my task much easier and credit should be given to her for many of the subulinid and cyclophorid names. Any errors are the sole responsibility of the present author.

The many anatomical drawings are by Miss PATRICIA RILL, a zoology student at Roosevelt University in Chicago and were prepared under the sponsorship of National Science Foundation Grant G-16419. All photographs were taken by the author and printed by the Division of Photography, Field Museum of Natural History.

SYSTEMATICS

The species are listed in rough phylogenetic order, utilizing a classification adopted from WENZ, ZILCH and H. B. BAKER with modifications by the present author. Since this collection contained only a few specimens of each species, comparable material from adjacent areas was not available, and no modern systematic studies have been published on the mollusks of Southeast Asia, little information could be contributed towards speciation and distributional problems. Under these circumstances, detailed listing of synonymies was considered unnecessary. Literature citations have been restricted to the original description and a single key reference to the earlier literature, unless new synonymy was involved.

Despite the limited data on distribution and generally inadequate descriptions found in much of the previous literature, many times it proved possible to suggest that typological species from neighboring areas might be synonymous with, or at most subspecifically distinct from, the Thailand material. Although available sets were inadequate to propose new synonymies, even simple collation of the very widely scattered literature serves a useful function.

Fortunately, a large percentage of the collection had been preserved in alcohol. This allowed preparation of several comments about generic and subfamily classification, particularly concerning the Thiaridae and Helicarionidae. For most other taxa, previously recorded data on the anatomy was so fragmentary that meaningful comparative remarks were impossible. By itself, the present collection was insufficient to permit detailed morphological studies and such an attempt would have been beyond the scope of this review. Thus a very uneven treatment of this collection has been presented, ranging from a simple recording of locality records to fairly comprehensive studies of the pallial and genital anatomy.

Following each locality record, in parenthesis, I have given the original field number, *or* the collector, and the date of collection. Often several species were collected under the same number, with 1844 being especially rich in new and unusual forms.

Class Bivalvia

FAMILY UNIONIDAE

Trapezoideus misellus (Morelet 1865)

Unio misellus Morelet 1865. Journ. de Conchyl. 13, pp. 21–22 (Siam); HAAS 1919. Syst. Conch. Cab. IX (2) 2, pp. 266–270, pl. 32, figs. 6–9, pl. 33, figs. 1–5.

Kwae Noi near Sai Yok (Palle Johnsen, 1962).

A single young shell, 32.7 mm. long, 18.4 mm. high, width 9.3 mm., is referred to this species, although perhaps resembling more closely illustrations of the Burmese *T. foliaceus* (Gould 1843). The identification can only be called tentative, since the extent of local variation within this genus is still unknown.

Class Gastropoda

Subclass Prosobranchia

Order Monotocardia

Superfamily Architaenioglossa (= Cyclophoracea)

FAMILY CYCLOPHORIDAE

Leptopoma **(*Trocholeptopoma*)** ***annamiticum*** Moellendorff 1900

Leptopoma (*Trocholeptopoma*) *annamiticum* Moellendorff 1900. Nachr. d. Malak. Gesell. 32, p. 134; KOBELT 1902. Das Tierreich 16, p. 18; KOBELT 1906. Syst. Conch. Cab. I (19) 2, p. 468, pl. 58, figs. 6–8.

Cauda, near Nhatrang, Vietnam (Knudsen, X.1959).

Two examples, height 10.8 and 11.1 mm., are typical of this little known species.

Lagochilus aff. ***kobelti*** Sykes 1903

see *Lagochilus kobelti* Sykes 1903. Proc. Zool. Soc. London 1903 part 1, pp. 194–195, pl. 20, figs. 13–15.
Chieng Dao at 1,100 meters (784, 15.VII.1958).

Compared with a paratype of *L. kobelti* (FMNH 73142), the single worn shell from Chieng Dao differs only in having the spiral ribs of equal size. In *L. kobelti* there are two major and many minor spiral ribs. The Thailand shell was 6.47 mm. high, diameter 6.67 mm., with $5^3/_8$ whorls.

Numerous *Lagochilus* have been described from southeast Asia. They must be carefully revised when sufficient material is available, since many of the named forms are probably synonymous.

Cyclophorus (Annularia) speciosus (Philippi 1847)

Cyclostoma speciosus Philippi 1847. Zeits. f. Malak. 4, p. 123; KOBELT, 1902. Das Tierreich 16, p. 133.
Sai Yok near Kwae Noi (P. Johnsen)
Doi Sutep at 1,100 meters (1107, 5.IX.1958)
Doi Sutep at 1,000 meters (1634, 22.X.1958)
Chieng Dao (1113, 6.IX.1958)
between Bo Luang and Omkoi at 1,100 meters in dipterocarp forest (B. Hansen, I.1964).

Dead adults from Sai Yok (diameter 59.1 mm.) and Bo Luang (diameters 45.9, 51.9, 52.9 mm.) and one live collected male from Doi Sutep (specimen 1107, diameter 52.1 mm.) were unquestionably this species. It is not possible to relate it to extra-limital forms at present, although very probably *speciosus* is a geographic race of a widely distributed species complex.

Cyclophorus (Glossostylus) fulguratus (Pfeiffer 1854)

Cyclostoma (*Cyclophorus*) *fulguratum* Pfeiffer 1854. Proc. Zool. Soc. London 1852, p. 63; KOBELT 1902. Das Tierreich 16, p. 112; GUDE 1921. Fauna British India, Moll. 3, pp. 61–62.
Ban Mussoe (Degerbøl, VII.1959)
near Ban Kao (P. Johnsen, 7–15.XI.1961)
Koh Chang (Degerbøl, 4.IV.1959).

The Koh Chang adult male (diameter 41.8 mm.) and Ban Kao adults (diameter 29.4, 33.6, 34.6 mm.) are typical. *C. fulguratus* has been reported from a number of localities in Burma and the Tonkin area of Vietnam.

Rhiostoma dalyi Blanford 1902

Rhiostoma dalyi Blanford 1902. Proc. Malac. Soc. London 3, pp. 34–35, fig. 1; Blanford 1903. *op. cit.* 3, p. 281.

Chieng Dao at 400 (808) and 1,100 (784) meters.

The live collected adult female (808) had almost exactly the same sized shell as a paratype of *dalyi* (FMNH 71336) from Pitsanuloke, Thailand. Measurements of the Chieng Dao shell are: height 12.8 mm., diameter 22.2 mm., H/D ratio 0.577, whorls 5–; of the paratype: height 13.7 mm., diameter 22.3 mm., H/D ratio 0.615, whorls $4^3/_4$.

Rhiostoma housei (Haines 1858)

Cyclostoma housei Haines 1858. Ann. Lyceum Nat. Hist., New York 6, p. 157, pl. 5, figs. 12–15 (Siam); Moellendorff 1895. Proc. Zool. Soc. London 1895, p. 152 (Samui Islands, Siam); Kobelt 1910, Syst. Conch. Cab. I (19), 3, pp. 757–758, pl. 110, figs. 8–10, pl. 113, fig. 2.

Pterocyclos marioni Ancey 1898. Ann. Musée d'hist. nat. de Marseille, série II, Bull. I (1), p. 137, pl. 9, fig. F (Luang-prabang, Laos and Mont Hou, Tonkin); Dautzenberg 1900. Journ. de Conchyl. 48, p. 70.

Chieng Dao at 1,100–1,200 meters (784, 801).

A live adult male (diameter 21.5 mm. with $4^5/_8$ whorls) and a dead example (diameter 25.0 mm. with $4^7/_8$ whorls) are referred here with slight hesitation. The only recorded locality for *housei* (Moellendorff, *loc. cit.*) may have been based on material of the species later described as *R. samuiense* Tomlin 1931. *R. jalorensis* Sykes 1903 from Biserat, Jalor, Malaya appears similar, but is a larger shell with a much bigger siphonal tube. Two species, *R. smithi* Bartsch 1932 and *R. tomlini* Salisbury 1949, described from Kao Sabap, near Chanthaburi, S. E. Thailand appear to be synonyms, since paratypes of *R. tomlini* (FMNH 71338) have the form and siphon of *R. smithi*. Their main difference from *R. housei* lies in their much larger size.

We have no data concerning geographic variation in *Rhiostoma*. It is not impossible that all of the names mentioned above represent extreme variants of one species.

The operculum of the male was pulled off in order to examine the head region, but no dissections were attempted. The male organ is a short (2.2 mm.) finger-like projection, situated about 1 mm. behind and very slightly below the right tentacle with a groove extending from base to tip of the penis. Most cyclophorids have the male organ directly below the right tentacle, but this difference may have no systematic importance.

Dioryx bacca (Pfeiffer 1862)

Alycaeus (*Dioryx*) *bacca* Pfeiffer 1862. Proc. Zool. Soc. London 1862, p. 275; KOBELT 1902. Das Tierreich 16, p. 337.
Chieng Dao at 1,100–1,200 meters (784, 801, 15–17.VII.1958).

The eleven specimens showed comparatively little variation in size or form – height 5.55–6.94 mm. (mean 6.36 mm.), diameter 4.97–6.14 mm. (mean 5.77 mm.), H/D ratio 1.04–1.15 (mean 1.12) and $3^3/_4$ to $4^1/_4$ whorls.

Chamalycaeus aff. ***fimbriatus*** Bevay and Dautzenberg 1912

see *Alycaens* (*sic*) (*Charax*) *fimbriatus* Bavay and Dautzenberg 1912. Journ. de Conchyl. 60, pp. 52–54, pl. 6, figs. 13–18.
Chieng Dao at 1,800 meters (794, 16.VII.1958).

Two partly broken specimens probably represent a new species that seems most similar to the Tonkinese form cited above. The one measurable shell is 2.17 mm. high, diameter 3.16 mm., with slightly more than $3^3/_4$ whorls.

FAMILY PUPINIDAE

Pupina (Tylotoechus) arula (Benson 1856)

Pupina arula Benson 1856. Ann. Mag. Nat. Hist. (2) 17, p. 230; GUDE 1921. Fauna Brit. India, Moll. 3, pp. 193–194.
Doi Sutep at 1,100 meters (1844, 8.XI.1958).

A single live collected example (height 7.52 mm., diameter 5.3 mm., with $4^5/_8$ whorls) is referred here. Although smaller than the type of *arula* (height 9 mm.) from Yanglan, Tenasserim, the difference probably is not significant. *Pupina lowei* de Morgan 1885 and *P. siamensis* (Moellendorff 1902) (see Arch. f. Mollusk. 86, pl. 2, fig. 15) may be either subspecies or synonyms. Various sets of shells in the FMNH collection from Perak labeled both *lowei* and *arula* do not seem separable.

Pupina artata Benson 1856

Pupina artata Benson 1856. Ann. Mag. Nat. Hist. (2) 17, p. 230; GUDE 1921. Fauna Brit. India, Moll. 3, p. 193.
Chieng Dao at 1,100 meters (784, 15.VII.1958)
Doi Sutep at 1,100 meters (1762, 31.X.1958).

The dead, worn example from Chieng Dao was 6.34 mm. high, diameter 4.38 mm., with $5^5/_8$ whorls. A live collected shell from Doi Sutep was 6.21 mm. high, diameter 4.71 mm., with slightly less than $5^3/_8$ whorls.

Pollicaria myersii (Haines 1858)

Cyclostoma myersii Haines 1858. Ann. Lyceum Nat. Hist., New York 6, p. 157, pl. 5, figs. 9–11 (Siam); KOBELT 1902. Das Tierreich 16, p. 290.

on limestone outcrops 20 km. east of Wang Sapung near Loei, North Thailand at 300 meters (B. Hansen, 29.II.1964).

Available material is insufficient to determine the relationships of several taxa described from the area between Malaya and Peninsular Burma, then east to the Tonkin area of North Vietnam. DAUTZENBERG and FISCHER (1905 pp. 171–173) synonymized *gravida* Benson 1856, *crossei* Dautzenberg and d'Hamonville 1887 and *rochebruni* Mabille 1887. The much larger *P. elephas* (de Morgan 1885) from Malaya seems well differentiated, but *P. mouhoti* (Pfeiffer 1862) and *P. meyersi* (Haines 1858) are very close to *P. gravida*. They differ in having the parietal-palatal margin angulated, while in the *gravida* series it is evenly rounded. *P. mouhoti*, described from "Lao Mountains, Camboje", is known from Lao Kay, Tonkin (FMNH 25420, FMNH 63086) and has a red-orange lip. *P. myersii*, described from "Siam", has a yellowish-white lip. As suggested by VON MARTENS (1867, p. 67), they may be synonymous.

The two examples collected by Hansen are 30.7 and 32.3 mm. high, diameter 18.4 and 17.9 mm., whorls 6 and $5^{7}/_{8}$, respectively. The less worn individual has a deep reddish-purple body color and the lip is burnt orange. It is unusual in having a weakly malleated sculpture on the last part of the body whorl, a feature not seen in other specimens of *Pollicaria* examined. The lip is flared backwards and distinctly rimate, not solidly reflected as in *P. gravida*. Despite the unusual sculpture, it seems best to refer this to *P. myersii*.

FAMILY VIVIPARIDAE

Generic classification is still unsettled. In utilizing *Bellamya* for the Southeast Asian forms I am following VAN BENTHEM JUTTING (1956 pp. 318–326).

Bellamya (Bellamya) ingallsiana (Lea 1856)

Paludina ingallsiana Lea 1856. Proc. Acad. Nat. Sci., Philadelphia 1856, p. 110 (Siam); KOBELT 1907. Syst. Conch. Cab. I (21 A), pp. 200–202, pl. 41, figs. 3–6, 11, 12.

Bangkok, (Dana Expedition, IV.1929).

Eight adults and subadult specimens belong to this species. *B. ingallsiana* is the oldest name for what seems to be a very widely distributed species in Southeast Asia. The following specific names seem to be based on local variations: *B. penangensis* (Martens 1900) from Penang, Malaya; *B. martensiana* (Frauenfeld 1864) (= *cingulata* Martens, not Mathéron) from Thailand; *B. noetlingi* (Kobelt 1907) from Meungyaw, "Indochina"; *B. kelantanensis* (Kobelt 1907) from Kelantan, Malaya; and *B. perakensis* (Martens 1908) from Perak. The Javanese *B. javanica* (von dem Busch 1844) is related, but seems distinct.

Bellamya (Mekongia) moreleti fruhstorferi (Kobelt 1907)

Vivipara moreleti fruhstorferi Kobelt 1907. Syst. Conch. Cab. I (21 A), pp. 211–212, pl. 43, figs. 5–8; PRASHAD 1928. Mem. Indian Mus. 8 (4), p. 174, pl. 19, fig. 32.

Ban Kao on Kwae Noi River (Palle Johnsen)
Beach of Kwae Noi, north of Ban Kao (Palle Johnsen, 20.XI.1961).

Three dead adults, 20.5, 20.7, 22.8 mm. high are practically identical with the type figures. These are the first localities reported for this species. The anatomy of *Mekongia* has not been studied, but the striking difference in shell form from that of typical *Bellamya* seems sufficient to warrant its retention as a subgeneric name.

FAMILY AMPULLARIIDAE

Pila ampullacea (Linné 1758)

Helix ampullacea Linné 1758. Syst. Nat., Ed. 10, p. 771; VAN BENTHEN JUTTING 1956. Treubia 23 (2), pp. 329–332, figs. 38, 42, 43.

Kwae Noi River, south of Ban Kao (Palle Johnsen, 21.XI.1961).

A single dead adult of this widely distributed species is 58.2 mm. high.

Pila polita (Deshayes 1830)

Ampullaria polita Deshayes 1830. Encycl. Meth. (Vers) 2 (1), p. 31; VAN BENTHEM JUTTING 1956. Treubia 23 (2), pp. 336–337, fig. 41.

between Loei and Udon, 250 meters (B. Hansen, 29.II.1964)
Mekong River at Vientiane, Laos (Palle Johnsen, 14.II.1962).

The three dead specimens from Vientiane are 53.2, 63.5 and 66.6 mm. high. Those from near Lowei are 60.6, 61.7, 65.6 and 66.2 mm. high.

Superfamily Cerithiacea

FAMILY THIARIDAE

With the qualifications expressed below, this classification follows that of MORRISON (1954).

Paludomus siamensis Blanford 1905

Paludomus siamensis Blanford 1905. Proc. Malac. Soc. London 5, p. 283, pl. 8, fig. 3. – Upper Menam River, Thailand.
Sai Yok (Palle Johnsen, 1962)
Ban Kao (Palle Johnsen, XI.1961).

All nine specimens were juveniles, the largest reaching only 10.2 and 12.1 mm. in height. The operculum is typical of *Paludomus*.

Melanoides tuberculata (Müller 1774)

Nerita tuberculata Müller 1774. Hist. Verm., p. 191; VAN BENTHEM JUTTING 1956. Treubia 23 (2), pp. 412–418.
Muaklek, 40 km. from Saraburi (Palle Johnsen, 19.II.1962).
Sai Yok (Palle Johnsen, 1962).

Two juveniles of this ubiquitous species have the shell sculpture of the diploid race (see JACOB 1959).

Brotia variabilis (Benson 1836)

Melania variabilis Benson 1836. Journ. Asiatic Soc. Bengal 5, pp. 746–747; PRESTON 1915. Fauna Brit. India, Moll. 4, pp. 23–24.
Kwae Noi River at Sai Yok (Palle Johnsen, 1962)
Kwae Noi River north of Ban Kao (Palle Johnsen, 20.XI.1961).

Both individuals were collected dead.

Brotia binodosa (Blanford 1903)

(Fig. 1)

Melania binodosa Blanford 1903. Proc. Malac. Soc. London 5, pp. 282–283, pl. 8, fig. 2 (common in large rivers of Siam).
Tungsalaeng Luang waterfall at 200 meters (B. Hansen, 19.II.1964).

Four decollated individuals, 22.7, 17.7, 15.7 and 15.5 mm. high, are obviously this species although much smaller than BLANFORD's type (length 42 mm.). Two have the distinct subperipheral cords shown by the type, two are smooth below the periphery.

One individual with soft parts yielded interesting data on the process of development in this species. Although the apical portion could not be pulled from the shell, the head with brood pouch came out intact. MORRISON (1954, p. 383) demonstrated the presence of an egg transfer groove on the neck and briefly discussed the young of *B. baccata* (Gould). Groove and head structures of *B. binodosa* (fig. 1 *a*) are essentially the same, but the young apparently differ. There is no evidence of apical asymmetry as found by Morrison, and the young were at several devel-

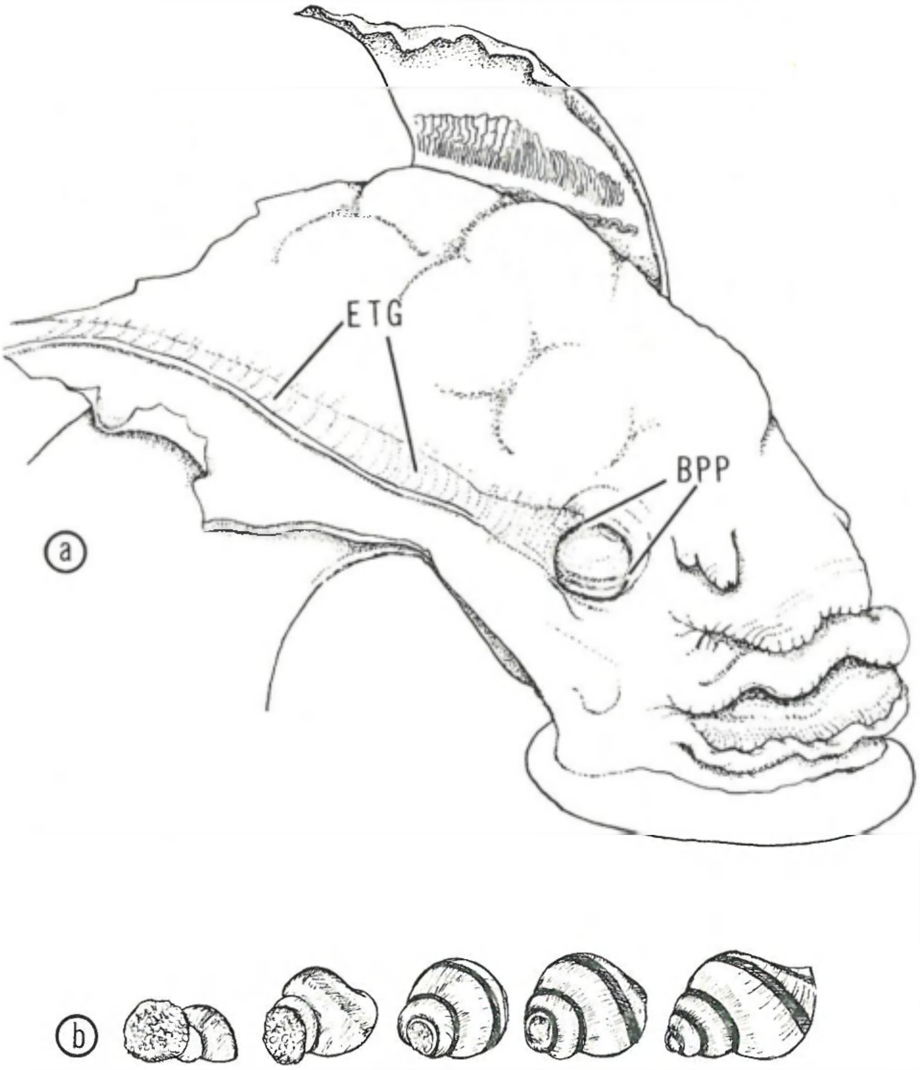

Fig. 1. *Brotia binodosa*: *a*, Head and part of visceral hump with pallial roof removed, showing egg transfer groove (ETG) and brood pouch pore (BPP) with a young snail nearly expelled; *b*, young taken from brood pouch.

opmental stages, those nearest the external pore being much larger than those in the rear portion of the brood pouch. Each embryo was enclosed by a thin membranous sac. Depending on the size of the embryo, there were small to large amount of light green granular nutritive material clustered about the shell apex. Careful dissection of several egg capsules showed that the apical shell covering did not form until after all the nutritive material had been utilized. Only in embryos ready to be expelled from the brood pouch was the apical whorl covered by shelly layers. A series of developmental stages is shown in figure 1 *b*. Probably the young are nourished through the digestive gland. Since thiarids normally have decollated shells with an apical plug, such a form of nourishment with delayed apical shell secretion causes no problems in shell deposition.

Paracrostoma paludiformis (Yen 1939)

(Fig. 2; Pl. 1, fig. H–J)

Semisulcospira paludiformis Yen 1939. Abhl. senckenberg. naturf. Gesell. 444, p. 55, pl. 4, fig. 73 (Lu-ho-wan, Hainan Island).

Tungsalaeng Luang waterfall at 200 meters (B. Hansen, 19.II.1964).

The five shells are referred here after a great deal of hesitation and puzzlement. In both shell and soft anatomy they are anomalous. Quite possibly they represent a new genus and species, but it seems best to refer them tentatively to the above taxa. *Paracrostoma* Cossman 1900 (synonyms: *Acrostoma* Brot 1870 not Le Sauvage 1826 and *Brotella* Rovereto 1899 not Kaup 1858) is based on *Thiara hügeli* Philippi from the Khasi Hills of India. The soft parts håve not been dissected. On conchological grounds it has been synonymized with both *Sulcospira* and *Brotia*. A specimen (Pl. I G) of *A. hügeli* from "Pondicherry" (FMNH 33529) is probably var. *compacta* Nevill 1884 since it is less elongated than the type figures. The Thailand shells (Pl. I H–J) differ in having a slightly subangulate periphery, more ovoid form and dark reddish coloration within the aperture. Published figures of typical *hügeli* and *assamensis* Nevill 1884 (and see PRESTON 1915, p. 31 for references) are all of lanceolate shells and obviously differ from both the Thailand and Indian shells.

The most similar illustration is of *Semisculcospira paludiformis* Yen 1939 from Hainan Island. The only conchological distinction lies in *paludiformis* having "undeutliche Spiralen" and lacking a subangulated periphery. Unfortunately the types and only known material of *S. paludiformis* were destroyed during World War II (ZILCH, personal communication), so that direct comparisons cannot be made. Despite the minor differences in sculpture and variable spire height, *hügeli*, its varieties, *paludiformis* and the Thailand specimens show many more similarities than differences and seem conchologically distinct from other Oriental melanians. The similarity of the Thailand shells to the figures of *paludiformis* is so great that I have little hesitation in utilizing that specific name, despite the impossibility of direct comparison at this time.

The generic reference is based on the soft parts, radula and operculum. The latter two (figures 2 *c*, *d*) are quite compatable with the structures found in *Brotia* (see van Benthem Jutting 1956 p. 366, figs. 69 a, 70), but the presence of male animals is not. All *Brotia* whose soft parts have been examined are ovoviviparous parthenogenetic females. There is an egg transfer groove on the right side of the head leading to a subhaemocoelic brood pouch on the back of the neck. The five Thailand specimens contained two animals with these female characters and three males which lacked both groove and brood pouch. Since the smallest (height 15.9 mm.) and second largest (height 23.0 mm.) shells contained females and the largest (height 25.6 mm.), a male, there can be little doubt that bisexuality rather than adult-juveniles is involved. The egg transfer groove (figure 2 *a*) appears narrower than in *Brotia binodosa* (figure 1 *a*) because the head of the latter is so swollen

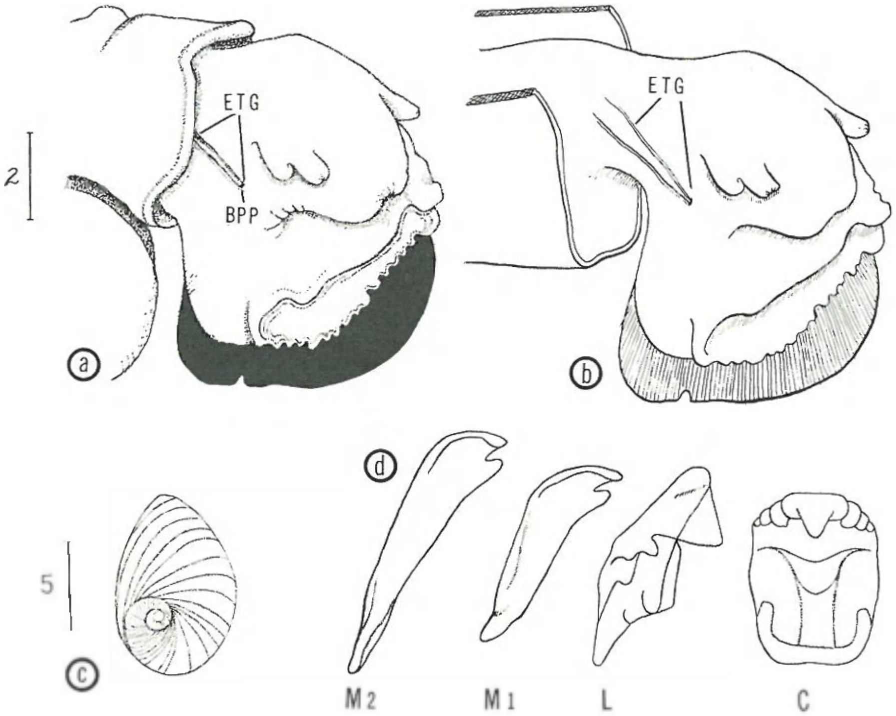

Fig. 2. *Paracrostoma paludiformis*: *a*, head of preserved specimen; *b*, head with egg transfer groove expanded; *c*, operculum; *d*, isolated radular teeth.

with embryos. When the Thailand females' groove is examined carefully and expanded (figure 2 *b*) no differences from *Brotia* can be seen. The brood pouch of one female was empty, the other filled with loose, greenish granular material visually identical with the nutrient materials associated with the embryos of *Brotia binodosa*. This raises intriguing possibilities as to the method of egg encapsulation. Quite possibly the egg, either fertilized or unfertilized, is passed down the egg transfer groove, enters the brood pouch (fertilized in transit or on arrival?) and then stimulates formation of an egg capsule around a clump of nutritive materials previously secreted in the brood pouch. This would be a most interesting topic for investigation by an Asian naturalist.

The close similarities between *Brotia binodosa* and *Paracrostoma paludiformis* in regard to operculum, radula, egg transfer groove and brood pouch suggest probable phyletic affinity. The difference of parthenogenicity in *Brotia*, versus evident bisexuality in *Paracrostoma paludiformis*, is of considerable biologic interest. The North American viviparid genus *Campeloma* has been found to include parthenogenetic and bisexual species (references in CHAMBERLAIN 1958), hence *Brotia* and *Paracrostoma* (in the sense used here) could be synonymous. Since the shells of *hügeli* and *paludiformis* are ovate and without strong spiral or radial sculpture, whereas *Brotia* has an elongate terebriform shell usually with strong sculpture, I have chose to retain generic separation. Rather than add to the complicated melaniid synonymy, I prefer to use *Paracrostoma*, although realizing that *hügeli* may be anatomically distinct.

MORRISON (1954) defined three fresh-water families of "melanians" on the basis of dioecious versus parthenogenetic reproduction and variations in the female egg-laying organs. He claimed that these represented parallel lines of descent from three different marine families. Morrison's Thiaridae was defined by "reproduction parthenogenetic; no males present in species; brood pouch not uterine, but adventitious (subhaemocoelic) in the neck region, with opening on right side of neck". In every respect except the apparent dioecious reproduction, the Thailand specimens of *Paracrostoma paludiformis* conform with *Brotia*, an undoubted thiarid in the sense of Morrison. The five available specimens were poorly preserved, both females and one male breaking off during the extraction process and a second male had the apical whorls immediately disintegrate upon extraction. Only the largest male came out intact, but somewhat "mushy", hence examination could not be attempted. JACOB (1957–1958, 1958) examined cytologically *Thiara scabra* (Müller 1774), *Tarebia granifera* (Lamarck 1822) (as *Melanoides lineatus* Gray) and *Melanoides tuberculata* (Müller 1774). He found 0.01 $^0/_0$ of *T. granifera* were males and a polyploid race of *M. tuberculata* averaged 3 $^0/_0$ males, but these were "chromosomally sterile" since no functional sperm were produced. The finding of a "thiarid" species with apparently dioecious reproduction is thus not improbable. Few Oriental melanians have been dissected and much more work must be done before an adequate classification can be established. The few specimens available for this study did not permit adequate morphological examination or any real contribution to classification. They do, however, suggest that Morrison's definition of Thiaridae may have to be altered to include dioecious reproduction.

Subclass Pulmonata
Superorder Basommatophora

FAMILY ELLOBIIDAE

Ellobium **(*Ellobium*)** ***aurismidae*** (Linné 1758)

Bulla aurismidae Linné 1758. Syst. Nat., ed. 10, p. 728; VAN BENTHEM JUTTING 1959. Treubia 7 (83), p. 114.

Soi Dao Mt. at 600 meters, Chantaburi District (K. Larsen, 1963).

A single rather small specimen, height 74.5 mm., with the spire angle (ca. 90°) larger than in most other examples seen, is referred here. Despite the large size and long nomenclatural history, little data has been published concerning this species. There are many records from Indonesia, and tropical Australia, and New Guinea, but it has not been reported from the Philippines, although apparently common in Borneo. Early records from "Malakka", Tonkin, and Siam seem reasonable in view of the above record, but whether the many museum shells labeled "India" indicate a range extension into Burma, Pakistan or India is uncertain.

Generally *Ellobium* is considered to be an inhabitant of mangrove or brackish-water areas. The occurence of a specimen at 600 meters elevation in evergreen forest is most remarkable. Although dead, traces of epidermis still remain on the shell. It is conceivable that the specimen was carried from the shore zone to this elevation by humans, or that the shell was mislabeled. Without confirmation by further collecting, this locality should be considered questionable, although I have no doubt the shell was taken in Thailand.

Superorder Systellommatophora
Order Soleolifera

FAMILY VERONICELLIDAE

Semperula siamensis (Martens 1867)

Vaginulus siamensis Martens 1867. Preuss. Exped. Öst-Asien, Zool. 2, p. 68, pl. 5, fig. 3; HOFFMAN 1925. Jenais. Zeits. Naturwissen. 61, pp. 256–257.

Chieng Dao at 400 meters (808, 18.VII.1958).

Four examples, 25–31 mm. long, probably belong to this species.

FAMILY RATHOUISIIDAE

Atopos sp.

Ban Mussoe (B. Degerbøl, 22.VII.1959).

A single specimen, 23.9 mm. long, is nearest to *Atopos punctata* Collinge 1902, but differs in having a black granular color band midway on each side of the body. The dorsum is distinctly keeled and the surface pustulose with scattered black granules. No comparative material was available and nearly all described species are known from only single specimens or a few individuals. Specific identification is not possible.

Atopos ranges from Northern Queensland and the Bismarck Archipelago to the Abor Hills of northeast Assam, "Cochinchina" and the Philippines. The practically unknown genus *Rathouisia* has been collected in the Yangtze River valley of China (*R. leonina* Heude 1885) and at Ch'êng-k'ou, northeast Ssu-ch'uan (= Szechwan) Province (108°47′ long., 31°56′ lat.), China (*R. tigrina* Heude 1885 and *R. pantherina* Heude 1890).

Superorder Stylommatophora
Order Orthurethra

FAMILY ENIDAE

Coccoderma ceratina (Reeve 1849)

Bulimus ceratinus Benson *in* REEVE 1849. Conch. Icon., *Bulimus*, pl. 77, fig. 569; GUDE 1914. Fauna Brit. India, Moll. 2, pp. 230–231.

Chieng Dao at 1,800 meters (794, 16.VII.1958).

A single adult, height 13.3 mm., diameter 6.9 mm., with 7 whorls, is placed in this species. Unlocalized sets of *C. nilagerica* (Pfeiffer 1846) in FMNH compare almost exactly in sculpture and form, but the Thailand shell is less elongated and has a distinctly greater angle to the spire. *C. nilagerica* and *C. vicaria* (Blanford 1870) are known from the Shan States of neighbouring Burma.

This species has not been dissected, so its systematic position is unknown. On the basis of shell form and sculpture, I prefer to place it in *Coccoderma*, rather than the essentially Chinese *Mirus*.

Order Sigmurethra

Suborder Aulacopoda

Superfamily Limacacea

FAMILY HELICARIONIDAE

Relatively detailed dissections were made of seven species, six previously undescribed. Information from these dissections suggested a re-evaluation of family classification, since current subfamily arrangements and systematic criteria were contradicted by the new data. A detailed review of literature relating to Indian, Burmese and Malayan specimens was supplemented by a less extensive survey of papers covering Indonesian and Australian taxa. The Pacific Ocean taxa have been reviewed by H. B. BAKER (1938, 1940, 1941). Additional information is contained in the standard classifications (THIELE 1931 and ZILCH 1959).

The proposed readjustments in subfamily groupings and diagnostic characters obviously can be no more than preliminary, but do account for the findings in this study and provide a more coherent picture in respect to geographic distribution. No attempt has been made to integrate the African taxa, and there is a great need for detailed examination of Indonesian, Philippine Island and Melanesian forms in order to test the hypotheses presented below.

