

On the Caobangiidae, a New Family
of the Polychaeta,
with a Redescription of
Caobangia billeti Giard

MEREDITH L. JONES

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On the Caobangiidae, a New Family of
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ABSTRACT

Jones, Meredith L. On the Caobangiidae, a New Family of the Polychaeta, with a Redescription of *Caobangia billeti* Giard. *Smithsonian Contributions to Zoology*, number 175, 55 pages, 25 figures, 11 plates, 3 tables, 1974.—The type-species of *Caobangia* Giard, *C. billeti* Giard, is redescribed, primarily in terms of its setal morphology. The description of six new species of *Caobangia* extends the distribution of the genus from North Vietnam to Thailand, Burma, Ceylon, India, Bangladesh, Java, Sabah, Sarawak, and certain of the Philippine Islands. The genus is associated with gastropod molluscs of the families Thiariidae, Pleuroceridae, and Viviparidae, and with the bivalve family Unionidae. Detailed observations on the external morphology and the anatomy of species of *Caobangia*, as well as their setal structure and distribution, have contributed to the decision to erect a separate family, the Caobangiidae, for the genus. Familial characters are: the presence of neurosetal palmate hooks on the first setiger; the absence of hooks of any sort on the following thoracic setigers; the presence of two types of avicular hooks in the posterior region; and the recurving of the gut, within the body, such that the anus opens anteriorly, in the region of the second to fourth thoracic setiger. Anatomical observations on the branchial crown and its supporting skeleton, the nervous system, the nephridial ducts, and the reproductive system of these hermaphroditic, larviparous, freshwater polychaetes are reported. Further comments are made on larval morphology, settling, and metamorphosis, as well as on the molluscan associates and their habitats, and some basic questions of biological import posed by the morphology, anatomy, and development of *Caobangia* are propounded.

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On the Caobangiidae, a New Family of the Polychaeta, with a Redescription of *Caobangia billeti* Giard

Meredith L. Jones

Introduction

In 1893 Giard described a bizarre sabelliform polychaete from the fresh waters of what was then known as Tonkin, in southeast Asia. The specimens were associated with a freshwater snail, identified by Giard as a species of *Melania*, and were found in blind-ending, teardrop-shaped burrows in the calcium carbonate shell of the snails. In the course of his description of *Caobangia billeti*, which was unaccompanied by figures, Giard described a number of unusual and peculiar anatomical and morphological characters: the gut is recurved within the body and the anal opening is in the anterior part; the branchial crown is supported by an extensive internal structure; aside from the placement of setal fascicles, there is no trace of the usual annelid segmentation; the species has an hermaphroditic mode of reproduction, fertilization is internal, and larvae develop within the body of the adult; the worms are capable of making burrows in the calcium carbonate of snail shells; and unique palmate neuropodial hooks are present on the first setiger.

Giard's description was based on material collected by Albert Billet who, upon his return from Tonkin (now North Vietnam), summarized his two years of natural history observations at the village of Cao Bang in northern Tonkin and mentioned

that the host snail of *Caobangia billeti* was closely related to *Melania aubryi* Hende [sic] (Billet, 1896-98:64). In reporting upon the molluscs collected by Billet, Fischer (1898:327, pl. 18: fig. 42) identified the host snail as *Melania aubryana* Heude and presented a figure of the snail shell bearing holes, the burrow openings characteristic of *Caobangia*. Since these reports, the only other citation in the literature based upon what might be considered to be actual material is that of Lamy and André (1936:954, fig. 3), who reproduced Fischer's figure in demonstrating that *Caobangia* is one of a number of annelids that burrow in mollusc shells.

The remainder of the literature concerned with *Caobangia* falls into a number of categories: (1) as a sabellid of the subfamily Fabriciinae or as a curious freshwater polychaete (Chamberlin, 1919; McIntosh, 1922; Zenkevitch, 1925; Monro, 1939; Hartman, 1951, 1959; and Wesenberg-Lund, 1958); (2) as a polychaete with a polytrochous larval stage in its life cycle (Dawydoff, 1959); (3) as a suggested member of a new sabellid subfamily, the Caobangiinae [sic] (Chamberlin, 1919); and (4) as a point of discussion in the somewhat heated exchanges between Mesnil (1901a and b) and Nusbaum (1901). Further, it is curious to note that three extensive studies of the Sabellidae (Bush, 1904; Rioja, 1923; and Johansson, 1927) all cite Giard's paper in their bibliographies, but do not mention *Caobangia* in their texts.

It is unfortunate that Giard's description was

Meredith L. Jones, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

somewhat ambiguous, in part, for it led Nusbaum (1901) and Hartman (1951) to conclude that the anal opening was on the ventral surface rather than the dorsal. In addition, Banse (1957:98-99) concluded that Giard had made a bad choice of words and really meant that the posterior end of *Caobangia* was reflected under the ventral surface of the worm, in much the same manner as is the case in the Sabellariidae. Mesnil (1901a:272) and Lamy and André (1936:954) also came to the same conclusion.

It would seem that the remoteness of the type-locality and the small size of *Caobangia* account for the fact that, aside from the initial collections, no new material has been obtained for some 75 years. It came, therefore, as a pleasant surprise to find that the shells of snails from Thailand, preserved in 70 percent ethanol and brought to my attention by Dr. Joseph P. E. Morrison, Division of Molluscs, National Museum of Natural History, Smithsonian Institution, contained a considerable number of well-preserved specimens of *Caobangia*. A preliminary report on these, as well as on other well-preserved material from Sabah [=British North Borneo], was concerned with the confirmation of Giard's observations on *Caobangia* and conjectures as to the method of burrow-formation (Jones, 1969).

Preliminary observations of the collections from Thailand and Sabah led me to believe that the structure of the palmate neuropodial hooks of the first setiger would serve to discriminate among species of *Caobangia*. Since these hooks are relatively large and were felt to be impervious to the effects of drying (lamentably, curatorial procedures for the molluscs do not coincide with those for the worms), I conducted a search of certain of the southeast Asian gastropod holdings of our Division of Molluscs for snail shells showing signs of *Caobangia* borings; these ultimately included the families Thiaridae, Pleuroceridae, and Viviparidae. Where *Caobangia* bore holes were found, indeed, the palmate hooks were also found and their structure has served as the basis of the systematic section to follow. Further, these observations have formed the basis for increasing the number of species in the formerly monotypic genus to seven and have allowed the extension of the distribution of the genus from North Vietnam to Thailand, Burma, Ceylon, India, Bangladesh, Java, Sabah,

Sarawak, and certain of the Philippine Islands. I feel certain that further investigations will reveal the genus to be widespread throughout the whole of southeast Asia.

In spite of the fact that type-material of *Caobangia billeti* does not exist in the collections of the Museum National d'Histoire Naturelle, Paris, I do not feel that any real purpose would be served in designating a neotype for the species, since the material upon which such a designation would have to be based is most unsatisfactory because of its dried and fragmented condition; it is suitable only for setal observations.

Where numbers have permitted, paratypic material has been deposited in the collections of the following institutions: Allan Hancock Foundation, Los Angeles (AHF); British Museum (Natural History), London (BMNH); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museum National d'Histoire Naturelle, Paris (MNHN); National Science Museum, Tokyo (NSMT); Rijksmuseum van Natuurlijke Historie, Leiden (RNHL); Universitetets Zoologiske Museum, Copenhagen (UZMC); Zoological Institute, Academy of Sciences, Leningrad (ZIL); Zoologische Museum, Amsterdam (ZMA); and Zoologisches Museum, Hamburg (ZMH).

Since the collections of two divisions of the National Museum of Natural History, Smithsonian Institution, are involved in the present study, it was decided to preface catalog numbers (which still carry the old designation for the United States National Museum: USNM) of the Division of Molluscs with "USNM-M" and those of the Division of Worms with "USNM-W."

With a few exceptions, so noted below, identifications of the molluscs, with which various species of *Caobangia* are associated, are those appearing on labels accompanying the individual molluscan species. These have been accepted, out of hand, as valid.

In view of the unique characters of the genus *Caobangia*, its long-time obscurity, and the equivocal nature of portions of Giard's description, I felt that the relatively large number of well-preserved specimens might be utilized in enlarging on an otherwise straight forward systematic account. Thus, a series of observations follows, not only on taxonomically important characters, but also on the branchial crown and its supporting skeleton,

the nervous system, the nephridial ducts, and the reproductive system, the latter including comments on larval morphology and metamorphosis. All of these observations have contributed to my judgment that the genus *Caobangia* should be separated from other sabelliform polychaetes in a separate family, the Caobangiidae.

I would here thank the following colleagues for their kind help and cooperation which have contributed so much to this paper: Dr. Joseph P. E. Morrison, Division of Molluscs, National Museum of Natural History, Smithsonian Institution, for his first drawing my attention to specimens of *Caobangia* and for subsequent discussions and identifications of certain freshwater snails; Dr. Joseph Rosewater, also of the Division of Molluscs, for other discussions of the problems presented by *Caobangia* and for the use of some photographic equipment, especially the Faxitron Model 8050 X-ray apparatus which produced Figure 5b; Dr. Rolph A. M. Brandt, then of the SEATO Medical Research Project, Thailand (now of the School of Tropical Medicine, Bangkok, Thailand), who made the original Thai collections and augmented these with others; Prof. E. Fischer-Piette, Museum National d'Histoire Naturelle, Paris, and Dr. Kenneth Boss, Museum of Comparative Zoology, Harvard, both of whom made available to me specimens from their mollusc collections; Mr. Prasong Temcharoen, now of the Academy of Natural Sciences, Philadelphia, for assistance in determining the location of certain collection sites in Thailand and Laos, as well as for a snail identification; and to Dr. Marian H. Pettibone, Division of Worms, National Museum of Natural History, Smithsonian Institution, for her cheerful and careful reading of the manuscript, which benefited greatly from her comments and criticisms.

Materials and Methods

The polychaete specimens upon which this study was based were obtained by decalcifying freshwater mollusc shells that showed the characteristic bore holes of *Caobangia*; this was done by placing the shell in several changes of 5 percent nitric acid in 70 percent ethanol.

Histological observations were based on ethanol-fixed specimens or, in the case of a few specimens, especially provided by Dr. Brandt, on Bouin's fixed

material. Paraffin sections were cut at five or seven microns and were stained in Mallory's Triple Stain. Whole specimens, as well as decalcified molluscan shell debris, were mounted in glycerine jelly.

Localities were determined by the use of various gazetteers (War Department, 1944; National Intelligence Survey, 1952, 1953, 1962, 1964, 1966a, 1966b, 1968) and certain maps (especially "East Asia Road Map," Series 1306, Edition 1-AMS (FE), U. S. Army Map Service, 1965, Sheets 1 and 2, and "Continental Southeast Asia," Series 1206, Edition 4-AMS (FE), U. S. Army Map Service, 1965).

Characteristics of the Genus *Caobangia* Giard

Habitat: Figures 1-5 (*C. brandti*).

External morphology: Figures 6-8, 20 (*C. abbotti*, *C. brandti*).



FIGURE 1.—*Brotia* (*Paracrostoma*) *pseudosulcospira pseudosulcospira* Brandt (USNM-M 704230): Showing truncated apex of snail shell due to boring of *Caobangia brandti*, new species (scale line is 10 mm).

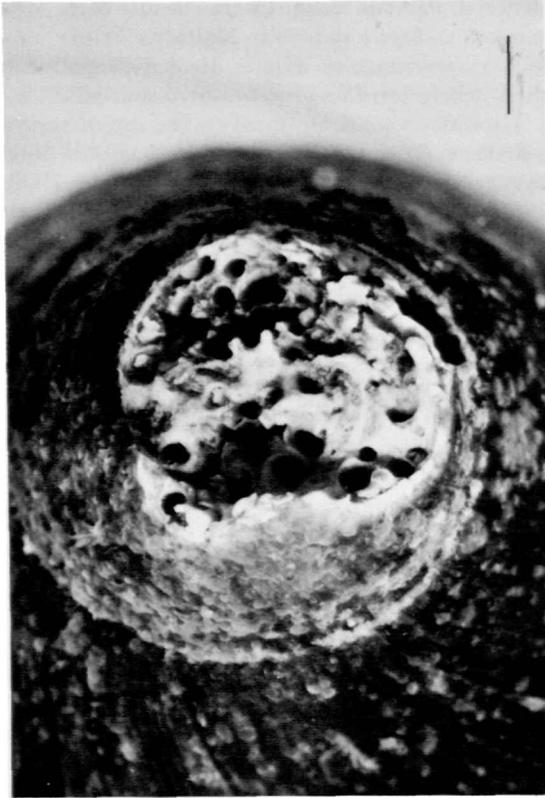


FIGURE 2.—*Brotia* (*Paracrostoma*) *pseudosulcospira pseudosulcospira* Brandt (USNM-M 704230): View of apex of snail shell showing bore holes of *Caobangia brandti*, new species (scale line is 1 mm).



FIGURE 3.—*Hyriopsis delaportei* (Crosse and Fischer) (USNM-M 704236): Surface of a generally tangential split of clam shell, showing transverse and longitudinal views of burrows of *Caobangia brandti*, new species (scale line is 1 mm).

Internal anatomy: Figures 6, 21; Plates 1-11 (*C. abbotti*, *C. brandti*).

Species of *Caobangia* bore into the shells of both gastropod and bivalve molluscs (Figures 1-5). As many as 28 adult *Caobangia* have been counted from a single snail shell. The effect of these numerous bore holes, usually restricted to the apex of the snail shell (Figure 3), weakens this portion of the shell and results in a truncated profile (Figure 1). In the case of borings in bivalve shells, there are many more specimens distributed throughout the available surface (Figure 5). The teardrop-shaped burrows, which are lined with a thin, secreted membrane, never connect with one another, and the burrows are most often found in the columellar area of the snails (Figure 4). Occasional bore holes may be found between adjacent

whorls of snail shells. Thus, adult specimens of *Caobangia* appear to be restricted to the thicker regions of calcium carbonate, although encapsulated metamorphosing larvae have been encountered all over the shell.

Specimens of *Caobangia* are herein reported from the shells of the pleurocerid gastropods *Paludomus*, *Hemimitra*, *Ganga*, and *Tanalia*; from the thiarid gastropod genera *Brotia*, *Balanocochlis*, *Stenomelania*, and *Antimelania*; from the viviparid gastropod genera *Anulotaia*, *Cipangopaludina*, and *Mekongia*; and from the unionid bivalve genus *Hyriopsis*.

Since type-material of *Caobangia billeti* Giard does not exist, the following morphological account is based on well-preserved specimens of *C. brandti* from Thailand and *C. abbotti* from Sabah, Malay-



FIGURE 4.—*Brotia* (*Brotia*) *binodosa binodosa* (Blandford) (USNM-M 704232): Apical view of partly decalcified snail shell, showing *Caobangia brandti*, new species (USNM-W 50857), in situ beneath the periostracum (scale line is 1 mm).

sia (Figures 6–8); that of the setae (Figure 11) comes from observations of dried specimens of *C. billeti* from That Khe, about 55 km from the type-locality and in the same river system.

Caobangia species include sabelliform polychaetes up to 5 mm in length with the branchial crown (BC) composed of three pairs of radioles (DR, MR, VR), each provided with pectinately or bipectinately arranged pinnules (Figures 6, 20). The body tapers from its widest (posterior) part, called the basal end by Jones (1969:830–831),¹ to

¹In my earlier treatment of *Caobangia* I was, perhaps, somewhat overzealous in emphasizing the internal anterior migration of the ascending gut and the opening of the anus so far forward. In changing terminology from “basal” to “posterior” and from “apical” to “anterior” I do not mean to lessen this emphasis, but do so merely to avoid confusion.

the narrowest (anterior) region bearing the branchial crown.

The first four setal fascicles are more crowded than the next three. There is no collar, although a rudimentary ventral process may be present (Figure 8c). On the ventral surface there are usually relatively large pigmented areas (VP) at the level of the first to second or third setal fascicles and another at the level of the sixth to seventh (Figures 6a, 7, 8c). In addition, smaller pigmented patches are distributed along the length of the ascending gut (Figures 7, 8c). In all adult specimens, developing eggs and larvae are readily seen through the body wall in the posterior third of the body. Histological sections have shown the presence of both eggs and sperm in all animals sectioned.

The first apparent thoracic segment bears a dorsal bundle of limbate capillary setae (LCS) and a ventral group of palmate hooks (PH) with a central fang encircled by a series of 4–15 teeth (Figures 6, 9, 11a–d). The hooks are oriented such that the teeth are directed posteriorly and somewhat dorsally (Figure 9). One of the lateral teeth in the arcuate series is quite often longer and/or stouter than the others; this tooth is always ventralmost (Figure 9c–f). New palmate hooks are generated at the ventral end of a given series, as suggested by the location of worn hooks and of embedded developing hooks (Figure 9b,e). The number of teeth in the arcuate series, as well as the relative length of the lateral teeth of the series, provide criteria for specific determinations. The setae of the second to seventh setal fascicles (SF) are composed usually of unilimbate capillaries of two types; upper, longer capillaries identical to the capillaries of the first fascicle, provided with nearly uniform, narrow limbations; and lower, shorter capillaries with basally widened limbations (Figures 6a, 10, 11d,e).

In the ventral part of the abdomen a somewhat shortened version of the limbate capillaries (SBS) are present in fewer numbers per fascicle (Figures 6a, 11f). These are associated with more dorsal, low, short-necked avicular hooks (AH), arranged in 3–14 rows (Figure 6a). The hooks are provided with a single larger tooth and numerous small teeth, 10–14 rows with about five or six per row (Figure 11e). The first row may have as many as 116 hooks on each side; more posteriorly, the number of hooks per row decrease until the last row is

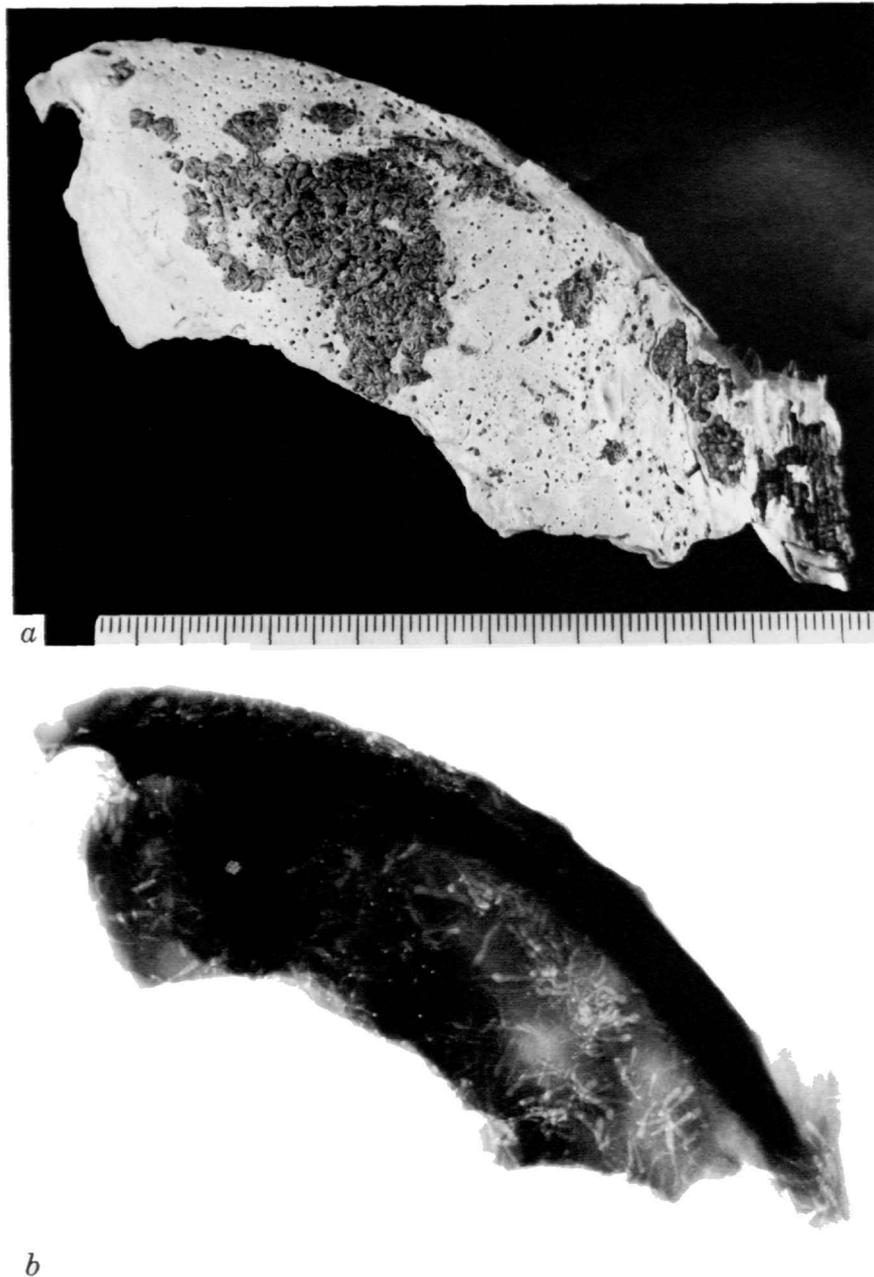


FIGURE 5.—*Hyriopsis delapointei* (Crosse and Fischer) (USNM-M 704236): *a*, outer surface of broken left valve showing bore holes of *Caobangia brandti*, new species, and external tubes of freshwater sabellid, *Monroika* sp. (center); *b*, X-ray photograph of the same valve, showing the shape and number of burrows, as well as their lack of common orientation.

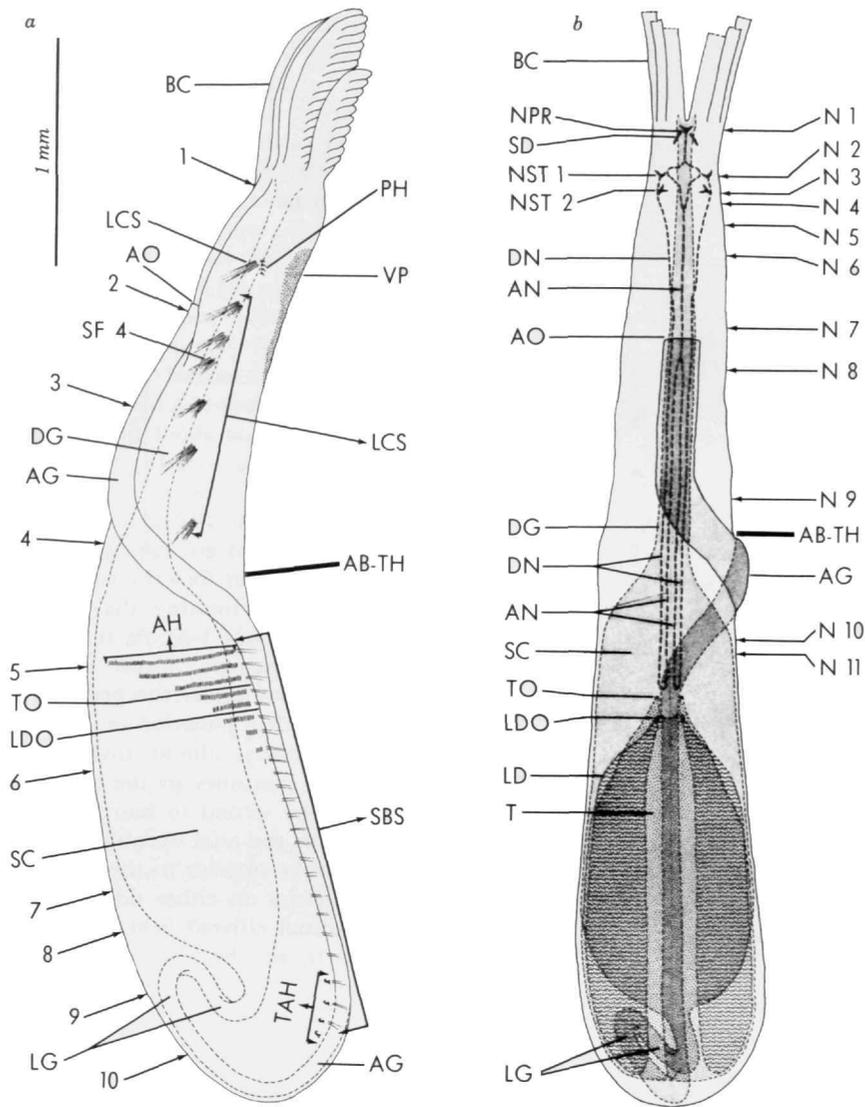


FIGURE 6.—Idealized and generalized drawings based upon *Caobangia abbotti*, new species: *a*, lateral view, showing external morphology and location of various types of setae; *b*, dorsal view, showing internal structures (setae and tips of branchial crown omitted). (1-10 = levels at which sections in Plates 1-5 were taken. AB = abdomen, AG = ascending gut, AH = low avicular hooks, AN = ascending nephridial duct, AO = anal opening, BC = branchial crown, DG = descending gut, DN = descending nephridial duct, LCS = limbate capillary setae, LD = larval duct, LDO = larval duct opening, LG = loops of gut, N 1-II = levels at which sections in Plates 8d-10d were taken, NPR = nephridiopore, NST 1 and 2 = first and second nephrostomes of the descending nephridial duct, PH = palmate hook(s), SBS = short limbate and brushlike setae, SC = stomachic chamber of the descending gut, SD = sperm duct, SF4 = fourth thoracic setal fascicle, T = "testis," TAH = tall avicular hook(s), TH = thorax, TO = external opening of the "testis," VP = ventral pigmented area; fine stippling = gut, coarse stippling = "testis," wavy lines = larval ducts.)

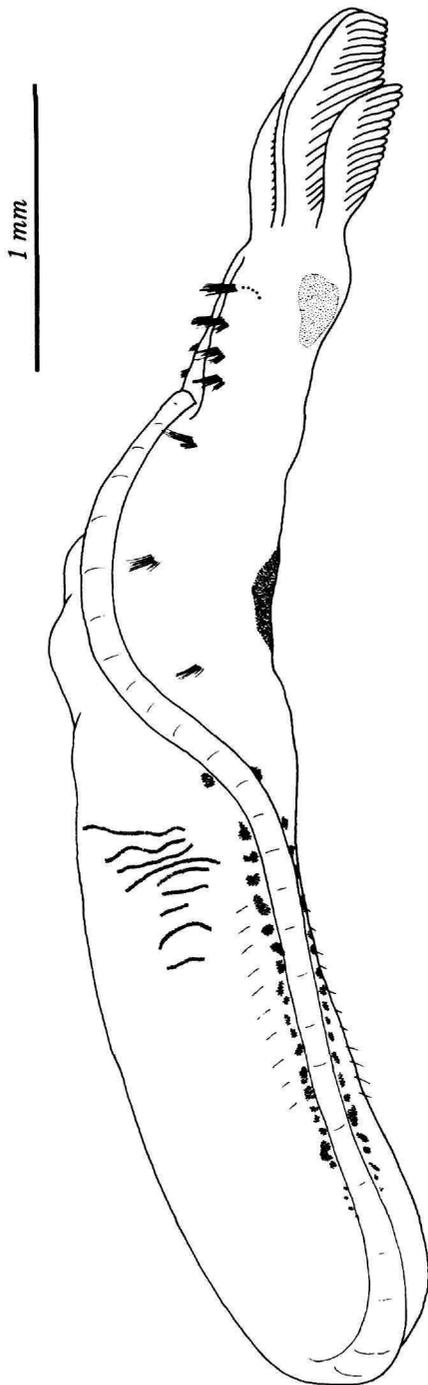


FIGURE 7.—*Caobangia brandti*, new species: lateral (anterior) to ventral (posterior) view (specimen twisted).

represented by but one or two hooks. Posterior to the region of avicular hooks, the limbate capillaries lateral to the ascending gut become still shorter and may be bilimbate or unilimbate (Figures 11*g-i*; the mucronate setae with symmetrical and asymmetrical limbations, respectively, of Giard, 1893: 475²). In most cases the abdominal limbate capillaries finally are replaced by brushlike setae with blunt tips, and having a generally frayed appearance (Figures 11*j,k*, 12*e,f*). These last are usually accompanied by some tall, long-necked avicular hooks (TAH) (Figures 6*a*, 11*m*).

The mouth, located at the center of the branchial crown, leads to a narrow passage, the descending gut (DG); at about the midpoint of the body, the gut enlarges to form a stomachic cavity (SC) which occupies most of the posterior half of the worm (Figure 6, Plates 1-4, 7, 10). More posteriorly, a narrowed gut emerges, forms several loops (LG), and turns forward within the curve of the posterior end, forming the ascending gut (AG) (Figure 6, Plates 1-5). As it progresses anteriorly, the ascending gut forms an increasingly pronounced ridge under the body surface (Figures 7, 8*c*). Somewhat posterior to the seventh setiger it curves dorsally, almost invariably on the right side, and continues in the middorsal line to the level of the second to fourth setiger where it terminates in the anal opening (Figure 6, AO). The dorsal areas anterior to the anus and between the setal fascicles on either side together form a wide longitudinal ciliated field (LCF) which continues anteriorly to the base of the branchial crown (Plates 1, 8, 9).

The separation of abdomen and thorax is assumed to be just posterior to the seventh setiger, in the region of the dorsal turn of the ascending gut, anterior to the first row of low avicular hooks (Figure 6, AB-TH). The latter, together with their ventrally placed capillary setae, are felt to represent the "inverted" condition of abdominal setae of other sabelliform polychaetes.

Caobangia Giard, 1893

TYPE-SPECIES.—*C. billeti* Giard, 1893, by monotypy.

GENDER.—Feminine.

DIAGNOSIS.—Small sabelliform polychaetes burrowing in shells of freshwater molluscs; 3 pairs

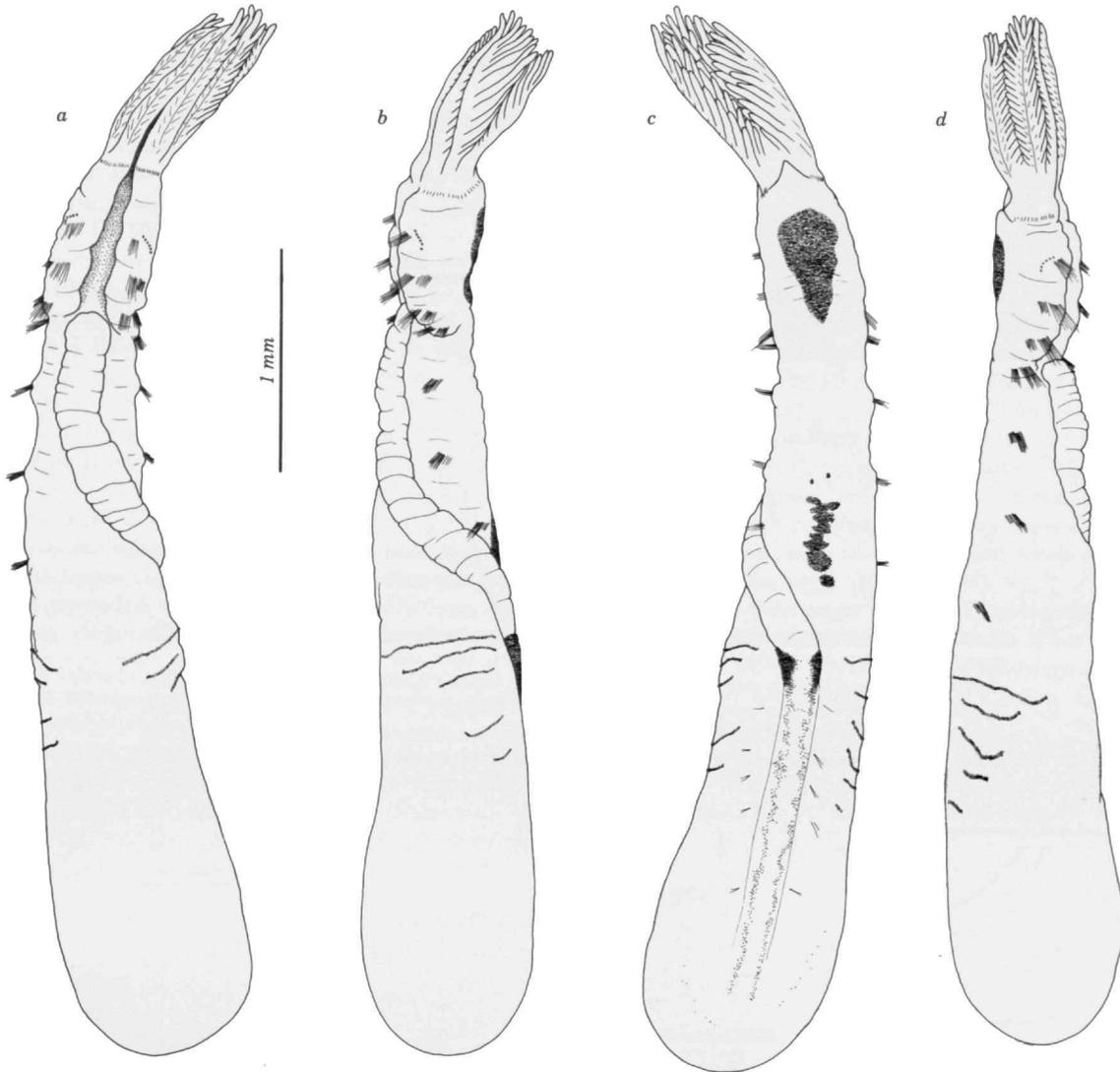


FIGURE 8.—*Caobangia abbotti*, new species: *a*, dorsal view; *b*, lateral view, right side; *c*, ventral view; *d*, lateral view, left side.

of radioles; thoracic region with 7 setal fascicles of limbate capillary setae (notopodial); palmate hooks on first setiger (neuropodial); abdominal region with short limbate capillary neurosetae and

notopodial avicular hooks, short in midregion, tall in posterior region; terminal portion of gut opening on dorsal surface of anterior thoracic region; hermaphroditic and larviparous.

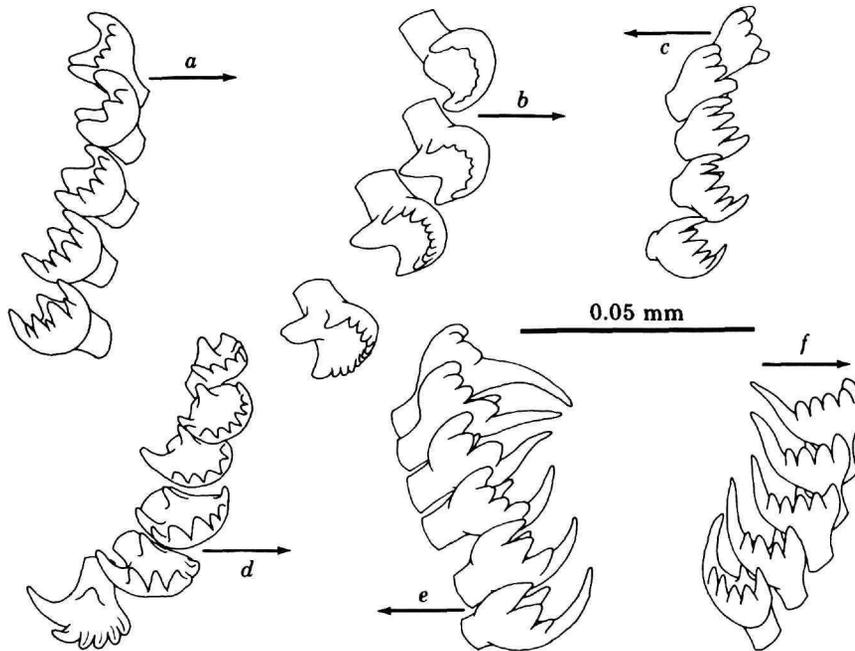


FIGURE 9.—*Caobangia* spp., palmate hooks from first thoracic setigers: *a*, *C. brandti*, new species, right side (USNM-W 50615); *b*, *C. abbotti*, new species, right side (USNM-W 50644); *c*, *C. morrisoni*, new species, left side (USNM-W 50640); *d*, *C. smithi*, new species, right side (USNM-W 50611); *e*, *C. indica*, new species, left side (USNM-W 50636); *f*, *C. ceylonica*, new species, right side (USNM-W 50632). (All emergent hooks of each series are shown in actual orientation; dorsal is top of figure, anterior ends of specimens are indicated by arrows.)

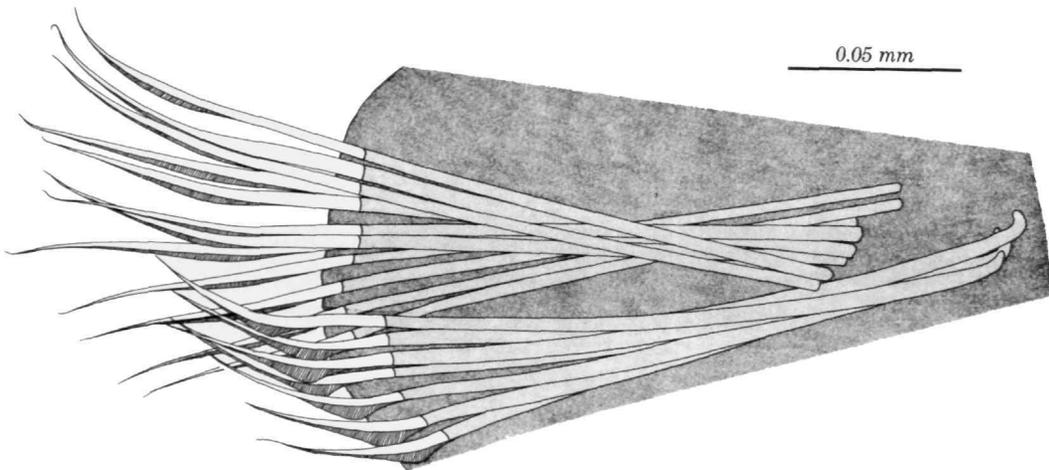


FIGURE 10.—*Caobangia abbotti*, new species: Anterior view of third right thoracic setal fascicle, showing relationship of longer (upper) and shorter (lower) limbate capillary setae.

Caobangia billeti Giard

FIGURE 11

Caobangia billeti Giard, 1893:473-476.—Billet, 1896-98:64.—Fischer, 1898:329, pl. 18: fig. 42.—Lamy and André, 1936:954, fig. 3.

MATERIAL EXAMINED.—[1]² That Khe, Tonkin [North Vietnam] (22°16'N, 106°28'E), from *Melania aubryana* Heude [= *Brotia* sp., fide J. P. E. Morrison] MNHNP, Lavezzari Collection, USNM-W 50643, dry material.

DISPOSITION OF ADDITIONAL MATERIAL.—MNHNP AE 1094.

DESCRIPTION.—Since all material was obtained from a dried snail shell, little can be said of the overall morphology of the specimens referred herein to *C. billeti*; however, all setal types characteristic of the genus have been recognized. The palmate hooks from the first setiger (Figure 11a-c) bear from 7 to 12 teeth in the arcuate series, the ventral lateral tooth may be rather stout, and both lateral teeth are usually somewhat longer than the others. The upper capillary setae of the 7 thoracic setigers are provided with narrow, relatively long limbations (Figure 11d); the lower capillary setae of the

² Bracketed numbers appearing in this and following "Material Examined" sections are keyed to localities shown on the maps of Figures 18 and 19.

second to seventh setigers bear limbations which are basally broad and abruptly narrowing apically (Figure 11e). Abdominal avicular hooks have a rather low profile (Figure 11l). According to Giard (1893), the abdominal hooks may be disposed in 3 or 4 rows, with up to 100 hooks in the first row and decreasing numbers in subsequent rows; in the specimens from That Khe, as many as 4 rows were observed. The anterior abdominal capillary setae are short and narrowly limbate (Figure 11f) and are ventral to the low avicular hooks. Posterior to the avicular hooks, several types of capillary setae are distributed along both sides of the ridge of the ascending gut: narrowly limbate capillaries give way to broadly unilimbate or bilimbate capillaries, and these, in turn, to capillaries with very short, broad limbations (Figure 11g-k). Those of the latter type are, perhaps, comparable to the brush-like setae of other species of *Caobangia*; they are usually abruptly bent at their tips. Dorsal to the latter are tall, long-necked avicular hooks; these are rather small, with the single basal tooth nearly appressed to the neck (Figure 11m).

REMARKS.—*Caobangia billeti* is known only from the type-locality, Cao Bang, and from That Khe; both are in North Vietnam, in the drainage of the Kiang River, which terminates at Canton, China, about 750 km to the east (Figure 19).

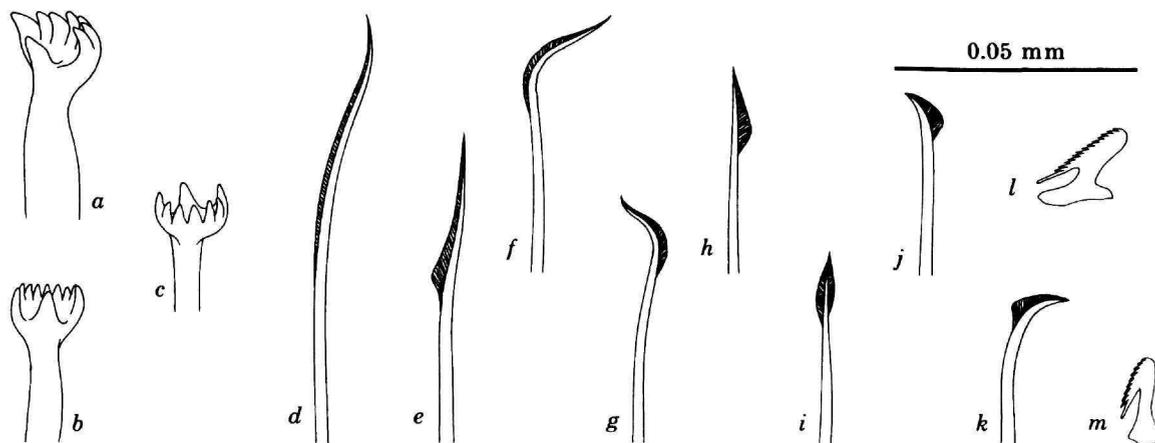


FIGURE 11.—*Caobangia billeti* (USNM-W 50643): a-c, palmate hooks from first thoracic setiger; d, longer thoracic limbate capillary seta; e, shorter thoracic limbate capillary seta; f, anterior abdominal limbate capillary seta; g-i, middle abdominal short limbate capillary setae; j, k, posterior abdominal brushlike (?) setae; l, anterior abdominal low avicular hook; m, posterior abdominal tall, long-necked avicular hook.

Caobangia brandti, new species

FIGURES 1-5, 7, 9a, 12

Caobangia sp. [in part] Jones, 1969: figs. 1, 4-8.