BLANFORD and GODWIN-AUSTEN (1908) presented the first comprehensive classification of the Indo-Malayan zonitoid snails, recognizing six subfamilies, with thirteen genera of uncertain affinities. THIELE (1931) synthesized data from previous studies and recorded these genera among eleven of the eighteen groupings in the Ariophantidae. H. B. BAKER (1941) reviewed the Polynesian-Micronesian helicarionids and attempted "a somewhat iconoclastic classification" that resulted in recognition of four large and twelve more narrowly defined subfamilies. ZILCH (1959) prepared a synthesis of THIELE and H. B. BAKER, marked primarily by raising BAKER's larger subfamilies to family rank.

Basically, I believe BAKER was correct, and my proposed alterations are primarily in the content and definition of trends in the helicarioninine and the ariophantinine stocks. I suggest that the basic divisions should be:

Family Helicarionidae

Subfamily Euconulinae (Copied from H. B. Baker (1941 p. 208)) – epiphallus without lime-sac, flagellum or much calc; spermatophore simple and rarely with horny wall; spermatheca weak, obsolete or on male side (penial prepuce of atrium); stimulators or darts, when rarely present, penial; outer radular marginals (at least) usually multicuspid.

Tribe Euconuli – spermatheca on female side or absent; rarely ovoviviparous.

Tribe Microcysti – spermatheca opening into atrial prepuce of penis; ovoviviparous.

Subfamily Helicarioninae – dart apparatus absent; epiphallus slender with lime-sac at apex, a small knob to long sinuated appendage; penial retractor inserting much further down epiphallus and at most having a small retractor caecum.

Subfamily Ariophantinae – long cylindrical dart sac with muscular or calcareous papilla surrounded by its gland (frequently lost); epiphallus varying from large and sac-like to a small bulge; penial retractor rarely simple, usually with a large coiled retractor caecum or a large straight caecum except in genera with reduced shells.

Tribe Ariophanti – dart-sac and gland large; penial retractor with simple thick retractor caecum (rarely with vestiges of coiling); lime-sac short and thick; spermatheca usually short, spermatophore with close-set spines; shell large with reflected lip or reduced; tripartite sole, caudal horn, caudal foss and ectocones of radular marginals commonly reduced.

Tribe Macrochlamydi – typically with well developed shell; long and finger-like lime sac well removed from penial retractor, a prominent coiled retractor-caecum, same dart apparatus as in Ariophanti, relatively few and large tri-cuspid lateral and marginal teeth, but any one or several characters often reduced or lost.

Tribe Girasii – dart apparatus present or absent; shell often reduced drastically; penial retractor caecum small and straight or absent; tail usually triangular in cross-section, caudal horn and foss larger than in other tribes; lime-sac more as in Ariophanti, epiphallus folded with lime-sac lying bound to penis and prominent.

Tribe Durgelli – dart apparatus present or absent; shell often reduced, tail elongated with greatly overhung caudal horn; lime-sac reduced to a small bump just lateral to insertion of penial retractor that has at most a small straight caecum, radular teeth tending to become minute, pectiniform and very numerous.

Tribe Parmarioni – dart apparatus almost always with calcareous papilla; spermatheca usually a very short sphere; penis with papilla; epiphallus with enlarged section above retractor insertion corresponding to lime-sac but much larger; no retractor caecum; shell greatly reduced.

Subfamily Dyakiinae – dart sac with glandular portion distinctly separate and extending above body of dart apparatus either as slender tubes or several lobes.

While the Euconulinae and Dyakiinae are quite distinctive in structure and appearance, the Helicarioninae and Ariophantinae cannot be readily separated. Our knowledge of their anatomy is based almost entirely on the early work of STOLICZKA and GODWIN-AUSTEN, who published illustrations and partial descriptions of the external body form, terminal genitalia, jaw and radula. H. B. BAKER's careful studies of the Oceanic species provide a guideline for comparisons, but a vast number of Indo-Malayan genera need to be restudied before any critical definitions will be possible, since forms transitional from the helicarioninine to ariophantinine genera probably live in the Indonesian-New Guinea area, if they do exist.

I believe most of the past confusion has been caused by failure to recognize that loss of the dart apparatus and reduction or loss of the retractor caecum is common in Indo-Burmese zonitoids; hence the references to the Helicarioninae of such genera as *Sesara*, *Rasama* and *Pseudaustenia*. Probably the Helicarioninae and Ariophantinae will either prove to be joined by insensible gradations, or differentiating criteria will be found in organs other than the genitalia.

In Australia and on the Pacific Islands the true Helicarioninae are represented by a number of genera. *Helicarion*, *s. s.*, *Epiglypta*, *Parmacochlea*, *Malandena*, probably most of Iredale's uncharacterized generic names, *Orpiella*, *Dendrotrochus* and possibly some of the Philippine genera (*Ryssota*, *Hemitrichia*, *Hemiglypta*, *Pseudohelicarion*, *Pareuplecta* and *Inozonites*) are genuinely primitive in lacking a dart apparatus and having only a vestigial retractor caecum. Baker's division into two "restricted subfamilies" – Helicarioninae with a retractor caecum and "Sesarinae" with only an apical lime-sac or flagellum on the epiphallus – does not seem warranted at present. As shown below, *Sesara* belongs to the Macrochlamydinine group and loss or gain of a minute retractor caecum is a common occurence. Quite possibly the Mascarene Ereptinae of Thiele are true Helicarioninae, but they may be more closely related to the many African genera. I do not accept any of the Indo-Burmese genera as being true Helicarioninae.

The Dyakiinae include a limited number of genera showing rather amazingly varied apical glandular appendages to the dart apparatus. Included are the genera *Staffordia* Godwin-Austen 1907 from the Dafla Hills of Assam; *Dyakia* Godwin-Austen 1891 from Tenasserim through Malaya and Indonesia to Borneo; *Pseudoplecta* Laidlaw 1932 from Malaya; *Elaphroconcha* Gude 1911 and *Asperitas* Gude 1911 from Indonesia; *Quantula* Baker 1941 from Malaya (introduced to Fiji), *Rhinocochlis* Thiele 1931 from Borneo; *Everettia* Godwin-Austen 1891 from Borneo; *Kalamantania* Laidlaw 1931 from Borneo; and *Sasakina* Rensch 1930 from the Lesser Sunda Islands.

Subfamily ***Ariophantinae***

The proposed division into five "tribes" purposefully attempts to indicate the relatively minor differences involved and the extent to which such changes may be found within apparently closely related species. All published data and the present dissections suggest that the characteristic dart apparatus, consisting of a central muscular tube opening through a papilla and surrounded by a coating of glandular tissue with a small retractor muscle originating (usually) off the columellar retractor, is common to all parts of the Ariophantinae with only minor modifications. An independent origin for this structure in more than one line seems rather improbable. There is no genus that shows the origin of the ariophantinine dart, unless the Malayan *Pseudoplecta* indicates an origin from the Dyakiinae. On the other hand, many genera seem to have lost the dart apparatus. With the limited anatomical data available, drawn mostly from the studies of GODWIN-AUSTEN, recognition of five trends of variation seems productive of clarity. Quite possibly convergence is involved in these groupings.

Primary importance has been given to the structure of the epiphallus and its position in regard to the penial retractor and its caecum. Changes in the dart apparatus, radula, caudal region, shell laps, mantle lobes and body form seem to correlate relatively well with the epiphallic changes. Four of the five tribes were involved in this study. Only the Parmarioni is extralimital. In these genera the lime-sac has expanded into a huge boat-shaped appendage, the spermatheca is very small and globose, the shell and visceral hump are greatly reduced, the penis has a functioning verge, and usually the dart apparatus has a calcareous dart. Besides the usually included *Parmarion* Fischer 1855, *Microparmarion* Simroth 1893, *Parmunculus* Collinge 1899, *Wiegmannia* Collinge 1901, *Philippinella* Moellendorff 1899, *Damayantia* Issel 1874, and *Is-*

selentia Collinge 1901, the Malayan genus *Apoparmarion* Collinge 1902 should be added. Although not having a calcareous dart, it shows the epiphallic expansion and reduced spermatheca. Quite possibly it represents a transition between the rather distinctive Parmarioni and the more conservative Macrochlamydi. LAIDLAW (1932 pp. 89–91) equated *Apoparmarion* with *Cryptaustenia*, a genus shown below to have very different genitalia.

Tribe Ariophanti

Included are the largest and most helicoid like species in the Helicarionidae. The dart apparatus is large; there is generally a prominent retractor caecum, occasionally coiled; the spermatheca is relatively prominent and the epiphallus is greatly enlarged at its head and far removed from the retractor insertion. Occasionally (*Euplecta* and *Hemiplecta*) there will be a distinct epiphallic flagellum, but usually the epiphallus will be a simply swollen tube equal in diameter to that of the penis with the vas deferens entering laterally on the epiphallus head much as in the Durgelli. In many genera the radular marginals are aculeate. According to Godwin-Austen, the spermatophore has very small and close-set spines, quite different from that of the Macrochlamydi.

The included genera – *Naninia* Sowerby 1842, *Xesta* Albers 1850, *Euplecta* Semper 1870, *Rhyssotopsis* Ancey 1887 (= *Haughtonia* Godwin-Austen 1899), *Hemiplecta* Albers 1850, *Cryptozona* Mörch 1872, *Ariophanta* Desmoulins 1829, *Indrella* Godwin-Austen 1901, *Ravana* Godwin-Austen 1901, *Ratnadvipia* Godwin-Austen 1899, and *Platymma* Tomlin 1938 – in general represent various experiments towards large size with reduced shell laps and mantle lobes. There have been various modifications to the foot, tail, radula and shell. Such genera as *Bensonies* H. B. Baker 1938 (= *Bensonia* Pfeiffer 1855 not Gray 1847) and *Oxytesta* Zilch 1956 (= *Oxytes* Pfeiffer 1855 not Giebel 1848) would appear to be Ariophanti, but retain the long lime-sac and coiled retractor caecum of the Macrochlamydi and are best retained in this group. The distinction is a very fine one and may have to be abandoned.

Only juvenile or dead specimens of four species were included in this collection.

Cryptozona granulosa (Moellendorff 1902)

Xestina granulosa Moellendorff 1902. Nachrb. d. Malak. Gesell. 34 (9/10), p. 156.

Chieng Dao at 1,100 meters (784, 15.VII.1958)
1,100–1,200 meters (801, 17.VII.1958)
Phu Kradeng at 1,300 meters (1926, 26.XI.1958).

Three juvenile specimens are either this species or an undescribed relative.

Hemiplecta **(*Hemipleceta*)** ***neptunus*** (Pfeiffer 1861)

Helix neptunus Pfeiffer 1861. Proc. Zool. Soc. London 1861, p. 190; BLANFORD 1903. Proc. Malac. Soc. London 5, pp. 277–278; GODWIN-AUSTEN 1919. Rec. Indian Mus. 16 (2), pp. 199–202.
Kampaengpet (2120, 18.I.1958).

A single juvenile example matches the sculpture and color pattern of adults in FMNH collection.

Hemiplecta **(*Hemiplecta*)** ***siamensis*** (Pfeiffer 1856)

Helix siamensis Pfeiffer 1856. Proc. Zool. Soc. London 1856, p. 32; MARTENS 1867. Preuss. Exped. Öst-Asien, Zool. 2, p. 71, pl. 6, fig. 6.
Sai Yok (P. Johnsen, XII.1961)
Ban Kao (P. Johnsen, 7–15.XI.1961; P. Johnsen, XI.1961).

Although slightly juvenile, the specimens are unquestionably this species.

Hemiplecta **(*Koratia*)** ***distincta*** (Pfeiffer 1850)

Helix distincta Pfeiffer 1850. Zeits. f. Malak. 1850, p. 69; BLANFORD 1903. Proc. Malac. Soc. London 5, pp. 277–278; GODWIN-AUSTEN 1919. Rec. Indian Mus. 16 (2), pp. 199–202.
9 km. north of Vientiane, Laos (P. Johnsen, 15.II.1962).

A single worn adult was collected.

Tribe Macrochlamydi

By far the largest and most varied grouping, it is possible to derive the structures found in the other tribes from genera and species of this group. Most characteristically, they have very small shell laps and mantle lobes; a large helicoid shell into which the animal can withdraw; a rather small caudal horn and a short tail; the radula has tricuspid central and laterals with bicuspid marginals (rarely unicuspid) that are less than 70 in number; the jaw has a median cutting edge; the spermatheca is long and finger-like; the penis large, with or without a verge; the penial retractor has a large coiled retractor caecum, rarely straight or free; at the head of the epiphallus, which is well removed from the penial retractor, lies a large finger-like or flagellar lime-sac appendage (sometimes reduced); and a large muscular dart apparatus is present in at least some species of most genera.

Any one or several of these characters may be altered, even within the same genus. As mentioned above, *Bensonies* and *Oxytesta* tend towards the Ariophanti. *Euaustenia* Cockerell 1898 and *Parvatella* Blanford and Godwin-Austen 1908 retain the genitalia of the Macrochlamydi, but have the body form, large shell laps and tail of the Girasii and are intermediate in shell form and visceral hump size.

Several genera are clustered around the variable grouping termed "*Macrochlamys*". This genus contains more than 100 described species with generally smooth depressed helicoidal shell and certainly will require alteration when restudied. Many species are typical, but *M. sufflava* Godwin-Austen 1910 and *M. atricolor* (Godwin-Austen 1875) have the coiled retractor caecum and a lime-sac like the Ariophanti; *M. zemoensis* Godwin-Austen 1907, *M. sathilaensis* Godwin-Austen 1907, and *M. richilaensis* Godwin-Austen 1907 from Sikkim and Bhutan have a long lime-sac, but the retractor caecum is uncoiled and free; while *M. pedina* (Benson 1865) has large laps, a very large lime-sac and a straight caecum. Several shell and radular variants also exist. *Sarika* Godwin-Austen 1907 is the eastern replacement of *Macrochlamys*, having a very large straight retractor caecum (as in many Ariophanti), but otherwise the same genitalia as *Macrochlamys. Syama* Blanford and Godwin-Austen 1908 differs from *Macrochlamys* only in lacking the dart apparatus, a character of doubtful generic value, while *Rhadella* Godwin-Austen 1914 is usually listed as a subgenus of *Macrochlamys. Dalingia* Godwin-Austen 1907 lacks the dart apparatus and has an enormously swollen epiphallic retractor caecum, but otherwise seems typical. Three little known genera from the Northeast Frontier Agency of India, *Rotungia* Godwin-Austen 1918, *Bapuia* Godwin-Austen 1918 and *Tadunia* Godwin-Austen 1918, vary only slightly in external body features (*Rotungia*) or shell characters.

Khasiella Godwin-Austen 1899 has a heavily sculptured, minutely perforated, often angulated shell, with the genitalia typical except for a nearly free short retractor caecum. *Holkeion* Blanford and Godwin-Austen 1908 from Burma and Northern Thailand retains the dart apparatus and lime-sac, but has practically no trace of a retractor caecum, the shell is sharply angulated and the shell laps are much larger than in *Macrochlamys. Taphrospira* Blanford 1905 has large shell laps, no dart apparatus, a shortened lime-sac, and the retractor caecum somewhat reduced in prominence, with the shell at once recognizable in having a distinctly channeled suture. A new genus, *Teraia*, from Thailand has the retractor caecum lost, but the lime-sac, dart apparatus and spermatheca typical; the shell differs in being openly umbilicated and with strong supraperipheral sculpture. *Sesara* Albers 1860 is shown below to have both the coiled retractor caecum and long lime-sac, although having a very distinctive shell.

All the genera mentioned in the previous paragraph are well characterized by shell features and show a more eastern distribution than the relatively featureless shells of the other Macrochlamydi.

Other genera are of less certain inclusion. *Microcystina* Mörch 1876 reportedly has a dart apparatus, but neither lime-sac nor retractor caecum, while the shell is a miniature duplicate of *Macrochlamys*. *Kaliella* Blanford 1863 apparently has a large lime-sac, but no retractor caecum and no dart apparatus. In addition, the radula is strikingly different in having tricuspid marginal teeth, as does the little known *Rahula* Godwin-Austen 1907 whose anatomy has not been studied otherwise. *Baiaplecta* Laidlaw 1956 (= *Pangania* Laidlaw 1932 not Poppius 1914) has the typical shell laps and genitalia of the Macrochlamydi, but unicuspid central and lateral teeth, although the marginals are the normal bicuspid type. Probably *Glyptobensonia* Moellendorff 1894 and *Vitrinula* Gray 1857 (= *Otesia* H. and A. Adams 1858) should be included. *Sivella* Blanford 1863 has a type species that has been reported from Sikkim to Malaya. Specimens from the type area have a long spermatheca and lime-sac, although lacking a dart apparatus and retractor caecum, and belong to this group.

Usually *Kaliella*, *Rahula*, *Sivella*, *Sesara* and *Tadunia* are placed in the Helicarioninae because they lack the dart apparatus, but I think this is a secondary loss.

Sivella castra (Benson 1852)

Helix castra Benson 1852. Ann. Mag. Nat. Hist. (2) 10, p. 349; GUDE 1914. Fauna Brit. India, Moll. 2, pp. 3–4.

Chieng Dao at 1,800 meters (794, 16.VII.1958).

There are no important differences from material of *S. castra* taken at Cherrapoonjee, Assam (FMNH 43601) and identified by GUDE. The single adult is 11.5 mm. in diameter, 5.7 mm. high, D/U ratio 4.00, with $6^{1}/_{8}$ whorls. It is questionable if the one species ranges from Sikkim to Malaya and this Thailand shell may belong to a trochomorphid genus. No Sikkimese examples were available and I have accepted GUDE's identification.

Genus ***Sesara*** Albers 1860

Type species. – *Helix infrendens* Gould 1844 by original designation.

The trochoidal to depressed-conoid shells included here are generally small (diameter 6–12 mm. except for *S. episema*), have an angulated periphery, are imperforate or minutely perforate, strongly costulate above periphery and smooth below with the lip of the adult shell thickened Several species have apertural lamellae. Only *S. infredens* (Gould 1844) and *S. parva* have been dissected.

The nineteen species range from the Khasi and Dafla Hills of Assam up to the Arbor Hills in the Sadiya Frontier Tract, then down to the level of Moulmein and Tavoy in Burma and east into Thailand (Doi

Sutep and Phitsanulok) and Laos ("Luang-Prabang"). A chronological list of the species and recorded localities follows:

Sesara infrendens (Gould 1844)
Moulmein and Tavoy, Burma
Sesara pylaica (Benson 1856)
Farm Caves, Moulmein
Sesara diplodon (Benson 1859)
Dafla Hills, Assam and Chittagong, Pakistan
Sesara galea (Benson 1859)
Teria Ghat, Khasi Hills
Sesara basseinensis (Blanford 1865)
south part of Arakan Range, Bassein Dist., Pegu
Sesara helicifera (Blanford 1865)
Arakan Range west of Prome, Burma
Sesara mamillaris (Blanford 1865)
Akoutoung, south of Prome, Pegu and Arakan Hills
Sesara ataranensis (Theobald 1870)
Ataran River near Moulmein
Sesara hungerfordiana Theobald 1876
Mizantoungon on Salwin near Moulmein
Sesara inermis Theobald 1876
Salwin Valley near Moulmein
Sesara ingrami (Blanford 1876)
Arakan Range, probably Pegu
Sesara episema Ponsonby 1894
"hills south of Assam"
Sesara penoti Ancey 1898
Luang-prabang, Laos
Sesara harmeri Gude 1900
Khasi Hills, Assam
Sesara mouleyitensis Gude 1901
Muleyit, almost due east of Moulmein
Sesara megalodon Blanford 1902
Pitsanuloke, Siam
Sesara bidentifera Blanford and Godwin-Austen 1908
Muleyit, west of Moulmein at 4,000 feet elevation$_2$
Sesara globosa Godwin-Austen 1918
between Renting and Rotung, Arbor Hills, Northeast Frontier Agency, India
Sesara parva new species
Doi Sutep, North Thailand.

Many of the taxa from near Moulmein may prove to be local variations of one species, but presently available specimens are totally insufficient to work out synonymies.

Sesara parva new species

(Fig. 3, 4, Pl. I, fig. D–F).

Diagnosis. – A small (diameter 6.01–7.52 mm.), depressed-conoid species of *Sesara* with two palatal teeth, the upper much larger, and only $5^1/_2$–$6^1/_4$ whorls.

The other species with only 2 palatal teeth, *S. penoti* Ancey 1898; *S. mouleyitensis* Gude 1901; and *S. bidentifera* Godwin-Austen 1908 are all distinctly larger (diameter 8–10 mm.) with 7 whorls. They have reduced ribbing with a more depressed form and a smaller upper palatal tooth (*penoti*); a much larger upper palatal tooth (*mouleyitensis*); or apparently have "subequal palatal teeth" (*bidentifera*).

Description of soft parts. – (Based on number 116). Body and tail short, retracted within shell. Pedal grooves (fig. 3 *a*) high on sides of foot, meeting above caudal horn (CH). Latter appressed to end of tail while contracted, probably slightly overhung when animal extended. Caudal foss (CF) a slit in middle of tail. Sole of foot tripartite, central portion less than half width of each side when contracted.

Mantle collar (MC) thick (fig. 3 *c*), with three small lappets: a small angulopalatal mantle lobe (not shown in drawing) extends a short distance along parietal margin; left mantle lobe (ML) relatively prominent,

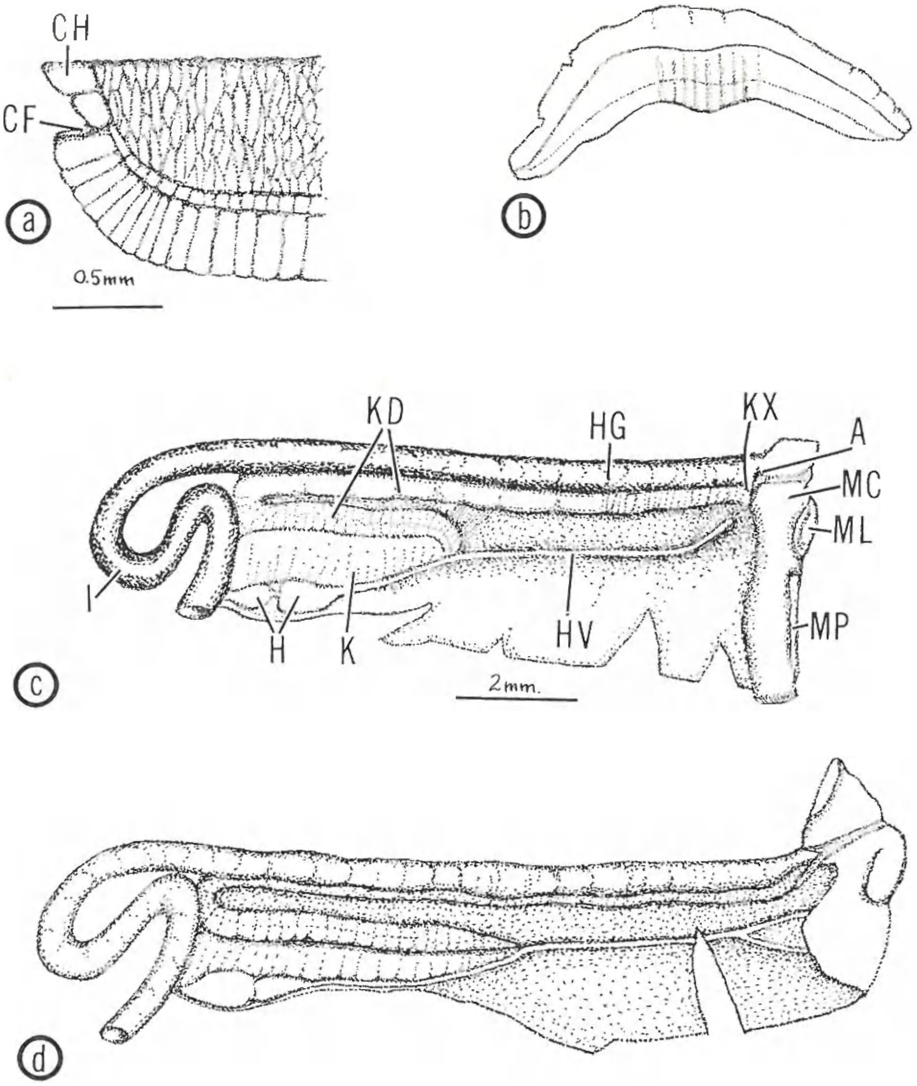

Fig. 3. *Sesara parva*, new species: *a*, tail of specimen 116; *b*, jaw of specimen 116; *c*, pallial region of specimen 116; *d*, pallial region of specimen 1797.

crescent shaped; basopalatal mantle lappet (MP) a long, slender ridge, largest at upper edge, tapering downwards. A lobe of mantle collar encroaches on lung surface opposite basopalatal mantle lappet. Respiratory pore, anus (A), and excretory chamber (LK) crowded together at parietal-palatal margin. Urinary chamber a transverse groove leading above anus, then out through pneumostome. Hindgut (HG) slender, paralleling parietal-palatal margin for length of pallial chamber. Ureter (KD) a closed reflexed tube, slightly narrower than hindgut, primary portion wider, separated by a narrow strip of lung roof. Kidney (K) 3.45 mm. long, fingerlike, tapering gradually anteriorly, base not flaring. Pericardium (H) slightly more than one-third length of kidney. Loop of intestine (I) abutting kidney base.

Genitalia (fig. 4 *a*) subadult. Ovotestis (G) imbedded in digestive gland above apical intestinal loop, consisting of small ovoid alveoli clustered along a single tubule. Hermaphroditic duct (GD) a simple tube to head of prostate-uterus, reflexed upwards into talon (GT). Albumen gland (GG) a fingerlike projection only slightly larger than talon, apparently with a prominent carrefour (X) as in *Durgella libas* (fig. 10 *a*). Prostate (D) more fully developed than uterus (UT). Vas deferens (VD) a slender tube bound into peniovidual angle, entering base of epiphallic lime sac (EF) at point opposite penial sheath (fig. 4 *b*). Lime sac and head of epiphallus (E) bound to basal portion of penis by a muscle sheath. Lime sac very large, somewhat sinuated, internally with a narrow tube along one margin, main portion filled with two rows of pustulations, entrance to epiphallus paralleling that of vas deferens. Epiphallus with longitudinal pilasters continuing past junction of coiled epiphallic retractor-caecum (ERC). Penial retractor (PR) attached to latter, originating on diaphragm. Epiphallus making an "S"-loop, entering penis, enlarging, becoming pustulose internally with two narrow longitudinal pilasters forming a groove in one wall leading to constricted neck of area surrounded by penial sheath (PS). Latter possessing a thin covering of muscle with fibers attaching to epiphallus. Internally a narrow tube with weak longitudinal pilasters passes through sheath, opening into a bulbous chamber with circularly arranged pustulations. This gradually narrows and opens into atrium (Y). The exact delineation between penis and epiphallus is uncertain. Probably it occurs just after "S" loop but may be just above penial sheath. No verge or penial stimulatory papillae developed.

Free oviduct (UV) and vagina (V) relatively long, simple tubes with longitudinal pilasters. Spermatheca (S) fingershaped, head reaching over two-thirds of way to albumen gland. Atrium (Y) short, torn in illustrated specimen. No dart apparatus.

Radular formula (37–34) – 7 – 1 – 7 – (34–37) with over 80 rows (fig. 4 *c*). Central distinctly larger than first lateral, mesocone very long, ectocones large and recessed far back on tooth. First lateral with prominent entocone, set further forward than the more prominent ectocone. On seventh lateral ectocone lost, base elongated and ectocone enlarged. By fifth marginal, ectocone only slightly less prominent than mesocone. Size of teeth gradually decreasing from seventh or eighth marginals,

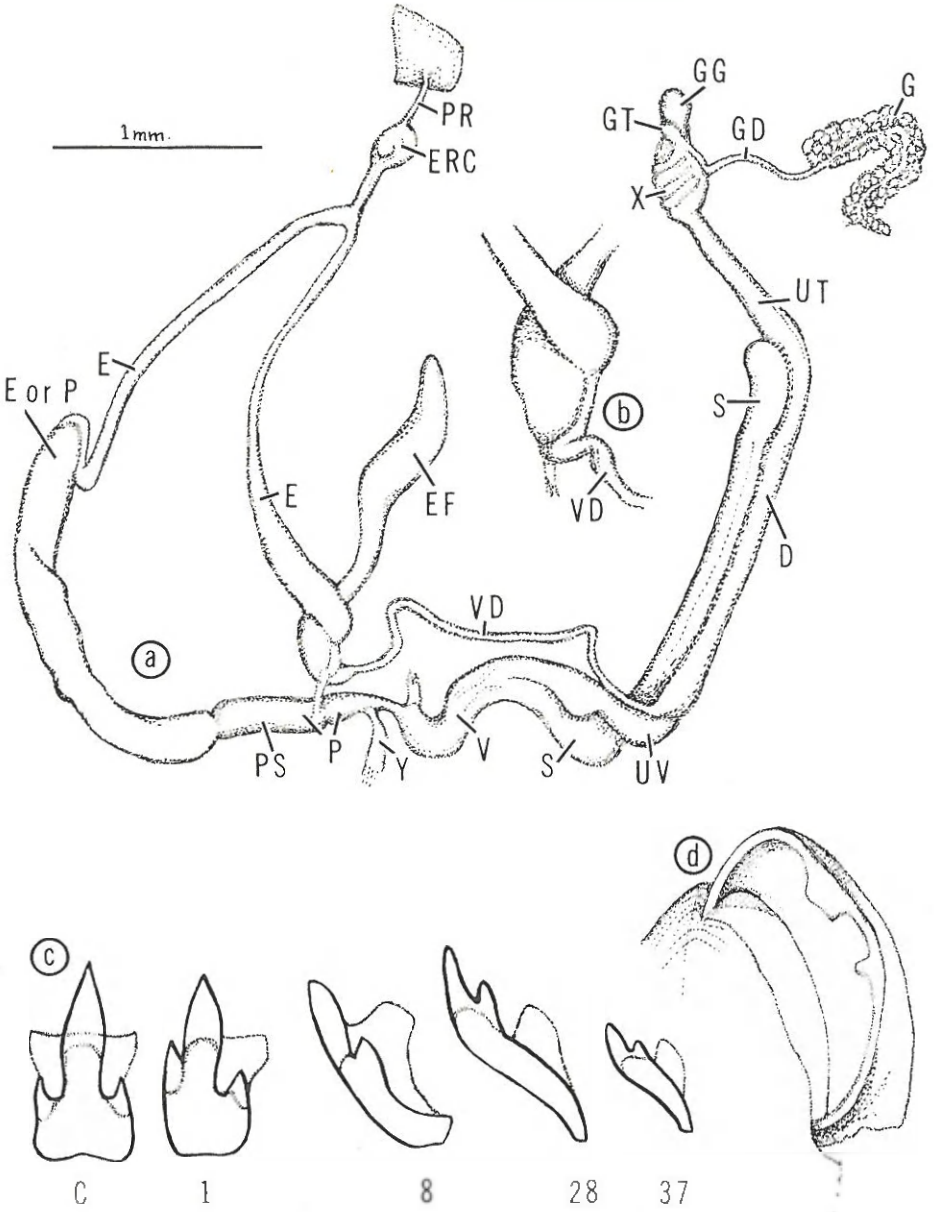

Fig. 4. *Sesara parva*, new species: *a*, genitalia of specimen 116; *b*, detail of vas-deferens-epiphallus junction; *c*, isolated radular teeth from specimen 116; *d*, palatal teeth of aperture.

cusps becoming narrower with a wider gap. Last five marginals showing reduction in ectocone, extreme foreshortening and outermost one or two marginals vestigial.

Jaw (fig. 3 *b*) with strong median projection and slight trace of vertical ridging on central portion.

Description of shell. – Shell rather small, depressed conoidal, dextral, with $5^3/_4$ normally coiled whorls. Apex and spire moderately and almost evenly elevated, sides of spire a little convex, rounded above, H/D ratio 0.549. Apical whorls $2^3/_4$, smooth and shining with vague opaque radial streaks on last apical whorl. Remaining whorls with low, slightly protractive radial ribs, about 102 on the body whorl, whose interstices are about 2–3 times their width, strong above periphery, absent from base of shell which is smooth and shining. Sutures shallow, whorls flatly rounded above blunt obtusely angulated periphery. Umbilicus completely closed, callus area slightly impressed with columellar lip inserting perpendicularly. Aperture oblong, distinctly narrowed by inward sinuation of palatal lip, portion above periphery extending much further forward than nearly straight basal portion. Palatal teeth two; inner teeth a squarish knob situated on lip edge just inside basal angle; outer tooth more than three times wider than high, situated on lower palatal lip slightly below middle of sinuation with upper edge gradually descending (fig. 4 *d*). Height of holotype 4.12 mm., diameter 7.52 mm.

Holotype. – Universitetets Zoologiske Museum, København. Doi Sutep, North Thailand at 800 meters elevation (number 2300). Collected by B. Degerbøl on 9.III.1959.

Paratypes. – Nineteen additional specimens, nine of them adults, were taken at Doi Sutep between 800–1,400 meters elevation from 18.IV.1958–9.III.1959. They are:

Sesara parva paratypes

Doi Sutep at 800 meters (2300, 9.III.1959),
1,000 meters (1671), 24.X.1958),
1,100 meters (1401a, 29.IX.1958, 1449, 4.X.1958, 1452, 4.X.1958, 1683, 25.X.1958, 1733, 28.X.1958, 1738, 28.X.1958, 1797, 3.XI.1958, 1844, 8.XI.1958, 2216, 14.II.1959, 2293, 8.III.1959),
1,300 meters (1508, 7.X.1958, 116, 18.III.1958),
1,400 meters (1588, 14.X.1958).

Two paratypes (number 2300) are FMNH 135277.

Remarks. – All six specimens collected in February, March and April were adults, while only four of the fourteen (1844, 1797, 1733 both examples) collected in October and November were adults. The juvenile shells were nearly adult in size, only lacking the lip thickening and tooth development. The presence of subadults in October-November and only adults in February-April gives only limited data as to the breeding season or life history since there is no way to determine the ages of the October juveniles.

Size and shape variation in the ten adults is height 3.53–4.77 mm., mean 4.15 mm.; diameter 6.01–7.53 mm., mean 7.00 mm.; H/D ratio 0.528–0.650, mean 0.595; whorls $5^1/_8$–$6^1/_4$. The two smallest adults had repaired injuries to the body whorl and may have been abnormally small. The elevation and shape of the spire varied moderately, with the holotype being one of the more depressed specimens.

Comparisons with other species are difficult. *S. megalodon* Blanford 1902 from near Phitsanulok has four palatal teeth and is 10.0 mm. in diameter (FMNH 43150), with a more elevated spire, $6^3/_4$ whorls, and a less angulated periphery. The middle palatal teeth of *S. megalodon* are as in *S. parva* and their shell sculpture is very similar. *S. mouleyitensis* Gude 1901 is also larger, more elevated, less carinated and has the outer palatal tooth much more prominent. No material of the unfigured *S. bidentifera* Godwin-Austen 1908 was seen, but this apparently has different palatal teeth and is much larger. The poorly figured *S. penoti* Ancey 1898 from Laos has smaller teeth, weaker sculpture and is much larger.

The combination of smaller size, fewer whorls, heavy sculpture and two unequal palatal teeth differentiate *S. parva* as a distinct species. The only previously dissected *Sesara* is the genotype, *Sesara infrendens* (Gould 1844). As figured by Stoliczka (1871, Journ. Asiatic Soc. Bengal 40, part 2, pl. 16, figs. 4–10 (Partly copied by Blanford and Godwin-Austen (1908, p. 242)) the genitalia show a highly complicated spermatophore, very large lime-sac, long spermatheca, long vagina and a long slender penis-epiphallus. The dart apparatus is absent. The penial retractor inserts on the epiphallus without trace of a retractor caecum.

Despite the shell lip formation, only juvenile genitalia of *S. parva* were seen. Compared with Stoliczka's illustrations, the most important difference is the presence of a prominent coiled retractor caecum on the epiphallus in *S. parva*. While no penial muscle sheath is shown for *S. infrendens*, this feature could have been overlooked. The straight hermaphroditic duct, small albumen gland, undifferentiated uterus and prostate of *S. parva* are juvenile characters and have no systematic importance.

The radula of *S. infrendens*, as figured by Stoliczka, has the central tooth distinctly smaller than the first lateral and there are ten lateral teeth. The absence of entocones on the figured first and second lateral teeth may reflect the poorer optical equipment of the 1870's, since these minute cusps are very difficult to observe. In *S. parva* the central tooth was distinctly larger than the first lateral, there are seven laterals and the entocones are clearly visible on the first two laterals.

Comparison of figs. 5 *c* and 5 *d* indicate that the degree of contraction within the shell can alter the pallial region rather considerably. Specimen number 116 (fig. 5 *c*) was contracted much further into the shell than specimen 1797 (fig. 5 *d*). Hence the kidney and primary ureter appear much shorter and wider in the first drawing than the second.

The prominent coiled retractor caecum and large lime-sac clearly indicate that, despite the absence of a dart apparatus, *Sesara* belongs to the Macrochlamydi.

Genus ***Sarika*** Godwin-Austen 1907

Type species. – *Helix resplendens* Philippi 1846 by monotypy.

The presence of a long, straight epiphallic retractor caecum is the main character separating *Sarika* from *Macrochlamys*. Godwin-Austen considered *Sarika* an eastern geographical replacement of the primarily Indian *Macrochlamys*, and probably most, if not all, of the "*Macrochlamys*" from Malaya, Thailand, former Indo-China and southern China should be transferred to *Sarika*. Both species reported on below showed the genitalia of *Sarika*, although only in *S.* aff. *hainesii* was it sufficiently adult to warrant illustrating.

Sarika sp.

(Pl. I, A–C).

Ban Kao near Kwae Noi (Palle Johnsen, 28.XI.1961; 15–20.XI.1961)

The two adults are planulate, tightly coiled shells, 15.0 and 14.3 mm. in diameter, H/D ratios 0.487 and 0.440, with 6+ and $5^3/_8$ whorls. They could not be identified with any known species.

Sarika obesior (Martens 1867)

(Figures 5, *b–c*)

Nanina resplendens Phil. var. *obesior* Martens 1867. Preuss. Exped. Öst.-Asien, Zool. 2, p. 72, pl. 12, fig. 6 (Petshaburi and Bang-Pra, Thailand).

Kampaengpet (2131, 19.I.1958)
Wang Dao (748, 11.VII.1958; 945, 3.VIII.1958)
Sitang (1896, 22.XI.1958)
Koh Kut (6.IV.1959)
Koh Chang (Degerbøl, 4.IV.1959)

Doi Sutep at 750 meters (1609, 17.X.1958)
800 meters (1480, 5.X.1958)
900 meters (1490, 5.X.1958)
1,000 meters (1344, 20.IX.1958; 1776, 1.XI.1958)
1,100 meters (1321, 18.XI.1958).
Doi Sutep (882, 26.II.1958; 2300, 9.III.1959).

The largest specimen (945) was only 22 mm. in diameter with $6^{1}/_{8}$ whorls. Most were less than 15 mm. At all stages of growth, these shells differ from those of *S.* aff. *hainesii* in having the last whorl rounded

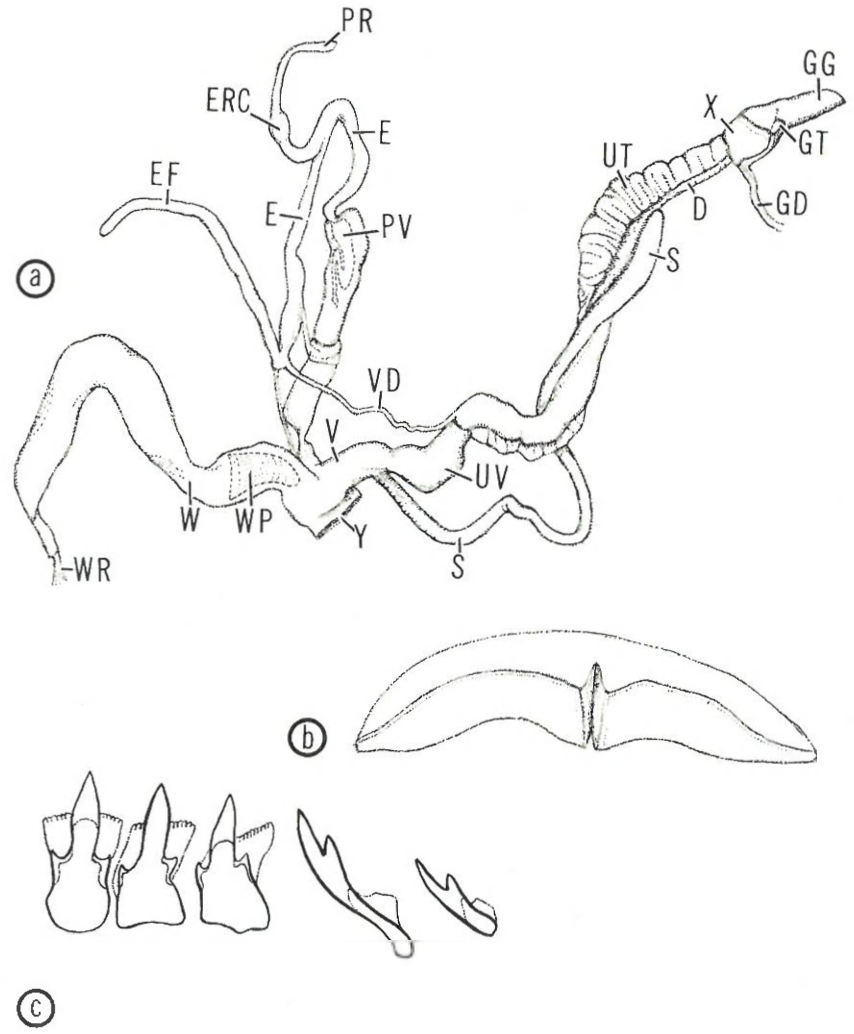

Fig. 5. *Sarika*: *a*, genitalia of *S.* aff. *hainesii*; *b*, jaw of *S. obesior*; *c*, isolated radular teeth of *S. obesior*.

rather than subangulated. The jaw (fig. 7 *c*) and radular teeth (fig. 7 *d*) are typical of *Sarika* and *Macrochlamys*.

Sarika aff. ***hainesii*** (Pfeiffer 1856)

(Fig. 5 *a*)

see *Helix hainesii* Pfeiffer 1856. Proc. Zool. Soc. London 1856, p. 32 (Siam); Martens 1867. Preuss. Exped. Öst.-Asien. Zool. 2, p. 73.

Koh Chang (3.IV.1959)

Doi Sutep at 1,000 meters (1671, 24.X.1958; 2002, 16.XII.1958; 1809, 4.XI.1958; 1173, 10.IX.1958; 2096, 11.I.1959, 1797, 3.XI.1958),
1,100 meters (2035, 21.XII.1958; 1579, 13.X.1958; 1452, 4.X.1958; 2216, 14.II.1958; 1762, 31.X.1958; 1844, 8.XI.1858; 1278, 15.IX.1958),
1,200 meters (2191, 7.II.1958),
1,300 meters (1508, 7.X.1958; 2066, 29.XII.1958; 2239, 20.II.1959),
1,400 meters (2245, 20.II.1959),
1,500 meters (2204, 15.II.1959),
1,550 meters (2089, 10.I.1959).

The largest example (Koh Chang), was still juvenile and only 21 mm. in diameter with $6^{1}/_{4}$ whorls. Most individuals were much smaller. All shells had the last whorl distinctly subangulated, thus distinguishing them from *S. obesior*. No authenticated material of *S. hainesii* was available, and I have thus left the identification tentative. Apparently this species is usually found at higher elevation than is *S. obesior*.

Despite the juvenile appearance of the shells, adult genitalia were extracted from one of the Doi Sutep examples (2191). Illustration of the genitalia serves to help define the Macrochlamydi, since the only recorded difference from *Macrochlamys* lies in the lack of a coiled head to the epiphallic retractor caecum. Lack of time prevented other than a cursory examination of the pallial region, which did not differ from that of *Sesara*, or other features of the anatomy.

A brief description of the genitalia (fig. 5 *a*) follows: – Ovotestis not removed. Hermaphroditic duct (GD slender, slightly sinuated, running to base of albumen gland (GG), then reflexed apically in a straight line and entering base of talon (GT). Latter opening into a large carrefour (X) heading prostaticuterine chamber. Carrefour walls with glandular tissue very similar to texture of albumen gland. Prostate and uterus typical, with common chamber and prominent "C"-shaped barrier providing functional separation. Uterus (UT) large and sacculated, prostate (D) a thinwalled sac of glandular tissue paralleling uterus.

Vas deferens (VD) a relatively short slender tube, entering head of epiphallus (E) near lower end of penial sheath. Epiphallic head attached to peniovidual angle by strip of connective tissue. Lime-sac (EF) distinctly longer than epiphallus, slender and fingerlike, slightly larger mid-apically than basally. Internally with two angled rows of single pustules flanking a longitudinal clear zone. Epiphallus proper with very weak longitudinal pilasters and numerous calcareous granules below insertion of penial retractor (PR). Latter attached on apex of epiphallic retractor caecum (ERC) and originating on diaphragm. Retractor caecum slightly bulbous at apex, rather thick walled with longitudinal pilasters ending at base of head. Lower part of epiphallus with weak longitudinal pilasters, entering penis (P) through a very long slender verge (PV). Verge very long and slender, coiled back upon itself, with the sides presenting a shingled appearance rather than being corrugated as the dart papilla. Location of pore on verge not determined. Lower one-third of penis surrounded by a muscle sheath. Apical portion to midpart of sheath with pustulose walls, lower portion with weak longitudinal pilasters extending into atrium. Area below muscle sheath with weaker pilasters than section within muscle sheath. Atrium (Y) rather short but wide, receiving dart apparatus (W), penial opening and vagina (V).

Free oviduct (UV) short, thinwalled, with internal glandular collar just above insertion of spermatheca (S). Spermatheca very long, fingerlike, reaching nearly to carrefour; without internal sculpturing. Vagina (V) short, weakly pilastered, clearly differentiated from atrium.

Dart apparatus (W) a long cylindrical tube with retractor muscle originating off columellar retractor muscle. In cross-section, dart apparatus a hollow muscular tube covered by a thin layer of glandular tissue and opening through a prominent dart papilla (WP) with smooth pointed tip and corrugated sides.

Teraia, new genus

Foot with tripartite sole and typical aulacopod grooves. Caudal foss cup-shaped, caudal horn very reduced, not overhung. Mantle collar with two minute lobes, no shell laps. Atrial and vaginal areas not differentiated. Free oviduct long. Spermatheca finger-shaped with stalk reaching far up spermoviduct. Dart apparatus compact, a tubular muscular core with surrounding glandular cover and membrane, a terminal retractor muscle, and opening through large dart-papilla. Epiphallus with long sinuated lime-sac, entering penis through functioning verge. Penial retractor epiphallic, without any retractor caecum. Radular central and laterals large, tricuspid. Marginals lanceolate and unicuspid.

Shell small to medium in size, depressed conoid, yellowish white, broadly umbilicated, with slight apertural lip callus. Base of shell nearly smooth, upper part with weak to strong radial sculpture. Apex smooth or sculptured.

Type species. – *Teraia thailandica* new species.

Great pleasure is taken in dedicating this genus to Mrs. W. S. S. VAN BENTHEM JUTTING VAN DER FEEN in recognition of her magnificent studies on the molluscan fauna of the Indo-Malayan region.

Several features in both shell and anatomy combine to warrant generic recognition for *Teraia thailandica*. The complete absence of any epiphallic retractor-caecum, the peculiar cup-shaped caudal foss without a caudal horn, lanceolate unicuspid marginal teeth and broadly umbilicated shell with prominent supra-peripheral sculpture combined with a smooth base, form a complex of characters that clearly differentiate *Teraia* from related genera.

The finger-like spermatheca with long stalk, prominent lime-sac, compact dart apparatus with dart-papilla (but no sign of a calcareous dart), obsolescent vagina and atrium, prominent lateral radular teeth, small mantle lobes, absence of shell laps, and general shell structure indicate affinity with the Macrochlamydi.

There are three genera that merit direct comparisons: –

Macrochlamys Benson 1832: usually has a well-developed caudal horn; a prominent coiled retractor caecum on the epiphallus; and an imperforate or minutely perforate shell, which at most is weakly sculptured above. The radular marginals may be bicuspid or unicuspid.

Taphrospira Blanford 1905: has a large caudal horn; a reduced retractor caecum on the epiphallus; a rather short lime-sac; and larger smooth shell with open umbilicus and channeled suture.

Khasiella Godwin-Austen 1899: has a well-developed caudal horn; a very small, uncoiled retractor caecum on the epiphallus; an imperforate or minutely perforate shell that may be angulated or rounded at the periphery and which generally has strong supra-peripheral sculpture. The radular marginals are bicuspid at first, becoming aculeate near the margin.

The complete absence of the epiphallic retractor caecum, very peculiar caudal termination (as in *Oxytesta*), and widely umbilicated shell are the key features characterizing *Teraia thailandica*. Of the three genera differentiated above, *Khasiella* is probably its nearest relative.

A search of the literature revealed three species, known from the shells only, that may be associated with *Teraia thailandica*. They are *Macrocyclis contempta* Bavay and Dautzenberg 1909 from "Lao Kay, Tonkin"; *Macrocycloides crenulata* Yen 1939 from Hongkong; and *Macrocycloides hainanensis* Yen 1939 from Hoihow, Hainan Island (Hai-K'ou on the north-central coast). Reference to the rhytidid genus *Macrocycloides* was a logical guess, since the greasy-white shell color, smooth base, supra-peripheral sculpture and open umbilicus are characters commonly found in the Rhytididae. The latter is Austro-Zelandic and Melanesian in distribution, with a very few Wallacean and Bornean species. No rhytidids are known from the Asian mainland. Transfer of these species to the helicarionid genus *Teraia* seems preferable, since they agree in sculpture, umbilicus and shape with *T. thailandica.* A single shell from Chieng Dao (specimen 794) is reported below as *T. crenulata*, since it shows no difference from the type figures of that species.

Teraia thailandica new species

(Pl. I, K–M, fig. 6, 13 *a*, *e*)

Diagnosis. – A large (diameter 9.5–10.4 mm.), depressed (H/D ratio 0.500–0.522) species with open umbilicus (D/U ratio 5.1–5.6), prominent apical radial ribbing, beaded radial ribbing on the lower spire, smooth base, and rather large apex.

T. crenulata (Yen 1939) has the apical whorls smooth, no beading on the ribs, is much smaller (diameter 6.2–6.7 mm.) and more elevated (H/D ratio 0.565–0.622). *T. hainanensis* (Yen 1939) and *T. contempta* (Bavay and Dautzenberg 1909) are smaller (diameters 6.4 and 7 mm.) with greatly reduced sculpture. The few sculptured *Macrochlamys* are immediately separable in having a closed or minutely perforate umbilicus.

Description of shell. – A medium sized, very depressed, conoidal shell with $4^1/_2$ regularly coiled whorls. Apex and spire slightly and evenly elevated, H/D ratio 0.500. Apical whorls $1^7/_8$, sculpture of prominent radial ribs, whose interstices are twice their width. Ribs becoming narrower, more crowded, less regular on lower whorls and inconspicuously, but regularly and closely, beaded on last $1^1/_4$ whorls (fig. 6 *f*). Ribs strong to periphery, then fading out rapidly. Base of shell smooth, shining, marked only by irregular growth wrinkles. Sutures impressed, whorls relatively evenly rounded, very slightly rounded above, with rounded periphery and basal margin. Umbilicus narrowly U-shaped, slowly and regularly decoiling, contained 5.62 times in the diameter. Aperture subovate, not deflected, with sinuated margin. Lip slightly thickened internally on basal and columellar margins. Parietal wall without callus. Height of holotype 4.77 mm., diameter 9.55 mm.

Description of soft parts. – Body rather short, tail dome shaped without distinct middorsal groove. Sole (fig. 6 *g*) evenly tripartite, pedal grooves very strong, high on foot. Caudal horn not developed, caudal foss (CF) a triangular slit near bottom of tail with a peculiar cup-shaped cavity (fig. 6 *g*) above sole margin.

Mantle collar (MC) rather large with two small accessory lappets (fig. 6 *h*): one bordering anal opening, a crescentic narrow lobe (ML); the other (MP) a narrow flap, flaring laterally on anterior edge and located on outer palatal section of mantle collar. Respiratory pore, anus (A) and excretory chamber crowded into parietal-palatal margin (fig. 6 *h*). Urinary chamber (LK) a sharply defined pit opening through a narrow groove running along top of anus with products apparently passing out the same pore as egested materials. Hindgut (HG) relatively small, opening well within mantle collar. Secondary ureter (KD) of equal width, obviously sacculated, opening slightly posteriorly of anus. Surface of lung roof with scattered black pigment granules, showing simple termination of principal pulmonary vein (HV). Remainder of pallial region not extracted. Internal edge of mantle collar extended backwards and rather thick.

Apical genitalia not extracted. Terminal portion (fig. 6 *a–e*) as follows. Uterus (UT) large and sacculated (fig. 6 *a*), prostate (D) reduced to a slender strip of tissue along uterine surface. Vas deferens (VD) a long, slender, slightly coiled tube entering at base of epiphallic lime sac (EL). Latter a quite long, finger like sinuous appendage without terminal expansion or attachment (fig. 6 *b*). Epiphallus (E) below entrance of kalk sac a much broader tube, internally with clusters of granules, narrowing after insertion of penial retractor (PR) to form a muscular tube about three times diameter of vas deferens. Penis (P) marked externally by sudden swelling, internally by a 0.6 mm. long verge (PV) with slightly corrugated sides and a blunt tip (fig. 6 *b*). The epiphallic pore (EP) opens in the center of the verge with a five-part rosette effect. Base of penis narrower, surrounded by a muscular sheath. Atrial area (Y) not clearly differentiated, gonapore ringed by a fleshy collar (fig. 6 *c*).

Free oviduct (UV) short and thickwalled, choked inside with pustulose glandular tissue, narrowing to form a collar just above entrance of spermatheca (S). Lower portion of free oviduct pebbled internally. Spermatheca a slender clubshaped organ whose head lies far above origin of vas deferens. Opening of spermatheca, free oviduct, penis and dart apparatus clumped so that no distinction of vaginal or atrial areas is possible (fig. 6 *c*).

Dart apparatus (W) a long cylindrical tube with small apical retractor muscle whose origin is unknown. Upper two-thirds with a glandular covering surrounding a thick sheath of circular muscles with a hollow core (fig. 6 *d*). Glandular coating absent from lower third of sheath, above covered by thin membrane continuing over basal portion.

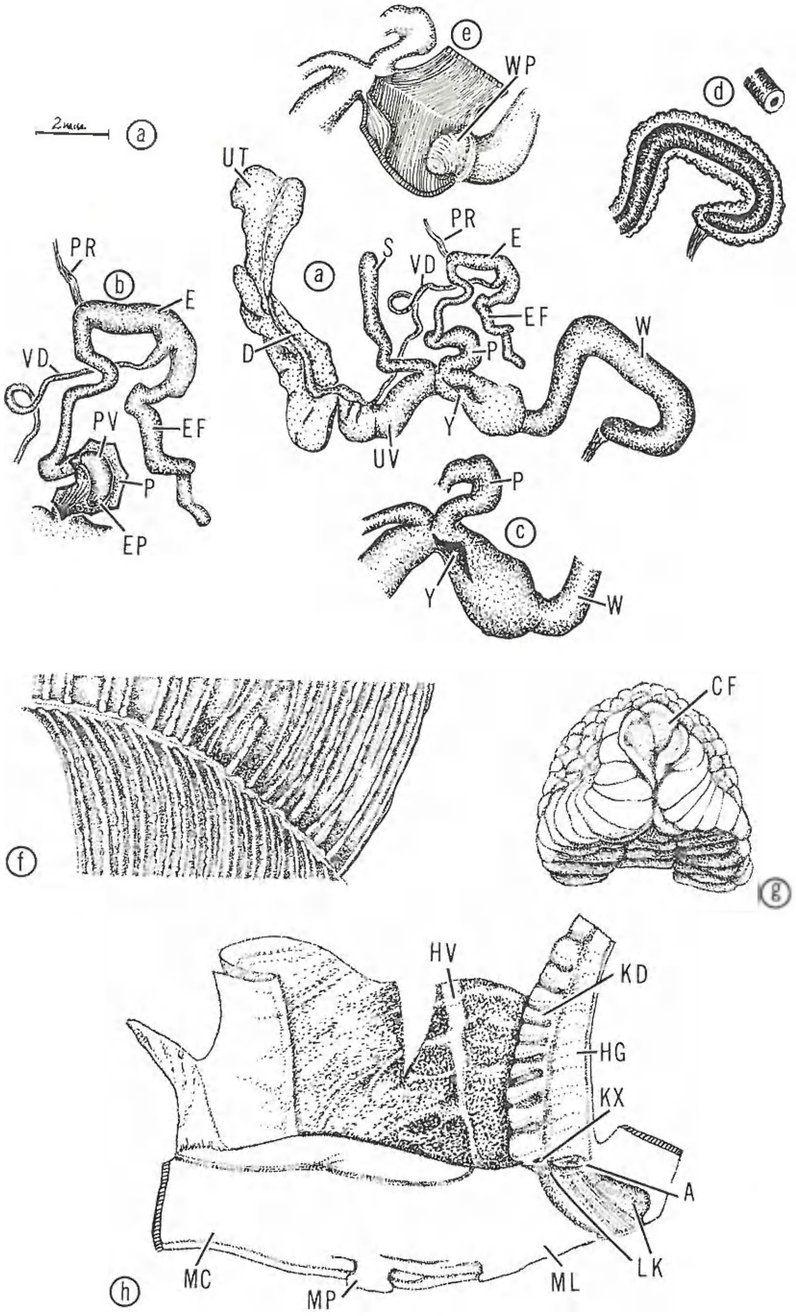

Fig. 6. *Teraia thailandica*, new species: *a*, genitalia anterior to albumen gland of holotype; *b*, details of penis and epiphallus; *c*, detail of atrial region; *d*, structure of dart apparatus; *e*, view of dart papilla; *f*, sculpture on penultimate and body whorl of holotype; *g*, caudal region; *h*, anterior part of pallial region. Figures *a–d* drawn by Miss Marcia Oddi.

Swelling at base of dart apparatus housing a large dart papilla (WP) with smooth tip and somewhat corrugated sides (fig. 6 *e*). Walls of lower dart apparatus with fine diagonal corrugations merging to form a "V" pattern opposite gonapore.

Radular formula 34–8–1–8–34 with about 100 rows. Central (fig. 13 *a*) equal in size to first lateral, mesocone moderately elongated, ectocones small. First lateral distinctly assymmetrical with prominent entocone and ectocone. Starting with 7th and 8th laterals, entocones and ectocones reduced, entocone disappearing after 1st marginal, ectocone after 2nd or 3rd marginals. Marginal teeth lanceolate with greatly reduced bases. Outer ten marginals very much reduced in size and shortened.

Jaw (fig. 13 *e*) thin, relatively featureless with slight median projection and weak striations, but no major sculpture.

Holotype. – Universitetets Zoologiske Museum, København. Doi Sutep, North Thailand at 1,100 meters elevation. Specimen number 1401 a. Collected by B. Degerbøl on 29.IX.1958.

Paratype. – Field Museum of Natural History Museum number 135276. Doi Sutep, North Thailand at 1,300 meters elevation. Specimen number 927. Collected by B. Degerbøl on 31.VII.1958.

Remarks. – In both specimens the soft parts were retracted far within the shell. Only part of the holotype could be extracted, hence the anatomical description is incomplete. No attempt was made to extract the more deeply recessed soft parts of the paratype.

Differences from the other species tentatively assigned to *Teraia* are given above in the diagnosis. While such Indo-Burmese genera as *Taphrospira*, *Khasiella* and *Sesara* show similar appearing shell sculpture and shape, the radular and genital differences outlined under the generic discussion at once separate *T. thailandica.*

Measurements of the two known specimens are: –

	Height	Diameter	H/D ratio	D/U ratio	Whorls
Holotype	4.77	9.55	0.500	5.62	
Paratype	5.43	10.40	0.522	5.13	

Teraia crenulata (Yen 1939)

(Pl. II, fig. A–C)

Macrocycloides crenulata Yen 1939. Abhl. Senckenberg. Naturf. Gesell. 444, p. 157, pl. 16, fig. 20 (Hongkong).

Chieng Dao at 1,800 meters (794, 16.VII.1958).

The single shell shows such minor differences from the holotype that I have no hesitation in using Yen's name, despite the geographic gap from Hongkong to Northern Thailand. The dimensions of Yen's type and the Thailand shell are: –

	Height	Diameter	H/D ratio	D/U ratio	Whorls
Holotype	3.5	6.2	0.565	4.77	$4^1/_2$
Specimen 794	4.2	6.7	0.622	4.90	$5^1/_8$–

To facilitate comparisons with *T. thailandica*, a description of the Thailand shell of *T. crenulata* follows: –

A rather small, depressed conoidal shell with slightly less than $5^1/_8$ tightly coiled whorls. Apex and spire moderately and evenly elevated, H/D ratio 0.622. Apical whorls slightly more than $2^1/_4$, surface smooth and shining. Remaining whorls with broad, rounded, protractively sinuated radial ribs, 101 on body whorl, whose interstices are about equal to their width. Ribs prominent to periphery, represented on base of shell only by irregular wrinkles. Sutures slightly impressed, whorls flatly rounded above and on base, periphery more sharply rounded. Umbilicus V-shaped, regularly decoiling, contained 4.90 times in the diameter. Aperture ovate, deflected about 10° from shell axis, margin sinuate. Columellar and basal lips with slight internal callus. Parietal wall without callus.

Tribe Durgelli

Originally proposed as a subfamily characterized by a reduced shell, very large shell laps, and the radula with very numerous pectiniform lateromarginal teeth, this taxon is expanded and defined by additional characters. The genitalia offer the most important features. The spermatheca is not finger-like, but consists of a broad collared base, a narrow stalk and a bulbous head. The vas deferens enters laterally on the small epiphallic head, which lies quite near the penial retractor insertion compared with its position in the Macrochlamydi. Mostly the vagina, atrium, penis and dart papilla sac share a common area and are not differentiated. The shell usually is small, vitriniform or helicoidal, very thin, sometimes without calcareous elements, and far too small for the animal to retract itself completely. The visceral hump is located far forward on the body, the tail is very long and slender and has a prominent caudal horn. The shell laps are quite large and can cover much of the shell when fully expanded. The radula varies from the typical ariophantine type (tricuspid central and lateral, bicuspid marginals) to the unicuspid teeth of *Sophina*, the minute serrated numerous lateromarginals of *Durgella*, and (possibly) the tricuspid marginals of *Muangnua*.

The reduced epiphallic head located near the penial retractor insertion and great reduction of the penial retractor caecum, together with the altered spermatheca and enlarged shell laps are the diagnostic characters. The tendency towards size reduction and loss of the lateral radular teeth are secondary developments.

Several genera have not been included in the Durgelli previously. *Eurychlamys* Godwin-Austen 1899 was placed in the Helicarioninae by THIELE (1931, p. 638) and the Euconulinae by H. B. BAKER (1941, p. 212). BAKER's suggestion was followed by ZILCH (1959, p. 279). Although it lacks a dart apparatus, the shortened spermatheca, large shell laps, no retractor caecum and small epiphallic head located near the penial retractor insertion agree with the Durgelli. The radular teeth are typical of the Macrochlamydi and the shell is the largest found in the durgelline series. While *Eurychlamys* might be considered intermediate, I think it best to place it in the Durgelli.

Sophina Benson 1859 from Tenasserim was placed in a distinct subfamily (Sophininae) by BLANFORD and GODWIN-AUSTEN (1908, p. 283), a judgment followed by THIELE and ZILCH. H. B. BAKER offered no suggestion as to where it might be classified. According to BLANFORD and GODWIN-AUSTEN (1908, p. 285), "The spermatheca is globular at the free end, but on a strong thick base. The vas deferens is given off from a bulbous expansion of the penis-tube (= epiphallus) close below the junction of the thick strong retractor muscle". It has the typical dart apparatus and moderately large shell laps of the Durgelli, but the radula is very unusual in having unicuspid teeth with strong angulation to the rows. The shell is umbilicated with a channeled columellar wall. Despite the unusual radula, the quoted description of the genitalia indicates placement in the Durgelli.

Satiella Blanford and Godwin-Austen 1908 contains a few large species from Southern India and Ceylon that have a vitriniform shell, large shell laps and the genitalia with a functioning verge. In other characters, the radula and genitalia seem typical of *Durgella*. *Sitala* H. Adams 1865 has a very different shell (trochiform with prominent sculpture) and retains tricuspid lateral teeth on the radula. The marginal teeth and genitalia are as in *Durgella*. *Sakiella* Blanford and Godwin-Austen 1908 from Pegu and Tenasserim has the radular teeth, tail and shell laps of the Durgelli. Other features of the genitalia have not been studied.

The other genera usually referred to the Durgelli, *Durgella* Blanford 1863 and *Ibycus* Heynemann 1862, are redefined below on the basis of new dissections and related to a third genus, *Cryptaustenia* Cockerell 1898, that usually has been placed in the Girasii.

This whole problem was brought into focus through dissection of two very similar species. A brief comparison provides the criteria for classification and can preceed the formal description.

Although agreeing in many characters, particularly in the genitalia and pallial regions, there are several contrasts between *Durgella libas* and *Cryptaustenia gadinodromica*. In *Durgella* the tail is less attenuated (fig. 7 *a*) and the visceral hump proportionately larger (fig. 7 *a*). *Durgella* has the central portion of the foot sole wider (fig. 7 *d*), the caudal horn less overhung (fig. 7 *c*) and the caudal foss somewhat recessed compared with *Cryptaustenia* (see figs. 10 *a*, *c*, *d*). Particularly obvious is the differing pattern of the slime network. In *Durgella* (fig. 7 *c*) it is a mosaic of varying rectangular patches; in *Cryptaustenia* (fig. 10 *c*) a few large elongated posteriorly slanting divisions. From preserved specimens it is difficult to be certain, but apparently the shell laps of *Cryptaustenia* are more strongly pebbled and larger than those of *Durgella*.

The pallial region of the larger *Durgella* (fig. 8) is more heavily vascularized, the kidney relatively smaller and only the reflexed secondary ureter grossly expanded. *Cryptaustenia* (fig. 11 *a*) has the kidney base flared and reflexed downward with a lobe extending somewhat forward, practically no lung roof space between the ureter arms, both parts of the ureter grossly expanded, reduced vascularization and the urinary chamber compressed with less distinct separation from the anal channel. All of these changes could be the result of size reduction.

The most obvious difference in the genitalia lies in *Durgella* (fig. 9 *a*) having a dart apparatus, which is lacking in *Cryptaustenia* (fig. 12 *a*, *b*). The hermaphroditic duct coiling and size differences in the albumen gland, ovotestis, prostate and uterus may be individual variations. The only significant distinction lies in the general compaction of the terminal genitalia in *Durgella*. Penis, vagina, atrium and spermatheca are shorter, more muscular and wider in *Durgella libas* than in *Cryptaustenia gadinodromica*. Internally (figs. 9 *b*, 12 *c*) the genitalia of both species has exactly the same structures, from the epiphallic pilasters to the muscular collar of the spermatheca, pustulose penis and penial stimulator situated below the penial muscle sheath.

The radulae are quite different. *Durgella libas* (fig. 13 *b*) has a wide, thin radula with a minute unicuspid central tooth and about 850 very small pectiniform bicuspid lateromarginal teeth per row. *Cryptaustenia gadinodromica* (fig. 13 *c*) has a narrower radula with much fewer and larger teeth. The central is tricuspid and only slightly smaller than the laterals, which number nine and have a small entocone far up on the mesocone and a larger, recessed ectocone. The about 50 marginals are subequally bicuspid, with elongated bases, but not serrated.

Both shells are globosely helicoid with about four whorls, few calcareous elements and fine incised spiral lines visible only under high magnification.

The nearly identical genitalia contrasts with the divergent body proportions, slime network, shell laps and radula. A literature survey showed a number of species from Sikkim to Tenasserim that, so far as anatomical features are known, agree with one or the other of the Thailand species. For convenience, they can be grouped into the generic units *Durgella* and *Cryptaustenia*, diagnosed as follows:

Durgella – visceral hump and shell larger; tail less elongated with only slightly protruded caudal horn; slime network a mosaic of small rectangular units; radula with unicuspid central and 300–900 minute pectiniform lateromarginal teeth per row; shell globosely helicoid; dart apparatus present or absent.

Cryptaustenia – visceral hump and shell smaller; tail very elongated with prominently protruding caudal horn; slime network organized into a very few zones slantly uniformly backwards; radula with tricuspid central and laterals (except *C. tavoyensis*), marginals elongately bicuspid, but not pectiniform, with about 120–180 teeth per row (except *C. aborense* and *C. tavoyensis*); shell globosely helicoid; dart apparatus present or absent.

Unfortunately, only the Thailand species have the pallial and genital systems studied in detail, so the diagnosis cannot include features from these systems. Species have been allocated on the basis of correlation with the above diagnoses, which are much too superficial to warrant being called descriptions.

The diagnoses serve to distinguish these two groups, but not to separate them from other genera. The peculiar basal penial stimulator and pustulose penis proper probably will be diagnostic. Two species from the same general region have similar genitalia, the radula with a large central and bicuspid, unserrated lateromarginal teeth (380–500 per row) and the shell vitriniform with two or three whorls, somewhat flattened with the body whorl very wide. The little-known *Ibycus fissidens* Heynemann 1862 from Sikkim at 5,600 feet elevation seems similar enough, that I include *I. khasiacus* (Godwin-Austen 1883) from the West Khasi Hills and *I. minutus* (Godwin-Austen 1876) from Toroputu Peak in the Dafla Hills, Jaintia Hills and Noa Dehing, Assam in a third genus, *Ibycus*.