MATERIAL EXAMINED.—Thailand: [1] Maenam Kaek [Kaek River] at Sakunothayan Waterfall [Wang Nok Nang Aen Waterfall], about 33 km east of Phitsanulok, Phitsanulok Province (16°51'N, 100°32'E), from *Brotia* (*Paracrostoma*) *pseudosulcospira pseudosulcospira* Brandt (USNM-M 704230), coll. R. A. M. Brandt, 6 January 1968 (USNM-W 50663, holotype; USNM-W 50614, 50622-26, 50630, paratypes), wet and dry material; [2] Maenam Kaek at Gaeng Song Waterfall, about 45 km east of Phitsanulok, Phitsanulok Province (16°49'N, 100°36'E), from *Brotia* (*Paracrostoma*) *pseudosulcospira armata* Brandt (USNM-M 704231), coll. R. A. M. Brandt, 6 January 1968 (USNM-W

50615, paratypes), wet and dry material; [3] Kaek Noi River at Thung Salaeng Luang Botanical Garden, about 71 km east of Phitsanulok, Phitsanulok Province (16°52'N, 100°47'E), from *Brotia* (*Brotia*) *binodosa binodosa* (Blanford) (USNM-M 704232), coll. R. A. M. Brandt, 16 December 1967 (USNM-W 50616, 50627-29, paratypes), wet and dry material; [4] Huai Chieng Nam [part of the Kaek Noi River], about 90 km east of Phitsanulok, Phitsanulok Province (16°48'N, 100°55'E), from *Brotia* (*Brotia*) *binodosa subgloriosa* Brandt (USNM-M 704233), coll. R. A. M. Brandt, 17 May 1966 (USNM-W 50617, paratypes), wet and dry material; [5] Maenam Chi [Chi River] near Sarakham, Maha Sarakham Province (16°12'N, 103°17'E), from *Anulotaia* cf. *mekongensis* Brandt (USNM-M 419887), coll. H. M. Smith, 21 March 1929 (USNM-W 50618, paratypes), dry material. Laos: [6] Sedone River at Pakse (15°08'N,

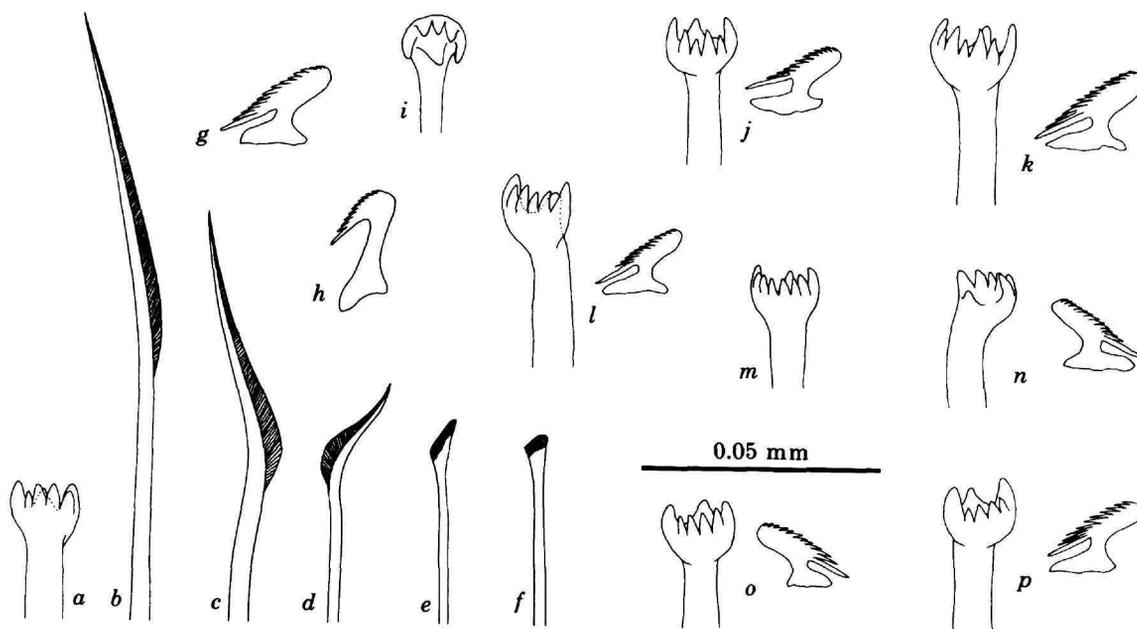


FIGURE 12.—*Caobangia brandti*, new species: a, palmate hook from first thoracic setiger; b, longer limbate capillary seta from third thoracic setiger; c, shorter limbate capillary seta from same; d, shorter limbate capillary seta from anterior abdomen; e, f, posterior abdominal brush-like setae; g, anterior abdominal low avicular hook; h, posterior abdominal tall, long-necked avicular hook (a-h, USNM-W 50614); i, palmate hook (USNM-W 50617); j, palmate and avicular hooks (USNM-W 50615); k, same (USNM-W 50616); l, same (USNM-W 50617); m, palmate hook (USNM-W 50618); n, palmate and avicular hooks (USNM-W 50619); o, same (USNM-W 50620); p, same (USNM-W 50621).

105°48'E), from *Cipangopaludina chinensis* Gray (USNM-M 704234), coll. R. A. M. Brandt, 14 March 1968 (USNM-W 50619, paratypes), dry material; [7] Mekong River at Ban Don Det, south of Khong Island, Sithandone (14°07'N, 105°48'E), from *Mekongia jullieni* (Deshayes) (USNM-M 704235), coll. R. A. M. Brandt, 13 March 1968 (USNM-W 50620, paratypes), dry material; [8] Mekong River at Ban Seo, south of Khong Island, Sithandone (14°06'N, 105°51'E), from *Hyriopsis delaportei* (Crosse and Fischer) (USNM-M 704236), coll. R. A. M. Brandt, 6 March 1968 (USNM-W 50621, paratypes), dry material.

DISPOSITION OF ADDITIONAL PARATYPES.—AHF Poly 1090; BMNH ZB 1973.121; MCZ; MNHNP AE 1092; NSMT Pol. P 102; RNHL 14772; UZMC; ZIL; ZMA Pol. 2600; ZMH 13529.

DESCRIPTION.—The external morphology of *C. brandti* agrees with the account given above in characterizing the genus (Figure 7). The first thoracic setiger has 4 to 8 long unilimbate capillaries and 3 to 5 palmate hooks. Palmate hooks bear from 5 to 9 teeth above the central fang (Figures 9a, 12a,i-p). The terminal teeth in the series are subequal in length and stoutness, and they may be slightly longer and stouter than the more central teeth, which may alternate in length. Thoracic setigers 2 to 7 bear unilimbate capillary setae in progressively decreasing numbers: from 7 to 1 longer upper ones and from 5 to 1 shorter ventral ones (Figure 12b,c). The abdominal segments begin at a point where the ascending gut has a midventral location. There may be as many as 11 rows of low avicular hooks (Figure 12g,j-l,n-p); each row is accompanied by 1 or 2 short limbate capillary setae just lateral to the ascending gut. The first row may be composed of up to 65 individual hooks, their numbers decreasing progressively. One individual with 11 rows showed the following sequence: 54; 56; 20; 34; 32; 23; 12; 1; 3; 1; and 2. At or beyond the last rows of hooks the accompanying limbate capillary setae are replaced by yet shorter capillaries and these, in turn, by single blunt, brushlike setae (Figure 12d-f). Finally, the last 2 to 5 of the brushlike setae are accompanied by single, tall, long-necked avicular hooks (Figure 12h). As many as 27 setal fascicles have been observed, which suggests the presence of at least that number of obscured segments. Apart

from the inner ends of the setal fascicles and, to some extent, the extensions of the branchial crown skeleton, the internal anatomy shows no segmentation.

REMARKS.—*Caobangia brandti* differs from *C. billeti* in having relatively longer thoracic setae, the upper ones having a basally expanded limba-tion, in having palmate hooks with fewer terminal teeth, in having more rows of abdominal avicular hooks and fewer of them in the first transverse row, and in having larger, long-necked avicular hooks. Further, *C. brandti* is confined to the drain-ages of the Mekong and Chao Phraya rivers (Figure 19). It should be noted that *C. brandti* was found in association with various thiarid and viviparid gastropods, as well as with the unionid bivalve *Hyriopsis delaportei*.

I take pleasure in naming this species for Dr. R. A. M. Brandt, School of Tropical Medicine, Bangkok, Thailand, who most kindly supplied me with the preserved material and identifications of these Thai and Laotian molluscs.

Caobangia abbotti, new species

FIGURES 8, 9b, 10, 13, 20

Caobangia sp. [in part] Jones, 1969: figs. 2, 3.

MATERIAL EXAMINED.—Malaysia, Sabah: [1] Mile 4, Tambunan Trail, Ranau (05°58'N, 116°41'E), from *Brotia pageli* (Thiele) (USNM-M 608099), coll. B. C. Walton, 30 August 1953 (USNM-W 50669, holotype; USNM-W 50644, 50654-60, paratypes), wet and dry material; [2] Gomatong, near Kinabatangan (05°42'N, 118°23'E), from *Brotia pontificalis pageli* (Thiele) (MCZ 185605), coll. H. G. Keith (USNM-W 50645, paratypes), dry material; [3] Penokok River, near Kiau, Mt. Kinabalu (06°03'N, 116°31'E), from *Brotia pontificalis agrestis* (Reeve) (USNM-M 590308), elevation 4,000 feet (USNM-W 50646, paratypes), dry material. Malaysia, Sarawak: [4] Robin River at Dana Amu (01°03'N, 110°26'E), from *Brotia pontificalis* von dem Busch (MCZ 227189), coll. D. Thomas, 1956 (USNM-W 50647, paratypes), dry material. Republic of the Philip-pines, Mindanao Island, [5] San Ramon River, San Ramon [30 km northeast of Zamboanga] (07°00'N, 121°55'E), from *Balanocochlis glans*

Philippi (USNM-M 591929), coll. M. E. McDonald, "attached to large rocks in rushing current" (USNM-W 50648, paratypes), dry material; [6] San Ramon River, San Ramon (07°00'N, 121°55'E), from *Balanocochlis glans* Philippi (USNM-M 543951), coll. R. T. Abbott, 1945 (USNM-W 50649, paratypes), dry material. Palawan Island: [7] Qwahig River, Puerto Princesa (09°44'N, 118°44'E), from *Stenomelania* sp.

(USNM-M 259372) (USNM-W 50650, paratypes), dry material. Samar Island: [8] Basey (11°17'N, 125°04'E), from [?] *Antimelania asperata* (Lea), (USNM-W 311026), coll. M. Smith (USNM-W 50651, paratypes), dry material; [9] Stream just east of Napuro (12°02'N, 124°42'E), from *Stenomelania* sp. (USNM-M 543943), coll. R. T. Abbott, 7 July 1945, water temperature 80°F (USNM-W 50652, paratypes), dry material. Luzon Island: [10]

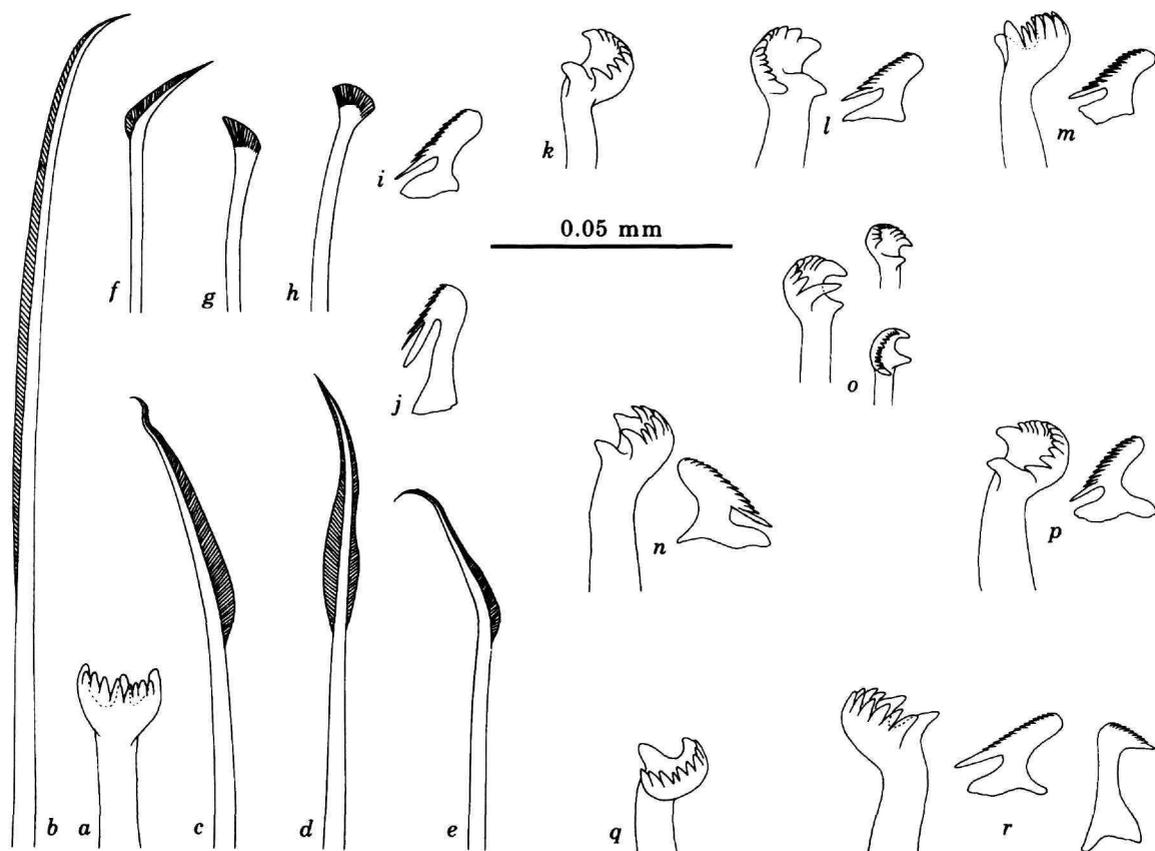


FIGURE 13.—*Caobangia abbotti*, new species: a, palmate hook from first thoracic setiger; b, longer limbate capillary seta from second thoracic setiger; c, shorter unilimbate capillary seta from same; d, shorter bilimbate capillary seta from same; e, abdominal limbate capillary seta associated with low avicular hooks; f, short abdominal limbate capillary seta; g, h, abdominal brushlike setae; i, low avicular hook; j, tall, long-necked avicular hook (a-j, USNM-W 50644); k, palmate hook (USNM-W 50645); l, palmate and avicular hooks (USNM-W 50646); m, same (USNM-W 50648); n, same (USNM-W 50649); o, one adult (left) and two juvenile (right) palmate hooks (USNM-W 50650); p, palmate and avicular hooks (USNM-W 50651); q, palmate hook (USNM-W 50652); r, palmate, low avicular, and tall, long-necked avicular hooks (USNM-W 50653).

Jovellar River, Jovellar (13°04'N, 123°36'E), from *Brotia dactylus* Lea (MCZ 96693), coll. P. de Mesa (USNM-W 50653, paratypes), dry material.

DISPOSITION OF ADDITIONAL PARATYPES.—AHF Poly 1091; BMNH ZB 1973.122; MCZ; MNHNP AE 1091; NSMT Pol. P 103; RNHL 14773; UZMC; ZIL; ZMA Pol. 2601; ZMH 13530.

DESCRIPTION.—The external morphology of *C. abbotti* agrees with the account given in the section on generic characteristics (Figures 8a-d, 20). There are from 4 to 9 ventral palmate hooks in the first setiger, and from 5 to 11 dorsal, very long, limbate capillary setae, provided with narrow limbations. The palmate hooks bear from 7 to 15 small teeth in an arc distal to the central fang and, although the terminal teeth of the series are stouter than the others, they may be subequal, to perceptibly longer than the others (Figures 9b, 13a,k-r). Thoracic setigers 2 to 7 bear unilimbate capillary setae in progressively decreasing numbers: from 14 to 2 longer upper ones, and from 10 to 1 shorter ventral ones (Figures 10, 13b-d). The anterior abdominal region usually has from 3 to 8 transverse rows of low avicular hooks (14 rows on one specimen) (Figures 8, 13i); the first row may contain as many as 116 individual hooks, their numbers decreasing progressively. One individual with 6 rows showed the following sequence: 104; 75; 58; 26; 8; and 5. The hooks are accompanied by up to 5 short capillary setae (Figure 13e). Posterior to the region of hooks the limbate capillary setae are similar, but shorter; in the posterior region they are blunt and brushlike (Figure 13f-h). The last 2 to 4 brushlike setae may be accompanied by from 1 to 3 tall, long-necked hooks (Figure 13j). As many as 37 obscured segments are reflected by the 37 fascicles observed along the length of the body of one specimen.

REMARKS.—*Caobangia abbotti* differs from *C. billeti* in the size of long-necked avicular hooks and the length of dorsal thoracic capillary setae, from *C. brandti* in the length and type of limbations of the dorsal thoracic capillary setae and the number of low avicular hooks in the first abdominal row, and from both in the number of teeth on the palmate hooks and in the number of rows of abdominal low avicular hooks.

Caobangia abbotti is distributed throughout the Philippine Islands and Borneo (Figure 18). It should be noted that differences in the shapes of

long-necked hooks and in the lengths of the end teeth in the distal series of teeth of the palmate hooks may, ultimately, necessitate the erection of a separate species for the Philippine populations (cf. Figure 13j and r); this must await the availability of more material. *C. abbotti* has, thus far, been found associated with the thiarid snail genera *Brotia*, *Balanocochlis*, *Stenomelania*, and *Antimelania*.

I take pleasure in naming this species for Dr. R. Tucker Abbott, Delaware Museum of Natural History, Greenville, whose contributions to malacology are too numerous to list here and who has contributed to this study in having collected valuable material.

Caobangia morrisoni, new species

FIGURES 9c, 14

MATERIAL EXAMINED.—Indonesia, Java: [1] Bogor (06°35'S, 106°47'E), from *Brotia* sp. (USNM-M 261804), coll. O. Bryant and W. Palmer, 1909–1910 (USNM-W 50639, holotype; USNM-W 50640, paratypes), dry material; [2] Bogor (06°35'S, 106°47'E), from *Brotia* sp. (USNM-M 261804A), coll. O. Bryant and W. Palmer, 1909–1910 (USNM-W 50641, paratypes), dry material; [3] Tjirebon [Cheribon] (06°44'S, 108°34'E), from *Brotia testudinaria* (von dem Busch) (MCZ 215007), coll. A. J. de Wilde (USNM-W 50642, paratypes), dry material.

DISPOSITION OF ADDITIONAL PARATYPES.—AHF Poly 1093; BMNH ZB 1973.124; MNHNP AE 1093; ZIL.

DESCRIPTION.—Since *C. morrisoni* is represented only by dry material, its description must be restricted to setal morphology. Palmate hooks from the first thoracic setiger bear from 5 to 11 distal teeth above the single central fang; the terminal teeth are subequal and somewhat longer and stouter than the others (Figures 9c, 14a,b,j-l). Capillary setae of the thoracic region are provided with limbations which are but slightly inflated proximally; the lower capillary setae of the second to seventh setigers have proximally inflated limbations (Figure 14c,d). Abdominal capillary setae are similar to those previously described for *C. brandti* (Figure 14e-g). The anterior low avicular hooks are unremarkable (Figure 14h). The pos-

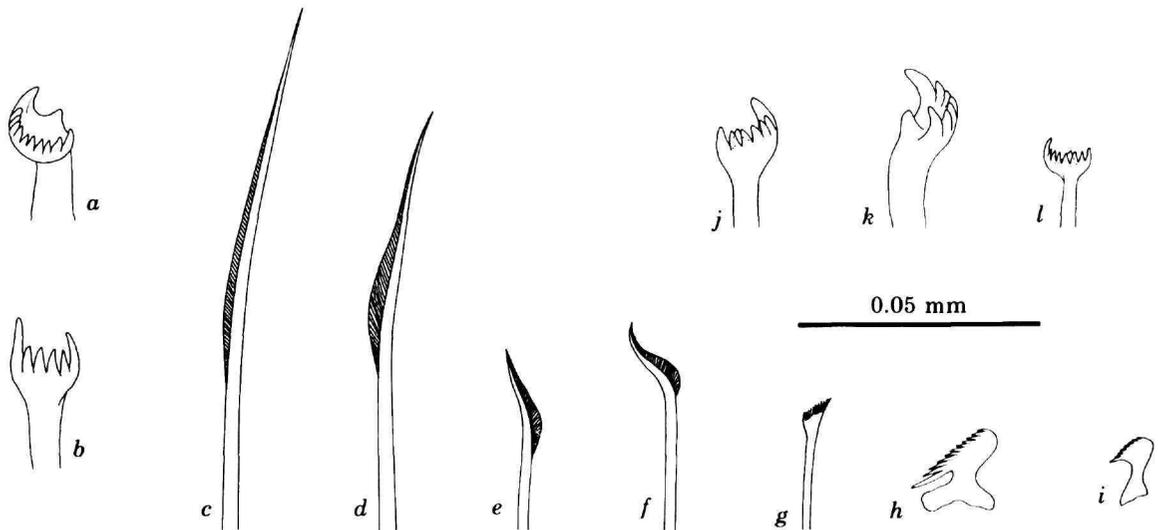


FIGURE 14.—*Caobangia morrisoni*, new species: *a*, palmate hook from first thoracic setiger; *b*, embedded palmate hook; *c*, longer limbate capillary seta from second thoracic setiger; *d*, shorter limbate capillary seta from same; *e*, anterior abdominal limbate capillary seta; *f*, abdominal short limbate capillary seta; *g*, posterior abdominal brushlike seta; *h*, low avicular hook; *i*, tall, long-necked avicular hook; *j*, *k*, palmate hook (s); *l*, same, from juvenile. (*a-e* and *h-j*, USNM-W 50640; *f*, *g*, *k*, and *l*, USNM-W 50642).

terior long-necked avicular hooks are relatively small, and there is a nearly perpendicular angle between the single large tooth and the shaft (Figure 14*i*).

REMARKS.—*Caobangia morrisoni* differs from *C. billeti*, *C. brandti*, and *C. abbotti* in the smaller size of its long-necked avicular hooks and their shape, as reflected by the angle between the shaft and the single tooth; further differentiation lies in the intermediate nature of the limbation of the relatively short dorsal capillary setae of the thoracic region.

Caobangia morrisoni is presently restricted to the Indonesian island of Java and has been found in association only with snails of the thiarid genus *Brotia* (Figure 18).

I take pleasure in naming the species for Dr. J. P. E. Morrison, National Museum of Natural History, Smithsonian Institution, who not only first drew my attention to specimens of *Caobangia*, but who has been continually helpful in identifying freshwater molluscs of southeast Asia for me and in retrieving from the collections additional speci-

mens bearing the characteristic bore holes of *Caobangia*.

Caobangia smithi, new species

FIGURES 9*d*, 15

MATERIAL EXAMINED.—Thailand: [1] Huai Charao, Charao Village, Mae Ramat District, Tak Province (16°58'N, 98°34'E), from *Brotia costula siamensis* Brot (USNM-M 704237), coll. R. A. M. Brandt, 26 April 1967 (USNM-W 50605, holotype; USNM-W 50606, paratypes) dry material; [2] Salween River at Ban Chao Noi, Mae Hong Son Province (approximately 18°26'N, 97°35'E),³ from *Brotia* cf. *baccata* (Gould) (USNM-M 420480a), coll. H. M. Smith, 14 January 1933 (USNM-W 50607, paratypes), dry material; [3]

³ Certain of Smith's collection sites remain unknown; approximate latitudes and longitudes for this locality and two others were deduced from dates and towns in Smith's known itinerary during the period 13–15 January 1933 (Deignan, 1945:5–6) and from an item-by-item perusal of the dates of locality records in Smith's (1945) monograph.

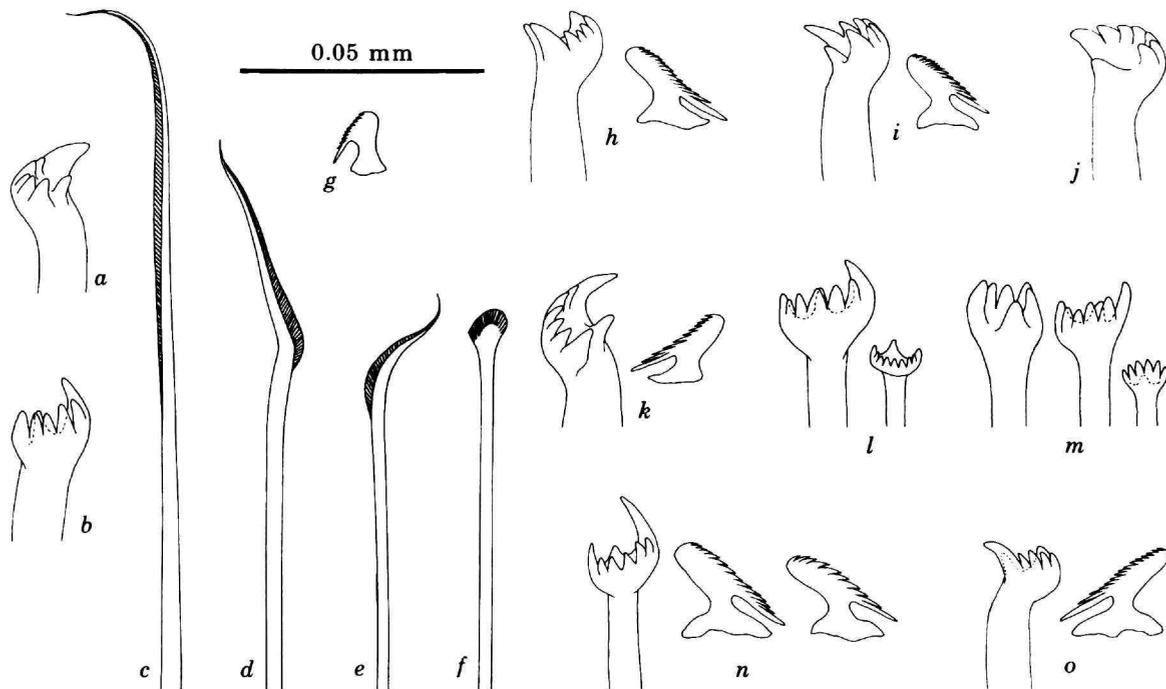


FIGURE 15.—*Caobangia smithi*, new species: *a*, *b*, palmate hooks from first thoracic setiger; *c*, longer limbate capillary seta from third thoracic setiger; *d*, shorter limbate capillary seta from same; *e*, short limbate capillary seta from abdomen; *f*, abdominal brushlike seta (*a-f*, USNM-W 50661); *g*, tall, long-necked avicular hook (USNM-W 50610); *h*, palmate and avicular hooks (USNM-W 50607); *i*, same (USNM-W 50606); *j*, palmate hook (USNM-W 50609); *k*, palmate and avicular hooks (USNM-W 50610); *l*, adult (left) and juvenile (right) palmate hooks (USNM-W 50611); *m*, two adult (left) and one juvenile (right) palmate hooks (USNM-W 50612); *n*, palmate and two avicular hooks (USNM-W 50613); *o*, palmate and avicular hooks (USNM-W 50661).

Salween River at Ta Ta Fang [=Ban Tha Phang], Mae Hong Son Province, (18°04'N, 97°43'E), from *Brotia* cf. *baccata* (Gould) (USNM-M 420471), coll. H. M. Smith, 31 January 1933 (USNM-W 50608, paratypes), dry material; [4] Maenam Moei, west of Mae Sot, Mae Sot District, Tak Province (16°42'N, 98°32'E), from *Brotia costula siamensis* Brot (USNM-M 704238), coll. R. A. M. Brandt, 27 April 1967 (USNM-W 50609, paratypes), dry material; [5] Huai Um Meng [=Huey Um Mong], Ching Mai Province (18°25'N, 98°22'E), from *Brotia* sp. (USNM-M 420441), coll. H. M. Smith, 30 December 1931, "mountain stream, 800 m altitude" (USNM-W 50610, paratypes), dry material. Burma: [6] Salween River at Ban Mae Hiek (approximately

18°50'N, 97°27'E), from *Brotia* cf. *baccata* (Gould) (USNM-M 420467), coll. H. M. Smith, 13 January 1933 (USNM-W 50611, paratypes), dry material; [7] Salween River at Chong Jam (approximately 18°03'N, 97°42'E), from *Brotia* cf. *baccata* (Gould) (USNM-M 427278a), coll. H. M. Smith, 15 January 1933, "attached to rocks in swift water" (USNM-W 50612, paratypes), dry material; [8] Pegu,⁴ from *Paludomus conica* (Gray) (USNM-M 31430)

⁴At least three populated areas in Burma are known as "Pegu": (1) 21°59'N, 95°32'E, near Mandalay, in the drainage of the Irrawaddy River (cf. Figure 19); (2) 24°29'N, 96°10'E, also in the Irrawaddy drainage (cf. Figure 18); and (3) 17°21'N, 96°30'E, a city of nearly 50,000 inhabitants on the Pegu River. I am inclined to believe that the third Pegu is a valid locality for these specimens.

(USNM-W 50613, paratypes), dry material; [9] Pegu, from *Brotia gloriosa* (Anthony) (USNM-M 43604) (USNM-W 50661, paratypes), dry material.

DESCRIPTION.—All specimens of this species have been dried, and the description is based on setal morphology. Palmate hooks of the first setiger bear from 4 to 10 teeth above the single central fang; both terminal teeth are longer, and usually stouter, than the other teeth; the ventralmost terminal tooth may be longer than the dorsalmost (Figures 9*d*, 15*a,b,h-o*). Upper capillary setae of the thoracic region are provided with narrow limbations similar to those of *C. billeti* (Figure 15*c*). Lower capillary setae of the same region show typical proximally inflated limbations (Figure 15*d*). Abdominal capillary setae are typical (Figures 15*e,f*). The low avicular hooks of the transverse rows are also typical (Figure 15*h,i,k,n,o*). The posterior long-necked avicular hooks are small and similar to those of *C. morrisoni* (Figure 15*g*).

REMARKS.—*Caobangia smithi* differs from *C. brandti* in the relative development of the limbation of the upper capillary setae of the thoracic setigers. Other capillary setae and the low avicular hooks do not serve to discriminate between *C. smithi* and other species of *Caobangia*. Long-necked avicular hooks are shorter and smaller than those of *C. billeti*, *C. brandti*, and *C. abbotti*; the angle between the single tooth and the shaft is more acute than is the case in *C. morrisoni*.

Caobangia smithi is known from the drainages of the Salween and Pegu-Sittang Rivers; there is a record (Huai Um Meng, USNM-M 420441, USNM-W 50610) from the drainage of the Chao Phraya River of Thailand which will be discussed below (Figure 19). Association has been observed with snails of the thiarid genus *Brotia* and the pleurocerid genus *Paludomus*.

I take pleasure in naming this species for Dr. H. M. Smith, who found time, while making collections of southeast Asian fish, to collect the snails from which most of the descriptive data of this species derive.

Caobangia indica, new species

FIGURES 9*e*, 16

MATERIAL EXAMINED.—India: [1] Kobo [40 km southwest of Sadiya in the drainage system of the

Brahmaputra River], Assam (27°47'N, 95°23'E), from ?*Antimelania menkiana* (Lea) (USNM-M 433497), coll. D. E. Hardy, 15 March 1944 (USNM-W 50635, holotype; USNM-W 50636, paratypes), dry material; [2] Teri Ghat [in the drainage of the Ganges River, near the Nepalese border], (27°19'N, 83°30'E), from *Hemimitra stephanus* (Benson) (USNM-M 31434) (USNM-W 50637, paratypes), dry material. Bangladesh: [3] Sylhet [in the drainage of the Meghna River, a tributary of the Ganges] (24°54'N, 91°52'E), from *Hemimitra stephanus* (Benson) (MCZ 256890) (USNM-W 50638, paratypes), dry material.

DISPOSITION OF ADDITIONAL PARATYPES.—AHF Poly 1092; BMNH ZB 1973.123; ZIL.

DESCRIPTION.—All specimens of this species have been dried and the description is based upon setal morphology. Palmate hooks of the first setiger bear from 4 to 7 teeth above the single central fang (Figures 9*e*, 16*a,i,j*). The terminal teeth are stouter than the others; the dorsalmost tooth is somewhat longer; the ventralmost tooth is from 2 to 3 times the length of the intermediary teeth. Upper capillary setae of the thoracic region are provided with a narrow limbation, and the lower capillary setae have an expanded limbation more basally (Figure 16*b,c*). Capillary setae of the abdomen become progressively shorter toward the posterior end of the worm and bear an expanded limbation (Figure 16*d,e*). The posterior brushlike setae are typical (Figure 16*f*). The anterior abdominal region has 4 to 7 transverse rows of low avicular hooks, similar to those of the other species of *Caobangia* (Figure 16*g,i,j*). The long-necked avicular hooks which accompany the brushlike setae are small and similar to those of *C. billeti* (Figure 16*h*).

REMARKS.—*Caobangia indica* differs from all species but *C. billeti*, in the size and shape of its long-necked avicular hooks and differs only from *C. brandti* with respect to the limbation of the dorsal thoracic capillary setae. The number of teeth on the palmate setae, as well as the extreme length of the ventralmost terminal tooth, differentiate *C. indica* from both of the above-mentioned species.

Caobangia indica is known from the Ganges River system (of which the Brahmaputra and Meghna are tributaries) and is here associated with pleurocerid (*Hemimitra*) and thiarid (*Antimelania*) snails (Figure 18).

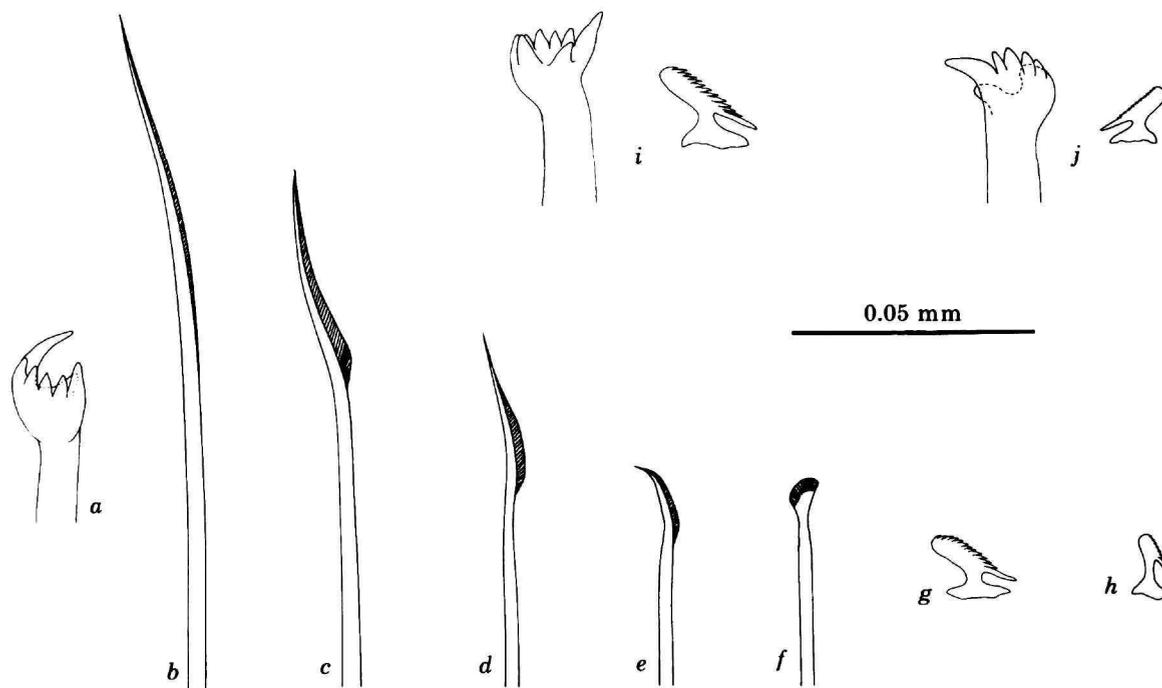


FIGURE 16.—*Caobangia indica*, new species: *a*, palmate hook from first thoracic setiger; *b*, longer limbate capillary seta from third thoracic setiger; *c*, shorter limbate capillary seta from same; *d*, anterior abdominal limbate capillary seta; *e*, abdominal short limbate capillary seta; *f*, posterior abdominal brushlike seta; *g*, low avicular hook; *h*, tall, long-necked avicular hook; *i*, *j*, palmate and avicular hooks. (*a-d* and *g*, USNM-W 50636; *e*, *f*, and *i*, USNM-W 50637; *h* and *j*, USNM-W 50638.)

Caobangia ceylonica, new species

FIGURES 9*f*, 17

MATERIAL EXAMINED.—Ceylon: [1] Mousakande Group, Gammaduwa [drainage of the Mahaweli River] (07°34'N, 80°42'E), from *Ganga abbreviata* (Reeve) (USNM-M 574104), coll. H. G. Deignan, 30 May 1944, "3,000 feet [elevation] in rocky pool of mountain torrent" (USNM-W 50631, holotype; USNM-W 50632, paratypes), dry material; [2] Andooloo, Bintenne [drainage of the Walawe River] (06°24'N, 80°48'E), from *Paludomus hanelyi* Dohrn (MCZ 74983), coll. E. L. Layard, 1864 (USNM-W 50633, paratypes), dry material; from *Tanalia aculeata* (Gmelin) (USNM-M 103704) [no specific locality given], coll. F. Stoliczka (USNM-W 50634, paratypes), dry material.

DESCRIPTION.—The description is based on setal morphology, since the species is represented only by dried material. Palmate hooks of the first setiger have from 5 to 9 teeth in the arcuate series above the single central fang (Figure 9*f*, 17*a,g,h*). The terminal teeth of the series are stouter than the rest, the dorsalmost being longer than the others, but the ventralmost is extremely long (up to 4 times the length of the intermediary teeth). Capillary setae of both the thorax and the abdomen (Figure 17*b-e*) are similar to those of *C. indica*. The anterior abdominal region may have up to 5 transverse rows of low avicular hooks, similar to those of all other species (Figure 17*f-h*). Long-necked hooks from the posterior region of the body were not observed.

REMARKS.—*Caobangia ceylonica* resembles *C. indica*, but differs in having a greater number of

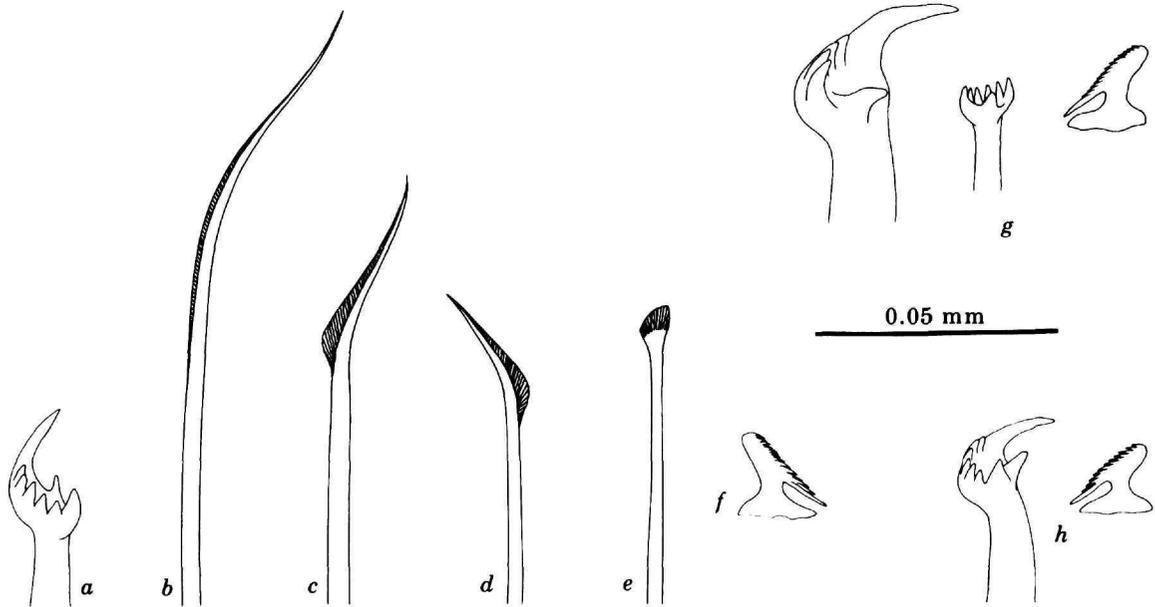


FIGURE 17.—*Caobangia ceylonica*, new species: *a*, palmate hook from first thoracic setiger; *b*, longer limbate capillary seta from second thoracic setiger; *c*, shorter limbate capillary seta from same; *d*, short limbate capillary seta from posterior abdomen; *e*, posterior abdominal brushlike seta; *f*, low avicular hook (*a-f*, USNM-W 50632); *g*, adult (left) and juvenile (center) palmate, and avicular (right) hooks (USNM-W 50633); *h*, palmate and avicular hooks (USNM-W 50634).

distal teeth on the palmate hooks and an even longer ventralmost terminal tooth.

Caobangia ceylonica is known only from Ceylon and associated only with pleurocerid snails of the genera *Ganga*, *Paludomus*, and *Tanalia* (Figure 18).

Comparison of Species of *Caobangia*

Seven species of the genus *Caobangia* can be discriminated, based primarily on the morphology of the palmate hooks of the first setiger. Although the actual number of teeth in the distal arcuate series may overlap (Table 1), application of the "two standard error overlap" rule of thumb (Table 2) suggests no real differences among *C. smithi*, *C. brandti*, *C. ceylonica*, and *C. morrisoni*. When the data are submitted to t-tests (Table 3), no significant differences (at the 95 percent level) are present only in the following comparisons: *C. brandti*-*C. ceylonica*; *C. brandti*-*C. smithi*; and *C.*

ceylonica-*C. smithi*. Were it not for the differing size and length of the terminal teeth of the arcuate series, it would be impossible to differentiate among these three species.

For the most part, the geographic distribution of the seven species (Figures 18 and 19) indicates discrete areas for each, whether confined to an island (*C. ceylonica* on Ceylon and *C. morrisoni* on Java), to neighboring islands (*C. abbotti* on islands of the Philippines and on Borneo), or to specific river systems on the mainland (*C. indica* from the Ganges, *C. smithi* from the Salween and Pegu-Sittang, *C. brandti* from the Mekong and Chao Phraya, and *C. billeti* from the Kiang). The single exception to this is the case of specimens of *C. smithi* associated with *Brotia* sp. from Huai Um Meng (Figure 19), mentioned above. Basically this species of *Caobangia* is restricted to the Salween/Pegu-Sittang drainages; this record places the species in the upper reaches of the Chao Phraya system of central Thailand. The most reasonable

explanation for this occurrence would seem to be that of "stream capture" or the eastward wandering of a population of *C. smithi* during the monsoon season. Morrison (1954:374) has determined that the thiarid gastropods are all parthenogenetic and ovoviviparous. Thus, a single specimen of the thiarid genus, *Brotia*, might well make its way be-

tween stream heads on either side of a divide and establish a clonal population in a new drainage system. The present observations are based upon relatively few localities, and it is quite possible that more intensive and/or widespread collections will uncover other similar cases of drainage transgression.

TABLE 1.—Frequency distribution of numbers of distal teeth on palmate hooks of first setigers of species of Caobangia

Numbers of distal teeth	<i>C. indica</i>	<i>C. smithi</i>	<i>C. brandti</i>	<i>C. ceylonica</i>	<i>C. morrisoni</i>	<i>C. billeti</i>	<i>C. abbotti</i>
4	5	2					
5	21	19	31	5	5		
6	18	74	75	30	16		
7	9	48	45	20	23	14	2
8		18	11	9	7	18	9
9		4	5	1	2	9	18
10		1			4	1	41
11					1	2	33
12						1	15
13							8
14							1
15							2

TABLE 2.—Summary of material examined and of number of distal teeth of palmate setae of species of Caobangia

Species	Number of snails	Number of localities	Number of hooks examined	Modal number of teeth	Range of number of teeth	Mean number of teeth	Two standard errors	Mean \pm 2 S.E.
<i>C. indica</i>	3	3	53	5	4-7	5.58	0.22	5.36-5.80
<i>C. smithi</i>	9	7	166	6	4-10	6.46	0.16	6.30-6.62
<i>C. brandti</i>	9	9	167	6	5-9	6.31	0.14	6.17-6.45
<i>C. ceylonica</i>	3	3	65	6	5-9	6.55	0.22	6.35-6.75
<i>C. morrisoni</i>	3	2	58	7	5-11	7.02	0.48	6.54-7.50
<i>C. billeti</i>	1	1	45	8	7-12	8.16	0.40	7.76-8.46
<i>C. abbotti</i>	9	8	129	10	7-15	10.46	0.38	10.08-10.84

TABLE 3.—Comparison of *t*-values (upper right) and their probabilities (lower left) derived from number of distal teeth of palmate setae of species of Caobangia

Species	<i>C. indica</i>	<i>C. smithi</i>	<i>C. brandti</i>	<i>C. ceylonica</i>	<i>C. morrisoni</i>	<i>C. billeti</i>	<i>C. abbotti</i>
<i>C. indica</i>		11.00	9.57	8.68	8.38	14.73	37.25
<i>C. smithi</i>	P < 0.001		1.41	0.67	3.17	8.93	45.82
<i>C. brandti</i>	P < 0.001	P = 0.10-0.20*		1.82	3.98	9.80	27.93
<i>C. ceylonica</i>	P < 0.001	P = 0.50*	P = 0.05-0.10*		2.50	6.28	33.42
<i>C. morrisoni</i>	P < 0.001	P = 0.001-0.01	P < 0.001	P = 0.01-0.02		4.40	15.49
<i>C. billeti</i>	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001		12.87
<i>C. abbotti</i>	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	

* Not significant at 95 percent level.