Certain distributional differences between *Durgella* and *Cryptaustenia* are worth noting. The former is well established in Burma and Thailand, but has been reported only from Cachar, Khasi Hills and Tezpur, Assam with one form in the Andaman Islands. *Cryptaustenia* has single species in Thailand and southern Tenasserim, but apparently is common from Sikkim to the Arbor Hills, then south through Assam and the Khasi Hills as far as Calcutta and Rajmahal – a much wider range in India.

On the basis of very fragmentary anatomical studies, three slug-like genera, *Cryptogirasia* Blanford and Godwin-Austen 1908, *Myotesta* Collinge 1901 and *Minyongia* Godwin-Austen 1916, probably are Durgelli. As indicated below (see pp. 65–67) they may be synonymous, but without new material for dissection their status cannot be determined. After much hesitation, a new genus from Thailand, *Muangnua*, is placed here, despite having tricuspid marginal teeth, no dart apparatus, apparently no lime-sac and a long, finger-like spermatheca. The affinities of this genus are very uncertain, but provisionally it seems closest to this group.

Radular features suggest that *Leptodontarion* Sarasin 1899 from Celebes is a durgelline genus and probably there are additional Indonesian relatives. The Malayan snails *Paraparmarion* Collinge 1902 and *Cryptosemelus* Collinge 1902 were described from external features and have not been dissected. Their elongated tails, small and forward placed visceral humps, large shell laps and thin shells make me guess that they are Durgelli. THIELE guessed they were Helicarioninae, H. B. BAKER guessed they might be Girasiinae.

Genus ***Durgella*** Blanford 1863

Type species. – *Helix levicula* Blanford 1859 by subsequent designation of GODWIN-AUSTEN (1881 p. 291).

The following species are included:

Durgella levicula (Blanford 1859)
    Phie Than, Tenasserim, Burma and Meetan, Mulé-it Range, Tenasserim, Burma
Durgella assamica Godwin-Austen 1881
    Panipputer Tea-garden near Tezpur, Assam
Durgella mairangensis Godwin-Austen 1907
    Mairang, North Khasi Hills, Assam
Durgella rogersi Godwin-Austen 1907
    Paphunta Valley, South Andamans
Durgella edeana Godwin-Austen 1910
    Silchar, Cachar, India
Durgella naharaniensis Godwin-Austen 1914
    Naharani, Upper Assam
Durgella libas new species
    Northern and western Thailand.

The anatomy of the following species are unknown, but they have been referred to *Durgella*, although some may be *Cryptaustenia*:

Durgella salius (Benson 1859)
    Teria Ghat, Khasi Hills, Assam
Durgella seposita (Benson 1859)
    near Darjiling, India
Durgella erratica (Godwin-Austen 1888)
    Pingoung, Shan Hills, Burma
Durgella concinna Blanford and Godwin-Austen 1908
    Thayet Myo, Prome and Akauktoung, Upper Pegu, Burma.

Species from Indonesia referred to *Durgella* seem misplaced, but their genital anatomy is unknown and taxonomic revision of these species is beyond the scope of this paper.

Of the species whose genital anatomy has been examined, *D. rogersi* and *D. assamica* lack the dart apparatus, while *D. levicula*, *D. mairangensis* and *D. libas* have a well-developed dart apparatus.

The genus is known from the Khasi Hills, Tezpur, and Cachar in India, Burma (north of Pegu, Shan Hills and Tenasserim), and Western Thailand as far south as Ban Kao and Sai Yok. Possibly species will be found in Laos, Vietnam, southwest China or Malaya. The species reported from Darjiling may be a *Cryptaustenia*.

Durgella libas new species

(Fig. 7–9, 13 *b*)

Diagnosis. – Shell large, diameter 10.6–12.5 mm. in adult specimens with $4^{1}/_{4}$–$4^{1}/_{2}$ whorls; calcareous elements few, sculpture of fine incised spiral lines in epidermis; umbilicus minutely open. Soft parts with very short and compact spermatheca, vagina and penis; radula with very tiny central tooth and pectiniform lateromarginals, formula ca. 425.1.ca. 425, teeth apparently much smaller and more numerous than in any other species of *Durgella*.

Durgella levicula (Blanford 1859) has a shell of $3^{1}/_{2}$–4 whorls, 7–9 mm. in diameter; much longer vagina, penis and spermatheca; radular formula + 170.1.170 +. *D. assamica* Godwin-Austen 1881 has a shell 9.5 mm. in diameter with 4 whorls; much longer spermatheca and penis, no dart apparatus; radula "as in *D. levicula*". *D. mairangensis* Godwin-Austen 1907 has a shell 7.5 mm. in diameter with 3 whorls; a weakly bilobed spermatheca and short thick dart apparatus; radular formula 320.1.320. *D. rogersi* Godwin-Austen 1907 apparently lacks the dart apparatus and "has very minute teeth" on the radula. *D. edeana* Godwin-Austen 1910 has a shell of 3 whorls, but otherwise is insufficiently described to be comparable with *D. libas*. *D. naharaniensis* Godwin-Austen 1914 has a shell 6.75 mm. in diameter with 3 whorls and a radula "very similar to that of *Durgella mairangensis*".

Description of soft parts. – Foot and tail very elongated, lightly pigmented (in alcohol), with markedly tripartite sole (fig. 7 *d*). Caudal horn (CH) greatly overhung (fig. 7 *c*); caudal foss (CF) indented with opening occupying middle of tail. Mid-dorsal groove very weak and foot

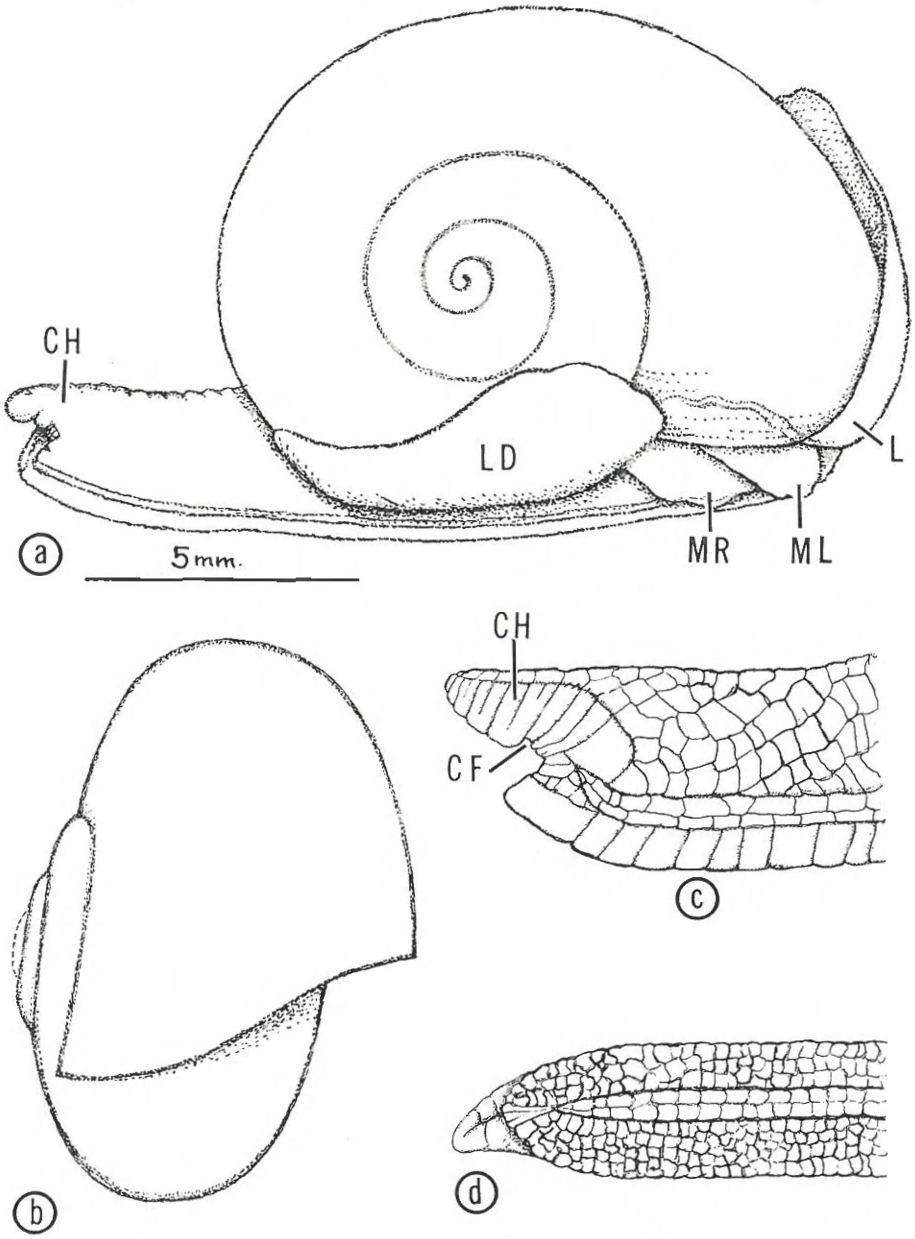

Fig. 7. *Durgella libas*, new species: *a*, side view of holotype (tail appears much shorter than in actuality because of body retraction and twisting); *b*, side view of shell, specimen 945, Wang Dao; *c*, side view of caudal region; *d*, bottom view of foot.

extremely narrow – only slightly broader than middle of tail. Cross-section of foot and tail bell-shaped. Pedal grooves aulacopod (fig. 7 *c*), rather high on foot.

Mantle collar narrow, lobes and laps large (fig. 7 *a*). Position of mantle lobes as in *Megaustenia siamensis*, but differing in size. Right mantle lobe very large, leaflike, reaching pedal grooves on side of foot with a flap extending upwards against base of shell lap, posterior $^1/_3$ of lobe free at base. Left mantle lobe differing from *M. siamensis* only in being much wider and thinner. Right shell-lap roughly triangular, very large, thin, capable of reaching shell apex. Main lobe of right shell-lap narrow at base, extending from pneumostome to posterior attachment of right mantle lobe, remaining portion a narrow thin band connecting posteriorly with left shell-lap. Left shell-lap very narrow across front of head followed by a sudden broad conical expansion, capable of reaching body whorl suture. About 2.5 mm. anterior of posterior left mantle lobe margin marks the end of the conical expansion. From there a gradually narrowing strip connects posteriorly to the right shell lap. Both lobes and laps have the basal portions irregularly pebbled, gradually becoming thinner and smoother towards the edge. Neither lobes nor laps have distinctive pigmentation.

Openings to pallial area as in *M. siamensis*, with secondary ureter opening into a distinct urinary chamber. Because of relatively normal whorl coiling, pallial chamber (fig. 8) very similar to that found in Polynesian and North American helicarionids. For entire length of pallial cavity, hindgut follows the palatal-parietal angle. Both kidney and pericardium terminate anteriad of intestinal loop and there is no shortening of the pallial cavity as in *Megaustenia*.

Pallial roof has extensive vascularization radiating from principal pulmonary vein (HV) and transversing two branches of ureter. Although prominent, venation is much reduced from that found in *Megaustenia*, and less extensive. Instead of a distinct respiratory flap just inside mantle collar, there is only a slender blood vessel, and the prominent vessel found in *Megaustenia* leading to the pericardium is lacking.

The kidney (K) is slender for the anterior $^2/_3$, then flares basally to give a roughly triangular appearance. The inner base of the kidney nearly touches the hindgut (HG), being separated by the membranes of the pallial roof and gut covering. There is a wide pocket between kidney and hindgut that is occupied by the two ureter branches and an expanse of lung roof. Although distinctly longer than pericardium, most of anterior extension is caused by very wide ureter. Both main and reflexed portions are quite broad with a complicated alveolar structure. Outer surface of primary ureter covered with black pigment, traces of which are also found along secondary ureter. Anterior end of secondary ureter narrows much more abruptly than in *Megaustenia*, then opens into an identical urinary chamber (LK) with the groove leading away from respiratory pore and anus (A).

Ovotestis (G) in second apical whorl, composed of short sacculated alveoli clustered along a branched tube embedded in digestive gland. Hermaphroditic duct (GD) slightly sinuated at first, then tightly folded until reaching surface of albumen gland. There it becomes a straight simple tube passing apically from base of albumen gland (GG) up to junction with talon (GT). Talon a simple blind pouch leading directly into a large carrefour (X), that appears to be a lobe of the albumen gland. Prostatic section (D) of same texture as albumen gland, uterine section (UT) sacculated and without any traces of embryos (fig. 9 *a*).

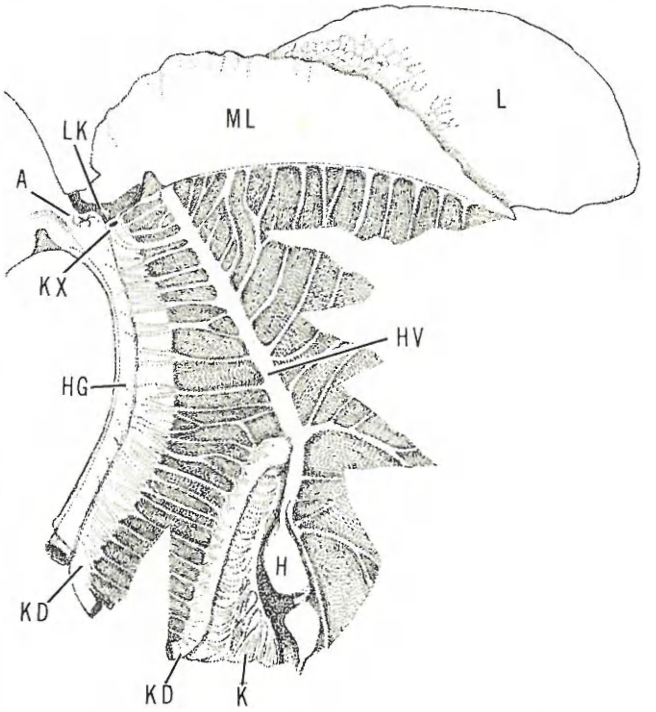

Fig. 8. Pallial region of *Durgella libas*, new species.

Vas deferens (VD) a slender tube passing down spermatheca to peniovidueal angle, then up to penis where it is tightly bound by connective tissue before entering laterally on tip of epiphallus. Epiphallus (E) with enlarged tip, containing an expanded terminal pilaster tapering towards insertion of penial retractor (PR). Latter prolonged into a slight retractor caecum. On inner wall of epiphallus opposite insertion of penial retractor, a pilaster forms, becomes very large, then tapers gradually to epiphallic pore (fig. 9 *b*). Penis (P) very large, thick-walled, "S"-shaped, with a thin muscular sheath around lower portion, although not easily detectable without dissection. Inside of penis densely papillose (fig. 9 *b*), but without pilasters. At base of penis, below sheath and lateral to free oviduct entrance, a small penial stimulator (PS) lies in a thin-walled pouch. Atrial chamber (Y) short but capacious.

Free oviduct (UV) relatively long, but recurved and internally sculptured with longitudinal pilasters. Spermatheca (S) with very short basal stalk, an extremely narrow neck, and an upper thin-walled sac that lies bound to "S"-loop of sperm-oviduct well above vas deferens origin.

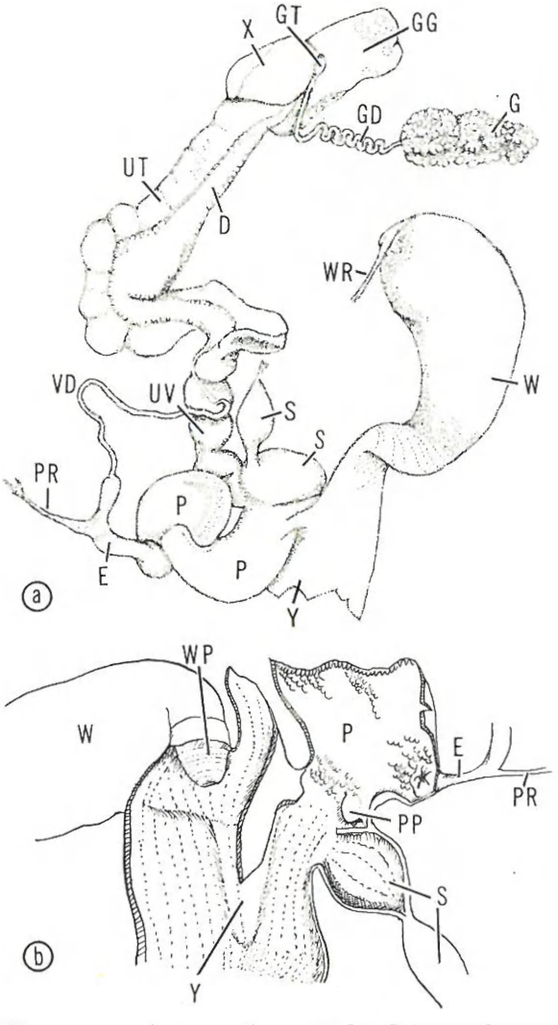

Fig. 9. *Durgella libas*, new species: *a*, entire genitalia; *b*, internal structures of terminal genitalia.
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Thick-walled basal portion in same position as spermathecal stalk of *Megaustenia siamensis*. Dart apparatus (W) as in latter species, but with longer basal stalk and proportionately larger head. Papilla (WP) of dart apparatus and retractor muscle identical. A muscular band connects base of spermatheca and dart apparatus. Many muscle fibers interconnect portions of terminal genitalia.

Radular teeth (fig. 13 *b*) very minute. Radular formula *ca.* 425–1–425 with 174 rows in mounted individual. Central tooth reduced to narrow elongated basal plate with low oblong elevated portion. Lateromarginal teeth very small, bicuspid with several tiny accessory ectoconal cusps. First lateromarginal with base opposite elevated portion of central tooth. Outermost teeth differ only in being somewhat shorter than inner lateromarginals.

Jaw very thin, without central projection, disintegrated while being mounted.

Description of shell. – Shell (fig. 7 *a*, *b*) globose, spire slightly elevated with barely impressed sutures. Calcareous elements few, most of shell membranous. Whorls 4+, body whorl three times width of penultimate at aperture. Surface nearly smooth, spiral incised lines visible under high magnification. Umbilicus a narrow crack. Diameter of holotype 12.3 mm.

Holotype. – Universitetets Zoologiske Museum, København. Wang Dao, North Thailand (number 945). Collected 3.VIII.1948 by B. Degerbøl.

Paratypes. – Seven of the fifteen additional specimens that have been referred to this species may be considered paratypes. They are: –

Wang Dao (1114, 6.IX.1958)
Doi Sutep at 1,000 meters (935, 1.VIII.1958; 385, 17.V.1958)
Chieng Dao at 1,800 meters (794, 16.VII.1958)
Doi Inthanon at 2,000 meters (283, 9.V.1958).

Eight juveniles from central west Thailand should not be considered paratypes, but have been placed here. They are: –

Ban Kao (P. Johnsen, 15–20.XI.1961)
Sai Yok (P. Johnsen, XII.1961).

One specimen from number 1114 is FMNH 135282 and two specimens from Sai Yok are FMNH 135281.

Remarks. – The name *libas* is the Greek form of "rill", in token appreciation of the excellent drawings illustrating this paper prepared by Miss PATRICIA RILL.

As in the case of *Austenia doisutepensis*, several probably related species have been described insufficiently to allow proper comparisons.

This is particularly true of *Durgella erratica* from the Shan Hills of Burma. Most other species are far enough removed geographically or differ enough in described features that no confusion seems probable. The geographically nearest species, *D. levicula*, differs in having a much longer penis and spermatheca, apparently much fewer radular teeth, and is smaller in size.

The material from Wang Dao, Doi Sutep, Chieng Dao and Doi Inthanon unquestionably seems to be one species. The examples collected July-September were adult, those in May (specimens 283 and 385) very young. The material from Ban Kao and Sai Yok was collected in November and December. The shells are 4.0–6.8 mm. in diameter and have $2^3/_4$ to $3^3/_8$ whorls. They appear to have a more solid, globular shell, but the genitalia is juvenile. Adult specimens from this area may show that these are populations of *D. levicula* rather than *D. libas*. They are too young for certain identification and have been referred here provisionally.

Genus ***Cryptaustenia*** Cockerell 1898

Type species. – "*Austenia planospira*" (= *Vitrina planospira* Benson 1859 not Pfeiffer 1853 and *Vitrina succinea* Reeve 1862) by original designation and monotypy.

The following species are included:

Cryptaustenia bensoni (Pfeiffer 1848)
    Bengal, Calcutta, Jessore, Chandanagore and Soorma River in Sylhet between Atgaon and Chatak
Cryptaustenia succinea (Reeve 1862)
    Sikhim and Bhutan
Cryptaustenia verrucosa (Godwin-Austen 1876)
    Toruputu Peak at 4,000 feet, Dafla Hills, Assam
Cryptaustenia durrangensis (Godwin-Austen 1907)
    Durrang District, Assam
Cryptaustenia silcharensis (Godwin-Austen 1907)
    near Silchar, Cachar
Cryptaustenia bensoni var. Godwin-Austen 1910
    Rajmahal, 180 miles up Ganges from Calcutta
Cryptaustenia moyongensis Godwin-Austen 1910
    Moyong, N.W. Khasi Hills
Cryptaustenia tavoyensis (Godwin-Austen 1910)
    Tavoy, Tenasserim
Cryptaustenia bicolor Godwin-Austen 1916
    Sadiya, Eastern Assam
Cryptaustenia arborense (Godwin-Austen 1916)
    Upper Rotung, Arbor Hills

Cryptaustenia gadinodromica new species
Doi Sutep, North Thailand.

These species were described from the shell only, but have been referred to *Cryptaustenia*:

Cryptaustenia ovata (Blanford 1871)
Darjiling
Cryptaustenia globosa (Godwin-Austen 1876)
summit Toruputu Peak, Dafla Hills, north of Assam
Cryptaustenia papillaspira (Godwin-Austen 1883)
North Khasi Hills
Cryptaustenia canefrii Blanford and Godwin-Austen 1908
near Bhamo, Burma
Cryptaustenia nonsingriensis Godwin-Austen 1910
Nonsingriang Wood, N.W. Khasi Hills
Cryptaustenia ovum Godwin-Austen 1910
Silcuri, Cachar
Cryptaustenia rarhiensis Godwin-Austen 1910
Rarhi Chu Valley, Sikhim
Cryptaustenia helva Godwin-Austen 1910
South Sylhet Hills.

The species in the first list have sufficient anatomical features illustrated or described to allow reasonably certain placement in *Cryptaustenia*. *C. verrucosa* is known only from a top view of the living animal and description of the shell. It may be misclassified. *C. tavoyensis* was described as a *Leptodontarion* (a genus based on a Celebes species whose genital anatomy remains unknown). Its body form and visceral hump position is identical to that of *C. gadinodromica*, but *C. tavoyensis* differs in having a unicuspid central radular tooth and about 300 bicuspid unserrated lateromarginal teeth in each half row. In genital features the latter seems quite compatable with *Cryptaustenia*. A photograph of the preserved soft parts shows that *C. bicolor* has the tail, slime network and visceral hump of *Cryptaustenia*, although no features of its internal anatomy are known. *C. arborense* is unusual only in having over 300 teeth per half row, although preserving tricuspid laterals and central tooth. Its radula is thus intermediate between that of typical *Cryptaustenia* and *C. tavoyensis*.

Two species probably erroneously referred to *Cryptaustenia* are *C. heteroconcha* (Blanford 1871) and *C. zemoensis* (Godwin-Austen 1907). The former, described from Darjiling, was not dissected until 1910 when Godwin-Austen obtained an animal from Siliguri, North Bengal. The partly described soft parts are compatable with *Cryptaustenia*, except for their being no clear epiphallus above the penial retractor insertion, but the large size (diameter of shell 20 mm.) makes me question this classification. Insufficient details were recorded to enable me to suggest an alternate, but I doubt this is a *Cryptaustenia*. *C. zemoensis* from Zemo Samdong, Sikhim has the coiled retractor caecum, long lime-sac and long spermatheca of the genus *Euaustenia* and may be transferred to that genus.

Cryptaustenia is known from the area covered by Darjiling and Sikhim east to the Dafla and Arbor Hills of the Northeast Frontier Agency, south through Assam to Rajmahal and Calcutta with two isolated records at Tavoy, Tenasserim and Doi Sutep, North Thailand.

Cryptaustenia gadinodromica new species

(Fig. 10–12, 13 *c*)

Diagnosis. – An elongated (preserved length 17.6 mm.) species of *Cryptaustenia* with yellow body color, black mid-dorsal tail stripe, no dart apparatus, radula with nine weakly tricuspid laterals and about fifty bicuspid, unserrated marginals, and shell helicoid with four whorls whose only calcareous elements lie near the sutures.

C. arborense (Godwin-Austen 1916) also lacks the dart apparatus, but the radula has four lateral plus nearly 300 marginal teeth and the body color is very different; *C. tavoyensis* (Godwin-Austen 1910) has a well developed dart apparatus, the radula contains over 300 bicuspid lateromarginal teeth in each half row, and the body is grey-green with black shell lobes; all other species of *Cryptaustenia* whose anatomy has been examined have a dart apparatus on the genitalia.

Description of soft parts. – Body extremely long and slender, length 17.6 mm., visceral hump large, located just behind head (fig. 10 *a*). Tail over twice as long as head and visceral hump, very narrow, "U"-shaped. Middorsal groove well defined, enclosed by a narrow black band extending from posterior overhang of visceral hump to anterior margin of caudal horn (fig. 10 *b*). Sole of foot tripartite, center portion one-half width of each side portion (fig. 10 *d*). Lower pedal groove well defined, upper less impressed, but indicated by a dark pigment band (fig. 10 *c*). Caudal horn (CH) very large and overhung (fig. 10 *c*). Slime network forming a regular pattern, somewhat exaggerated in drawings. Caudal foss (CF) opening at base of caudal horn, between lobes of pedal margins. Interior of caudal horn a shallow groove. Body color pinkish yellow, sole yellow, with a middorsal black band extending from visceral hump posterior to caudal horn (fig. 10 *b*).

Mantle collar narrow, widening posteriorly to form an umbilical flap between shell and foot. Right mantle lobe (MR) extending from

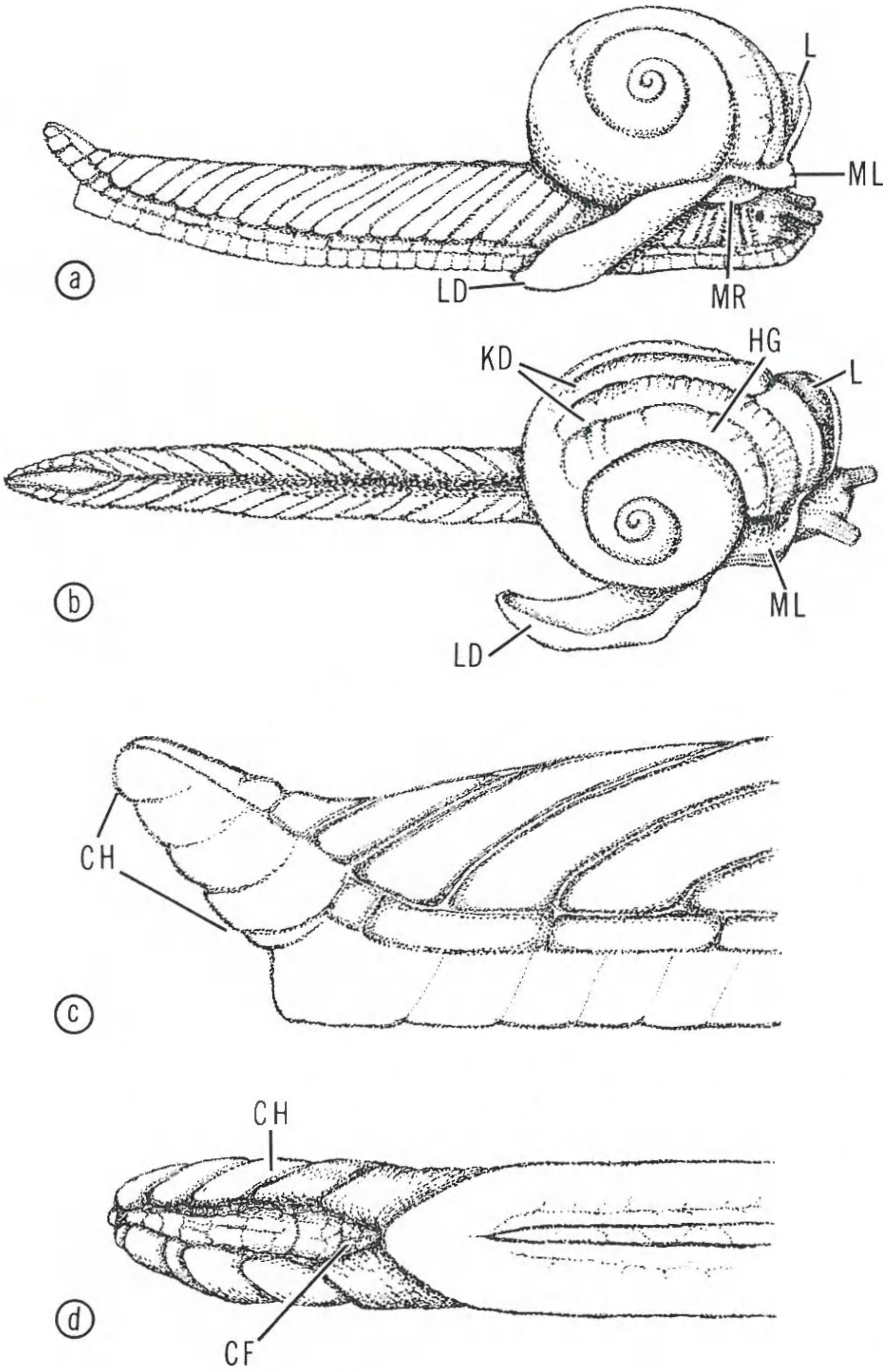


Fig. 10. *Cryptaustenia gadinodromica,* new species: *a*, side view of body; *b*, top view of body; *c*, side view of caudal region; *d*, bottom view of caudal region.

middorsal line around to posterior margin of visceral hump. Posterior part a free lobe, anterior part extending under left mantle lobe to middorsal line; central part extended upward, fusing with mantle collar at parietal-palatal angle. Left mantle lobe (ML) extending from parietal-palatal margin around middle of visceral hump on left side. Median portion of lobe larger, forming a small cephalic shield. Neither lobe extending

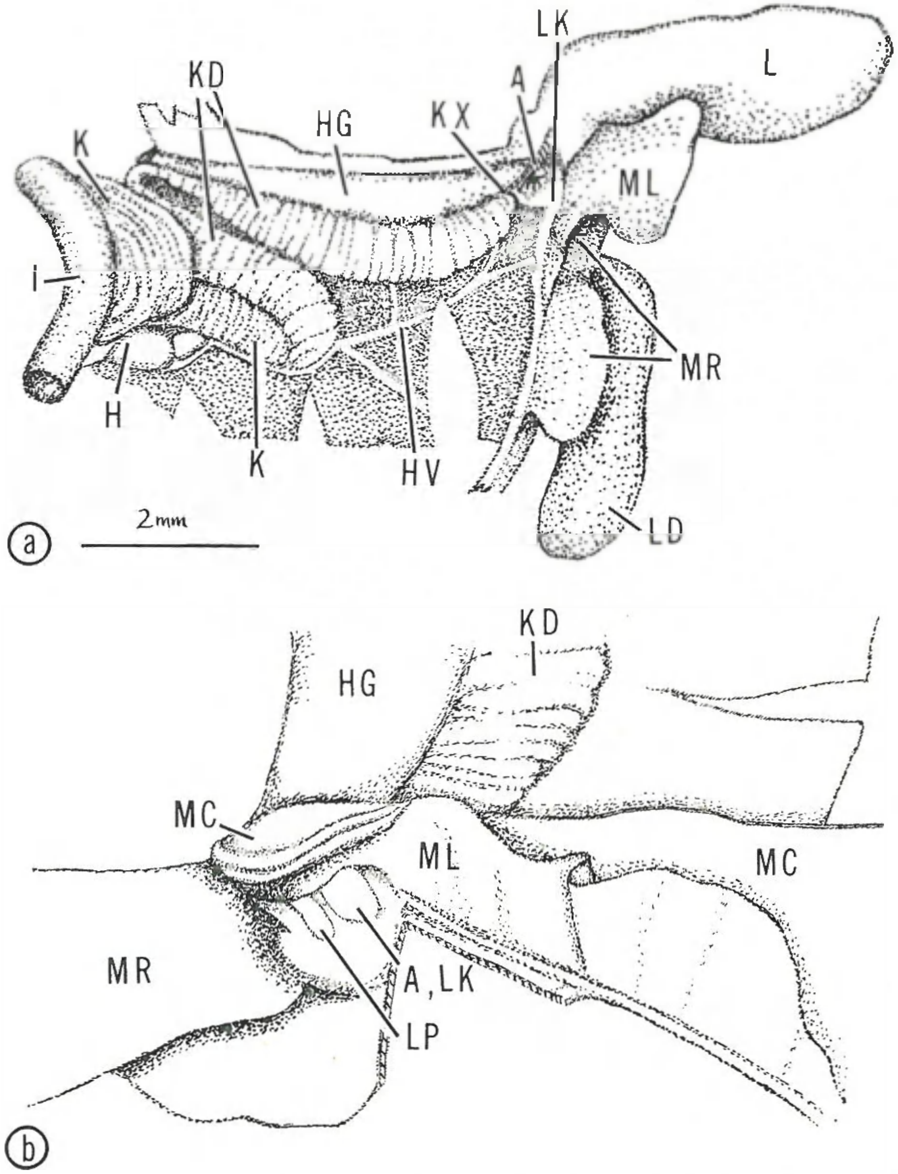


Fig. 11. *Cryptaustenia gadinodromica*, new species: *a*, pallial region; *b*, details of pallial openings and mantle lobes.

down sides of body for any distance. Right shell lap (LD) with one corner at parietal-palatal margin, running to umbilical margin with a narrow extension to posterior margin of visceral hump. Right shell lap extending upwards to cover shell apex, a large "U"-shaped lobe. Left shell lap (L) a large crescent, extending from parietal-palatal margin to left side of visceral hump. Mantle lobes nearly smooth, sprinkled with black markings. Shell laps with large pebblings, becoming smoother near tips, scattered black markings on surface.

Pallial region (fig. 11 *a*) rather short, constricted posteriorly. Hindgut (HG) slender, following parietal-palatal margin to end of pallial cavity. Pallial roof weakly vascularized, few branches from principal pulmonary vein (HV) running to inner edge of mantle collar.

Kidney (K) narrow and finger-like anteriorly, flaring greatly and reflexed downwards basally over intestinal loop (I) that protrudes into pallial cavity. Pericardium (H) angled outwards from normal position parallel to hindgut. Basal flaring and folding of kidney plus slight pericardial displacement results in pericardium seeming only one-half of kidney in length. If basal extension considered, then kidney 3.5–4 times length of pericardium. Ureter (KD) bulbous at tip and along kidney, sacculated internally, narrowing very abruptly at reflexion, re-expanding along, and wider than, hindgut. Only a very narrow strip of lung roof between ureter branches. Secondary ureter narrowing near pneumostome to opening (KX) into a deep urinary chamber (LK) to right of anus (A). Anus and urinary chamber share external pore located above and slightly to right of pneumostome (LP) (see fig. 11 *b*).