A fine potential taxonomic problem at the specific or subspecific level is posed by the two types of long-necked avicular hooks of *C. abbotti* (cf. Figure 13j from Sabah and Figure 13r from Luzon). The long-necked hooks are rather difficult to find in dried material, and adequate numbers of well-

preserved specimens from localities throughout the Philippines, as well as from other areas on Borneo, will clarify the situation one way or the other. Lacking this, there is no choice but to assume that a single species, *C. abbotti*, ranges throughout the Philippines to Sabah and Sarawak.

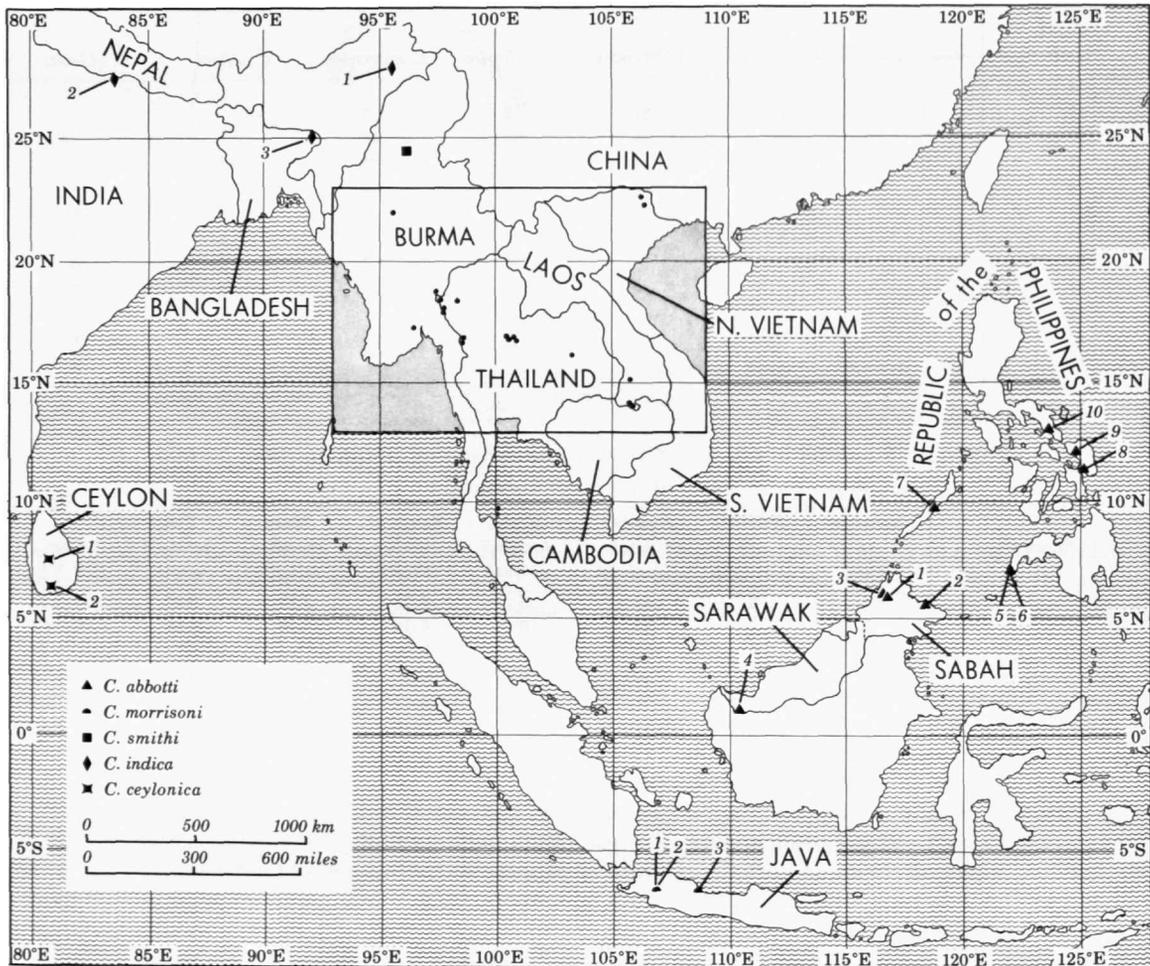


FIGURE 18.—Southeast Asia, showing localities of various species of *Caobangia*. Inset is shown in detail in Figure 19. Small circles in the inset indicate localities only, not individual species. Numbers accompanying species localities refer to numbers in the "Material Examined" section of each species account. The unnumbered locality of *C. smithi* is the northernmost "Pegu" (cf. text footnote 4). (Based on U.S. Navy Hydrographic Office Miscellaneous Chart No. 15,254, 1961.)

Key to Species of *Caobangia*

1. One or both terminal teeth of palmate hooks 2 or more times longer than others (Figure 9c,f) 2
 Terminal teeth less than 2 times longer than others (Figure 9a,b) 5
2. Terminal teeth equal or subequal in length (Figure 9c) *C. morrisoni*, new species
 Terminal teeth unequal in length 3
3. Longer terminal tooth about twice length of others (Figure 9d) *C. smithi*, new species
 Longer terminal tooth greater than twice length of others 4
4. Longer terminal tooth about 3 times length of others (Figure 9e) *C. indica*, new species
 Longer terminal tooth about 4 times length of others (Figure 9f) *C. ceylonica*, new species
5. Modal number of teeth in distal series 6 (Figure 9a) *C. brandti*, new species
 Modal number of teeth in distal series 8 (Figure 11a-c) *C. billeti*
 Modal number of teeth in distal series 10 (Figure 9b) *C. abbotti*, new species

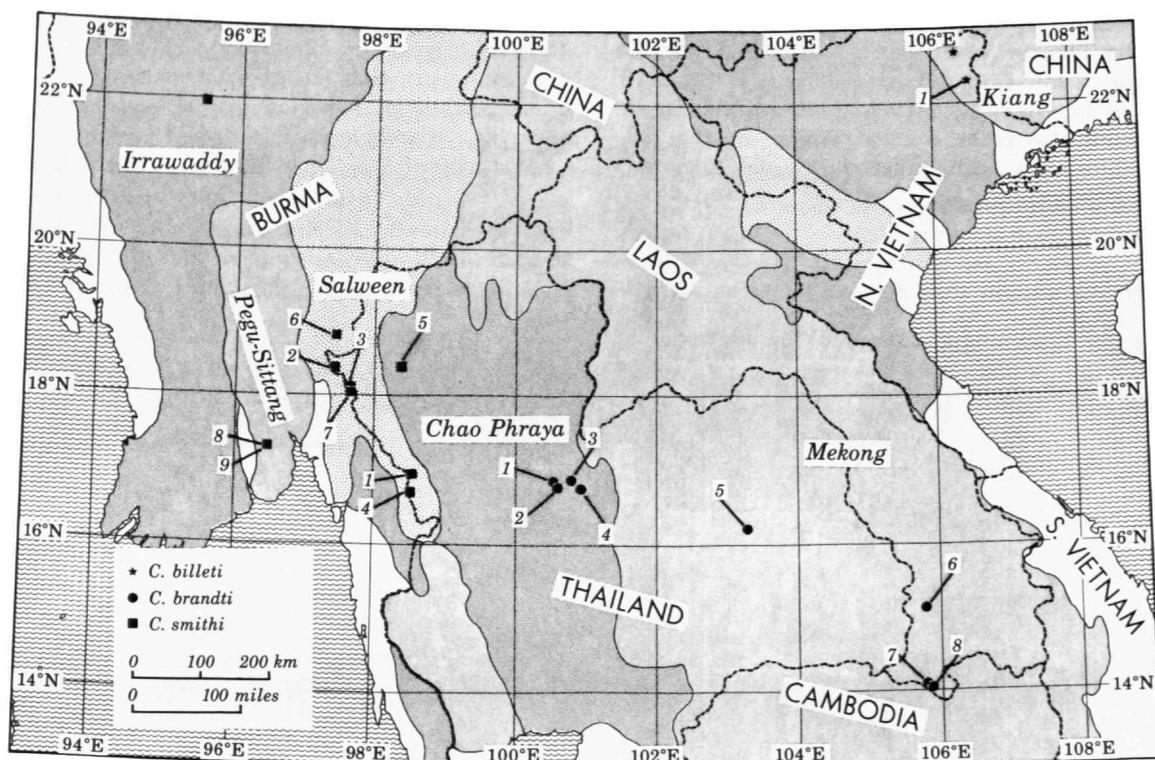


FIGURE 19.—Distribution of species of *Caobangia* in Burma, Thailand, Laos, and North Vietnam. Stippled areas represent drainages of pertinent large river systems (labeled in italics) and dashed lines show national boundaries. Numbers accompanying species localities refer to numbers in the "Material Examined" section of each species account. The unnumbered locality of *C. smithi* is a less likely "Pegu" (cf. text footnote 4), and the unnumbered locality of *C. billeti* indicates the location of Cao Bang, the type-locality. (Based on plate 24, volume 1, *The Times Atlas of the World*, 1958.)

Morphological Observations

BRANCHIAL CROWN AND SUPPORTING SKELETON (Figures 20, 21; Plates 6–8: *C. brandti*; *C. abbotti*).—In his original description, Giard (1893: 474) observed that the branchial crown of *Caobangia billeti* was supported by a hyaline cartilaginous skeleton and that the 24 to 32 or more ciliated tentacles each contained a blood vessel. These observations have been confirmed for all species of *Caobangia*. For the most part, the branchial crowns of specimens preserved in alcohol are strongly contracted, and it is difficult to observe details of their structure. A few specimens of *C. abbotti* from Ranau, Sabah, were in a more relaxed condition and allowed the following observations (Figure 20).

The material comprising the skeleton stains with aniline blue and the whole is made up of cylindrical units, one to two times as long as broad, each joined to the next to form the branching linear structure that is the skeleton (Figure 21, Plates 6, 7). The units have rather thick solid sides and

thinner common ends; each contains small quantities of what is assumed to be cytoplasm as well as a nucleus (Plate 6*b*). The skeletal structure conforms to the short description given by Person and Philpott (1969:5–6) for *Eudistylia polymorpha*.

There are three pairs of radioles, the two dorsal pairs (DR, MR) being better developed than the ventral pair (VR, Figure 20). The former bear bipectinately disposed pinnules and the latter has far fewer pinnules, which appear to be in a simple pectinate distribution. There is no palmate membrane connecting the radioles. As noted by Giard (1893) the radioles and pinnules are ciliated (CE), and supported by a cartilaginous skeleton (CS) accompanied by blood vessels (BV, Plate 6*c,d*).

At the base of the crown the skeletal elements are united in what might be called a "yoke" (SY), a U-shaped structure, open ventrally and closed dorsally (Figure 21, Plate 8*b*). Similar crown-support construction has been observed in histological sections of some four genera of the Sabeliidae, i.e., *Amphiglana*, *Euchone*, *Myxicola*, and three species of *Sabella*. In contrast to these, how-

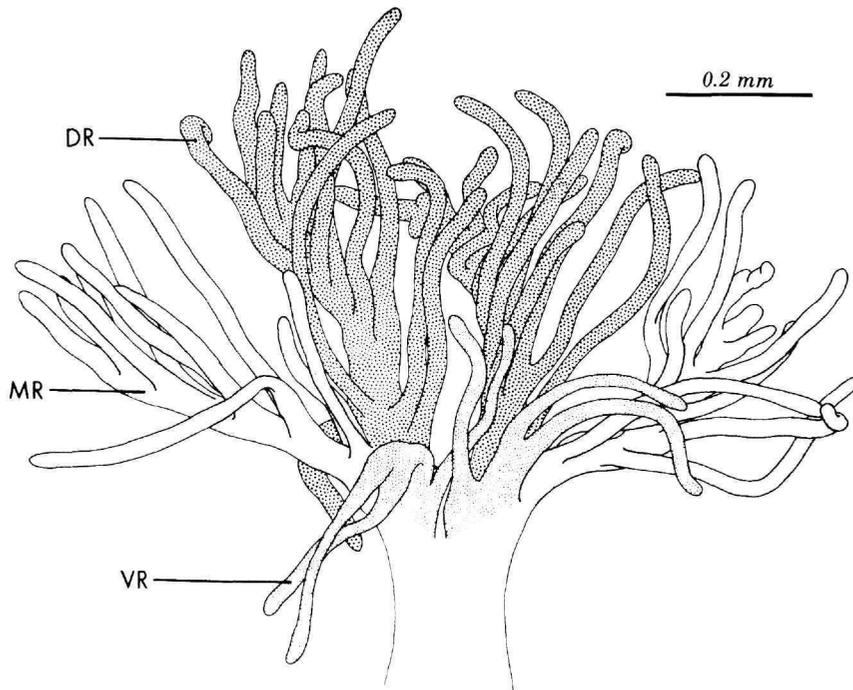


FIGURE 20.—*Caobangia abbotti*, new species: Branchial crown (USNM-W 50644). (DR = dorsal-most radiole, MR = middle radiole, VR = ventralmost radiole.)

ever, in *Caobangia* paired extensions of the cartilaginous skeleton (CSE) project posteriorly from the yoke and undergo a series of dorsoventral loopings, passing dorsal to a given setal fascicle; the extensions finally taper to an end at about the level of the fourth setiger (Figure 21, Plate 7a,b). Fibers of the longitudinal muscles (LM) of this region are inserted at all points along the length of these sinuous processes (Plates 6a,b; 7a,b).

NERVOUS SYSTEM (Plates 6, 7: *C. brandti*; *C. abbotti*).—The available preserved specimens of *Caobangia* all proved to be refractory to a number of histological staining techniques specific for nervous tissue. The account to follow is based on observations of sections treated with Mallory's Triple Stain and is rather incomplete.

The supraoesophageal ganglion (SPG) of *Caobangia* lies midway between the base of the branchial crown and the first thoracic setiger (Plate 7c,d). It is relatively large and is broadly joined, laterally and ventrally, by thick circumoesophageal commissures (CC), to a pair of relatively large masses, the suboesophageal ganglia (SBG), which, in turn, are joined by a rather thin connective, about one-fifth the diameter of the suboesophageal ganglia; the connective passes ventrally to the gut, just in front of the setal fascicles of the first setiger

(Plate 7c,d). Subsequent segmental ganglia (SGG) are situated ventrolaterally, are connected by very thin transverse commissures, and come to lie progressively closer to one another (Plate 7c). The first ganglionic pair posterior to the suboesophageal ganglia is just behind the first setal fascicle, and the second and third are ventral to their respective setal fascicles. Further observations of the ventral nerve cord were not possible.

The innervation of the branchial crown appears to arise from a pair of nerves that originate from each side of the anterior margin of the supraoesophageal ganglion. Each of these pass ventrally, at the base of the three pairs of radioles, and each of the radioles receives a pair of nerves (RN) that lie on each side of its cartilaginous support (Plate 6d).

NEPHRIDIAL DUCTS (Figure 6b; Plates 8b,c; 9, 10: *C. abbotti*).—Zenkevitch (1925:2-3, et seq.) proposed two so-called subtribes for the sabellid polychaetes: the Thoracogoneata and the Abdominogoneata.

The Thoracogoneata were considered to be sabellids with a pair of thoracic nephridia opening far anteriorly by a single common duct, with thoracic gonoducts, also opening far anteriorly by a single common duct, and with neither nephridia

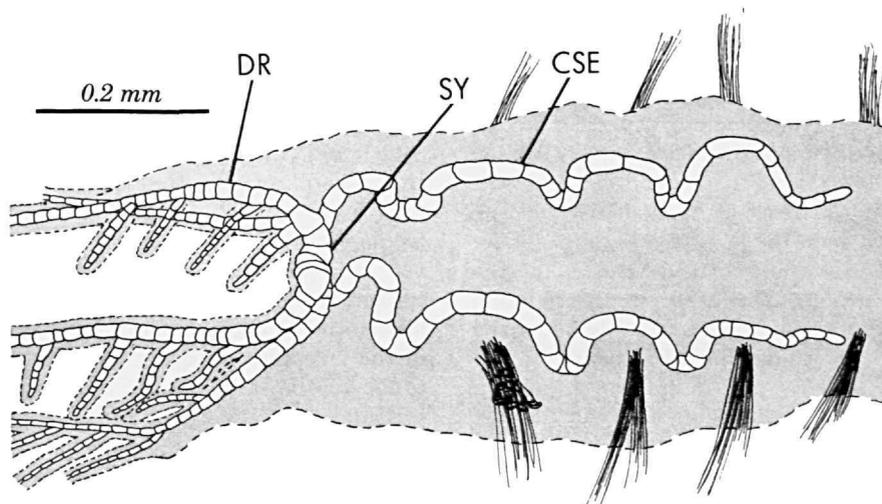


FIGURE 21.—*Caobangia brandti*, new species: Dorsolateral view of cartilaginous skeleton; part of the skeleton of the branchial crown is lacking, due to limited clearing of the specimen; the bases of the right setal fascicles have been omitted. (CSE = extension of cartilaginous skeleton, DR = right dorsal radiole, SY = skeletal yoke.)

nor gonoducts in the abdomen. The contrasting subtribe, the Abdominogoneata, was characterized by the possession of a pair of thoracic nephridia opening far anteriorly by a single common duct and by the presence of abdominal gonoducts opening from the abdomen by segmental ducts; the gonoducts, in this case, were considered to be modified abdominal nephridia. It is, perhaps, well to note that Hartman's (1951:380) interpretation of Zenkevitch's subtribe is somewhat at variance with the above.

On the basis of Giard's (1893) description, Zenkevitch (1925) placed *Caobangia* in the Thoracogoneata, along with the genera *Amphicorina* [=? *Oriopsis*], *Oria* [= *Oriopsis*], *Fabricia*, and *Manayunkia*; it is difficult to see how he arrived at this conclusion, in view of the sketchiness of Giard's description.

The nephridial system of *Caobangia* consists of one pair of ducts (AN, DN, Figure 6*b*, Plates 9, 10), each with two nephrostomes (NST 1, 2) in the coelomic cavity between the base of the branchial crown and the first setiger. The anterior nephrostome (NST 1) merges into the descending nephridial duct (DN) ventral to the cartilaginous extension from the yoke supporting the branchial crown. The second nephrostome (NST 2) joins directly with the same duct approximately 100 microns posterior to the first, between the cartilaginous extension and the gut. The paired descending nephridial ducts then move medially, ventral to the gut, then straight back to about the level of the transverse rows of abdominal avicular hooks, where they bend upon themselves and continue anteriorly, still ventral to the gut and medial to the descending nephridial canals, as paired ascending ducts (AN), to about the level of the fourth setiger where they join to form a single duct. At about the level of the nephrostomes, the single ascending duct splits, each branch moving laterally under the gut, then dorsally around the gut, over the dorsal surface of the skeletal yoke, uniting once again in the midline, dorsal to the gut. The united duct finally opens to the exterior as a nephridiopore within the area surrounded by the branchial crown (NPR, Figure 6*b*, Plate 8*b*), dorsal to the mouth opening. The descending nephridial ducts tend to have somewhat thinner walls than the ascending ducts. With one exception, the cell membranes of the tissue of the duct walls are obscure: at about

the level of the sixth thoracic setiger, the walls of the ascending ducts (AN) are composed of columnar cells (Plate 10*b*). Because of the general compression of the ducts, it was not possible to observe the presence of cilia in the lumen, except in the initial portions of the descending ducts (DN) near the nephrostomes (Plate 9*a,b*). These observations do not agree with the findings of Koechlin (1959, 1961) in the case of *Sabella pavonina*, for there are no large, voluminous regions in the nephridial canal of *Caobangia*, there are no histologically well-defined sections along its length, and there appears to be a more intimate association of blood vessels with the nephridial canal of the freshwater worms.

REPRODUCTIVE SYSTEMS (Figure 6*b*; Plates 1-6, 8, 10, 11: *C. brandti*; *C. abbotti*). —Giard (1893:476) noted that although he was unable to distinguish testes, since all specimens available to him were ovigerous, he was convinced that *C. billeti* was hermaphroditic. Giard also observed that the ovary was located in the loop of the gut and, on the basis of Billet's having seen well-developed larvae moving about in the *Caobangia* burrows, Giard suggested that an incubative chamber was formed by the external body surface of the adults, perhaps from the development of an area similar to the posterior ventral flattened area of *Euchone*.

Extensive regions of sperm and egg formation are to be found in specimens of *Caobangia*. There seems to be no special orientation of maturation of either spermatocytes or oöcytes, and mature and developing eggs or sperm both appear to be mixed, but in reasonably discrete areas which might be called an "ovary" (O) and "testis" (T), respectively. Both appear to be rather flattened unpaired structures, extending from one side of the coelom to the other and from about the level of the transverse rows of avicular hooks to near the basal end (Plates 5*c*, 11*a*). The "ovary" is dorsal to the "testis" and is closely applied to the ventral surface of the enlarged stomachic cavity of the gut, then to the ventral surface of the gut as it emerges from the stomachic region, and later as it moves beneath the posterior curve of the body. The "testis," in its turn, is closely applied to the ventral surface of the "ovary." At about the level of the transverse rows of avicular hooks the "testis" forms a pair of rather short ducts (TD) which lead to the body surface and open to the exterior (TO), adjacent to the ridge formed by the ascending gut (Figure 6*b*,

Plate 11*c,d*). At the margins of this ridge there are rather deep ciliated grooves (SG) which continue forward, along the ascending gut in its lateral and dorsal course to the dorsal surface of the body (Plates 2, 3*a,b*; 10*c,d*; 11*c,d*). At the level of the anal opening the ciliated grooves are lost in a pair of broad ciliated fields (LCF) on the dorsal surface, which ultimately merge with cilia on the floor of the inner surface of the branchial crown (Plate 1*b,d*). Although no sperm have been observed in the ciliated grooves, the short testicular ducts (TD) leading to them from the "testis" are filled with sperm (Plate 11*c,d*).