Ovotestis (GG) composed of small ovoid alveoli (fig. 12 *a*) clustered along duct imbedded in upper part of liver. Hermaphroditic duct (GD) markedly sinuated in middle portion, then straight across to base of albumen gland, reflexed up into talon (GT). Latter a simple blind pouch opening into carrefour (X). Uterus (UT) swollen, prostatic section (D) a relatively narrow band of tissue.

Vas deferens (VD) a very slender tube bound to peniovidual angle, entering laterally on expanded head of epiphallus (E). Epiphallus (fig. 12 *c*) with enlarged head containing apical knob from which weak pilasters run along upper margin past insertion of penial retractor (PR). Latter very short, thickened with glandular tissue at base (weak retractor caecum?), originating on diaphragm. On opposite side of epiphallus just below insertion of penial retractor, an elongately bulbous papilla arises, extending down to epiphallic pore (EP) with anterior half tapered to narrow ridge. Penis proper (P) with muscular sheath (PS) around lower half. Interior of penis pustulose, pustules somewhat longitudinally oriented. Upper part of penis swollen, area within sheath a narrower muscular tube. At base of penis, just below muscle sheath and just lateral to free

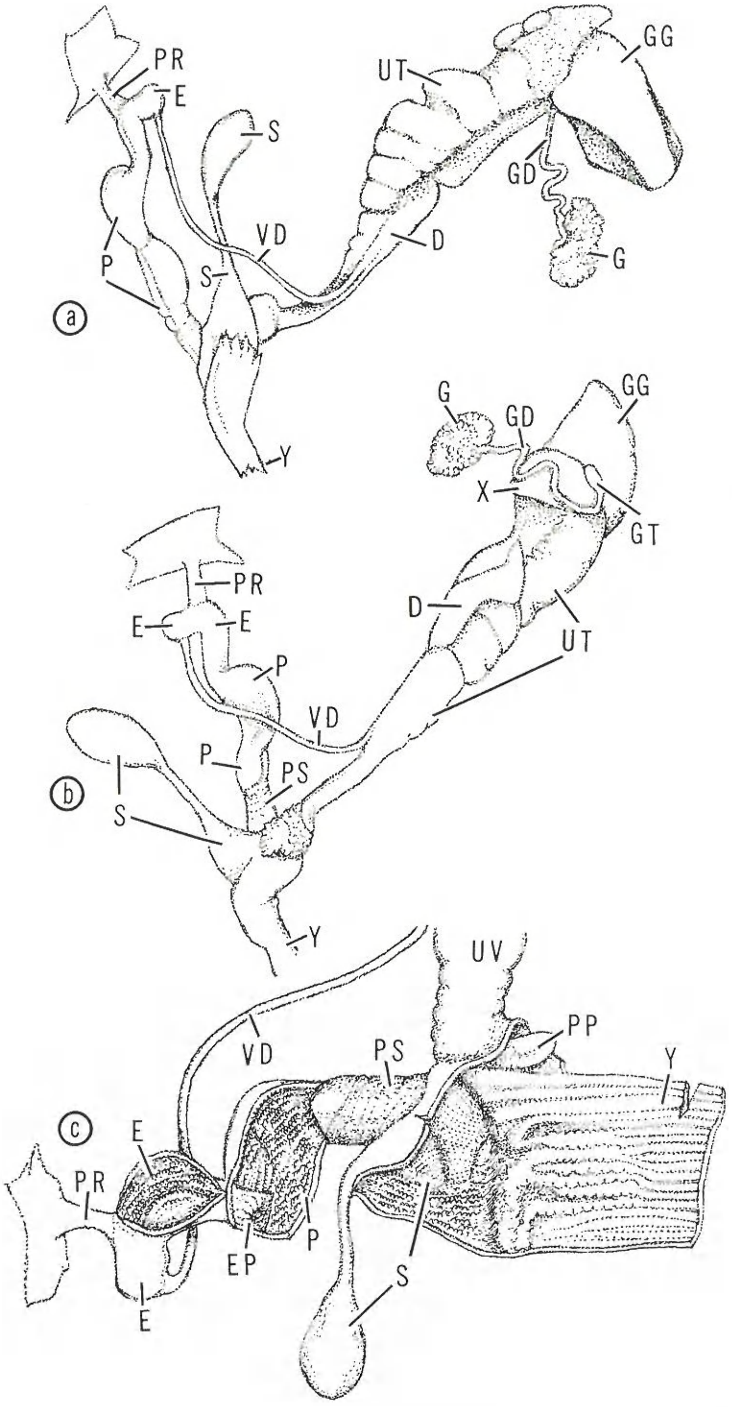


Fig. 12. *Cryptaustenia gadinodromica*, new species: *a* and *b*, views of genital system; *c*, internal structures of terminal genitalia.

oviduct (UV) entrance to atrium, lies a thin-walled pocket containing prominent stimulator (PP).

Free oviduct (UV) rather long and narrow, internally with longitudinal pilasters. Vagina obsolescent, free oviduct, penis and spermatheca opening simultaneously into atrium. Spermatheca (S) with two distinct portions. Basal portion conical, very thick-walled, coneshaped, internally with a thickened collar surmounted by slender pustulations that also cover walls of cone up to its narrowing to a slender tube leading to bulbous, thin-walled head. Atrium (Y) rather long, with numerous longitudinal pilasters, upper portion of those below spermathecal opening crenulated. No dart apparatus.

Radular formula *ca.* 50–9–1–9–*ca.* 50. Radula (fig. 13 *c*) fragmented so rows could not be counted. Central tooth slightly smaller than first lateral, mesoconal tip opposite tip of first lateral, but base distinctly not aligned. Ectoconal cusps set relatively far back. First lateral with entocone far up on mesocone, relatively small, persisting onto ninth lateral. Ectocone very large, subequal in tip size although set well back from tip, becoming slightly forward and larger on outer laterals. Entocone lost on first marginal, ectocone subequal to mesocone, base elongated. Ectocone and mesocone equal by eighth marginal. Outer marginals shorter than inner teeth, but still bicuspid.

Jaw very thin, without central projection, disintegrated while being mounted.

Description of shell. – Shell very thin, a membrane covering body surface, calcareous elements confined to a narrow zone bordering sutures and providing a solid framework for spire. Whorls four, rapidly and regularly increasing in width. Surface with very fine spiral incised lines, visible only under high magnification and side lighting. Color light greenish horn with vague radial darker streaks. Umbilicus closed. Diameter of visceral hump 5.6 mm.

Holotype. – Universitetets Zoologiske Museum, København. Doi Sutep, North Thailand at 1,100 meters elevation (number 1844). Collected by B. Degerbøl on 8.XI.1958.

Remarks. – During preliminary studies, this snail was informally christened "lean and racy" by members of my staff. The specific appellation *gadinodromica* is the Greek rendition of this very appropriate descriptive phrase.

Diagnosis of this species was difficult, since only the grossest anatomical details are known for other *Cryptaustenia.* Undoubtedly study of the genitalia in other species will enable more satisfactory criteria for discrimination.

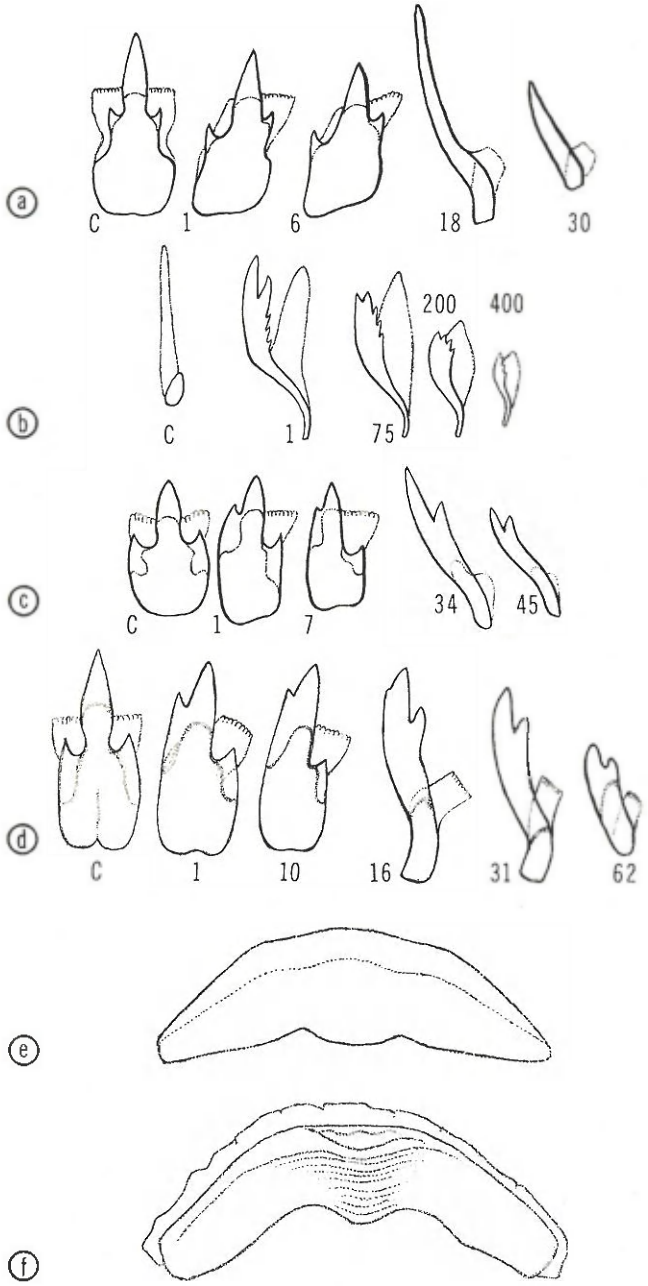


Fig. 13. Radulae and jaws: *a–d*, isolated radular teeth of – *a*, *Teraia thailandica* (holotype), *b*, *Durgella libas* (holotype), *c*, *Cryptaustenia gadinodromica* (holotype), *d*, *Austenia doisutepensis* (holotype), *e–f*, jaws of – *e*, *Teraia thailandica* (holotype), *f*, *Austenia doisutepensis* (holotype).

Sitala trochulus (Moellendorff 1883)

Nanina (*Sitala*) *trochula* Moellendorff 1883. Jahrb. d. Malak. Gesell. 10, p. 370, pl. 12, fig. 8 (near Wa-shau monastery, Lo-fou-shan, Kwangtun, China).
Chieng Dao at 1,800 meters (794, 16.VII.1958).

Comparisons with species of *S. trochulus* labeled "Yunnan-fu, Yunnan" (FMNH 76929) showed no differences. The relationships to Indian and Indonesian species remain to be determined.

Genus ***Muangnua*** new genus

Aulacopod sigmurethrous helicarionid slugs with shell reduced to a partially calcified cap having only single remnant of coiling and completely covered by fused shell laps. Mantle lobes forming large cephalic shield reaching nearly to eyes. Tail long, very slender, with hooked caudal horn. Color yellow with black stripes. Posterior of visceral hump rounded, resting in "V"-shaped body groove. Pallial region compressed, organs distorted, kidney bilobed with heart at left central margin. Stomach very large, both salivary glands on left side of body cavity, intestine forming three loops in visceral hump, hindgut "S"-curved. Free muscles uniting at anterior one-third of stomach. Jaw thin, without median projection or sculpture. Radula with tricuspid central, laterals and marginals, second largest cusp formed by increase in entoconal size, about 180 teeth per row. Genitalia without dart apparatus or (apparently) accessory penial organs, spermatheca long, reaching two-thirds of way to albumen gland.

Type species. – *Muangnua limax* new species.

The early history of Northern Thailand is chronicled in the famous Pongsawadan Mu'ang Nu'a. The generic name *Muangnua* recognizes the habitat in the "North Country" while *limax* is the Latin word for slug, hence "North Country slug" is an appropriate name for this beautiful animal.

Relationships are difficult to determine, both because of unusual structural features and insufficient knowledge of possible relatives. The following genera and species, while not necessarily phylogenetically related, showed at least superficial similarities and were considered as possible alternatives to description as a new genus.

Cryptogirasia rubra (Godwin-Austen 1875)

Parmarion rubra Godwin-Austen 1875. Journ. Asiatic Soc. Bengal 1875, part 2, pl. 6, pl. 2, figs. 4–4c (Kohima, Anghami Naga Hills).

Girasia ? rubra (Godwin-Austen) GODWIN-AUSTEN 1888, Land & Freshwater Moll. India 1 part 6, p. 228, pl. 61, figs. 4 a, b, c, d; COCKERELL 1893. Journ. of Malac. 2, part 8, p. 187.

Cryptogirasia rubra (Godwin-Austen) BLANFORD and GODWIN-AUSTEN 1908. Fauna Brit. India, Moll. 1, p. 204, fig. 64 D; GODWIN-AUSTEN 1916. Rec. Indian Mus. 8, pp. 556–559.

The internal anatomy has not been studied and only the original collection has been reported. The visceral hump seems pointed behind, not rounded and the color is orange-pink. For all practical purposes, this is a meaningless name. Until new collections in the vicinity of Kohima rediscover this species and allow study of its anatomy, use of the generic name is based only on guesswork.

"Parmarion" setchuanensis Heude 1885

Parmarion setchuanensis Heude 1885. Mem. hist. nat. l'empire Chinois 1, p. 99, pl. 26, figs. 4 a (Tchen-k'eou, = Ch'êng-k'ou, northeast Ssŭ-ch'uan (= Szechwan) Province at about 108°47′ long., 31°56′ lat.); MOELLENDORFF 1887. Jahrb. d. Malak. Gesell. 14, p. 34.

"*Limax*" *setchuanensis* (Heude) Yen 1938. Mitt. Zool. Mus. Berlin 23, p. 444 (citation as an Arionidae!).

In form of the visceral hump, this species is intermediate between *Cryptogirasia rubra* and *Muangnua limax*, having a rounded visceral hump, but a small knob that suggests the slightly exposed shell of *Myotesta* and *Galongia*. Both *Cryptogirasia rubra* and "*Parmarion*" *setchuanensis* have three dorsal stripes on the head. There is no description of the internal anatomy and no indication of the size. This is another meaningless name.

Myotesta fruhstorferi Collinge 1901

Myotesta fruhstorferi Collinge 1901 (December 30). Journ. of Malac. 8, part 4, p. 118 (Mt. Mausson, Tonkin at 2,000–3,000 feet); COLLINGE 1902 (April 10). Journ. of Malac. 9, part 1, pp. 11–13, pl. 1, figs. 1–4.

Ostracolethe fruhstorfferi Simroth 1901 (December 30), Zoolog. Anz. 25, no. 660, pp. 62–64 (Tonkin); SIMROTH 1902 (May 5). Zool. Anz. 25, part 670, pp. 355–357; SIMROTH 1904 (April 12). Zeits. f. Wissen. Zool. 76, part 4, pp. 61–672, pl. 32 (Mt. Mausson, Tonkin).

Despite minor discrepancies in the descriptions and illustrations, these are almost certainly based on the same species. SIMROTH's figures of the genitalia probably contain some mis-interpretations and show the spermatheca with a most unusual spermatophore.

Despite the simultaneous publication date, subsequent authors have utilized Collinge's generic name.

Differences from *Muangnua* are many despite the close external similarity. *Myotesta* has a short spermatheca; penis with a functioning verge and accessory epiphallic appendages; penial retractor fastened to body wall; jaw composed of several plates (?); radula with 630–640 lateromarginal teeth per row, central tooth unicuspid, other teeth bicuspid; shell flat, platelike, with no trace of spiral remaining.

Simroth maintained that the shell was barely visible through the posterior of the mantle hump, but Collinge denied this. Further collections are needed.

Myotesta punctata Collinge 1901

Myotesta punctata Collinge 1901. Journ. of Malac. 8, part 4, p. 119 (Mt. Mausson, Tonkin at 2,000–3,000 feet); Collinge 1902. Journ. of Malac. 9, part 1, pp. 13–14, pl. 1, figs. 5–11.

The genitalia shows the atrium, vagina and penis shortened and swollen (much as in *Durgella libas*); a much longer spermatheca; no accessory organs on the penis; and a large spermatophore studded with spines. Other features of the anatomy were not examined.

Minyongia kempi Godwin-Austen 1916

Minyongia kempi Godwin-Austen 1916. Rec. Indian Mus. 8, pp. 556–557, pl. 47, figs. 2–2g (Rotong and Kobo, Arbor Hills, Sadiya Frontier Tract, India).

This large (length 55 mm.) species may belong to *Myotesta*, but without new material, synonymization is premature. The pallial organs and visceral hump show somewhat different orientation to the pallial openings than in *Muangnua*, while the genitalia and radula show sharp divergences. In *Minyongia* the genitalia have: a short bulbous penis with single accessory organ; short pear-shaped spermatheca; and no dart apparatus. The radula is typical durgelline, consisting of an elongated, unicuspid central and over 300 bicuspid pectiniform lateromarginal teeth in each half row. The shell is reported as being a small oval disc covering just the heart, kidney and pallial sac, lying anterior to the pallial opening.

None of the characters cited by Godwin-Austen in his description of the genus *Minyongia* (erroneously spelled *Minyongai* in this one place) or the species *M. kempi* show any real differences from *Myotesta*. Godwin-Austen suggested that *Cryptogirasia* and *Minyongai* probably were synonymous. It is quite possible that all of the forms discussed above will be united into one genus.

While many anatomical details of the above taxa remain unknown, the very different tricuspid lateral and marginal radular teeth, long spermatheca and apparently simple genitalia provide systematically important criteria for separating *Muangnua*, and the external color pattern provides immediate visual separation. Determining the exact relationships of *Muangnua* is impossible at present. Tentatively I have placed it with the genera discussed above as a member of the Durgellinae, although the radula is very similar to that of *Kaliella* and the penis seems similar.

Muangnua limax new species

(Fig. 14–16)

Diagnosis. – A relatively small (length 21.6 mm.) sluglike snail with shell reduced to a cap-like structure completely enclosed by shell laps. Tail slender with three black stripes, head with two black stripes, vague black markings on visceral hump. Genitalia with long spermatheca and (apparently) no penial accessory organs or dart apparatus. Radula with tricuspid central, lateral and marginal teeth, about 180 per row.

Distinctions from previously known species are given under the generic discussion above.

Description. – Body 21.6 mm. long when only slightly retracted, mantle shield and visceral hump 9.7 mm. long (fig. 14 *b*). Foot narrow, tapering posteriorly (fig. 14 *e*), tail "U"-shaped in crossection. Caudal horn (CH) prominent, slightly overhung (fig 14 *d*). Caudal foss (CF) a transverse slit up under caudal horn. Posterior lobe of visceral hump sitting in "V"-shaped depression on top of foot (fig. 14 *b*).

Mantle lobes and shell laps fused, completely covering shell and visceral hump (fig. 14 *b*), without noticable delineation except at pallial openings. Pneumostome (LP, fig. 15 *a*) below and slightly behind anus (A) and excretory pores (fig. 15 *a*). Pneumostome in right mantle lobe, anus and excretory pore in angle of overlap between right mantle lobe and left mantle lobe. Right mantle lobe running along side of body to visceral hump anteriorly with a weak lobe on side of foot, but not reaching middorsal area. Cephalic lobe (= left mantle lobe) with sinuated right edge masking anus and excretory pore, but leaving pneumostome open, then extending forward almost to level of ommatophores.

Color light yellow with black markings (fig. 14 *c*). Tail with three black stripes: a darker middorsal line from base of "V"-groove, fading out two-thirds of way to caudal horn; each side with lighter stripe from middle of visceral hump to caudal horn. Each side of head with black stripe from just below and behind ommatophore back to base of cephalic shield and under its edges. Cephalic shield with a vague network of black markings that continue onto visceral hump. Latter with two short lateral stripes (fig. 14 *b*).

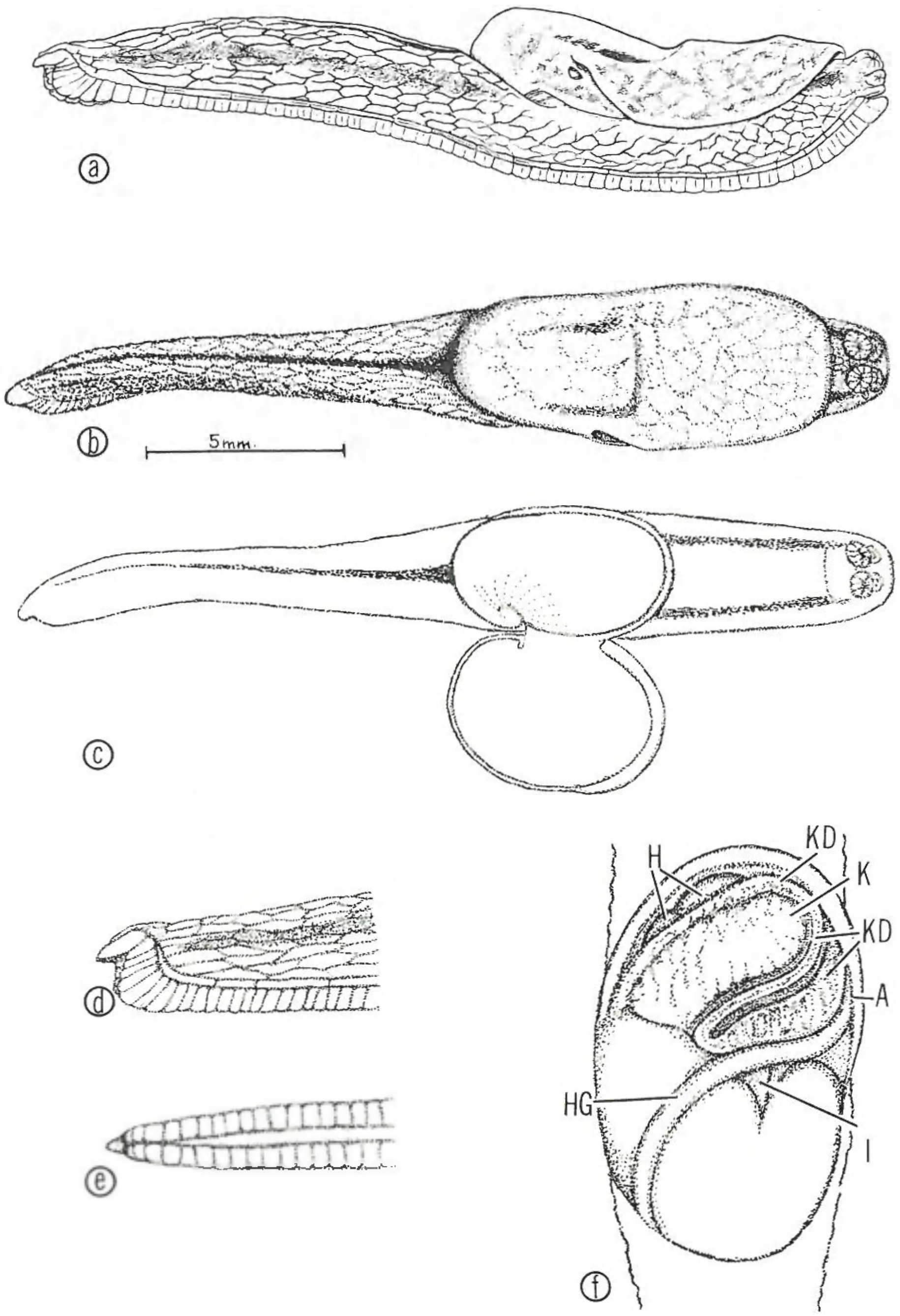


Fig. 14. *Muangnua limax*, new genus, new species: *a*, side view of body; *b*, top view of body; *c*, top view of body with mantle lobes removed, shell laps partly severed and twisted sidewards and shell plate showing; *d*, side view of caudal region; *e*, bottom view of caudal region; *f*, top view of visceral hump with shell laps and shell removed.

Shell completely enclosed by shell laps. Spire and most of body whorl calcified. No distinct coiling preserved, only a curve between visceral lobe and pallial roof cover, shown as a curved line on figure 14 *c*. Anterior edge of shell membrane reaching mantle collar in front and on sides, sharply delineated. Posteriorly, shell membrane extending slightly below middle of visceral hump, but calcareous element restricted to upper posterior surface of hump.

Pallial region (figs. 15 *a*, *b*) compressed, organ positions altered, although not as radically as in *Austenia doisutepensis*. Hindgut (HG) a very slender tube crossing from posterior left margin of visceral hump to anus in sinuated curve. At midpoint of body and visceral hump nearly perpendicular to body axis, then curving forward along right margin of pallial cavity to anus (A) (fig. 14 *f*). Unlike *Austenia*, the reduced hindgut does not protrude into pallial cavity. Kidney bilobed, primary lobe extending across entire pallial cavity from left to right, barely reaching pallial roof, but curved down over digestive gland where visceral hump bulges forward constricting pallial cavity. At left margin of pallial cavity, loop of intestine reaches surface of digestive gland, but does not bulge into pallial cavity. At left rear margin of pallial cavity, kidney (K) narrows, reflexes forward above heart (H), then extends as a thin wedge of tissue above enormously expanded ureter (KD). Latter continues anteriorly and medially, overlapping end of secondary ureter near right margin of pallial cavity. Primary ureter (KD) greatly swollen, reflexed and running below kidney back to just left of posterior midline of pallial roof, then reflecting along posterior margin over to right side and excretory pore. As is normal, ureter parallels hindgut in reflexed portion. Pericardium (H) lying under smaller kidney lobe, running along posterior left margin of pallial cavity. Principal pulmonary vein (HV) running across kidney and ureter surface to edge of pallial cavity, then along front edge to just short of pallial openings where it expands into a small vascularized area (fig. 15 *a*). Pneumostome (LP) slightly below and behind anus (A). Excretory pore (KX) slightly above and in front of anus. A blind pouch of ureter extends noticably in front of excretory pore along inner pallial margin. Urinary chamber reduced to an expanded groove between mantle lobes.

Free retractor muscles simple (fig. 16 *a*). Right ommatophoral retractor passing through penioviducal angle. Origin of rhinophoral retractors not traced. Right tentacular retractor (TR) passes posteriorly uniting with left tentacular and buccal retractor (BR) about one-third of way along stomach. Left tentacular retractor passing just under esophagus and uniting with two branches of buccal retractor just above junction of esophagus and stomach. Branches of buccal retractor equal in size. United muscular band passing along top of stomach, slightly

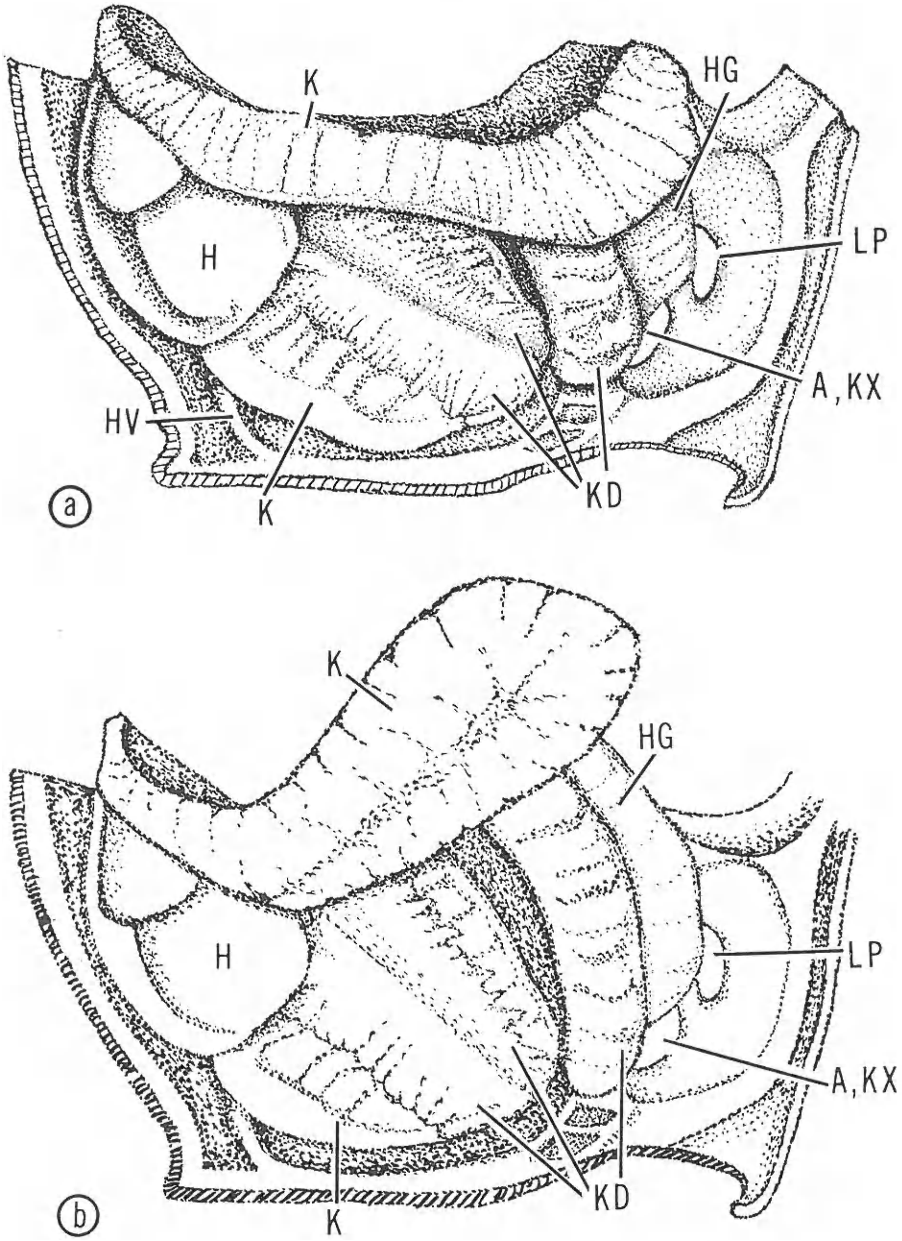


Fig. 15. Pallial region of *Muangnua limax*, new species: *a*, viewed from beneath with kidney lobe slightly lifted; *b*, with kidney lobe lifted and twisted to show ureter and hindgut.

right of middorsal line, into visceral hump to right of first intestinal loop. There a major branch attaches to remnants of parietal-palatal spire margin and a minor branch to the spire itself.

Digestive tract (fig. 16 *a*) rather similar to *Austenia*. Relatively elongated buccal mass (B) hiding short esophagus when viewed from above (? caused by retractor). Stomach (IZ) greatly enlarged, filling body cavity. Salivary glands (OG) paired, ducts opening into buccal mass on each side of esophageal duct. Right salivary gland moved to left side of body in front of left salivary gland, ducts crossing to right side of buccal mass. Intestine (I) a large tube rising straight up from stomach into visceral mass, barely visible through surface of digestive gland to left of parietal-palatal margin (fig. 14 *f*). It then reflexes down through visceral hump to right posterior margin, passes diagonally forward across base to left basal margin, narrows appreciably, loops up left front side of visceral hump and abuts on kidney base, passes down to midpoint of left side, then back to posterior margin before looping upwards across top and over to right margin as hindgut (HG). Latter an extremely narrow tube forming an extended "S"-loop. Intestinal loops expanded and exaggerated in fig. 16 *a*.

Genitalia (fig. 16 *b*) juvenile. No details of apical parts observed. Vas deferens (VD) bound to penioviducal angle passing up directly to attachment of penial retractor (PR). Latter attached to diaphragm just inside right anterior margin of mantle collar, well anterior to pallial openings. Vas deferens with longitudinal pilasters inside. Epiphallus not differentiated, angle of penis-epiphallus-vas deferens with slight indication of a retractor caecum (? ERC). Interior of penis-epiphallus with longitudinal pilasters, differentiated at two places. About one-fourth of way between retractor caecum and atrium, pilasters widen; nearly halfway one pilaster ends and a new one begins lateral to termination of first.

Free oviduct short, vagina (V) rather long. Spermatheca (S) fingerlike, reaching two-thirds of way to albumen gland. Atrium rather long. Dart apparatus absent.

Radula (fig. 16 *c*) with 120 rows, formula 78.11.1.11.78. Central tooth large and long with broad base. Mesocone very long and slender, extending far past edge of basal plate. Ectocones prominent, reaching nearly to edge of basal plate. First lateral with small entocone well out on mesoconal shaft, ectocone large and slightly offset. Succeeding laterals have basal plate elongated, entocone somewhat more prominent, ectocone only slightly less prominent. After 11th tooth, elongation of basal plate and increase in entoconal size accelerates, also ectocone rapidly becomes much smaller. By 20th tooth (9th marginal), teeth subequally bicuspid (entocone a little smaller than mesocone) with ectocone re-

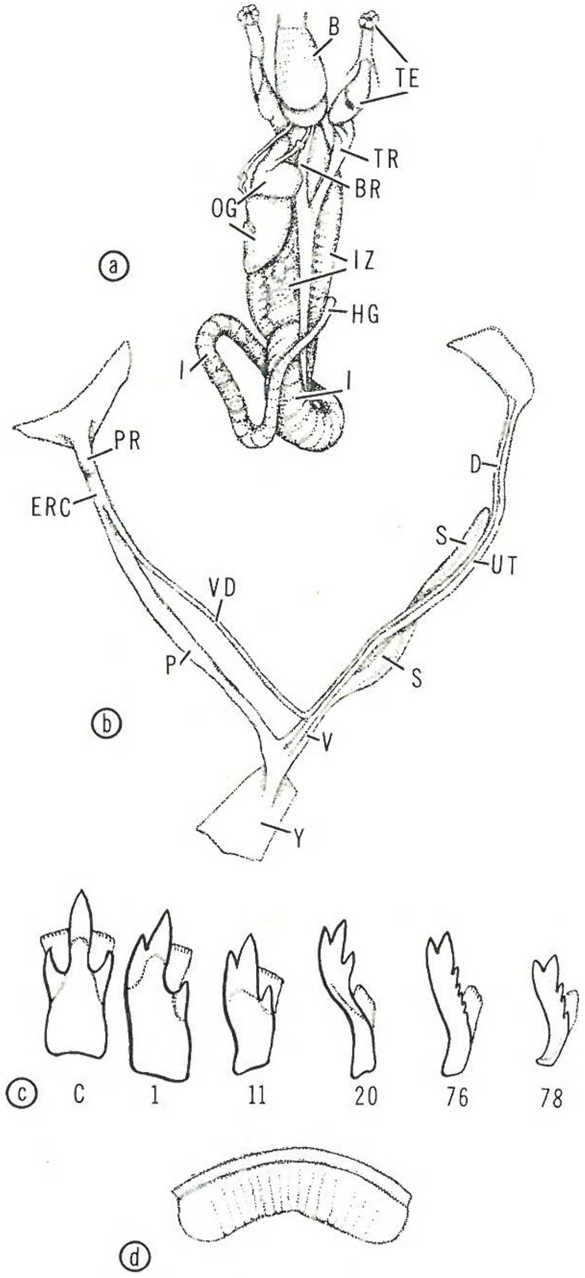


Fig. **16**. *Muangnua limax*, new species: *a*, digestive system and free muscles; *b*, genitalia; *c*, isolated radular teeth; *d*, jaw.

duced to a small side cusp. Starting in this region, tooth size decreases, but ectoconal prominence increases sharply so that most marginals are clearly tricuspid. By 35th marginal, ectocone and entocone equal in prominence and there are additional ectoconal cusps. Outer marginals with split ectoconal cusps, outermost marginals greatly shortened.