Ventral and lateral to the "ovary" and "testis" there is a pair of rather large ducts (LD) which, when not occupied, has thick walls (Plates 3*d*, 4*b*). The walls are capable of considerable extension for, at several levels, more posteriorly, developing embryos and larvae occupy their cavities (Plates 4*d*, 5*b,d*). The posterior ends of the ducts seem to be blind, but the anterior ends (LDO) open to the exterior, slightly in back of the openings of the ducts from the "testis" (TO, Figure 6*b*). Masses of yolk granules (YG) also are found in these ducts, as well as free in the coelomic cavity (Plates 4*c*, 5*a,c*; 11*c*). No specific site of yolk formation has been recognized. Further, no passageway has been observed between the ovary and the larval ducts, although such must exist.

It was mentioned above that the ducts from the "testis" have been observed to be filled with sperm. It should be noted that a second pair of short sperm-filled ducts (SD) can be seen in sections from the region of the floor of the branchial crown (Figure 6*b*, Plate 8*a*). These ducts open externally among the cilia at the margin of the mouth; internally they open directly into the coelomic cavity in the vicinity of the skeletal yoke and the supraoesophageal ganglion. No sperm have been observed free in the coelomic cavity. The source and destination of the sperm in these ducts are not known. It is possible that sperm from the "testis," after traversing the ciliated groove lying alongside the ascending gut, are moved to the floor of the branchial crown on ciliated fields on the dorsal surface, pass into the ducts, and then move posteriorly, internally, to fertilize ova of the same individual. It is also possible that sperm from a second individual are collected on the branchial crown, passed down the ciliary tracts of the pinnules and radioles

to the floor of the crown, and then selectively sorted and deposited in the ducts, through which they pass to fertilize the ova at the posterior end. The latter would seem to be the more reasonable alternative. Apart from the internal opening to the coelom, these structures bear a resemblance to the seminal receptacles of *Manayunkia baicalensis*, described by Zenkevitch (1925:18–20).

LARVAL MORPHOLOGY (Figures 22–25: *C. brandti*; *C. abbotti*).—Larvae of *Caobangia* can be dissected quite readily from the adult body. In the case of the two species from which larvae have been obtained, *Caobangia brandti* (Figure 22) and *C. abbotti* (Figure 24), larvae are from 0.60 to 0.95 mm in length and about 0.20 mm wide. They are provided with eyes (EY) in the form of pigment cups with lenses, and with the rudiments of a cartilaginous skeleton (DCS). They have an extensive pattern of ciliation which includes an anterior prototroch, a ventral neurotroch, a posterior telotroch, as well as anterior and posterior tufts of cilia and transverse bands of cilia (CB) which extend dorsally from the neurotroch between successive setal fascicles. At this stage there is a central core of yolk (YG) but no sign of either mouth or anus (Figure 24).

Segmentation is indicated by seven pairs of fascicles of two setae each (LLC and SLC). Apart from size, the setae are quite comparable to the adult thoracic setae, i.e., one is a longer limbate capillary seta and the other is a shorter limbate capillary seta (Figures 23*b,c*; 25*b,c*). In both species, there is an additional type of seta which has no counterpart in adults. Near the posterior end there are two palmate hooks (LPH) on each side on the dorsal surface (Figures 22, 23*e*, 24*a*, 25*e,f*). They are similar to the palmate hooks of the first thoracic setiger of adults but lack central fangs. This would not appear to be due to the small size of these emergent posterior hooks, for embedded developing palmate hooks with a central fang (DPH) can be seen within the body in their usual anterior position, associated with, and ventral to the first setal fascicle (Figures 23*a*, 24*a*, 25*a*). Another point of difference between the posterior palmate hooks of the larvae and the fanged palmate hooks of the adult lies in their individual orientation. Where the adult hooks are disposed such that the teeth of the arcuate series point away from the branchial crown, the larval posterior palmate hooks point toward the

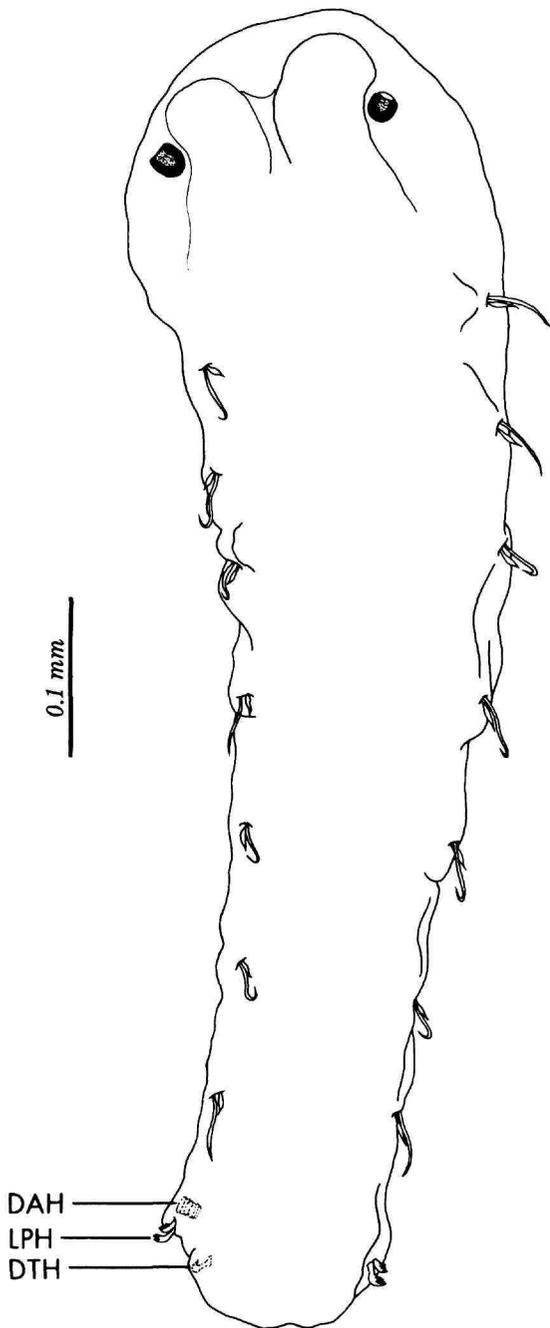


FIGURE 22.—*Caobangia brandti*, new species: Dorsal view of larva; cilia and yolk omitted. (DAH = embedded developing low avicular hooks, DTH = embedded tall avicular hook, LPH = larval palmate hooks.)

head end. The only other type of emergent seta may be the early counterpart of the adult brush-like abdominal seta (BLS, Figures 24, 25*d*). In addition to the palmate hooks of the first setiger, two other types of setae can be seen developing beneath the body surface. In the posterior region, up to six embedded low avicular hooks (DAH) are found just anterior to the posterior larval palmate hooks, and one or two embedded tall, long-necked avicular hooks (DTH) just posterior to them (Figures 22, 23*d,f*; 24*a*). From the distribution of the various types of setae, it would appear that the seven thoracic setigers of the adult arise from the seven larval setigers provided with the longer and shorter limbate capillary setae. It appears also that the posterior larval palmate hooks are adaptations for larval movement prior to encapsulation and metamorphosis, and that the point of linear elongation, corresponding to the pygidium of other polychaetes, lies in the region of the posterior palmate hooks of the larvae, between the developing low hooks and tall, long-necked avicular hooks.

LARVAL SETTLING AND METAMORPHOSIS.—It has been reported earlier (Jones, 1969:833–834) that liberated larvae of *Caobangia* settle on the periostracum of a given snail shell or upon bare calcium carbonate. The settled larvae then form a dome-shaped capsule over themselves and coil within it with their posterior end in the center. As a larva grows, the posterior end either penetrates the cap-

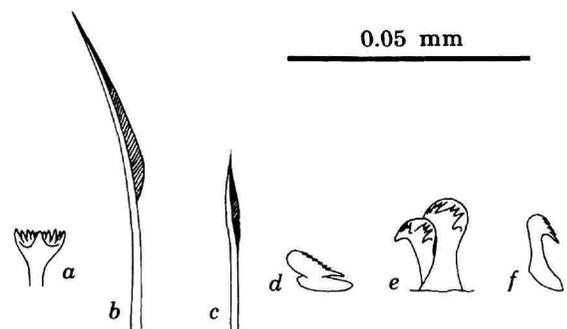


FIGURE 23.—*Caobangia brandti*, new species, larval setae: *a*, embedded palmate hook from first setiger; *b*, longer limbate capillary seta; *c*, shorter limbate capillary seta; *d*, embedded low avicular hook (foreshortened); *e*, larval palmate hooks from posterior region; *f*, embedded tall, long-necked avicular hook (slightly foreshortened).

sular floor or continually forms capsular material as it moves through the underlying periostracal layer and the carbonate matrix of the snail shell. Growth in length and girth, along with the dissolution of carbonate and the laying down of a burrow lining, result in the formation of the adult burrow. Whole mounts of such developing worms demonstrate that it is during this period of growth

that a diverticulum arises from the posterior end of the developing gut. This diverticulum, during the course of its linear growth, undergoes a looping, and then movement, internal to and within the body wall, anteriorly. This anterior growth proceeds along the ventral surface to a point just anterior to the first row of abdominal low avicular hooks, then shifts dorsally (almost invariably on the right

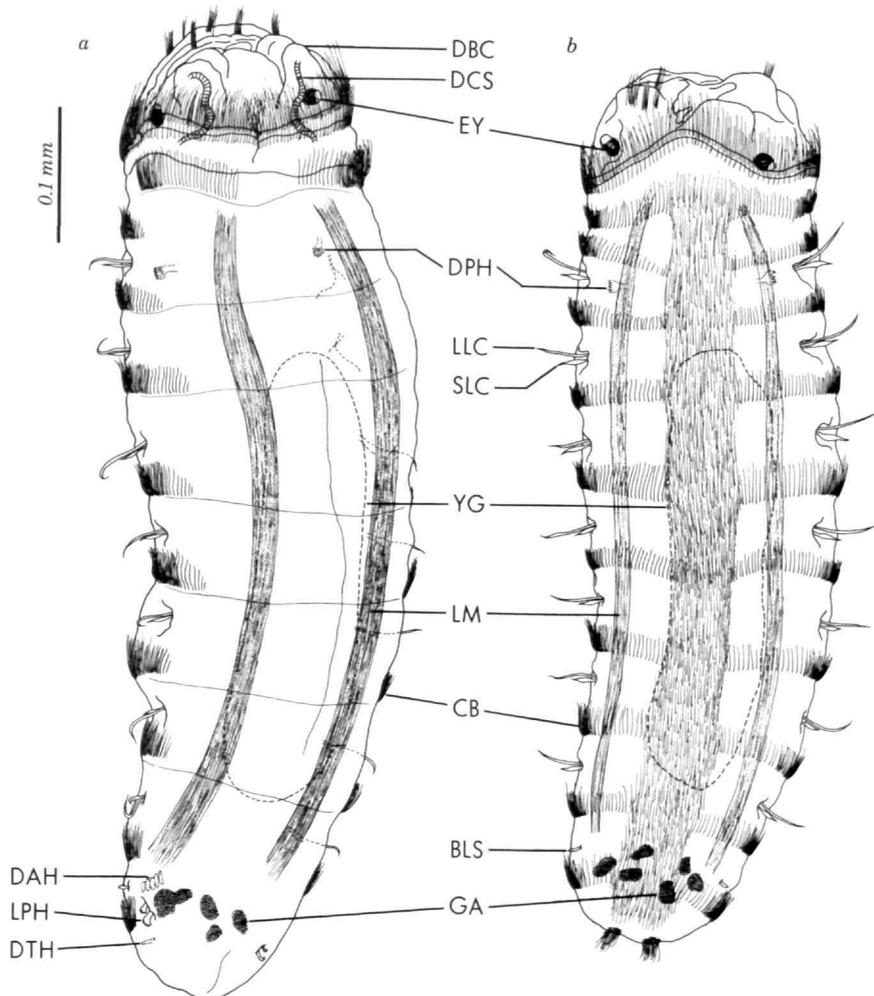


FIGURE 24.—*Caobangia abbotti*, new species: *a*, dorsal view of larva; *b*, ventral view of another larva. (BLS = brushlike seta, CB = ciliated band, DAH = embedded developing low avicular hooks, DBC = developing buds of branchial crown, DCS = developing cartilaginous skeleton, DPH = embedded developing palmate hook, DTH = embedded developing tall avicular hook, EY = eye, GA = granular aggregations, LLC = longer limbate capillary seta, LM = longitudinal muscles, LPH = larval palmate hooks, SLC = shorter limbate capillary seta, YG = area of remaining yolk granules.)

side), and continues on the dorsal surface to the level of the second to fourth thoracic setigers where growth stops and the anal opening is established. It was assumed that larval liberation was accomplished by the bursting of the adult body wall (Jones, 1969:833–834), but with the discovery of the larval ducts (LD) and their external openings (LDO), it is now felt that egress is through a “birth pore” (Figure 6a,b).

Observations have been made on two juvenile specimens of *C. abbotti* which had encapsulated on the periostracum of a snail shell, undergone linear growth, and had grown backward into a continually enlarged burrow in the calcium carbonate of the snail shell. In both cases the branchial crown was developed, the anal opening was at the third or fourth setiger, and there was a single row of emergent low avicular hooks in the abdominal region. One specimen (0.98 mm length; 0.12 mm wide at widest part, at the level of the low avicular hooks; 0.08 mm at first setiger) was provided with a palmate hook, a longer and a shorter limbate capillary seta on each side of the first setiger; the second to seventh setigers all had a longer and a shorter limbate capillary seta in each fascicle; there were eight low avicular hooks in each of the single rows, accompanied by a single brushlike seta; and there was a single, tall, long-necked avicular hook on each side. All of these were emergent.

The second juvenile (1.14 mm length; 0.19 mm wide at the level of the low avicular hooks; 0.08 mm at the first setiger) had two palmate hooks on one side of the first setiger and three on the other,

accompanied in both cases by two longer and one shorter limbate capillary setae; the second setiger had three longer and three shorter limbate capillary setae; the third setiger, three longer and one shorter; the fourth to seventh setigers each had a longer and a shorter limbate capillary seta in each fascicle; and the single rows of low avicular hooks, each accompanied by a single brushlike seta, had 11 on one side and 13 on the other. No tall, long-necked avicular hooks were observed.

The Taxonomic Status of *Caobangia*

Classically the Sabellidae have been characterized as having two body regions: the thorax, composed of relatively few segments, the first of which is provided with limbate capillary notosetae only, and the remainder with similar notosetae, as well as neurosetal avicular or long-handled hooks; and the abdomen, from a few to many segments, each provided with notosetal hooks and neurosetal limbate capillaries.

Rioja (1923) recognized three subfamilies of the Sabellidae: Sabellinae, with thoracic hooks avicular or with a prolonged base, with or without pickaxe setae, with an obvious faecal groove, and well-developed ventral scutes; Fabriciinae, with long-handled thoracic hooks; and Myxicolinae, with branchial filaments united all along their length, and abdominal hooks disposed in a nearly complete circle around the body.

Johansson (1927), on the other hand, recognized two subfamilies: Sabellinae, with “short stemmed” hooks in both the thorax and the abdomen, with longitudinal muscles which are not “nematoid,” with innervation of the branchial crown by a single pair of nerves, and lacking a so-called ciliated organ; and Fabriciinae (including *Myxicola*), with a few “long-stemmed” hooks in the thorax, with longitudinal muscles of the body usually “nematoid,” with the branchial crown innervated by “double” nerves, and with a ciliated organ associated with the supraoesophageal ganglion.

As mentioned above, Zenkevitch (1925) proposed two “subtribes” for the Sabellidae: Abdominogonata, with abdominal nephridia modified as gonoducts opening from their respective abdominal segments; and Thoracogonata, with gonoducts opening far forward, in the vicinity of the branchial crown. Hartman (1951) has considered the

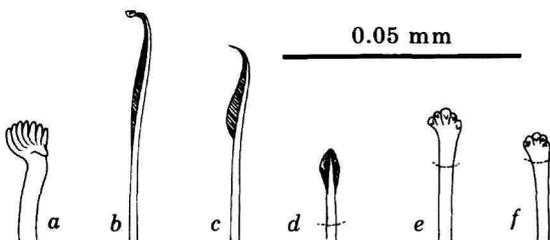


FIGURE 25.—*Caobangia abbotti*, new species, larval setae: a, embedded palmate hook from first setiger; b, longer limbate capillary seta; c, shorter limbate capillary seta; d, brushlike seta from posterior region; e, f, larval palmate hooks from posterior region.

Abdominogoneata to be equivalent to the Sabellinae and the Thoracogoneata to be equivalent to the Fabriciinae; she begs the question of where to place *Myxicola*, which Zenkevitch put among the Abdominogoneata.

Present-day usage may recognize Rioja's three subfamilies (Fauvel, 1927; Hartman, 1959; Uschakov, 1965) or Johansson's two subfamilies (Day, 1967); Zenkevitch's two subtribes are not utilized at all.

In his original description, Giard (1893:474) stated that the characters of *Caobangia billeti* were different enough to justify the erection of a new genus and "even probably a distinct family" ("même sans doute une famille distincte"). However, this observation was not followed up and *Caobangia* subsequently has been considered a curious sabellid. The only other gesture toward separating the genus from other sabellids was that of Chamberlin (1919:470) where he names Caobangiinae [sic] as a new subfamily in a dichotomous key. Chamberlin's usage has not been followed by subsequent workers, and, where considered at all, *Caobangia* has been placed with the Fabriciinae.

All seven species of *Caobangia* possess a number of morphological characters unique to the genus which justify the relegation of it to a new family, the Caobangiidae, the type-genus of which is here designated to be *Caobangia* Giard, 1893.

These morphological characters are: (1) the presence of neurosetal palmate hooks on the first setiger; (2) the absence of hooks of any sort on the following thoracic setigers; (3) the presence of two types of avicular hooks in the posterior region; and (4) the recurving of the gut within the body such that the anus opens far anteriorly. It is admitted that the presence of an anterior anus, as well as the internal development of larvae and the ability to form burrows in calcium carbonate may be better considered as adaptations to life in a freshwater environment, in association with molluscs.

Another argument in favor of erecting a separate family for *Caobangia* is concerned with the placement of the male and female gonadal openings. There is a single pair of openings from the "testis" and another single pair from the larval duct (as contrasts with a number of segmentally arranged gonoducts in Zenkevitch's Abdominogoneata, including *Myxicola*), and these paired openings are found at the anterior end of the abdomen (in con-

trast to the Thoracogoneata where a single duct, in the case of males, opens far anteriorly).

Finally, the presence of two pairs of nephrostomes associated with a pair of nephridial canals may also be considered to be a familial character.

General Comments on *Caobangia*

CONCERNING MOLLUSCAN ASSOCIATES.—It is of some interest that the easternmost species of *Caobangia*, *C. abbotti* (Figure 18), has been found in association with four genera of thiarid snails in the Philippines (including *Brotia*) and with one thiarid, *Brotia*, on the island of Borneo. Further, *C. morrisoni*, the southernmost species, from Java, and *C. billeti*, from North Vietnam, are both associated with *Brotia*. To the west, *C. ceylonica* is associated with three pleurocerid genera. To the northwest, *C. indica* has been found in the shells of one pleurocerid and one thiarid (not *Brotia*); the same is true of *C. smithi*, the adjacent species to the east, but the thiarid is *Brotia*. At the apparent center of the known distribution of *Caobangia* is *C. brandti* (Figure 19), which in northern Thailand and Laos occurs with a single thiarid (*Brotia*), three viviparid genera, and one unionid bivalve.

Although it may be the fortuitous result of an inadequate search through various museum collections, it would seem that the one gastropod common to six of the seven *Caobangia* species is the thiarid, *Brotia*. Similar to other thiarids, *Brotia* has a reproductive pattern of ovoviviparous parthogenicity (Morrison, 1954:374) and a brood pouch which may be "... very large, crowded with a great many relatively small young of uniform size" (Morrison, 1954:383). Morrison (1954:374) also has noted that these characteristics and the consequent ability to form clonal populations if a single snail reaches a new freshwater locality, either by stream capture or by adventitious transportation, account for the widespread distribution of the Thiaridae.

CONCERNING THE HABITAT OF MOLLUSCAN ASSOCIATES.—The few ecological notes accompanying the various molluscs considered in this work suggest that the molluscs, and the associated *Caobangia*, occur at medium elevations, from 800 to 1300 m. Further, most occur in fast-moving water [*Balanocochlis glans*, with *C. abbotti*; *Brotia* cf. *baccata*, with *C. smithi*; *Ganga abbreviata*, with *C. ceylonica*; and *Brotia pseudosulcospira pseudosulcospira* and

B. p. armata (Brandt, 1968:275)], although one, *Mekongia jullieni*, with *C. brandti*, was reported from a sand bank (Brandt and Temcharoen, 1971: 116) and *Brotia binodosa subgloriosa* was found "on sandy grounds . . . at comparatively quiet parts . . . but at Ban Palo it is also found in rapids" (Brandt, 1968:270).

It was noted earlier (Jones, 1969:834) that *Caobangia brandti* was found in so-called dead valves of the bivalve *Hyriopsis delaportei*. This suggested that it was possible that limestone outcrops along river or stream banks might serve as populational reservoirs which would allow the "infection" of new molluscs at that site, thus overcoming the continual down-river attrition of newly emerged larvae. It is interesting that Billet (1896-98:64) mentions such "rochers calcaires" in the vicinity of Cao Bang.

SOME BASIC QUESTIONS POSED BY *Caobangia*.—

1. What is the mechanism that mediates the inter-

nal anterior growth of the ascending gut such that it grows straight, beneath the ventral surface, moves dorsally on the right side, then straight to the mid-thoracic region?

2. Where is the usual prepygidial growth zone of other polychaetes? Is the caobangiid growth zone just posterior to the posteriormost row of low avicular hooks, or elsewhere?

3. If the caobangiids are not self-fertilizing hermaphrodites, how are sperm from one worm transferred to another? Are chemotactic behaviorisms implicated or are transfers merely fortuitous, depending on the vagaries of water currents? What is the source and fate of the sperm observed in the short anterior ducts?

4. Since *Caobangia* burrows are lined with an intact secreted membrane, and the various setae seem not to be unduly worn, how is enlargement of a given burrow accomplished?

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PLATE 1

Caobangia abbotti, new species: Transverse sections, five microns, Mallory's Triple Stain (USNM-W 50660); longitudinal locations indicated on Figure 6a: *a, b*, at 1; *c, d*, at 2; scale lines for *a, c*, 100 microns and for *b, d*, 50 microns.

- a.* Section at base of branchial crown.
- b.* Same section as *a*, more highly magnified, centered on descending gut.
- c.* Section just behind anal opening.
- d.* Same section as *c*, more highly magnified, centered between descending and ascending gut.

(AG = ascending gut, AN = ascending nephridial duct, BV = blood vessel, CS = cartilaginous skeleton, DG = descending gut, DN = descending nephridial duct, GA = granular aggregations, LCF = longitudinal ciliated field, LM = longitudinal muscle, SD = sperm duct, SF 3 = third thoracic setal fascicle, VNC = ventral nerve cord(s).)

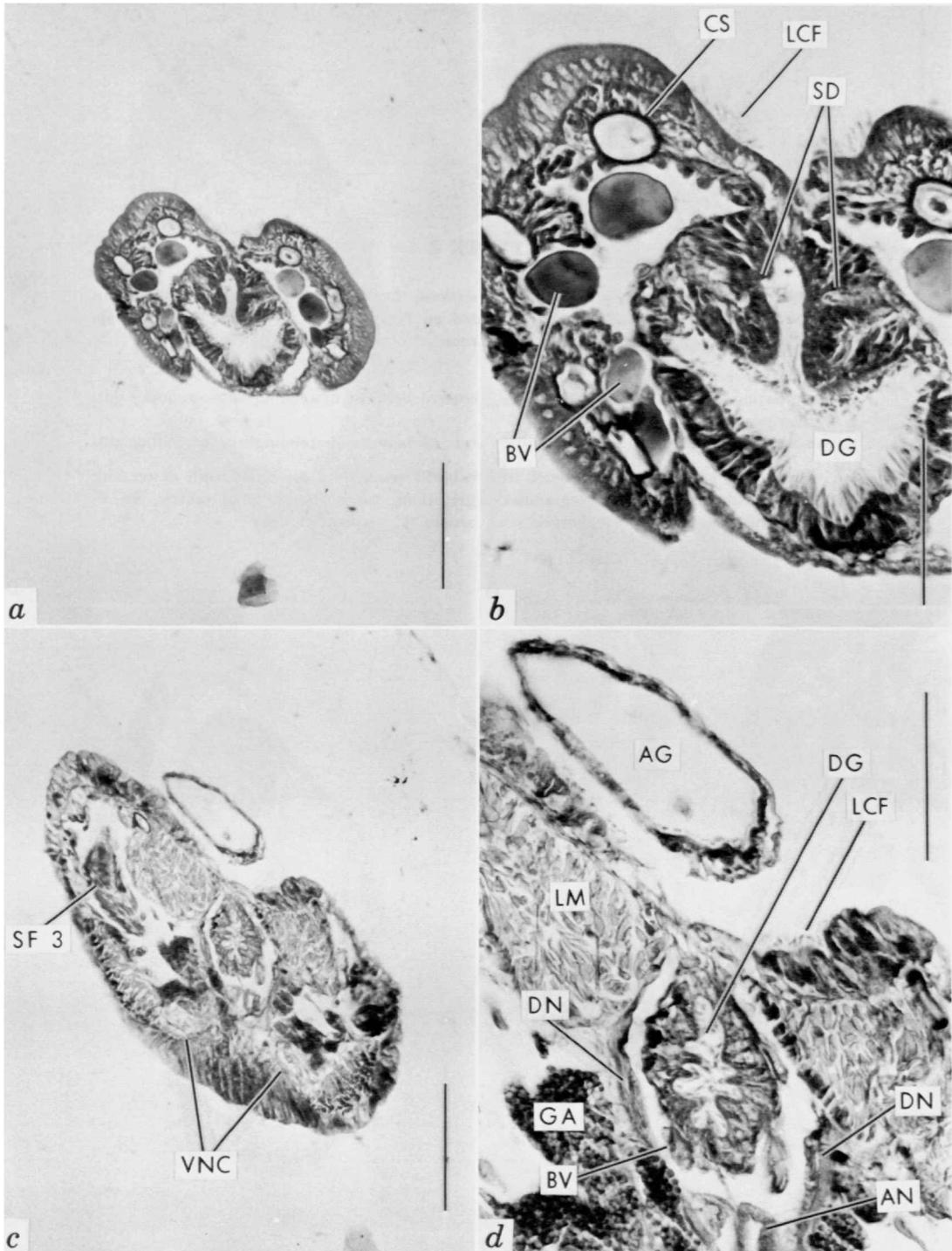


PLATE 2

Caobangia abbotti, new species: Transverse sections, five microns, Mallory's Triple Stain (USNM-W 50660); longitudinal locations indicated on Figure 6a: *a, b*, at 3; *c, d*, at 4; scale lines for *a, c*, 100 microns and for *b, d*, 50 microns.

- a.* Section between thoracic setigers 5 and 6.
- b.* Same section as *a*, more highly magnified, centered between descending and ascending gut.
- c.* Section near thoracic setiger 7.
- d.* Same section as *c*, more highly magnified, centered between descending and ascending gut.

(Ac = ascending gut, BV = blood vessel, BVS = blood vessel/sinus associated with descending gut, DG = descending gut, GA = granular aggregations, LM = longitudinal muscle, ND = nephridial ducts, SF 7 = seventh thoracic setal fascicle, SG = sperm groove.)

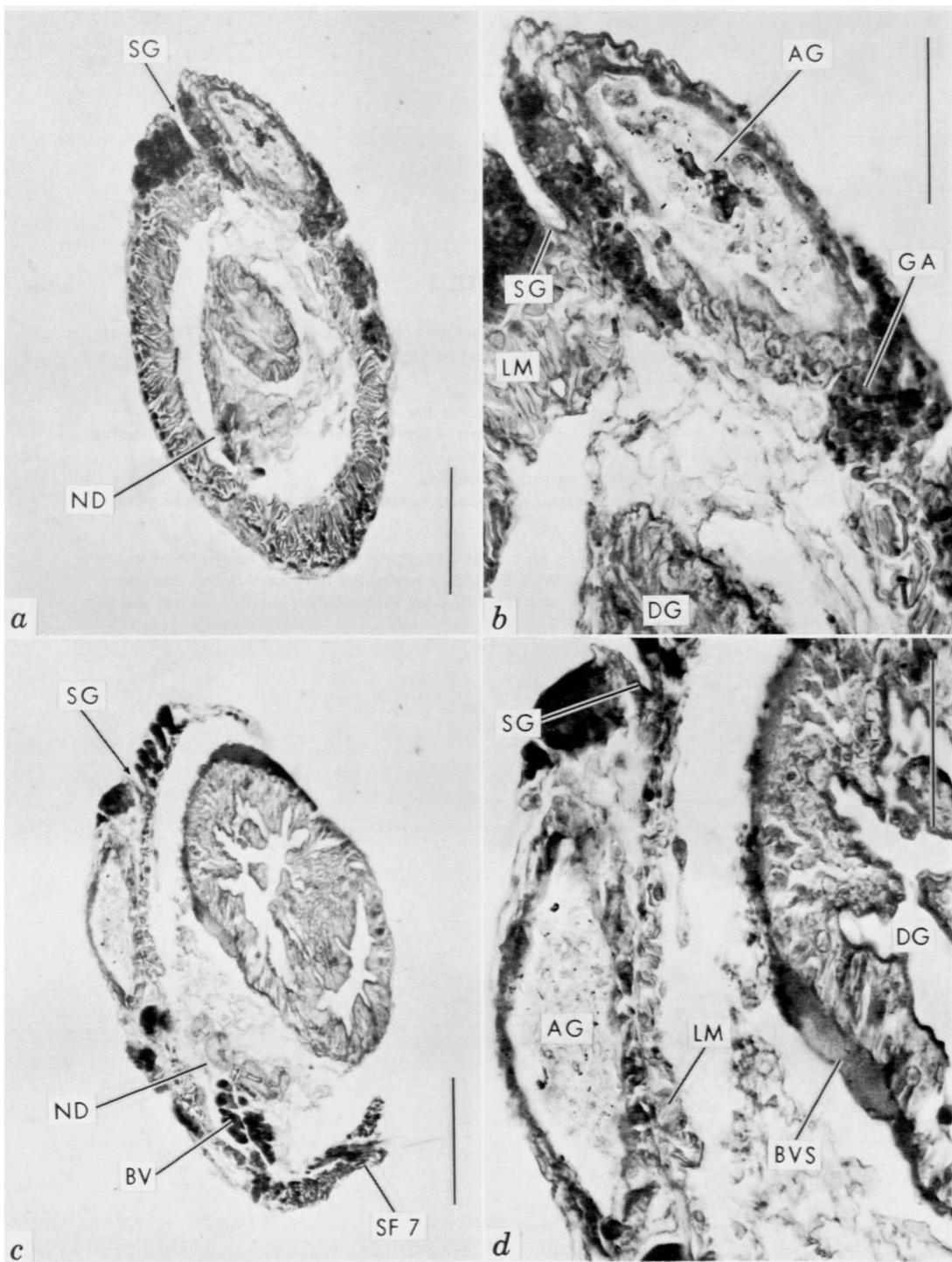


PLATE 3

Caobangia abbotti, new species: Transverse sections, five microns, Mallory's Triple Stain (USNM-W 50660); longitudinal locations indicated on Figure 6a: *a*, *b*, at 5; *c*, *d*, at 6; scale lines for *a*, *c*, 100 microns and for *b*, *d*, 50 microns.

- a*. Section approximately at the level of first row of low avicular hooks.
- b*. Same section as *a*, more highly magnified, centered between stomachic chamber and ascending gut.
- c*. Section midway along length of stomachic chamber.
- d*. Same section as *c*, more highly magnified, centered between stomachic chamber and ascending gut.

(AG = ascending gut, AN = ascending nephridial duct, BV = blood vessel, BVS = blood vessel/sinus associated with descending gut, DN = descending nephridial duct, LD = larval duct, ND = nephridial ducts, OCR = oöcytes, SC = stomachic chamber of descending gut, SG = sperm groove, YG = yolk granules.)

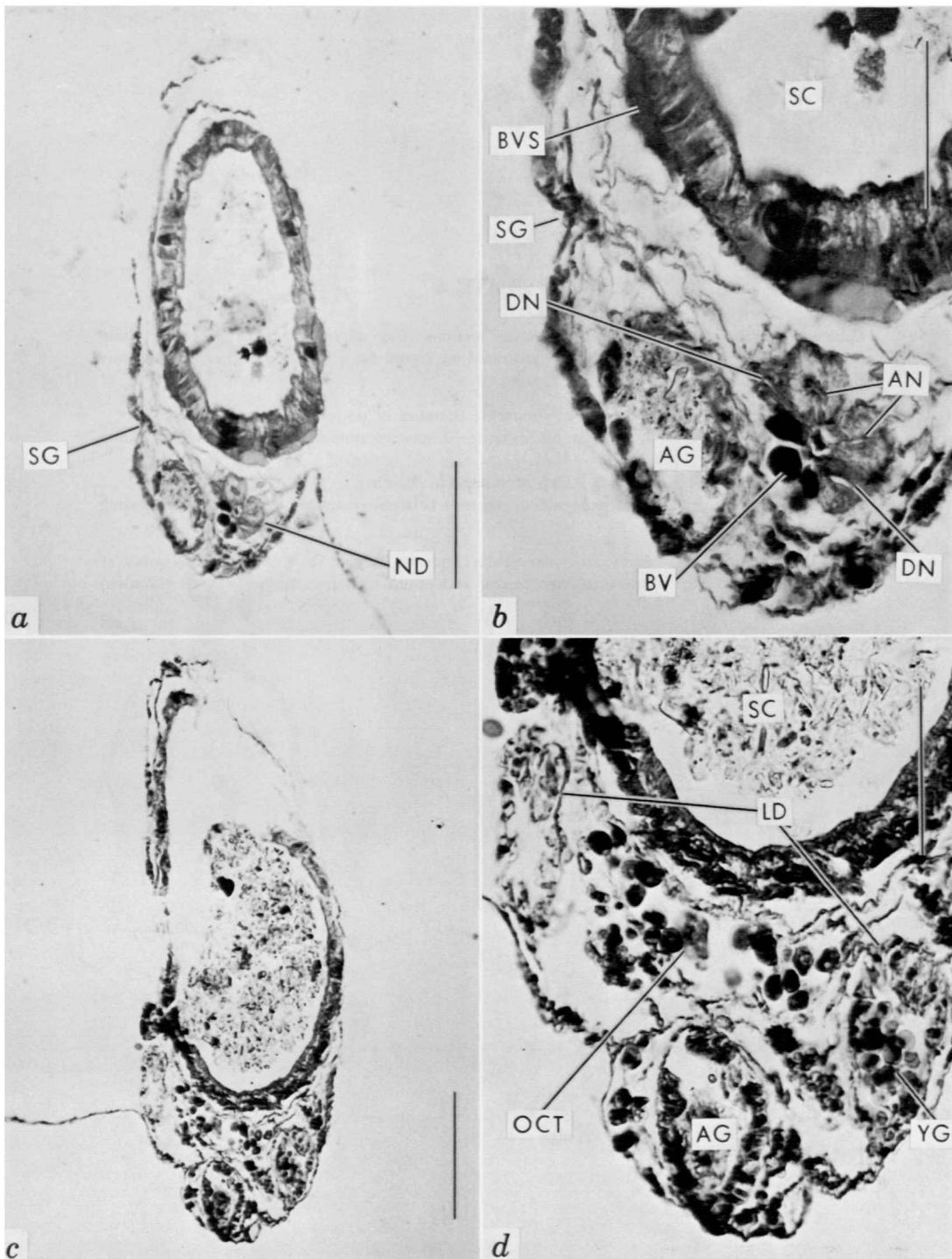


PLATE 4

Caobangia abbotti, new species: Transverse sections, five microns, Mallory's Triple Stain (USNM-W 50660); longitudinal locations indicated on Figure 6a: *a, b*, at 7; *c, d*, at 8; scale lines for *a, c*, 100 microns and for *b, d*, 50 microns.

- a.* Section through posterior fourth of stomachic chamber of descending gut.
- b.* Same section as *a*, more highly magnified, centered between stomachic chamber and ascending gut.
- c.* Section through more posterior region of stomachic chamber.
- d.* Same section as *c*, more highly magnified, centered between stomachic chamber and ascending gut.

(AG = ascending gut, L = larva, LD = larval duct, ocr = oöcytes, sc = stomachic chamber of the descending gut, scr = spermatocytes, sfa = abdominal setal fascicle, yg = yolk granules.)



PLATE 5

Caobangia abbotti, new species: Transverse sections, five microns, Mallory's Triple Stain (USNM-W 50660); longitudinal locations indicated on Figure 6a: *a*, *b*, at 9; *c*, *d*, at 10; scale lines for *a*, *c*, 100 microns and for *b*, *d*, 50 microns.

- a*. Section through posterior loops of gut.
- b*. Same section as *a*, more highly magnified, centered near ascending gut.
- c*. Section through region posterior to loops of gut.
- d*. Same section as *c*, more highly magnified, centered near ascending gut.

(Ac = ascending gut, BLS = brushlike seta, DG = descending gut, L = larva, LD = larval duct, LG = loops of gut, O = "ovary," ov = egg, OCT = oöcyte, SCT = spermatocytes, SFA = abdominal setal fascicle, T = "testis," YG = yolk granules.)

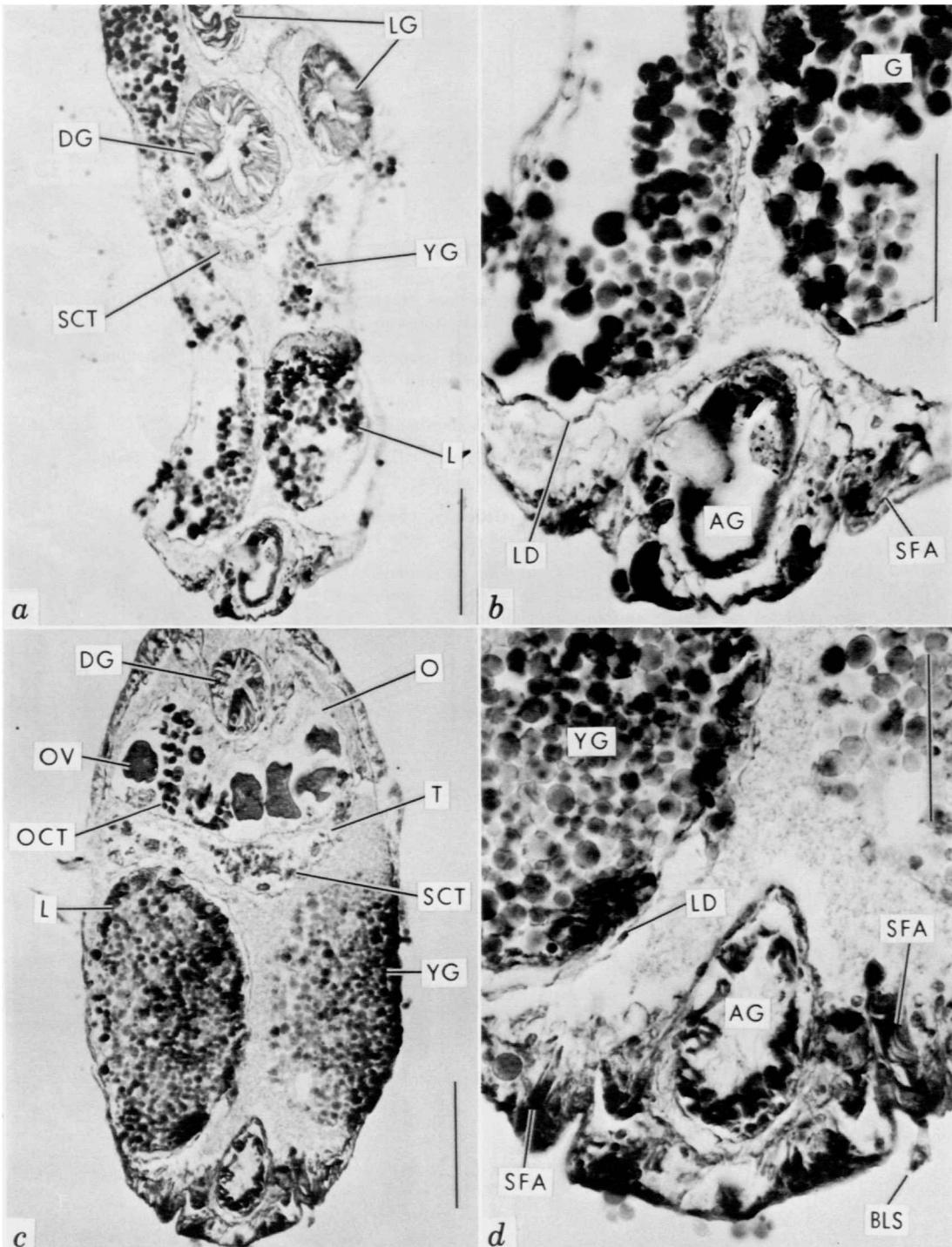


PLATE 6

Caobangia brandti, new species: Parasagittal sections, seven microns, Mallory's Triple Stain (USNM-W 50630); scale lines for *a* and *b*, 50 and 10 microns, respectively.

- a.* Section through base of dorsal radiole showing relationship of dorsal surface epithelium (right), cartilaginous skeleton, and ciliated epithelium of inner surface of branchial crown (left).
- b.* Same section as *a*, but more highly magnified, showing detail of cartilaginous skeleton.

Caobangia abbotti, new species: Transverse sections, five microns, Mallory's Triple Stain (USNM-W 50660); scale lines for *c* and *d* are 10 microns.

- c.* Section of ventralmost radioles, showing relationship of radiole to its pinnules.
- d.* Section of right dorsalmost and middle radioles at base of branchial crown.

(bv = blood vessel, ce = ciliated epithelium, cs = cartilaginous skeleton, lm = longitudinal muscle, lvr = left ventralmost radiole, mr = middle radiole, rdr = right dorsalmost radiole, rn = radiolar nerve, se = surface epithelium.)