Jaw (fig. 16 *d*) very thin, crescent shaped, without medial projection or sculpture.

Holotype. – Universitetets Zoologiske Museum, København. Doi Sutep, North Thailand at 1,100 meters elevation (number 1844). Collected by B. Degerbøl on 8.XI.1958.

Paratype. – A slightly younger individual, 16.0 mm. with visceral hump and cephalic shield 8.5 mm. long, was taken at the same time. It also is deposited in the Universitetets Zoologiske Museum København.

Remarks. – In solving the problems of organ displacement associated with shell reduction, *Muangnua limax* (figs. 14–16) offers some interesting contrasts with *Austenia doisutepensis* (figs. 20–22).

In body form, the visceral hump of *Muangnua* lies well forward of the body midpoint; in *Austenia* it lies nearer the tail than the head. *Muangnua* has a very narrow elongated tail and foot that is "U"-shaped in crossection; *Austenia* a short elevated tail that is triangular. Both genera have the left mantle lobe forming a cephalic shield reaching nearly to eye level. *Muangnua* has the shell completely covered by the shell laps, only a slight vestige of spiralization remaining, and only a small fraction of the shell calcified; *Austenia* has the shell laps covering less than half the shell, distinct spiral coiling preserved, and rather extensive calcification remaining. *Muangnua* has the central portion of the foot sole ending well before the tail tip, which is bluntly pointed; in *Austenia* the central portion is separated from the gently rounded foot end only by a narrow margin. *Muangnua* has a shallow transverse caudal foss under a narrow hooked caudal horn; *Austenia* a deep vertical caudal foss with only slightly protruding horn. *Muangnua* has an elongated slime network; *Austenia* a rectangular, shortened slime network. With mantle lobes removed, the pallial cavity and visceral hump of *Muangnua* are 25 $^0/_0$ of the total retracted body length; in *Austenia* they occupy 46 $^0/_0$ of total retracted body length. In *Muangnua*, body width is 20 $^0/_0$ of body length; in *Austenia* 34 $^0/_0$. Despite the lesser proportion of the body devoted to the pallial region and visceral humps, *Muangnua* has the pallial cavity much less compressed and distorted than in *Austenia*. In *Muangnua*, the front 50 $^0/_0$ of the combined pallial cavity-visceral hump dorsal surface is pallial cavity; in *Austenia* slightly less than 35 $^0/_0$. No organ position is the same. The hindgut in *Muangnua* forms an "S"-loop running from left posterior margin of the visceral hump to midline, at which point the secondary ureter runs alongside as the hindgut forms the second curve of the "S" along anterior right margin to anal opening; in *Austenia*, the hindgut runs diagonally forward from posterior left margin to anterior third of pallial-visceral mass, then turns at right angle to body axis, running directly to anus at right margin. In *Muangnua*, the hindgut lies completely at pallial roof surface; in *Austenia* it is rotated under a thin lobe of the kidney. The heart in *Muangnua* is located under the kidney at the left central anterior margin and is barely visible through the pallial roof; in *Austenia* the heart is still on the left central side and under the kidney, but lies more nearly perpendicular to the body axis. In both genera the kidney is an enlarged, bilobed sacculated organ occupying much of the pallial cavity, but in *Muangnua* the upper lobe lies transversely on the lung roof, reflexes at left posterior margin of pallial cavity and curves down over visceral hump as the latter's forward extension constricts the cavity; in *Austenia* the primary lobe hangs down all along the anterior margin, reverses at left posterior pallial cavity margin, where rotation of the hindgut-ureter junction results in part of the kidney lobe lying above the hindgut and perpendicular to the body axis. Both genera have the ureter reflexed, but in *Muangnua* the arms lie transversely across the body, the reflexion is only moderately left of center and clearly visible through the pallial roof; in *Austenia* the ureter lies almost perpendicular to the body axis, the reflexion lies considerably left of center, and the compression of the pallial cavity hides the ureter from view through the pallial roof.

The digestive systems show the typical slug stomach enlargement, but there are certain differences. In *Muangnua*, the salivary glands remain of equal size, but the right gland has shifted to the left side of the stomach and lies completely in front of the left salivary gland; in *Austenia* the glands are thinner and more platelike, the right gland being noticably thinner than the left. The intestine of *Muangnua* is large at first, then very narrow at the hindgut; in *Austenia* the intestine narrows only slightly. The pattern of intestinal looping is distinctive in the two genera (see figs. 16 *a* and 22 *c*).

The free muscles are quite different. In *Muangnua* they all unite less than one-third of the way along the stomach; in *Austenia* only the left tentacular retractor and buccal retractor unite at this point, the right tentacular retractor not fusing until the columellar area.

Since the genital systems of both taxa were immature, very few comparisons can be made. *Muangnua* apparently lacks a dart apparatus, has a long fingerlike spermatheca, no epiphallic lime-sac, possibly a small epiphallic retractor caecum, and possibly no penial muscle sheath or a functioning verge; *Austenia* has a large dart apparatus, long fingerlike spermatheca, prominent epiphallic lime-sac and retractor caecum, a large functional verge and a penial muscle sheath.

The jaw of *Muangnua* is a simple crescent; the jaw of *Austenia* has a prominent medial projection.

Radular differences are fundamental. In *Muangnua* the marginals and laterals are tricuspid because of an increase first in entoconal prominence, then ectoconal prominence; in *Austenia* tricuspid laterals have entocones reduced (lost on marginals) with marginals bicuspid through increase in ectoconal size.

The above comparisons clearly demonstrate that *Muangnua* and *Austenia*, despite their similar sluglike appearance, have reached this shape independently and are not closely related. Unfortunately, none of the other Oriental slug genera are known in sufficient anatomical detail to allow similar comparisons.

Despite the availability of only two juvenile specimens, the characteristics of this slug are so outstanding that description seems necessary. The reference to the Tribe Durgelli is with great hesitation, but until adult genitalia can be examined, the systematic position of *Muangnua* will remain uncertain.

Tribe Girasii

The term Girasiidae was first used by COLLINGE (1902 p. 73), but not defined. Subsequently it has been adopted, in a somewhat altered sense, by THIELE, H. B. BAKER and ZILCH. In this study, it recognizes an evolutionary trend towards reduction of the visceral hump and shell, accompanied by enlargment of the tail and alterations in the genitalia. Almost certainly the included genera are derivations from the Macrochlamydi, but the question of monophyletic or polyphyletic cannot be answered without much more study. Usually only the external body features, jaw, radula and genitalia have been studied; often only parts of these organ systems have been discussed.

The genera all show a greatly elevated, triangular tail with long vertical slit leading to the caudal foss and a barely or not overhung caudal horn. The shell laps and mantle lobes are very large and partly to completely fused, covering part or almost all of the shell and visceral hump. Usually a large cephalic shield, formed by the left mantle lobe, extends nearly to the level of the ommatophores. The shell is globosely vitriniform (*Megaustenia*) to vitriniform (*Austenia*) or a flat plate (*Pseudaustenia*) except in the questionable *Rasama*, which has a helicoidal shell. Reduction of the visceral hump and consequent shortening of the intestine resulted in enormous enlargement of the stomach, which often nearly fills the body cavity.

The genitalia normally have a large dart apparatus, the spermathecal head higher than the vas deferens origin and enlarged, the epiphallic retractor caecum reduced or absent. The epiphallus is unique in being sharply folded back upon itself, the head lying alongside the middle or lower part of the penis and usually bound to it by connective tissue. The distance from the lime-sac to the penial retractor is as large as that found in the Macrochlamydi, but the reflexion from the penial retractor and lack of a retractor caecum is quite different. Usually the lime-sac is short and bluntly pointed, lying parallel to the vas deferens. Although variable in form, neither the jaw nor the radula show important differences from the Macrochlamydi.

Every student has recognized that *Girasia* Gray 1855, *Austenia* Nevill 1878 and *Mariaella* Gray 1855 are related. Unquestionably *Galongia* Godwin-Austen 1916 and *Dihangia* Godwin-Austen 1916 are variations on the same theme. *Pseudaustenia* Cockerell 1891 has been placed in the Helicarioninae because it lacks a dart apparatus and has a verge. The form of the epiphallus, lime-sac, spermatheca, tail, caudal horn and shell laps agree with the genera mentioned above and I have no hesitation in transferring *Pseudaustenia* to the Girasii.

The status of *Rasama* Laidlaw 1932 (= *Sarama* Blanford and Godwin-Austen 1908 not Moore 1887) requires further study. Composed of a single species from Damsang Peak, Daling Hills, Western Bhutan, *Rasama kala* (Godwin-Austen 1883), which has a helicoidal shell with spiral sculpture, lacks a coiled caecum on the penial retractor, does not have a dart apparatus, but has the short lime-sac and enlarged tail of the Girasii. The shell laps are small, and it may be a Macrochlamydi or a Girasii. Pending further study, it is referred here.

Megaustenia Cockerell 1912 (= *Cryptosoma* Theobald 1857 not Milne-Edwards 1837) from Burma, Thailand, Malaya and South China has a large vitriniform shell, altered radular teeth, a functional although small verge, small lime-sac and a very short spermatheca. In many respects it seems intermediate between the Girasii and Macrochlamydi, but probably is more like the former.

Genus ***Megaustenia*** Cockerell 1912
(= *Cryptosoma* Theobald 1857 not Milne-Edwards 1837)

Type species. – *Vitrina praestans* Gould 1843 by original designation.

Supposedly the animal can retract within the shell and secretes an epiphragm during the dry season. The shell laps are smaller than in most Girasii and the radular teeth are strikingly modified. In having a verge, a small straight retractor caecum, and relatively large shell, *Megaustenia* is easily differentiated. The short spermatheca, large tail and caudal foss, dart apparatus and reflexion of the epiphallus decided its placement in the Girasii.

The following species are included:

Megaustenia praestans (Gould 1843)
  Mergui and Moulmein to the Shan States and Sawady, Upper Burma
Megaustenia birmanicum (Philippi 1847)
  near Mergui
Megaustenia heliciformis (Pfeiffer 1855)
  (= *Helix ophiria* Pfeiffer 1857)
  Mt. Ophir, Johore, Malaya
Megaustenia siamensis (Haines 1858)
  Siam
Megaustenia imperator (Gould 1859)
  Hongkong
Megaustenia khyoungensis (Godwin-Austen 1888)
  Shan Hills
? *Megaustenia austeni* (Collinge 1898)
  locality unknown
Megaustenia inusitatum (Godwin-Austen 1898)
  Eastern Burma about 300 miles northeast of Moulmein.

Possibly there are species of Tonkinese "*Helicarion*" and "*Vitrina*" that should be included in *Megaustenia*, but their anatomy is unknown.

Megaustenia siamensis (Haines 1858)

(Figs. 17–19)

Vitrina siamensis Haines 1858. Ann. Lyceum Nat. Hist. New York 6, p. 158. – Siam; MARTENS 1867. Preuss. Exped. Öst-Asien, Zool. 2, pp. 68–69; GODWIN-AUSTEN, 1898, Moll. India, 2: 52, 53, pl. 71 (anatomy); EHRMANN 1922. Sitz. ber. Naturf. Ges. Leipzig 45–48, pp. 4–8; COCKERELL 1929. Nautilus 43, (2), pp. 51–54.

Sai Yok near Kwae Noi (P. Johnsen, XII.1961)
Wang Dao (1754, 30.X.1958)
Sitang (1896, 22.XI.1958)
Chieng Dao at 1,000–1,200 meters (784, 15.VII.1958; 801, 17.VII.1958)
Doi Sutep (610, 29.VII.1958)
Doi Sutep at 1,100 meters (1273, 15.IX.1958; 1340, 20.IX.1958; 1452, 4.X.1958)
  1,500 meters (1146, 9.IX.1958).

The shell of the largest example (1340) was 18.5 mm. in diameter, another (1452) 18.3 mm., six between 14 and 16 mm., and the remaining six from 6.4 to 11.9 mm. There was no seasonal pattern in size evident from these few examples.

Some information on the anatomy has been presented by GODWIN-AUSTEN, EHRMANN and COCKERELL (see References above). The availability of good preserved material permitted supplementary notes and the preparation of more accurate drawings. These notes are based on dissections of individuals 1754 and 801, each figure representing a composite.

Foot and tail elongate (fig. 17 *a*) heavily pigmented, with weak mid-dorsal groove and indistinctly tripartite sole (fig. 17 *e*). Caudal foss very large with slightly overhung horn (fig. 17 *d*). Opening occupies full height of tail, which is roughly triangular in outline. Pedal grooves normal aulacopod pattern.

Mantle collar narrow, with large lobes and laps (fig. 17 *a*). Right mantle-lobe (MR) extending from mid-dorsal line laterally to point opposite posterior junction of foot and visceral hump. Pallial opening at upper margin of right mantle-lobe, a longitudinal slit of about 2 mm. (fig. 17 *b*). Left mantle-lobe (ML) extending from upper edge of pallial opening around to equivalent stopping point of right mantle-lobe, forming a flap-like covering for pallial opening (fig. 17 *c*). Surface of mantle-lobes heavily pigmented with pustulations, becoming markedly stronger near outer margin. Right shell-lap (LD) crescent shaped, uniting posteriorly with left shell-lap (L), starting from upper right-hand edge of pallial opening. Left shell lap much larger, extending from pallial opening to posterior junction and reaching high up on left side of body whorl. Surface of shell laps with very large pustulations and alternating dark and light coloration, except where laps join posteriorly. There the pustulations are greatly reduced in size and no dark pigmentation is present. Both shell laps narrow abruptly just before the posterior junction as shown for *M. praestans* (Gould 1843) in BLANFORD and GODWIN-AUSTEN (1908, p. 210, fig. 74 B, bottom right).

Pallial opening proper (fig. 17 *c*) or pneumostome (LP), opens below anus (A) and urinary chamber (LK). The latter passes above anal opening and leads into small groove at upper right margin of pallial opening, thus directing excretory products away from pneumostome.

Peculiarities in the pallial complex (fig. 18) reflect foreshortening of this region. In narrowing the distance between pneumostome and aorta, the intestinal loop was "pushed" into the pallial cavity resulting in a flap of the kidney (K) extending apically under the intestinal loop and beyond the reflexion of the ureter, while the pericardial sac lies on top of intestinal loop for part of its length. In snails with a fully developed shell and visceral hump, pallial cavity and hindgut follow parietal-upper palatal shell angle to the end of the pallial cavity. In *Megaustenia*, the

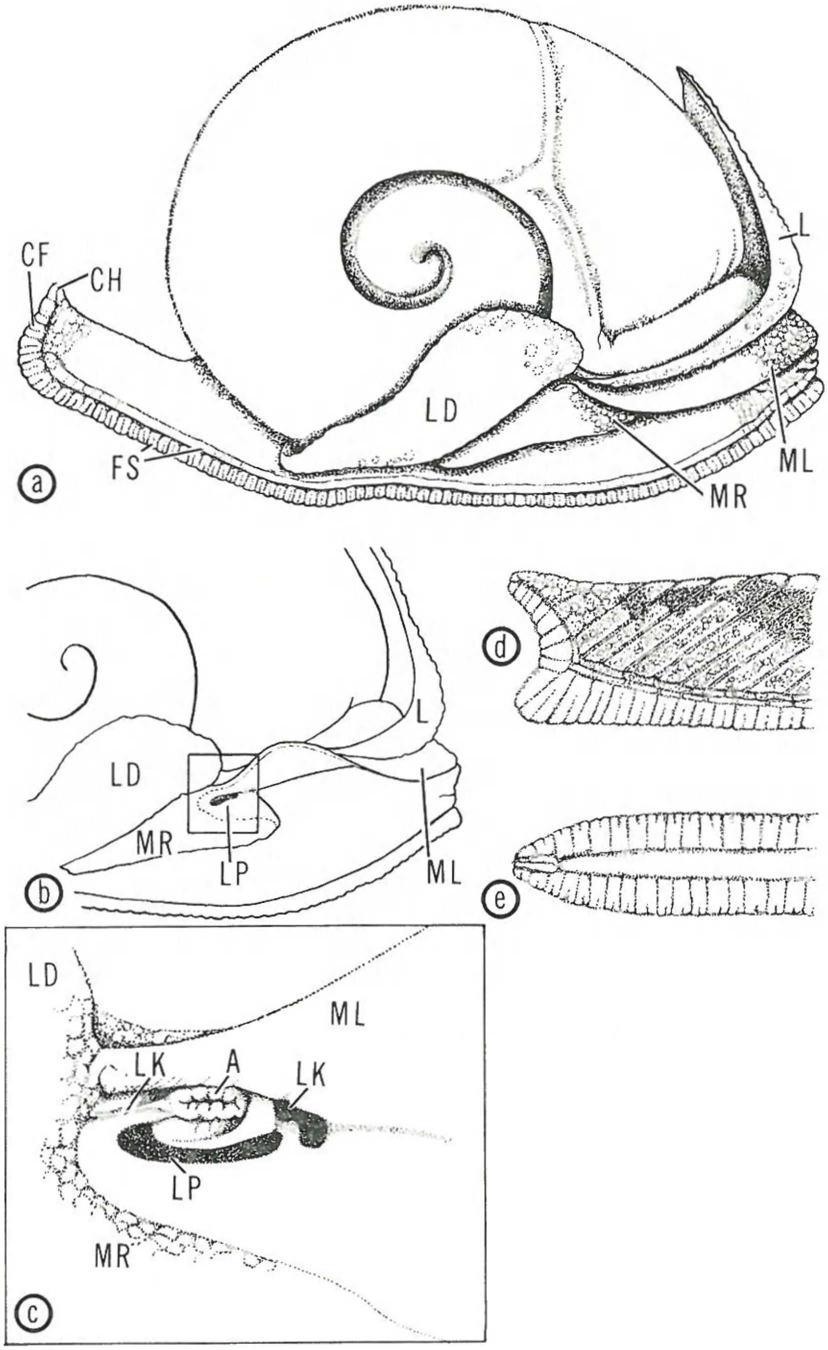


Fig. 17. *Megaustenia siamensis*: *a*, side view of body; *b*, location of pallial openings; *c*, details of pallial openings; *d*, side view of caudal region; *e*, bottom view of caudal region.

reduction in whorl number and foreshortening of the pallial area resulted in the hindgut leaving the parietal-upper palatal angle and slanting diagonally across the body. Columellar muscle (CR) attaches just apical of the point where the hindgut angles off.

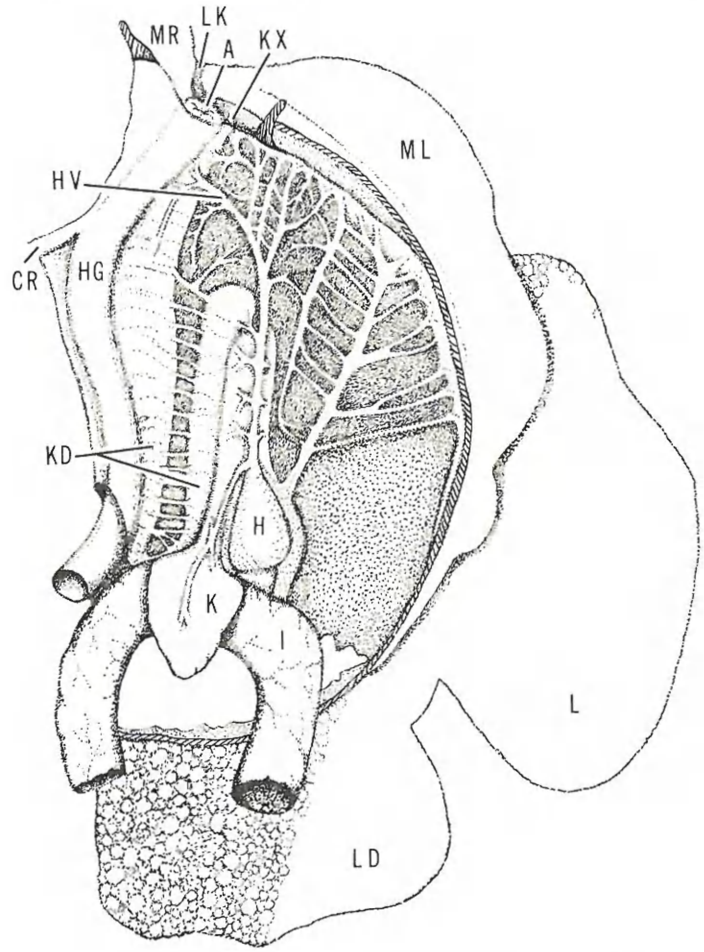


Fig. 18. Pallial region of *Megaustenia siamensis*.

Pallial roof very heavily vascularized with a flap of respiratory tissue just inside anterior edge of cavity receiving principal pulmonary vein and also another vessel that enters the pericardium. Branches of the blood vessels extend to both kidney and secondary ureter with several subsidiary branches joining the two loops of the ureter. The kidney (K) is relatively long, about $1^{1}/_{2}$ times the pericardial length, and narrow, partially lying on top of the pericardium with an expanded, wedgeshaped flap extending apically over intestinal loop. The ureter (KD) is bulbous anteriorly, narrows abruptly at posterior pallial margin, reflexes and is enormously enlarged near the end of the hindgut. It narrows significantly to the renal orifice (KX), which opens into a short urinary chamber (LK).

Most of visceral hump occupied by intestinal loops and digestive glands, the former being greatly enlarged and stuffed with bits of dead leaves in examined specimens. Apicad of pallial cavity, only the small albumen gland and very small ovotestis could be located. The rest of the genitalia (fig. 19 *a*) lies anteriorly.

Ovotestis (G) of clumped, short alveoli spaced along hermaphroditic duct which is imbedded in digestive gland. Hermaphroditic duct (GD) a simple tube without coiling or convolutions, anterior portion lying on surface of albumen gland (GG), running diagonally from anterior margin as a straight tube to talon (GT). This is a blind pouch lying on the albumen gland surface and marks a rough delineation between albumen gland and carrefour (X), with talon opening into lumen heading prostate-urine region. Prostate and uterus relatively slender, possibly seasonally underdeveloped, bound together for their entire length, central portion having a "C" shaped fold that may serve to separate sperm and egg passage.

Vas deferens a slender tube lightly bound to surface of free oviduct and vagina, passing across penioviducal angle, where it is very tightly joined by connective tissue, and immediately entering the epiphallus. Right ocular retractor muscle passing through penioviducal angle. The epiphallus is loosely anchored to the penial side of the atrium and is marked by a terminal caecum (EF) or lime-sac. Both caecum and epiphallus proper are lined with longitudinal smooth ridges. No indication of calcareous matter was found in the caeca opened. After an "S" loop, the epiphallus gives off a retractor epiphallic diverticulum to which the penial retractor muscle attaches. Origin of the penial retractor was not detected in the two animals dissected, although probably the diaphragm is involved, judging from attached tissue fragments. From retractor caecum, epiphallus makes a single angular turn before joining the penis through a verge that occupies most of the penial head (fig. 19 *c*). Verge (PV) crescent shaped with terminal pore covered by large triangular flap. Just below and slightly to one side of verge is a conical penial stimulator (PP) equal in size to the verge and with a papillose surface. Penial walls adjacent to verge and stimulator have a papillose surface, changing to longitudinal smooth pilasters in lower penial region. These ridges also continue into atrium (Y).

After prostate changes to vas deferens, a slender free oviduct (UV) descends to a common opening with the spermatheca (S) and a very

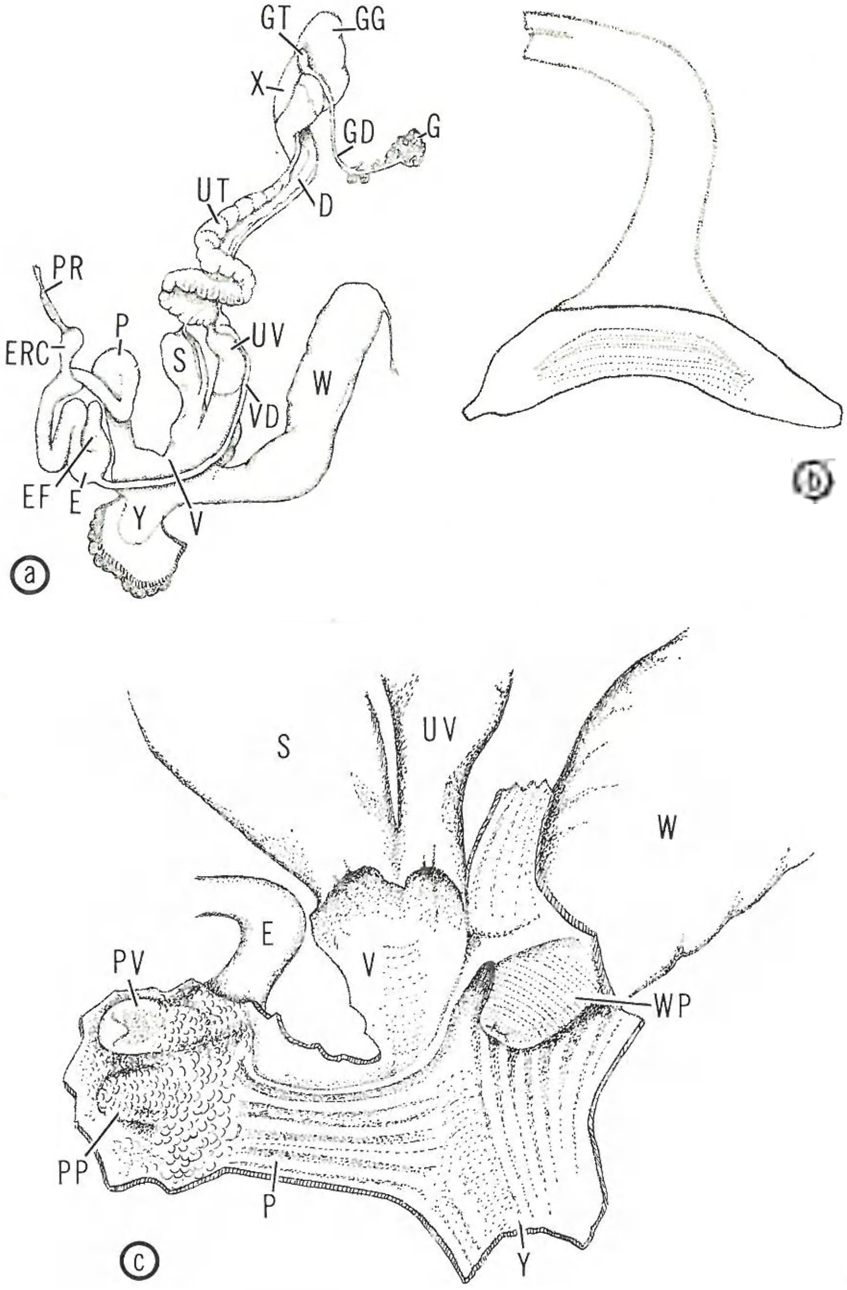


Fig. 19. *Megaustenia siamensis*: *a*, genitalia; *b*, jaw; *c*, internal structures of terminal genitalia.

short vagina (V) into which the dart apparatus opens. The spermatheca (S) is a squat, stalk-like object, bound to the side of the free oviduct and reaching only to the base of the prostate-uterus. The illustration (fig. 19 *a*) shows the severed connective tissue and the small strand that binds the head to the prostate-uterus. Internally, the spermatheca shows circularly arranged pustulations. These continue in less distinct fashion into vagina (V). Just below origin of vas deferens, free oviduct has a large papillose glandular collar, followed by two glandular, papillose ridges and a fine network of pustulations that gradually fade out just before spermathecal junction.

Dart apparatus (A) enters laterally on vagina at atrial junction. It consists of a dart papilla (WP) with central opening and circular wrinkling basally, with a very long head. This consists of an outer glandular zone surrounding a muscular tube that was filled with spongy tissue in opened examples. Apically there is a small retractor muscle that runs to the main columellar muscle just below its fusion with the tentacular retractors.

The jaw (fig. 19 *b*) lacks a median projection, but has a very well developed supporting membrane.

Radular structures were adequately discussed by GODWIN-AUSTEN (*loc. cit.*).

Genus ***Austenia*** Nevill 1878

Type species. – *Vitrina gigas* Benson 1836 by original designation.

Separated from *Girasia* Gray 1855 primarily in having an ear-shaped shell with distinct coiling, long spermatheca and less extensive shell laps, some nineteen species have been referred to *Austenia*. Only a few have been adequately described and figured. Some are known only from external features of one or two individuals, others from only the shell or radula.

The recorded geographic range extends from 9,500 feet elevation in Sikhim and the base of the Himalayas at Darjeeling, east through the Sadiya Frontier Tact (Abor Hills) in the disputed zone between India and Tibet, southeast at least to T'ēng-yüeh Chou (= Teng-Yue-Chow or Momein), Yunnan, China (app. 25° 98°30') and continuing south in a broad band from the Khasi Hills and Silchar throughout Burma to the Shan States and Tenasserim. There is no information as to whether *Austenia* reaches Peninsular Thailand and Malaya. (A record of *A. peguensis* from Belimbing, Ligeh, Malaya (COLLINGE 1902 pp. 76–77, pl. 4, figs. 13–14) is almost certainly erroneous, the figured genitalia showing a coiled lime-sac, totally different penis and large dart sac. The identity of this is unknown. An unnamed species of *Girasia* has been seen from Kuala Lumpur, Malaysia (FMNH 135300)). It probably reaches the northern parts of Laos and Vietnam and the first Thailand examples (Doi Sutep) are reported here.

The availability of well-preserved material allowed preparation of illustrations and descriptions of the external features, digestive tract and free muscles, radula, jaw, and the first study of the pallial region. Study of the nervous system was not possible and only juvenile genital structures could be observed. Comparisons with previously described taxa are almost impossible, since those named forms showing geographic proximity are known from the most fragmentary descriptions, while those that have been diagnosed adequately are from far distant localities and differ obviously in size, color and shell features.

Practically no features have been recorded for all nineteen forms. Nearly all species were named from only one or two individuals. We have no idea as to what constitute specific criteria, nor what is the range of variation either within or between populations. In order to have a name for the Doi Sutep animals, it was necessary to describe them as a new species. There were obvious differences from their nearest neighbors, even though only a very few characters of the latter had been described. Description as a novelty was considered preferable to use of "*Austenia* sp." or almost certain erroneous use of an essentially unidentifiable name.

The most recent summary of *Austenia* is BLANFORD and GODWIN-AUSTEN (1908 pp. 191–198). Subsequently described forms and their type localities are: –

Austenia annandalei Godwin-Austen 1910
    Siliguri, North Bengal
A. rotunda Godwin-Austen 1910
    Cachar and Silchar
A. tigris Preston 1914 (shell only)
    Naga Hills, Assam
A. rotungensis Godwin-Austen 1914
    Rotung, Abor Hills, Sadiya Frontier Tract, northeast India
A. aborense Godwin-Austen 1916
    Rotung, Abor Hills
A. alba Godwin-Austen 1916
    Rotung, Abor Hills at 1,300 feet
A. siyomensis Godwin-Austen 1916
    Damda, Siyom Valley, Abor Hills
A. dawnaensis Godwin-Austen 1918
    west base Dawna Hills, Tenasserim, Burma at 1,400 feet.

Only the first, second and fourth are sufficiently characterized to be identifiable.

Austenia doisutepensis new species

(Figs. 13 *d*, *f*, 20–22; Pl. II D)

Diagnosis. – A small, body length in preservative 22–30 mm., species of *Austenia* with subequally bicuspid marginal radular teeth, bluish-grey smooth mantle lobes and shell laps that leave much of the shell exposed, light brown foot sole and sides of body below visceral hump. Shell with $1^3/_4$ to 2 whorls, apex flat (not protruded), posterior margin of shell very shallow, calcareous elements absent from front portion of shell that is covered by the shell laps.

Austenia peguensis (Theobald 1864) from near Pegu, Burma has granulated mantle lobes and shell laps that almost completely cover the shell, unicuspid outer radular marginals, body color brown, and apex of shell distinctly protruding. *Austenia shanensis* (Godwin-Austen 1899) from east of Fort Stedman, Shan Hills, Burma differs in having the outer radular marginals unicuspid while the inner teeth have the ectocone far below the mesocone. *Austenia dawnaensis* Godwin-Austen 1918 from the west base of Dawna Hills, Tenasserim, Burma at 1,400 feet elevation has a strongly granulose mantle; its internal anatomy is unknown.

Description of soft parts. – Foot relatively broad, tripartite, rounded anteriorly, tapering slightly posteriorly (fig. 20 *b*). Tail short, high, sharply keeled middorsally, triangular in crossection. Caudal horn (CH) not overhanging, caudal foss (CF) a long vertical slit in tail (fig. 20 *c*). Pedal grooves typically aulacopod (fig. 20 *d*). Sides of body light brownish-white with grey spots that become much more frequent anteriorly and posteriorly, until upper part of tail appears solidly grey. Sole of foot greyish-yellow without spots. Mantle lobes and shell laps very dark grey above, lobes becoming lighter posteriorly and on outer edges, margins yellow-white. All parts of shell laps on top of body dark grey.

Right mantle lobe (MR) small, thick with a short lobate anterior extension, outer margin barely extending below upper foot margin (fig. 20 *a*). Lower part of right mantle lobe extends only to posterior margin of foot. From end of posterior lateral portion, a thin flap extends across the foot to join with the left mantle lobe and reaching posteriorly to overlap the lower posterior shell margin. Left mantle lobe (ML) greatly expanded and completely fused with left shell lap (L), forming a cephalic shield extending to level of eye stalks and slightly down sides of foot (fig. 20 *b*). Posteriorly the left mantle lobe's lateral extension ceases at rear of visceral stalk, with a flap from the left shell lap joining the lobe and passing under the body to unite with the right shell lobe.

Right shell lap (LD) fused with right mantle lobe on lower margin and with left shell lap anteriorly. Right shell lap (L) forming a pocket

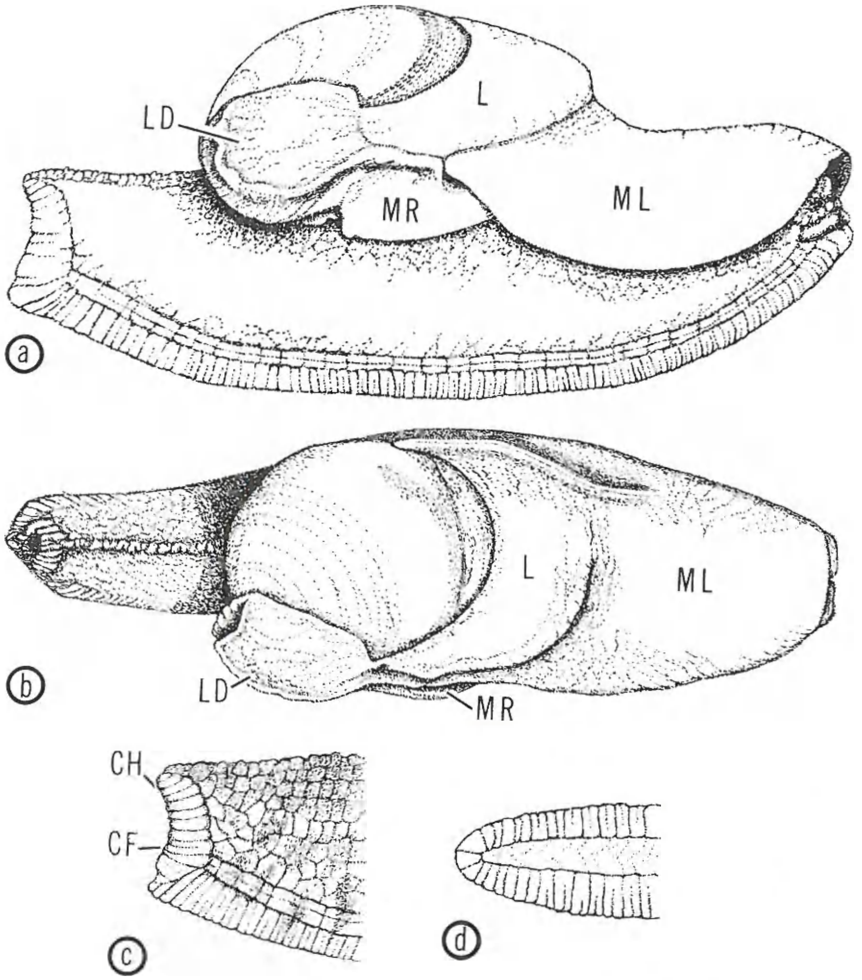


Fig. 20. *Austenia doisutepensis*, new species: *a*, side view of body; *b*, top view of body; *c*, side view of caudal region; *d*, bottom view of caudal region.

covering apex and posterior one-fourth of shell, with a distinct sinuated ridge running from pallial openings to near the posterior inner margin. Left shell lap fused on the right with right shell lap, in front and on the left side with the left mantle lobe. Upper margin of left shell lap a smooth concave curve, with lap covering anterior one-third of shell. On left side of body a ridge located just above foot margin runs from posterior one-third of mantle lap to posterior margin of shell lap.

Gonopore on right side of head, slightly behind right ommatophore and almost opposite inferior tentacle.

The extreme reduction of the visceral hump (fig. 21 *a*) and shell had drastic effects on the pallial region (figs. 21 *a–c*). Instead of lying parallel to the parietal-palatal margin as in most shelled forms (*Durgella*, fig. 8, for example) the hindgut and ureter rotated 90° to lie transversely across the body, essentially perpendicular to the longitudinal axis of the animal. This was accomplished without anterior prolongation of the mantle cavity and accompanied by a reduction in height of the cavity. Although the pallial cavity width remained essentially unchanged, the extreme *length* reduction and rotation required rather severe alterations in organ sizes, positions and relationships. Because of extreme compression, two figures (figs. 21 *b*, *c*) were required to illustrate the pallial area.

Figure 21 *b* shows the pallial cavity with one kidney lobe twisted downwards and backwards, partly severed from the hindgut-ureter margin. The hindgut is partially lifted downwards and backwards from where it nestles in a groove of the kidney. Figure 21 *c* shows a downwards and forwards rotation of the kidney to show the ureter and kidney in perspective. For comparison with figure 21 *a* the pallial area has been severed and turned over to expose the inside with the left edge becoming the right margin.

In *Megaustenia siamensis* (fig. 18) an intestinal loop is pushed into the pallial cavity, partly separating the kidney lobe and heart. In *Austenia* the hindgut protrudes into the pallial cavity with a lobe of the kidney extending dorsally and the ureter-hindgut junction rolled inwards and downwards so that part of the kidney is rolled around the hindgut. The dotted line in figure 21 *a* indicates the anterior margin of the visceral hump. The intestinal loop that normally borders the posterior of the kidney lies ventral to the pallial cavity and anterior of the hindgut (fig. 22 *c*). Although reaching the digestive gland surface, it does not protrude into the pallial cavity. The pallial region is thus reduced to a slim crescent shaped cavity lying anterior to and partly on top of the visceral hump.

Kidney proper (K) bilobed, major lobe paralleling mantle collar and only separated from it by a narrow (0.75 mm.) strip of lung roof. Right margin of kidney terminates considerably short of the respiratory pore. At the left margin the kidney forms a thin strip of tissue reaching the end of the pallial region. Here the kidney roofs the pallial cavity and a large flat lobe extends along hindgut, almost reaching right margin. Main lobe rather thick, but secondary lobe very thin, although much wider. Ureter very large, initially forming a swollen pendulous sac occupying almost entire right half of pallial cavity. This enfolds the kidney, then narrows abruptly as it passes along the main kidney lobe towards left margin. Since the pallial cavity does not have the usual shape, reflexion of ureter occurs medially of kidney termination. Technically, kidney does not reach hindgut, since rotational compression of the pallial region wrapped a kidney lobe partly around hindgut. There is no morphological connection.

The normally extensive pallial roof is thus reduced to two narrow strips of tissue, one separating the two branches of the ureter, the other the kidney from the mantle collar.

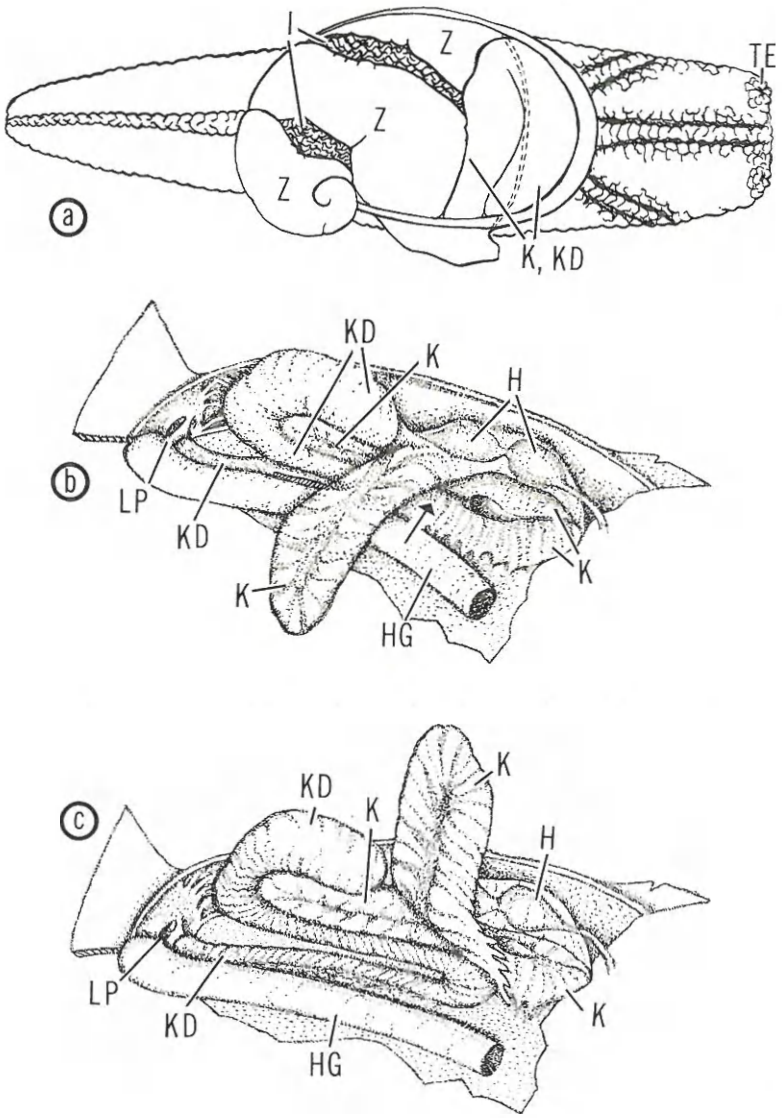


Fig. 21. *Austenia doisutepensis*, new species: *a*, top view of body with mantle lobes, shell laps and shell removed; *b*, pallial region with kidney lobe twisted backwards; *c*, pallial region with kidney lobe twisted forward. Both views of the pallial region from beneath.

Pericardium normally lies parallel to kidney and attached to lung roof, or lies partly under kidney and partly on lung roof. In *Austenia* it is wholly under kidney and pericardial sac has no direct contact with lung roof. Principal pulmonary vein thus passes along kidney surface to its right tip, crosses short strip of lung roof, giving off a branch to ureter, then enters a small area of extensive indistinct vascularization reaching respiratory pore (LP). A narrow zone of vascularization extends along mantle collar edge, paralleling kidney and ending slightly past middorsal line.

As a consequence of compression, the anal, excretory and respiratory pore relationships have changed rather markedly. The respiratory pore opens well below upper margin of right mantle lobe under a lateral flap of the left shell lobe. Excretory and anal openings higher, situated just below mantle collar and beneath lateral flap of cephalic shield although still within right mantle lobe border. Anus opens directly above left margin of pneumostome. Excretory pore at same level, but towards midline. Urinary chamber reduced in size, its groove passing above anus and thence apparently outward through channel between mantle lobes. Within mantle collar, hindgut comes to a blind ending, then reflexes to anus.

Free retractor muscles rudimentary (fig. 22 *b*). Right ommatophoral retractor (TER) passing through penioviducal angle. Rhinophoral retractors (TVR) uniting very quickly with ommatophoral retractors (TER). The right tentacular retractor (TR) passes posteriorly to unite directly with the columellar retractor (CR). Left tentacular retractor passing underneath esophagus and uniting with buccal retractor (BR) about one-third of way to columellar retractor. Columellar retractor a small broadened plate extending into visceral hump to parietal margin and weakly attached to shell. Buccal retractor split into two branches attaching laterally on buccal mass – right branch distinctly smaller than left. Retractor of dart apparatus (WR) originating on columellar retractor above union of tentacular retractors.

Digestive tract (fig. 22 *c*) relatively simple. Esophagus (BE) a short narrow duct connecting buccal mass (B) with enormously enlarged stomach (IZ). This occupies entire rear three-fourths of body cavity. Liver ducts enter near posterior margin. Intestine (I) completely buried in digestive gland (Z), wider at entrance into visceral hump than at anus, tapering gradually. Initial loop ascending vertically through digestive gland, visible at surface just to left of apex, descending along posterior edge and base, then running forward to right front margin of visceral hump. At this point it ascends and passes diagonally across visceral hump top to left side near midpoint of hump. For part of this traverse it is clearly visible through floor of pallial cavity. From left midmargin,

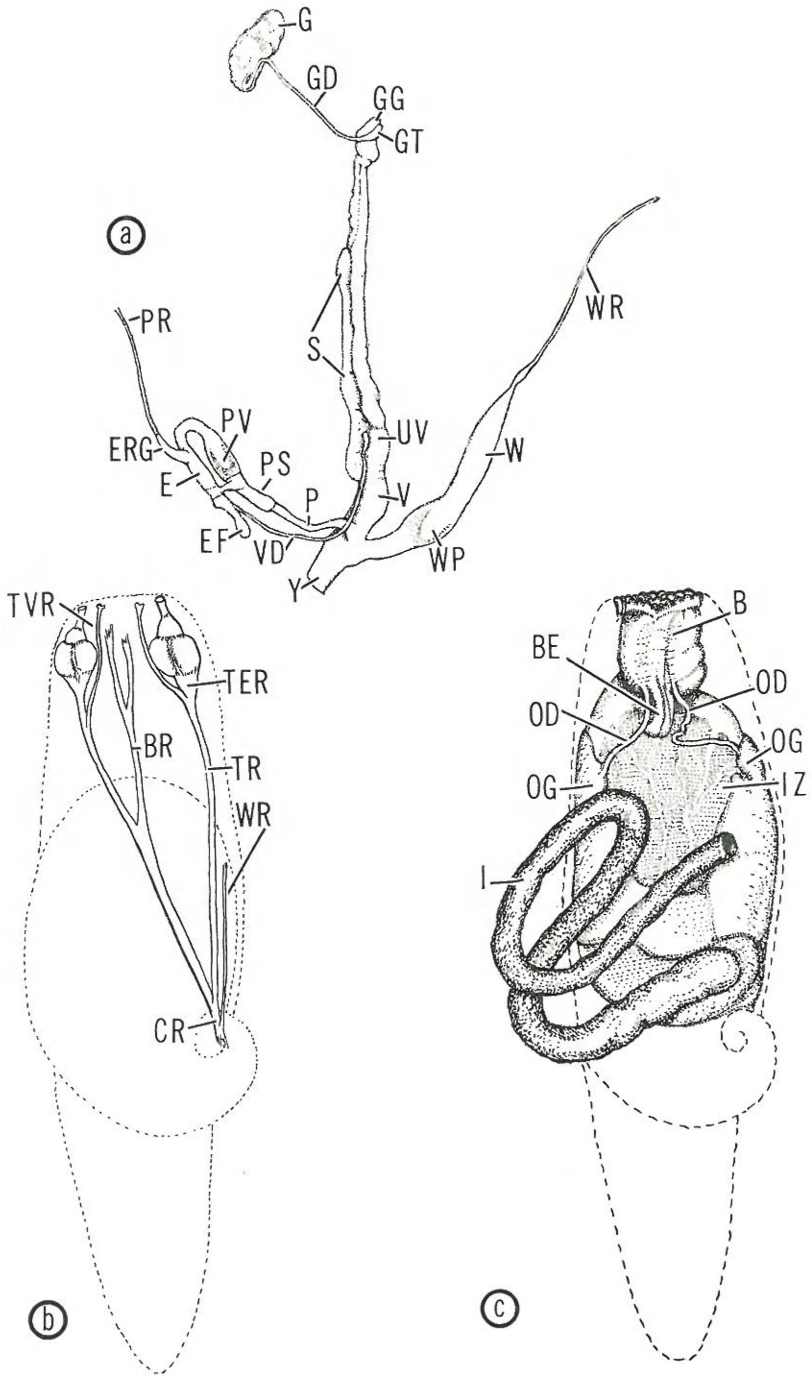


Fig. 22. *Austenia doisutepensis*, new species: *a*, genitalia; *b*, free muscles; *c*, digestive system.

intestine loops downward, buried in the digestive gland, to the left base of the visceral hump, then ascends to the upper surface on the posterior left side, curves forward to the edge of the pallial cavity (visible at surface of digestive gland) and swings transversely towards the anus, but buried under the kidney-ureter surface. Salivary glands paired, thin sheets of tissue united posteriorly across the stomach, right lobe distinctly larger. Twin ducts of salivary glands entering buccal mass at top sides of esophagus. Intestinal length exaggerated and expanded greatly to left and front in order to show position of loops.

Genitalia (fig. 22 *a*) of all dissected individuals immature. Ovotestis (G) and part of hermaphroditic duct (GD) buried in digestive gland. Talon (GT) a blind pouch equal in size to juvenile albumen gland (GG). Spermoviduct not clearly differentiated. Vas deferens (VD) passing along free oviduct (UV) and vagina (V), bound in peniovidučal angle, passing up penis, then entering epiphallus laterally at base of lime-sac (EF). Epiphallus reflexed at insertion of penial retractor (PR) entering penis (P) apparently through a verge (PV). Just below level of verge, a muscular sheath (PS) covers the penis, with a band extending around the reflexed epiphallus just apicad of vas deferens insertion. Inside of penis to midpoint of sheath pustulose, becoming longitudinally ridged to base of muscle sheath. Lower portion of sheath without clear sculpture, a simple tube. Penis entering atrium (Y) above level of dart apparatus. Penial retractor (PR) with short retractor caecum (ERC).

Free oviduct (UV) relatively short. Spermatheca (S) long and fingerlike, reaching two-thirds of way to albumen gland. Vagina (V) larger than free oviduct, leading straight into atrium. Dart apparatus (W) with upper glandular portion opening through a dart papilla (WP). Dart retractor muscle (WR) attaching to columellar retractor. Atrium (Y) quite prominent, vagina opening directly, penis laterally above and opposite opening of dart apparatus.

Radular formula 50–(13–14)–1–(13–14)–50 with 108 rows in specimen 1844; 44–13–1–13–44 in specimen 1448. Central tooth (fig. 13 *d*) equal in size to first lateral, mesocone large, ectocones small. First lateral with prominent ectocone, entocone slightly larger and set nearer mesoconal tip. After tenth lateral, entocones reduced and set nearer mesoconal tip, lost on marginals. After entocone is lost (beginning of marginals) ectocone increasing in size and tooth elongating rapidly until by 14th marginal, ectocone and mesocone nearly equal in size and tooth shape aculeate. On outer marginals, ectocone becomes reduced compared with mesocone and the tooth shortened. In 1448 outermost eight marginals vestigal, bicuspid, only slightly larger than wide; next seven shortening rapidly; middle 24 very aculeate; first 5 marginals lengthening rapidly.

Jaw (fig. 13 *f*) a simple crescent with prominent median projection. Faint, transverse growth striae, but no prominent sculpture present.

Description of shell. – Shell (Pl. 2 D) with $1^3/_4$ whorls, apex very slightly raised. Basal portion nearly entirely open. Surface without sculpture, smooth and shining. Calcareous elements restricted to portion not enclosed by left shell lap. Length of holotype 9.4 mm., width 6.2 mm.

Holotype. – Universitetets Zoologiske Museum, København. Doi Sutep, North Thailand at 1,100 meters elevation (specimen 1844). Collected by B. Degerbøl on 8.XI.1958.

Paratype. – Fourteen additional specimens were taken at Doi Sutep between 1,000 and 1,570 meters from 7.X.1958 to 20.II.1959. They are:

Doi Sutep at 1,000 meters (1671, 24.X.1958; 2002, 16.XII.1958)
1,100 meters (1738, 28.X.1958)
1,300 meters (1498, 7.X.1958; 2239, 20.II.1959)
1,500 meters (1559, 11.X.1958; 2204, 15.II.1959)
1,570 meters (2089, 10.I.1959)
Doi Sutep (1452, 4.X.1959).

Two specimens from number 1498 are FMNH 135280.

Remarks. – The body length of preserved specimens ranged from 12.6–29.3 mm. Both the largest and smallest individuals were collected at the same time (1498, 7.X.1958). No pattern of size difference could be detected.

Differences from the three geographically nearest named forms are given in the diagnosis. Since these three taxa were very inadequately characterized, no more detailed diagnosis is possible.

Color was the most variable external feature, most individuals showing at least a few lighter spots on the cephalic shield.

Suborder Holopoda

Superfamily Achatinacea

FAMILY SUBULINIDAE

Subfamily ***Subulininae***

Glessula latestriata Moellendorff 1899

(Pl. II *e*)

Glessula latestriata Moellendorff 1899. Nachrb. d. Malak. Gesell. 31, p. 166 (Kalow, southern Shan States at 5,000 feet elevation); Pilsbry 1909. Man. Conch. (2) 20, p. 100.

Doi Sutep at 500 meters (1643, 22.X.1958)
900 meters (1703, 26.X.1958)
1,000 meters (1173, 10.IX.1958 and 1776, 1.XI.1958)
1,100 meters (1059, 2.IX.1958, juvenile).

The several adults of this previously unfigured species were 7.9–11.2 mm. high with 6 to $6^5/_8$ whorls.

Lamellaxis (Allopeas) gracile (Hutton 1834)

Bulimus gracilis Hutton 1834. Journ. Asiatic Soc. Bengal 3, p. 93; VAN BENTHEM JUTTING 1952. Treubia 21, pp. 378–380.
Chieng Dao (780, 14.VII.1958).

Five specimens are the slender variant of this widely distributed culture snail.

Curvella puta (Benson 1857)

Bulimus puta Benson 1857. Ann. Mag. Nat. Hist. (2) 19, p. 330; GUDE 1914. Fauna Brit. India, Moll. 2, pp. 351–352.
Chieng Dao at 1,800 meters (794, 16.VII.1958).

A single, probably subadult specimen of this Burmese species is 6.73 mm. high, diameter 4.25 mm., whorls $5^1/_2$.

Prosopeas walkeri (Benson 1863)

Spiraxis walkeri Benson 1863. Ann. Mag. Nat. Hist. (3) 11, p. 90; BLANFORD 1903. Proc. Malac. Soc. London 5, p. 280 ("Lampun, Siam"); GUDE 1914. Fauna Brit. India, Moll. 2, pp. 363–364.
Doi Sutep at 1,000 meters (2178, 4.II.1959).

A single worn shell with $9^3/_8$ whorls, height 15.8 mm., is referred here. The very similar *P. anceyi* Pilsbry 1906 from Tonkin differs in having a shallower suture and more heavily callused columellar region. These may not be important, but insufficient material is available to access their value.

Superfamily Polygyracea

FAMILY CORILLIDAE

The systematic position of the Corillidae has been uncertain for a long time. PILSBRY (1905 pp. 288–289) indicated that the kidney lacked a ureter and opened on the right side through a simple pore. H. B. BAKER (1955) established the Order Mesurethra, based on possession of this type of kidney and included the Corillidae on the basis of PILSBRY's dissection of *Corilla humberti* (Brot 1864). Pilsbry (*loc. cit.*) had suggested that the Corillidae was an aberrant helicoid group and placed it next to the Camaenidae. Thiele (1931 p. 585) placed the Corillidae between the Sagdidae and Thyrophorellidae and before the Zonitidae. Zilch (1960 pp. 594–596) included the Corillidae, Sagdidae and Polygryidae in a superfamily Polygyracea, and placed this taxon just before the Helicacea.

Dissection of *Plectopylis simplex* (fig. 24) demonstrated the presence of a very thin sigmurethrous ureter and simple genitalia. Apparently Pilsbry mistook the ureter for the sac that often surrounds the hindgut, since his drawings of the pallial region in *Corilla humberti* shows the two arms of the ureter. This means that the Corillidae belong to the Sigmurethra. The simple genitalia, lack of pedal grooves, undivided foot sole, and weakly ribbed jaw all suggest that placement in the Polygyracea would be correct. As a Mesurethran relict, the corillid distribution seemed anomalous, but as a Polygyracean, it makes sense.

Genus **Plectopylis** Benson 1860

Gude never had much material from Siam or Cochin China, but felt that many forms might be found in these areas. Two sets collected by B. Degerbøl in Northern Thailand are new species. It must be remembered that Gude seldom had more than a few examples and we still do not know the extent of variation within or between populations. On the basis of present specific concepts, both taxa are unquestionably new species. Further study may show they are only subspecifically separable from Burmese taxa.

Plectopylis (Chersaecia) degerbolae new species

(Fig. 23 *a*, *b*, Pl. II, F–H)

Diagnosis. – A medium-sized, sinistral species of the *Chersaecia* section of *Plectopylis* characterized by a continuous upper parietal lamella that stops short of the parietal barrier; a very short lower parietal lamella that stops short of the barrier; and six palatal teeth, all simple but with small accessory posterior teeth.

Of the possibly related species, the smaller *P. peracta* (Blanford 1865) has a third parietal lamella and lacks the posterior accessory teeth; *P. shanensis* (Stoliczka 1873) has more parietal folds, some of which fuse with the parietal barrier, a total of nine accessory palatal denticles, and is larger; *P. leiophis* (Godwin-Austen 1874) has at least one of the parietal lamellae fusing with the barrier, lacks posterior accessory palatal denticles, and is somewhat smaller; and *P. kengtungensis* Gude 1914 has much more complex palatal dentition and a uniquely constructed parietal barrier.

Description. – Shell sinistral, planulate, of medium size, with slightly more than $5^7/_8$ tightly coiled whorls. Apex and first whorl of spire slightly protruding, remaining whorls flatly coiled, body whorl sharply descending just before aperture, H/D ratio 0.370. Apex smooth, shining, light brown in color, somewhat bulbous. First whorl of spire narrowing rapidly, sculpture of irregular growth wrinkles. Remaining whorls with narrow, crowded, protractive ribs and faint traces of lower spiral cords, becoming obsolete on body whorl. Sutures shallow, whorls evenly rounded laterally, somewhat flattened above. Umbilicus wide, cup-shaped, last whorl uncoiling more rapidly because of body whorl descension, contained 2.13 times in the diameter. Color light yellow-brown, lips white. Aperture ovate, rather abruptly deflected, inclined about 45° from the shell axis. Lips thickened and reflected with narrow grooves at palatal margins. Parietal wall with two lamellae; upper extending from just above midpoint of parietal lip posteriorly for one-quarter whorl, stopping short of parietal barrier; lower a very short (1.4 mm.) lamellar trace midway between upper parietal and columellar margin and situated just below posterior end of upper parietal lamella (fig. 23 *a*). Vertical parietal plate U-shaped with arms of "U" pointed posteriorly, lower much longer, with upper edge slightly fluted, the indentions lying opposite the major palatal teeth. Palatal teeth six, (fig. 23 *b*) major portion situated between end of parietal lamellae and parietal barrier; upper five with smaller accessory posterior teeth; lowest palatal with accessory tooth reduced to a small lateral bump midway between lowest and next lowest palatal. Upper palatal a low lamella near upper palatal margin, posterior portion distinctly separated, long and ridgelike. Second palatal a high crescentic lamella, horizontal, accessory tooth distinctly separated, ridgelike. Third, fourth and fifth palatals, lower, longer, joined to accessory portions, slanted from the horizontal with posterior end lowest. Sixth palatal greatly reduced in size, situated on columellar wall, with accessory tooth a faint ridge on basal margin. Height of holotype 6.0 mm., diameter 16.0 mm.

Holotype. – Universitetets Zoologiske Museum, København. Doi Sutep, North Thailand at 1,000 meters elevation (number 1173). Collected by B. Degerbøl on 10.IX.1958.

Paratypes. – Six subadult specimens collected at the type locality on 25.X.1958. Two of these are FMNH 135274.

Remarks. – Despite the presence of only a single adult example, the characters of this species are so distinctive that no hesitation is felt in describing it as new. While at first glance it is quite different from *P. simplex* in its larger size and parietal dentition, the near identity of the palatal teeth and parietal barrier suggests that they may be closely related.

Present knowledge of variability in *Plectopylis* is insufficient to allow conclusions as to its nearest relatives. Great pleasure is taken in naming this species after its collector, B. Degerbøl.

Plectopylis (Chersaecia) simplex new species

(Fig. 23 *c–g*, 24, Pl. III, A–C)

Diagnosis. – A small, sinistral species of the *Chersaecia* section of *Plectopylis* characterized by having only a single very short parietal

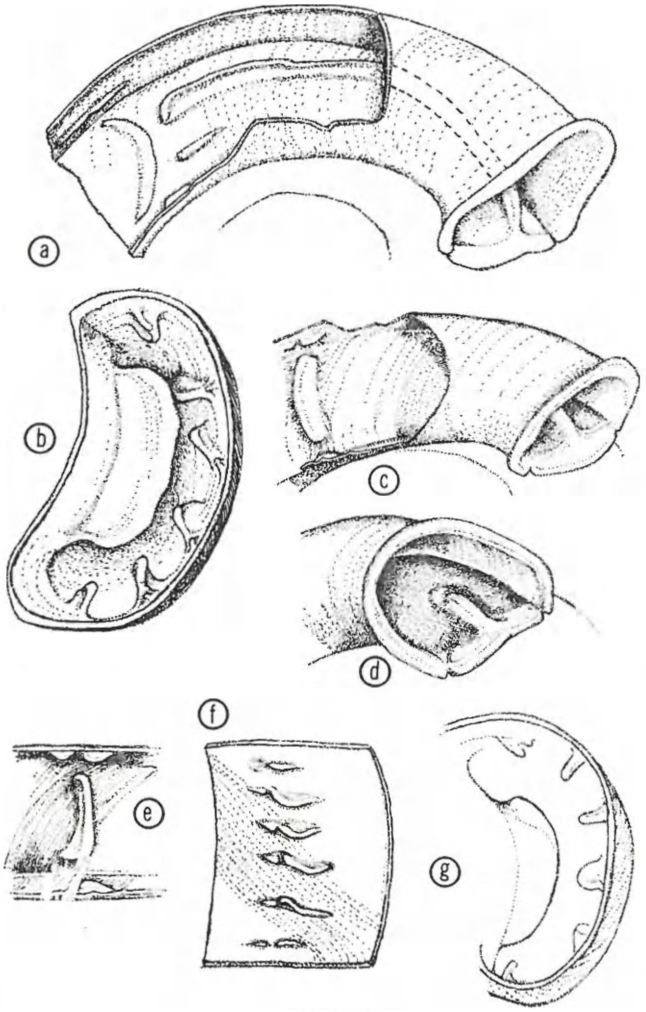


Fig. 23. Apertural barriers in *Plectopylis*: *a–b*, *P. degerbolae* – *a*, relative position of parietal lamellae and barriers, *b*, parietal barriers and palatal teeth viewed from behind; *c–g*, *P. simplex* – *c*, parietal barrier, *d*, aperture showing trace of parietal lamella; *e*, detail of parietal barrier, *f*, palatal teeth of a paratype, *g*, palatal teeth and parietal barrier viewed from the front.

lamella joined to the lip; no accessory parietal lamellae; and six palatal teeth with posterior accessory denticles.

Most species with the simple short parietal tooth are dextral and much larger (*P. schlumbergeri* Morlet 1886 and allies). Only *P. muspratti* GUDE 1897 is comparable. It differs in having an accessory parietal tooth below the barrier and several of the palatal teeth are connected. The larger *P. degerbolae* has nearly identical palatal dentition, and parietal barrier, but is easily differentiated by its long parietal lamella.

Description. – Shell small, sinistral, planulate, with slightly more than $5^1/_2$ normally coiled whorls. Apex barely emerging, remaining whorls flatly coiled, body whorl descending slightly just before aperture, H/D ratio 0.356. Apex very slightly expanded, first whorl of spire narrowing noticeably. Sculpture of apex and first whorl of spire consisting of irregular growth wrinkles, changing to narrow, crowded radial ribs with faint spiral ribs visible on unworn sections of the shell. Sutures moderately impressed, whorls slightly flattened above with evenly rounded outer margins. Umbilicus deep, cup-shaped, wide, last whorl uncoiling slightly more rapidly, contained 2.35 times in the diameter, with rounded margins. Color light yellow-brown, lip white. Aperture ovate, moderately deflected, inclined about 35° from the shell axis. Parietal lip elevated, reflected, rather narrow with noticeable grooves at palatal margins; palatal lip thick, reflected. Parietal wall with single very short lamella coming off parietal lip (fig. 23 *d*). Parietal barrier high, U-shaped, lower arm of "U" longer, arms pointing posteriorly, upper edge slightly flattened in two areas (fig. 23 *c*). Palatal teeth six, (fig. 23 *f*), major portion of each tooth located just anterior to top of parietal barrier, with accessory posterior denticles. Upper palatal a small crescentic lamella whose side is parallel to the wall of the previous whorl, with a very small accessory denticle clearly separated from tooth; second through fifth palatals high crescentic lamellae, slightly slanted from the horizontal and directly joined to the accessory tooth; sixth palatal tooth reduced in size, located on columellar wall with accessory posterior denticle distinctly separated and nearly on basal margin of aperture. Height of holotype 4.4 mm., diameter 12.3 mm.

Holotype. – *Universitetets Zoologiske Museum, København*. Chieng Dao, North Thailand at 1,200–1,300 meters elevation (number 797). Collected by B. Degerbøl on 16.VII.1958.

Paratypes. – Five adults and two subadults were collected with the type. Two of these are FMNH 135278.

Remarks. – Size and shape variation of the six adult shells is: height 4.18–4.57 mean 4.37; diameter 12.3–12.9 mm., mean 12.5 mm.; H/D ratio 0.334–0.366, mean 0.348; D/U ratio 2.11–2.35, mean 2.24; whorls $5^1/_2$–$5^7/_8$. Compared with most of the species of *Plectopylis*, the dentition is quite simple in character, hence the name *simplex*. *P. muspratti* Gude 1897 is the only species with which it could easily be confused. The differences are given in the diagnosis above.

Soft parts were partially extracted from the two illustrated specimens. In both cases the upper spire broke off and was left inside the shell, but sufficient organ systems were obtained to allow classification of the group as a primitive helicoid, most probably the geographic analog of the North American Polygyridae.

Brief descriptive notes of the animal follow.

Foot holopod with broadly rounded tail that lacks any sign of a caudal foss or horn. Head retracted so that expanded length of body not observed.

Pallial region (fig. 24 *a*) elongated, hindgut paralleling parietal-upper palatal margin past end of pallial cavity. Mantle collar (MC) thick, parietal-palatal margins somewhat elongated with a glandular

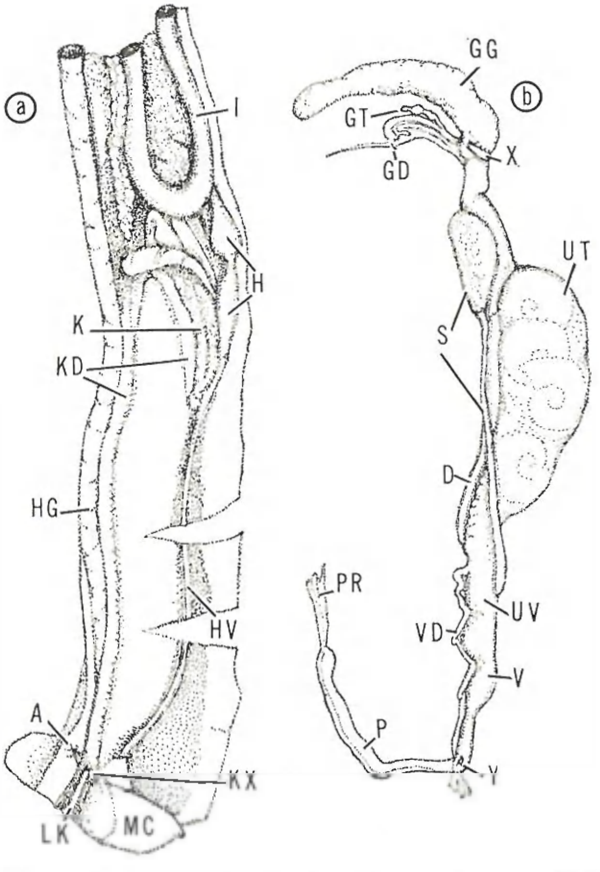


Fig. 24. *Plectopylis* (*Chersaecia*) *simplex*, new species: *a*, pallial region; *b*, genitalia.

extension onto pallial roof. Kidney (K) slightly less than 25 % longer than pericardium, slender, flaring basally and extending slightly back over intestinal loop. Ureter (KD) sigmurethrous, reflexing along hindgut in a wide, very thin band, opening (KX) into a dark pigmented urinary chamber (LK) that parallels anal passage. Pericardium (H) quite elongated and slender. Principal pulmonary vein (HV) running forward to edge of mantle collar extension. Hindgut (HG) slender, with well developed muscle running along past posterior margin. Looping of intestine behind kidney normal, digestive gland unusual in consisting of fingerlike lobes.

Apical genitalia not extracted, lower portions (fig. 24 *b*) adult. Ovotestis not seen. Hermaphroditic duct (GD) a straight tube to middle of albumen gland (GG), recurving and broadening, then running parallal along side albumen gland to large carrefour (X). Talon (GT) a slender, sinuated stark white duct along side of upper broadened hermaphroditic duct area. Carrefour with a solidified internal calcareous mass, opening into sharply differentiated prostate (D) and uterus (UT). Prostate enlarged below head portion, wide, becoming narrower and thinner where brood portion of uterus expands. Upper third of uterus slender, lower two-thirds grossly expanded with well-developed embryos.