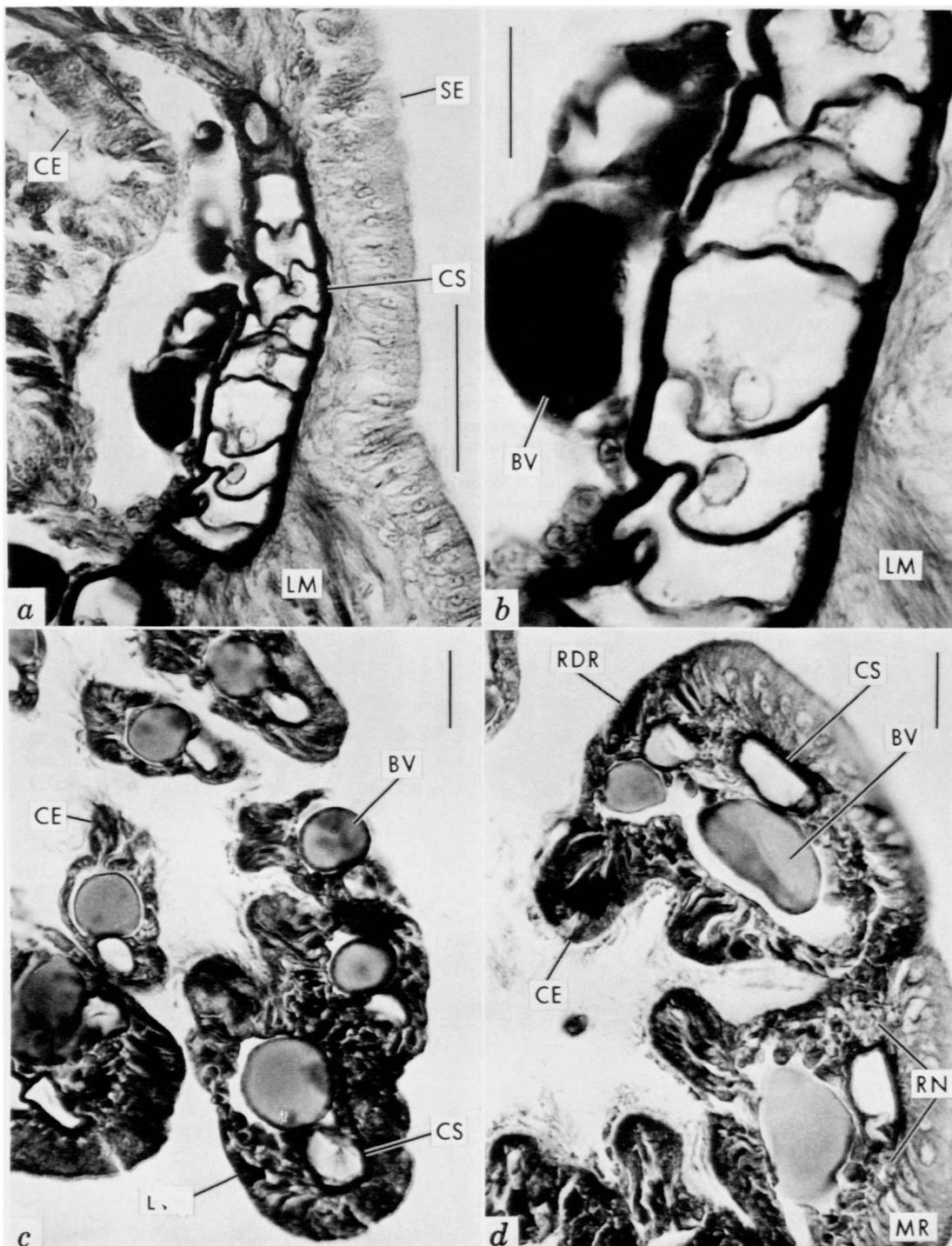


PLATE 7

Caobangia brandti, new species: Parasagittal sections, seven microns, Mallory's Triple Stain (USNM-W 50630); dorsal to the right, branchial crown above; scale lines for *a*, *c*, and *d*, 100 microns and for *b*, 50 microns.

- a.* Section showing cartilaginous extension from skeletal yoke.
- b.* Section showing relationship of setal fascicles to cartilaginous extension.
- c.* Section showing elements of the nervous system.
- d.* Nearly sagittal section of the region just behind the branchial crown.

(cc = circumoesophageal commissure, cse = extension of cartilaginous skeleton, dg = descending gut, lm = longitudinal muscle, mo = mouth region, nd = nephridial ducts, rn = radiolar nerve, sbg = suboesophageal ganglion, sf 1-3 = first to third thoracic setal fascicles, scg = segmental ganglia, srg = supraoesophageal ganglion, sy = skeletal yoke.)



PLATE 8

Caobangia abbotti, new species: Transverse sections, five microns, Mallory's Triple Stain (USNM-W 50660); longitudinal locations of *b*, *c*, and *d* indicated on Figure 6*b*, N 1, N 2, and N 3, respectively; scale lines are 50 microns.

- a*. Section at level of sperm ducts, 10 microns behind that shown in Plate 1*a*.
- b*. Section at level of skeletal yoke, 40 microns behind that of *a*, above.
- c*. Section through first nephrostome of descending nephridial duct.
- d*. Section through second nephrostome of descending nephridial duct.

(AN = ascending nephridial duct, BV = blood vessel, DG = descending gut, GA = granular aggregations, LCF = longitudinal ciliated field, LM = longitudinal muscle, NPR = ascending nephridial duct just prior to nephridiopore, NSr 1 and 2 = first and second nephrostome of descending nephridial duct, SD = sperm duct, SY = skeletal yoke.)

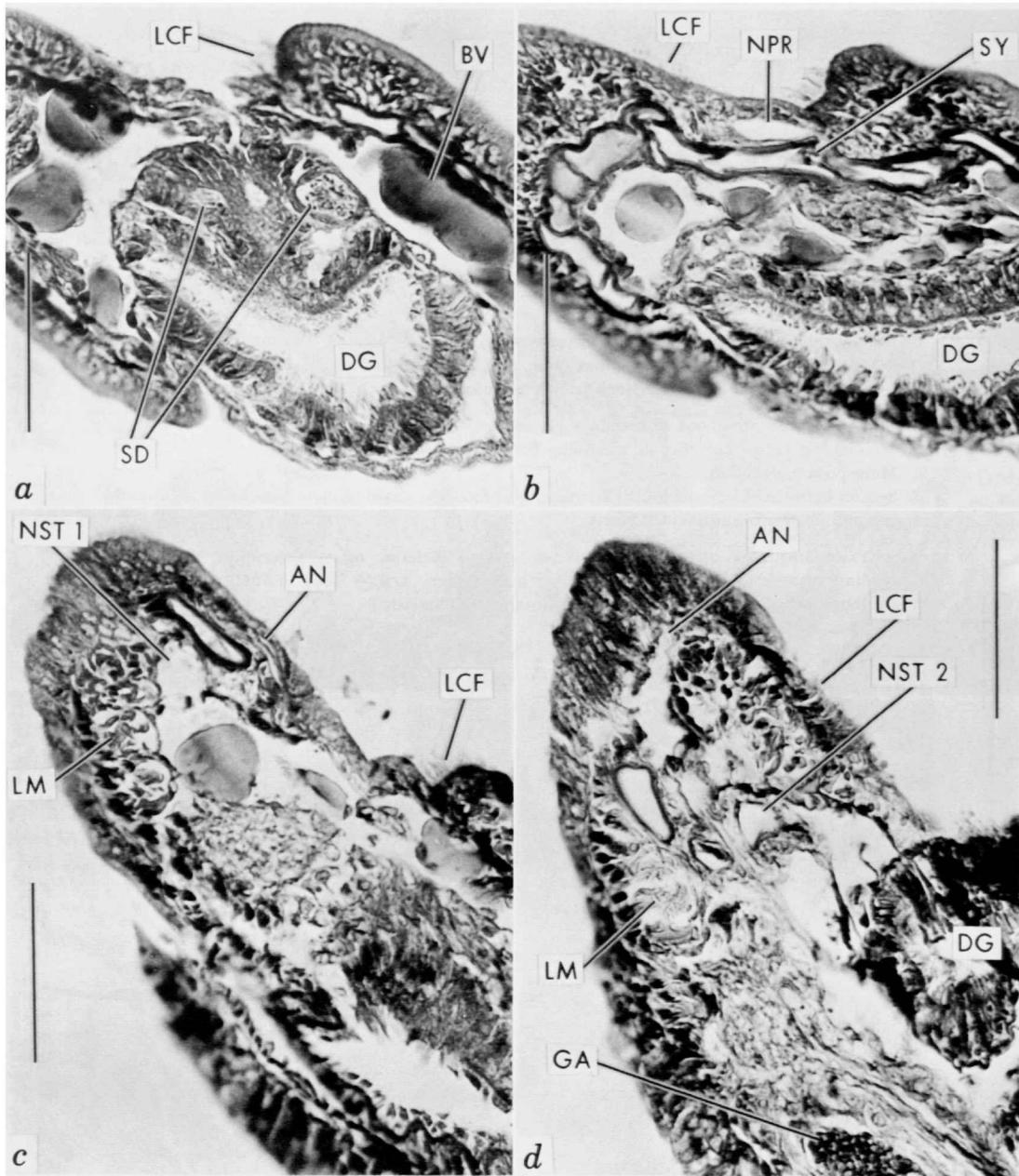


PLATE 9

Caobangia abbotti, new species: Transverse sections, five microns, Mallory's Triple Stain (USNM-W 50660); longitudinal locations of *a*, *b*, *c*, and *d* indicated on Figure 6*b*, N 4, N 5, N 6, and N 7, respectively; scale lines are 50 microns.

- a*. Section at about the level of first thoracic setiger.
- b*. Section just before splitting of ascending nephridial duct.
- c*. More posterior section.
- d*. Section between third and fourth thoracic setal fascicles, showing close association of ascending and descending nephridial ducts.

(AN = ascending nephridial duct, CS = cartilaginous skeleton, DG = descending gut, DN = descending nephridial duct, GA = granular aggregations, LCF = longitudinal ciliated field, LM = longitudinal muscle, SF 4 = fourth thoracic setal fascicle.)

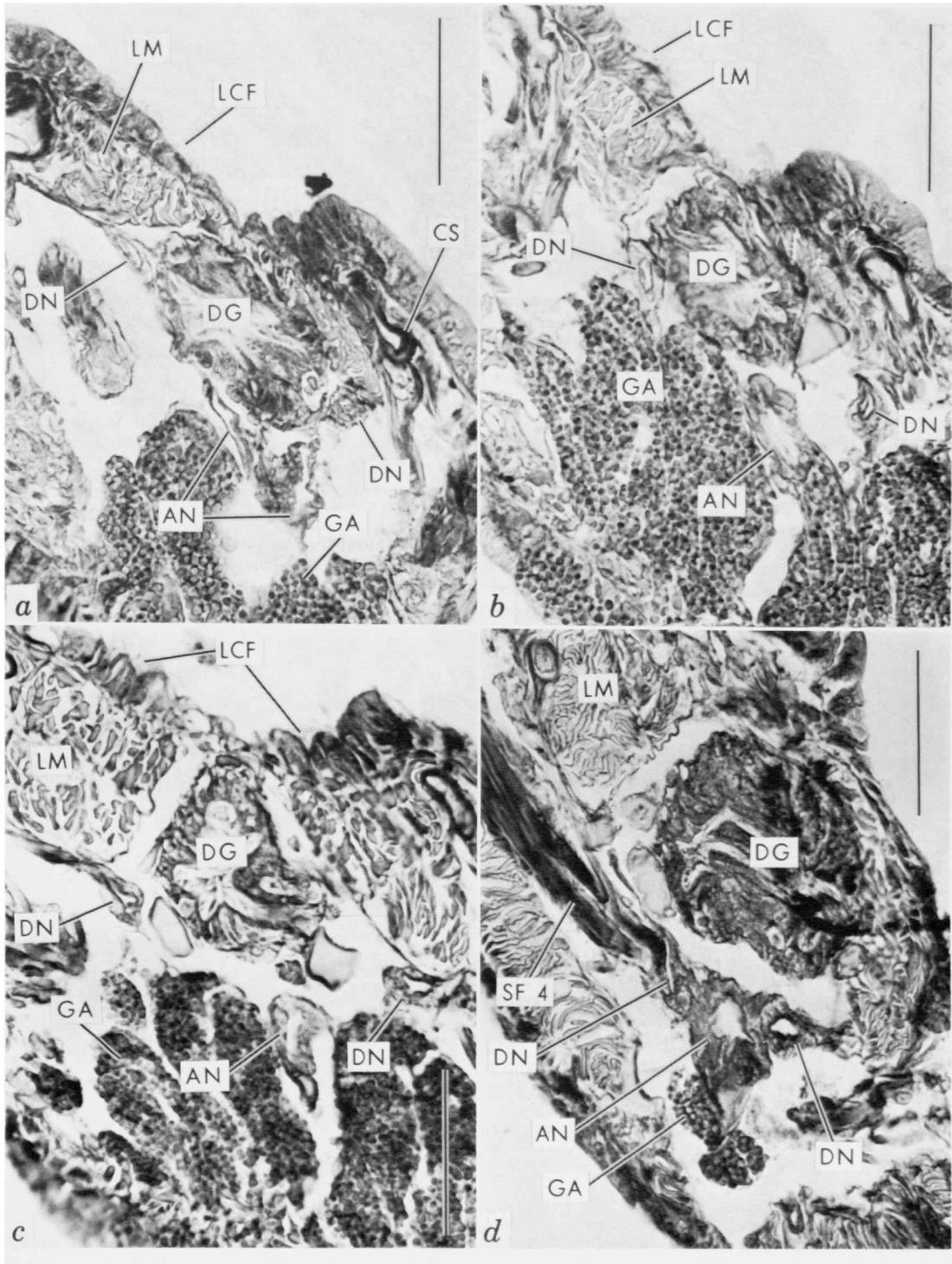


PLATE 10

Caobangia abbotti, new species: Transverse sections, five microns, Mallory's Triple Stain (USNM-W 50660); longitudinal locations of *a*, *b*, *c*, and *d* indicated on Figure 6*b*, N 8, N 9, N 10, and N 11, respectively; scale lines are 50 microns.

- a.* Section just anterior to fifth thoracic setal fascicle.
- b.* Section between sixth and seventh thoracic setal fascicles, showing association of nephridial ducts with numerous blood vessels.
- c.* Section from abdominal region, showing size difference of ascending and descending nephridial ducts.
- d.* Section close to transition between descending and ascending nephridial ducts, showing similar size.

(AG = ascending gut, AN = ascending nephridial duct, BV = blood vessel(s), BVS = blood vessels/sinus associated with stomachic chamber, DG = descending gut, DN = descending nephridial duct, LM = longitudinal muscle, NM = mesentery supporting nephridial ducts, SC = stomachic chamber of descending gut, SF 5 = fifth thoracic setal fascicle, SG = sperm groove.)

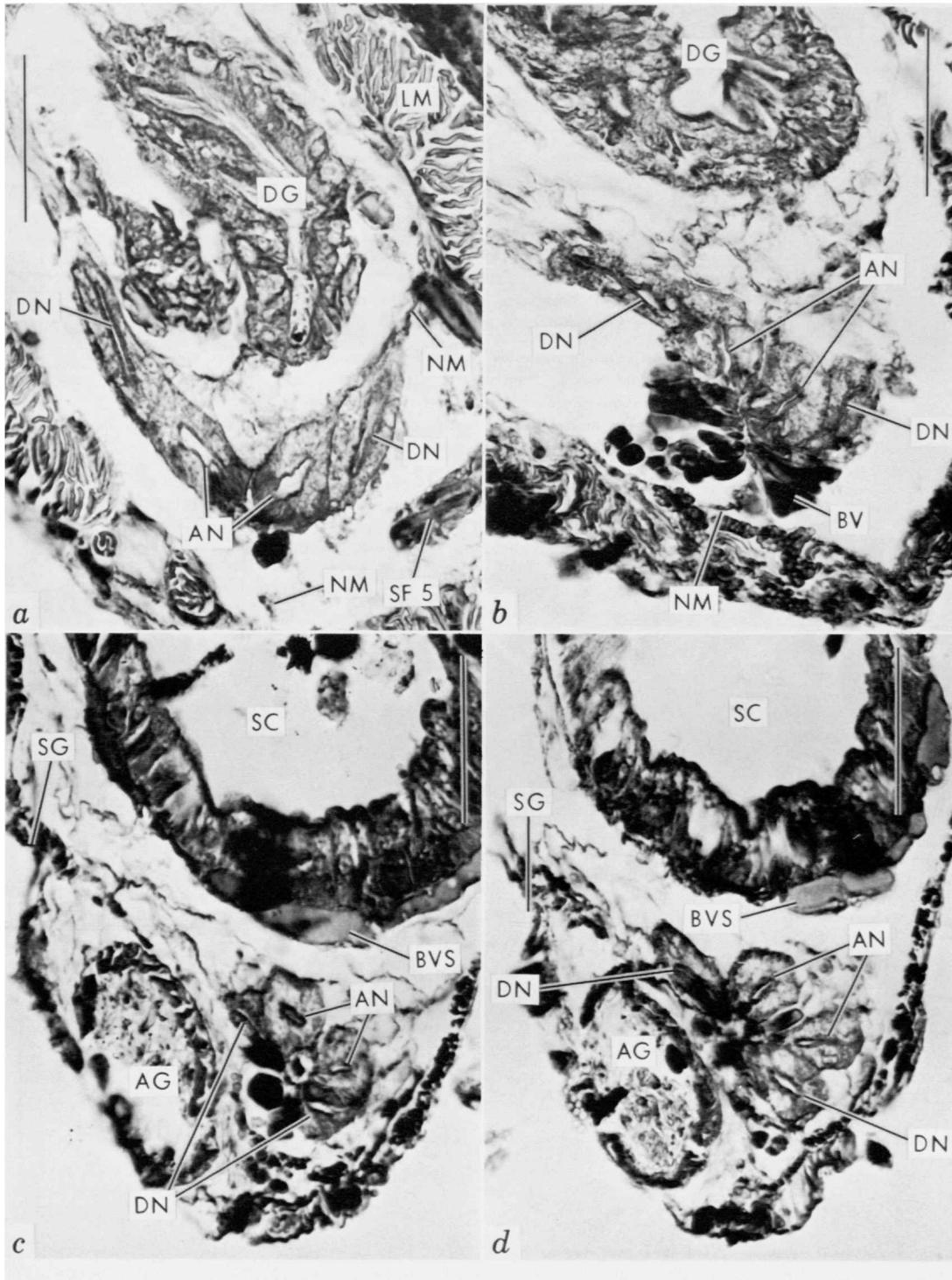
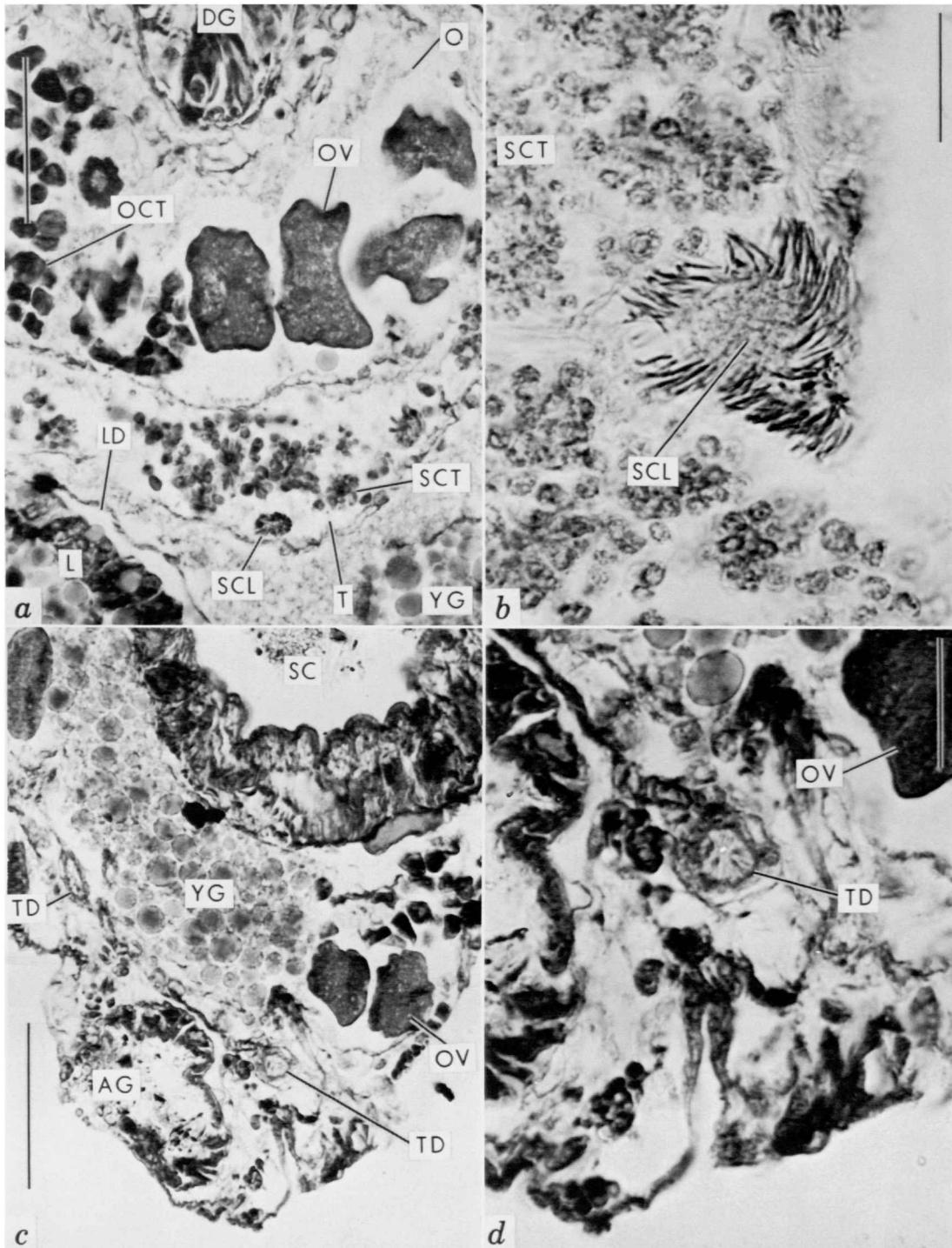


PLATE 11

Caobangia abbotti, new species: Transverse sections, five microns, Mallory's Triple Stain (USNM-W 50660); scale lines for *a* and *c*, 50 microns, for *b* and *d*, 10 microns.

- a.* Same section as Plate 5*c*, through posterior region beyond stomachic chamber and loops of gut, showing relationship of "ovary," "testis," and larval ducts.
- b.* Section through "testis," showing spermatocytes and cluster of nearly mature sperm.
- c.* Section posterior to opening of duct from "testis" to sperm groove; actual opening is 10 microns anterior to this section.
- d.* Same section as *c*, more highly magnified.

(AG = ascending gut, DG = descending gut, L = larva, LD = larval duct, o = "ovary," ov = egg, OCT = oöcyte(s), SC = stomachic chamber of descending gut, SCR = spermatocyte(s), SCL = cluster of sperm, T = "testis," TD = testicular duct, YG = yolk granules.)



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