Vas deferens (VD) an irregularly coiled tube passing along short free oviduct and along vagina to penioviducal angle. There it becomes an integral part of the fibers surrounding the penis, ascends penis laterally to its head, entering through small penis papilla. No epiphallic differentiation observed. Penis (P) a relatively short muscular tube with a thick apical retractor muscle (PR) attaching to diaphragm. Internally, penis with about eight corrugated longitudinal pilasters, those situated next to the vas deferens distinctly larger. At apex of penis two large pilasters flank a small vergic papilla with basal epiphallic pore. Gonopore located behind and below left tentacle. Atrium (Y) extremely short.

Free oviduct (UV) very short, only slightly narrowed from base of uterus. Spermatheca (S) with very long slender stalk and a pendulous enlarged head lying above broadened area of uterus with tip of head nearly reaching carrefour. Vagina (V) very long, upper part broad and stuffed with gelatinous tissue. Several sheets of muscular fibers bind atrial and vaginal areas to body wall.

Jaw crescentic, composed of about 27 plates cemented together, those near the center much narrower than the outer ones. Edge neither serrated nor projecting.

Radular formula 15–9–1–9–15 with 85 rows. Central very slender and elongated, basal plate equal in length to laterals, cusped portion tiny with only mesocone present. Laterals with square basal plates, large mesocone and prominent recessed ectocone. First marginal has entocone developed and tooth noticeably smaller than laterals. Outer marginals with basal plates wider than long, ectocone reduced and split, mesocone reduced in size.

So little has been published on the anatomy of the Corillidae that comparisons are almost impossible. The jaw and radula agree with the figures of *Plectopylis pinacis* (Benson 1859) as published by GODWIN-AUSTEN (1899–1914 pp. 201–204, pl. 114, figs. 2 *a–d*), while the genitalia differs only in having the vas deferens bound to the penis. *Corilla*, as described by PILSBRY (1905) and GODWIN-AUSTEN (*op. cit.*, p. 200), differs in having a flagellar appendage to the spermatheca, a well developed epiphallus and quite different radular teeth.

Superfamily Helicacea

FAMILY CAMAENIDAE

Ganesella (Ganesella) coudeini (Bavay and Dautzenberg 1900)

Helix (*Ganesella*) *coudeini* Bavay and Dautzenberg 1900. Journ. de Conchyl. 48, pp. 113, 443–444, pl. 9, figs. 13–15 (Bac-Kan, Tonkin).

Doi Sutep at 1,000 meters (1671, 24.X.1958)
1,100 meters (1762, 31.X.1958 and 1797, 3.XI.1958).

Specimens from "Langson, Tonkin" (FMNH 41362) identified by Dautzenberg as *G. coudeini* show a few minor differences. The whorls are less rounded, spire more elevated, periphery more angulated and lip slightly more reflexed. Despite this, I have little hesitation in considering the Thailand shells conspecific. The three Doi Sutep adults were 7.5–8.0 mm. in diameter, H/D ratio 0.698–0.722, D/U ratio 5.23–6.78, with $5^1/_4$–$5^1/_2$ whorls. The Tonkinese shells were 8.0–8.1 mm. in diameter, H/D ratio 0.795–0.805, D/U ratio 6.84–7.18, with $5^7/_8$ whorls.

Chloritis (Trichochloritis) sp.

(Pl. III, D–F)

Doi Sutep at 1,700 meters (1780, 2.XI.1958).

A single adult shell, height 21.4 mm., diameter 35.1 mm., with $5^7/_8$ whorls, is very similar in shape and form to *Chloritis* (*Trichochloritis*) *remoratrix* (Morlet 1892), although the latter is much smaller (diameter 24 mm.). Several rather similar species have been reported from southeast Asia and Southern China. Almost all of them have not been collected subsequently. The extent of variation within a species is unknown and it is impossible to assign a meaningful name to the Doi Sutep specimen. Figures are presented in order to allow comparison with subsequent collections.

Chloritis sp.

Doi Sutep at 1,300 meters (927, 31.VII.1958).

A juvenile shell differs in spire elevation and coiling from the shell discussed above. While obviously belonging to a distinct species, identification is impossible.

Amphidromus glaucolarynx (Dohrn 1861)

Bulimus glaucolarynx Dohrn 1861. Proc. Zool. Soc. London 1861, p. 207, pl. 26, fig. 7. LAIDLAW and SOLEM 1961. Fieldiana: Zoology 41 (4), pp. 524–525, fig. 17.

Sai Yok (Palle Johnsen 206, 28.XI.1961; 1610, XII.1961)
near Ban Kao (3013, 7–15.XI.1961).

The two very young dextral shells from Sai Yok probably are this species; two dextral adults, height 34.3 and 35.4 mm., from near Ban Kao belong to color form *fasciatus* Martens 1867.

Amphidromus metabletus Moellendorff 1900

Amphidromus metabletus Moellendorff 1900. Nachrb. d. Malak. Gesell. 32, pp. 22–23; LAIDLAW and SOLEM 1961. Fieldiana: Zoology 41 (4), p. 528.

near Cauda, Nhatrang, Vietnam (Knudsen, X.1959).

One dextral adult, 39.6 mm. high, and five juveniles, one dextral and four sinistral, were collected.

Amphidromus atricallosus (Gould 1843)

Bulimus atricallosus Gould 1843. Proc. Boston Soc. Nat. Hist. 1, p. 140; LAIDLAW and SOLEM 1961. Fieldiana: Zoology 41 (4), pp. 530–531.

Soi Dao Mt., Chantaburi District (K. Larsen, 1963).

A single juvenile, height 34 mm., with $5^7/_8$ whorls, is the *leucoxanthus* color phase of this common species.

Amphidromus xiengensis Morlet 1891

Amphidromus xiengensis Morlet 1891. Journ. de Conchyl. 39, pp. 27, 232, 240–241, pl. 5, fig. 4; LAIDLAW and SOLEM 1961. Fieldiana: Zoology 41 (4), pp. 564–565.

Wang Dao (945, 3.VIII.1958).

A single worn adult, height 31 mm., apparently belongs to the common and variable form *clausus* Pilsbry 1900.

Amphidromus sp.

Ban Kao (Palle Johnsen 1597, 15–20.XI.1961)
Thailand (Palle Johnsen 656, 4.I.1962).

Two dextral juveniles are too young for identification.

FAMILY BRADYBAENIDAE

Aegista (Plectotropis) emensa (Godwin-Austen 1888)

(Pl. III, G–J)

Helix (*Trachia*) *emensus* Godwin-Austen 1888. Proc. Zool. Soc. London 1888, p. 242 (Hlindet, Burma); Gude 1914. Fauna Brit. India, Moll. 2, p. 220, fig. 84.

Helix (*Plectotropis*) *oldhami* Blanford 1903 (not Benson 1857). Proc. Malac. Soc. London 5, p. 278 ("Lampun, Siam").

Doi Sutep at 700 meters (1604, 17.X.1958)
900 meters (1490, 1.VII.1960)
Doi Sutep (2143, 14.I.1960).

Variation in the three Doi Sutep adults suggests that *A. clara* (Godwin-Austen 1888) from Hlindet is a synonym of *A. emensa*. The relevant dimensions are:

Specimen	Height	Diameter	H/D ratio	Whorls	D/U ratio
1604	7.2	14.2	0.507	$6^{1}/_{2}-$	2.73
1490	7.0	13.7	0.511	$6^{1}/_{8}$	2.98
2143	6.5	11.7	0.555	$6^{3}/_{8}+$	2.60
FMNH 40434 Lampun, Siam	6.3	15.2	0.414	$6^{1}/_{2}-$	2.42
clara (type)	—	9.5	—	5	—
clara (type figure, enlarged)	8.1	15.3	0.523	5	3.06
emensa (type figure)	7.9	13.5	0.585	7	2.65
FMNH 40381 Pato, Burma as *clara*	5.3	10.1	0.525	$5^{3}/_{4}$	2.73

The diameter and umbilical differences between the types of *clara* and *emensa* are effectively bridged by the Doi Sutep examples. Probably the two are synonymous. Similarly, one of the "Lampun" shells Blanford reported as *oldhami* (FMNH 40435) does not seem separable. Gude

(1914 p. 213) had referred to this as similar to *Planispira nilagerica* (Pfeiffer 1845).

Without dissections, classification will remain uncertain. Because of the papillose shell surface, I'm tentatively referring these to *Aegista*, although they may be found to belong to the *Trachia-Planispira* complex.

Pseudobuliminus (Giardia) siamensis (Redfield 1853)

Bulimus siamensis Redfield 1853. Ann. Lyceum Nat. Hist. New York 6, p. 15; MARTENS 1867. Preuss. Exped. Öst-Asien, Zool. 2, pp. 81–82, pl. 19, fig. 7.

Cauda, near Nhatrang, Vietnam (Knudsen, 27.XI.1959).

Three subadult shells are unquestionably this widely distributed species.

DISTRIBUTIONAL NOTES

A clear majority (32) of the 56 species (Table 1) came from one of two localities – Doi Sutep or Chieng Dao. Despite these mountain masses being only a few miles apart and on the same drainage system, only three species – *Cyclophorus speciosus* (Philippi 1847), *Megaustenia siamensis* (Haines 1858) and *Durgella libas* new species – were found at both. Of the 32 species, 26 were represented only from the one locality in this collection. This faunistic difference probably is more apparent than real. The Chieng Dao material was all taken during the middle of August, while the Doi Sutep specimens were gathered at intervals from September 1958 to the following March. Hence the collection may have been biased by seasonal factors. In addition, unquestionably only part of the fauna at each place was obtained.

If 18 objects are drawn from a sample of 30, 40 or 50 different items on two occasions, simple probability calculations indicate that, respectively, 21.6 %, 9.1 % and 4.7 % of the time there will be three items duplicated. These figures are large enough to suggest that the two "random samples" of molluscan species could be non-duplicating partial samples of the entire fauna. It is equally apparent, however, that there are some real faunal distinctions. Different species of *Pupina*, *Teraia* and *Plectopylis* occur at Chieng Dao and Doi Sutep, but *Cyclophorus*, *Megaustenia* and *Durgella* have the same species at both locations.

Without comprehensive collections from both places, no decision as to the degree of similarity or difference is possible and any speculation concerning faunistic affinities or divergences is meaningless. While species in any one area obviously are not randomly distributed and vary greatly

TABLE 1

Species from Chieng Dao and Doi Sutep

Chieng Dao	Doi Sutep
Lagochilus aff. *kobelti*	*CYCLOPHORUS SPECIOSUS*
CYCLOPHORUS SPECIOSUS	*Pupina arula*
Rhiostoma dalyi	*Sarika obesior*
Rhiostoma housei	*Sarika* aff. *hainesii*
Dioryx bacca	*MEGAUSTENIA SIAMENSIS*
Chamalycaeus aff. *fimbriatus*	*Muangnua limax*
Pupina artata	*Sesara parva*
Semperula siamensis	*Austenia doisutepensis*
Coccoderma ceratina	*Teraia thailandica*
Sitala trochulus	*DURGELLA LIBAS*
Sivella castra	*Cryptaustenia gadinodromica*
Cryptozona granulosa	*Plectopylis degerbolae*
MEGAUSTENIA SIAMENSIS	*Glessula latestriata*
Teraia crenulata	*Prosopeas walkeri*
DURGELLA LIBAS	*Ganesella coudeini*
Plectopylis simplex	*Chloritis* (*Trichochloritis*) sp.
Lamellaxis gracile	*Aegista* (*Plectotropis*) *emensa*
Curvella puta	

Species common to both localities capitalized.

in their relative abundance, collections by non-specialists on the basis of "I picked up whatever was seen" can approximate random sampling of the fauna. From experience with collecting in other continental areas, I consider that a fauna of 30 to 50 land snail species would be a conservative estimate for each of the two mountains. As demonstrated above, a sample of 18 species from each could contain only three in common, even if the faunas were identical. Although the different species of *Pupina*, *Teraia* and *Plectopylis* demonstrate that the faunas are not identical, the probability calculations suggest that the apparently large difference could be merely a sampling artifact. Differences undoubtedly exist, but probably are grossly magnified by the incomplete sampling.

The remaining 24 species included 16 recorded from one locality, 7 from two localities and only 1 from three localities. Of these, 10 were found in the Kwae River basin, 4 are from Cauda, near Nhatrang, Vietnam, and the other 10 from scattered places in northern and southeastern Thailand.

With such limited data, no important distributional data could have been expected. It was quite surprising to equate Thailand specimens with *Paracrostoma paludiformis* (Yen 1939) from Hainan and *Teraia crenulata* (Yen 1939) from Hongkong, but available data suggested no criteria for separation. Otherwise the collection provided the first Thailand records for a number of species and genera. None of these range extensions could be called surprising, but they do confirm a general pattern of land snail distribution that has not been emphasized sufficiently.

There are several genera with virtually identical ranges, extending from the Himalayan slopes of Sikhim through the Northeast Frontier Agency, Assam and Upper Burma into South China (occasionally as far as Hainan), then ranging south into Tenasserim, Thailand, Laos and North Vietnam, sometimes extending into Malaya, Cambodia and/or South Vietnam. *Sivella*, *Sesara*, *Durgella*, *Cryptaustenia*, *Plectopylis* and *Dioryx* fit this pattern most closely, although each may be absent from one or two of the fringes. *Austenia* is the same, but apparently absent from China and Vietnam. *Megaustenia*, *Rhiostoma* and *Pollicaria* are absent from India and the Himalayan kingdoms and only *Megaustenia* extends into China. *Sarika* probably is nearer the first group, but does not reach India and may touch Indonesia and the Philippines. Other genera show the India to China range, but have spilled through Malaysia into Indonesia (*Lagochilus*, *Cyclophorus*, *Cryptozona*, *Prosopeas*, *Glessula*, *Curvella*, *Amphidromus*) or even as far as the Solomon Islands (*Pupina*, *Atopos*, *Leptopoma*, *Chloritis*) or Japan (*Chamalycaeus*, *Ganesella*, *Aegista*). *Hemiplecta* ranges from Burma, Thailand and Vietnam through Indonesia to the Philippines and probably New Guinea, but is absent from China and India. *Pseudobuliminus* is known from Thailand to Formosa and the new genus *Teraia* possibly extends from Thailand to Hainan. *Muangnua* is recorded from only the one locality, but seems related to forms from Assam, China and Vietnam. *Sitala*, *Coccoderma* and *Semperula* are not sufficiently defined at present to permit range delineation.

Whole families (Clausiliidae, Succineidae, Vertiginidae) were absent from this collection and the 32 genera mentioned above are a very incomplete sample of the Thailand snail fauna. They do indicate that the richest part of the Oriental fauna, found from at least Sikhim to South China, is very well represented in Northern Thailand at least to the level of Doi Sutep. The land snail fauna shows only slight changes in generic composition within this area. Only when the sprawling Indian sub-continent is entered or Peninsular Thailand approached are there major faunal shifts.

APPENDIX

The symbols utilized on all text figures are modified from a system developed by H. B. Baker. Although explained in the text, it was considered desirable to present a single key to the abbreviations.

A	anus
B	buccal mass
BE	esophagus
BPP	brood pouch pore
BR	buccal retractor muscle
C	central tooth of radula
CF	caudal foss
CH	caudal horn
CR	columellar retractor muscle
D	prostatic portion of spermoviduct
E	epiphallus
EF	epiphallic flagellum
EP	opening or epiphallus into penis; epiphallic pore
ERC	epiphallic retractor caecum
ETS	egg transfer groove
FS	pedal grooves
G	ovotestis
GD	hermaphroditic or ovisperm duct
GG	albumen gland
GT	talon
H	heart or pericardium
HG	hindgut
HV	principal pulmonary vein
I	intestine
IZ	stomach
K	kidney
KD	ureter, both arms
KX	external opening of ureter
L	lateral tooth of radula AND left shell-lap of mantle
LD	right shell-lap

LK	urinary chamber
LP	pneumostome
M_1	first marginal tooth of radula
M_2	second marginal tooth of radula
MC	mantle collar
ML	left mantle lobe
MP	posterior left mantle lappet
MR	right mantle lobe
OD	ducts of salivary glands
OG	salivary gland(s)
P	penis
PP	penial papilla or pilaster
PR	penial retractor muscle
PS	penial sheath
PV	penial verge or vergic papilla
S	spermatheca
TE	ommatophore
TER	ommatophoral retractor muscle
TR	tentacular retractor
TVR	rhinophoral retractor
UT	uterine section of spermoviduct
UV	free or post-uterine oviduct
V	vagina
VD	vas deferens
W	dart apparatus on female side
WP	papilla of dart apparatus
WR	retractor muscle of dart apparatus
X	carrefour
Y	atrium of genitalia
Z	digestive gland or "liver'.

ADDENDUM

Several months after completion of this study, I learned of a recent paper by **Tadashige Habe** (1964). Based mostly on specimens collected in the vicinity of Bangkok, there is little systematic overlap with material reported on above. With a single exception, we agreed in our classification of the few species common to both collections. **Habe** used *Sinotaia* as the generic name for the species described as *Paludina ingallsiana*; I used *Bellamya*. The exact affinities of the African viviparids (*Bellamya*) and Asiatic (*Sinotaia*) are unknown. I prefer to follow a conservative classification and use *Bellamya* in a broad sense until anatomical distinctions are demonstrated.

REFERENCES

ANNANDALE, N., 1920: The Apple Snails of Siam – Journ. Siam Soc. Nat. Hist., Supplement **7**, (1), pp. 1–24.

BAKER, H. B., 1938: Zonitid snails from Pacific Islands. Part I. – Bernice P. Bishop Museum, Bull. **158**, pp. 1–102, pls. 1–20.

— 1940: Zonitid snails from Pacific Islands. Part II. – Bernice P. Bishop Museum, Bull. **165**, pp. 103–201, pls. 21–42.

— 1941: Zonitid snails from Pacific Islands. Parts 3 and 4. – Bernice P. Bishop Museum, Bull. **166**, pp. 202–370, pls. 43–65.

— 1955: Heterurethrous and aulacopod. – Nautilus, Vol. **64**, part 4, pp. 109–112.

BENTHEM JUTTING, W. S. S. VAN, 1956: Systematic studies on non-marine Mollusca of the Indo-Australian Archipelago. V. Critical revision of the Javanese fresh-water gastropods. – Treubia **23**, (2), pp. 259–477, 135 figs.

BLANFORD, W. T., 1902: On *Rhiostoma dalyi*, n. sp., and *Sesara megalodon*, n. sp., obtained by the late Mr. W. M. Daly in Siam. – Proc. Malac. Soc. London **5**, pp. 34–35.

— 1903: Notes on Mr. W. M. DALY's collections of land and fresh-water Mollusca of Siam. – *op. cit.*, pp. 274–284, pl. 8.

— & GODWIN-AUSTEN, H. H., 1908: Mollusca. Testacellidae and Zonitidae. – The Fauna of British India. London: TAYLOR and FRANCIS, pp. i–xxxii + 1–311, 90 figs.

CHAMBERLAIN, N. A., 1958: Life history studies of *Campeloma decisum*. – Nautilus **72**, (1), pp. 22–29.

COLLINGE, WALTER E., 1902: On the non-operculate land and fresh-water molluscs collected by members of the "Skeat Expedition" in the Malay Peninsula, 1899–1900. – Journ. of Malac. **9**, (3), pp. 71–95, pls. 4–6.

DAUTZENBERG, P. and FISCHER, H., 1905: Liste des Mollusques récoltés par M. le Capitaine de Frégate Blaise au Tonkin, et description d'espèces nouvelles. – Journ. de Conchyl. **53**, part 2, pp. 85–234, pls. 3–6.

GODWIN-AUSTEN, H. H., 1881: On the land-molluscan genus *Durgella*, W. T. Blanford; with notes on its anatomy and description of a new species. – Journ. Linn. Soc. London, Zool. **15**, pp. 291–296, pls. 20–21.

— 1889–1914: Land and freshwater Mollusca of India, **2**, pp. 18 + 442, pls. 63–158.

— 1919: On the generic position of *Helix distincta* Pfr. of Siam. – Rec. Indian Museum **16** (2), nr. 10, pp. 199–202, 2 figs.

GUDE, G. K., 1903: A classified list of the helicoid land shells of Asia. – Journ. of Malac. **10**, (1), pp. 5–9.

— 1921: Mollusca. – III. Land Operculates. – The Fauna of British India. London: Taylor and Francis, pp. xiv + 1–386, 40 figs.

HAAS, F., 1952: Some non-marine mollusks from Northwest and Southwest Siam. – Soc. Nat. Hist. Bull. Siam, **15**, (1), pp. 21–25.

HABE, T., 1964: Freshwater molluscan fauna of Thailand. – Nature and life in Southeast Asia, **3**, pp. 45–66, 2 pls.

HAINES, W. A., 1858: Descriptions of four new species of terrestrial shells from Siam. – Ann. Lyceum Nat. Hist. New York **6**, pp. 157–158, pl. 5.

JACOB, J., 1957–1958: Cytological studies of Melaniidae (Mollusca) with special reference to parthenogenesis and polyploidy. – I and II. Trans. Roy. Soc. Edinburgh **63**, (2), nr. 16, pp. 341–351, 4 pls. and nr. 20, pp. 433–443.

— 1959: Cytological studies of Melaniidae with special reference to parthenogenesis and polyploidy. – Annamalai Univ., pp. viii + 1–186, 69 pls.

LAIDLAW, F. F., 1932: Notes of Ariophantidae from the Malay Peninsula, with descriptions of new genera. – Proc. Malac. Soc. London, Vol. **20**, Part 2, pp. 80–94, 9 figs.

MARTENS, E. VON, 1867: Die Preussische Expedition nach Öst-Asien. – Zool. Theil, **2**, pp. 61–86.

MOELLENDORFF, O. VON, 1894: On a collection of shells made by Mr. Roebelin on Kau Samui in 1884 and 1892. – Proc. Zool. Soc. London, 1894, pp. 146–156, pl. 16.

— 1902: Binnenmollusken aus Hinterindien. – Nachrb. d. Malak. Gesell. **34** (9–10), pp. 153–160.

MORLET, L., 1891: Contributions à la faune Malacologique de l'Indo-Chiné. – Journ. de Conchyl. **39**, pp. 230–243.

MORRISON, J. P. E., 1954: The relationships of the Old and New World melanians. – Proc. U.S. Nat. Mus. **103**, (3325), pp. 357–394, pl. 11.

PILSBRY, H. A., 1905: Anatomical and systematic notes on *Dorcasia*, *Trigonephrus*, n. gen., *Corilla*, *Thersites* and *Chloritis*. – Proc. Malac. Soc. London, Vol. **6**, Part 5, pp. 286–291, pls. 13–14.

PRESTON, H. B., 1915: Mollusca. Freshwater Gasteropoda & Pelecypoda. – The Fauna of British India. London: Taylor and Francis, pp. i–xix + 1–244, 29 figs.

SALISBURY, A. E., 1949: A new species of *Rhiostoma*. – Proc. Malac. Soc. London **28**, (1), pp. 41–42, pl. 3 b, figs. 1–4.

SUVATTI, CHOTE, 1938: Molluscs of Siam-Bangkok: Bureau of Fisheries, pp. 91.

THIELE, J., 1931: Handbuch der Systematischen Weichtierkunde, lief. **2**, pp. 377–778, figs. 471–782.

TOMLIN, J. R. LE B., 1929: The land shells of Kaw Tao. Journ. Siam Soc. Nat. Hist. Supplement **8** (1) pp. 15–17.

— 1931: Two new species of *Rhiostoma*. – Proc. Malac. Soc. London, **19**, (5), pp. 227–228, pl. 6.

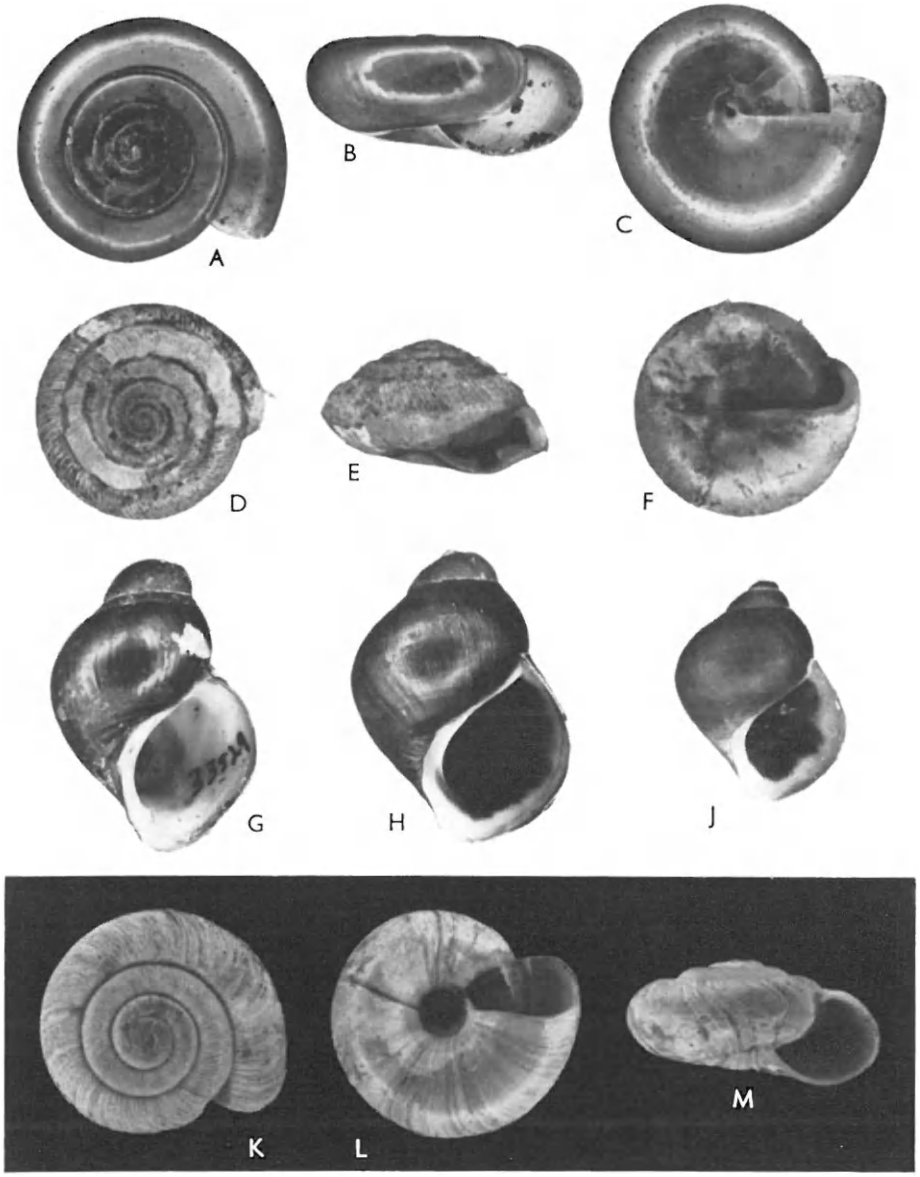
— 1932: Shells from a cave at Buang Bep, Surat, Peninsular Siam. – Jour. Siam. Soc. Nat. Hist. **8**, (4), pp. 315–320.

YEN, T.-C., 1939: Die chinesischen Land- und Süsswasser-Gastropoden des Natur-Museums Senckenberg. – Abhl. senckenberg. naturf. Ges. **444**, pp. 1–234, 16 pls.

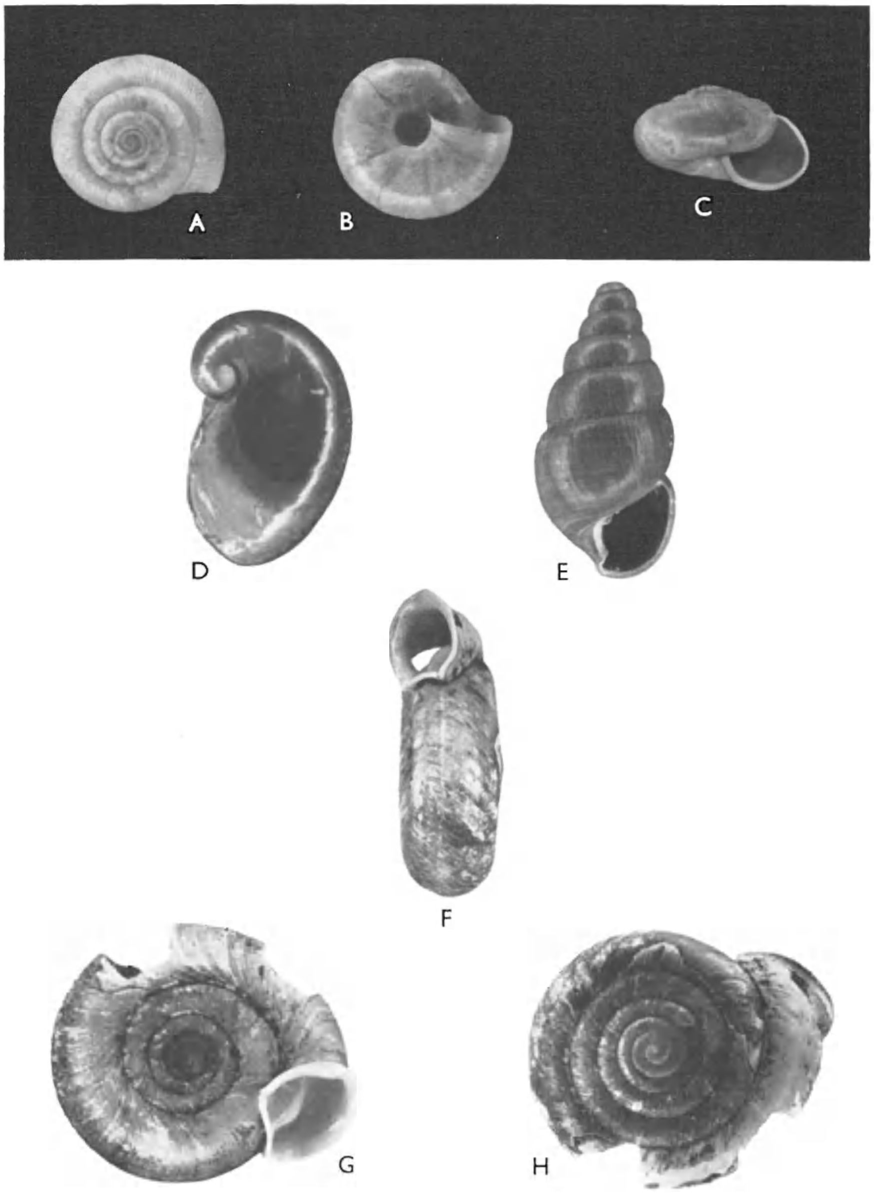
ZILCH, A., 1959: Gastropoda Euthyneura. – Handbuch der Paläozoologie, Band **6**, Teil 2, Lief. 2, pp. 201–400, figs. 702–1434.

— 1960: Gastropoda Euthyneura. – Handbuch der Paläozoologie, Band **6**, Teil 2, Lief. 3, pp. 401–600, figs. 1435–2111.

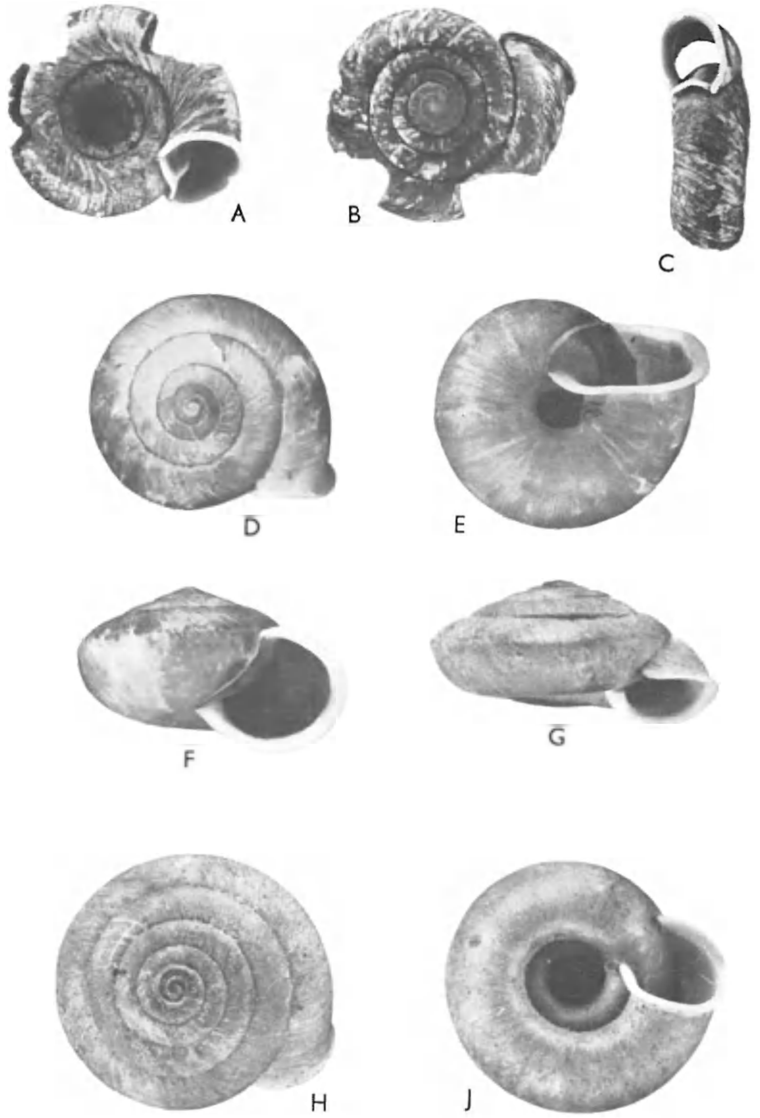
PLATES



A–C: *Sarika* sp., Ban Kao. D–F: *Sesara parva*, new species, specimen 2300, Doi Sutep at 800 m. G: *Paracrostoma hugeli*. H–J: *Paracrostoma paludiformis*, adult and juvenile. K–M: *Teraia thailandica*, new genus, new species, holotype, specimen 1401 a, Doi Sutep at 1,100 m.



A–C: *Teraia crenulata*, specimen 794, Chieng Dao at 1,800 m. D: *Austenia doisutepensis*, new species, paratype, specimen 1844. E: *Glessula latestriata*, specimen 1643, Doi Sutep at 500 m. F–H: *Plectopylis* (*Chersaecia*) *degerbolae*, new species, holotype, specimen 1173, Doi Sutep at 1,000 m.



A–C: *Plectopylis (Chersaecia) simplex*, new species, holotype, specimen 797, Chieng Dao at 1,200–1,300 m. D–F: *Chloritis (Trichochloritis)* sp., specimen 1780, Doi Sutep at 1,100 m., diameter 35.1 mm. G–J: *Aegista (Plectotropis) emensa*, specimen 1490, Doi Sutep at 900 m., diameter 13.7 mm.