A Genus of Dorid Nudibranch

Previously Unrecorded from the Pacific Coast of the Americas, with the Description of a New Species

BY

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(11 Text figures)

INTRODUCTION

THE CENTRAL CALIFORNIA coast offers a wide variety of marine habitats supporting an extremely diverse marine fauna. The genus *Hallaxa* is previously unrecorded from the west coast of the Americas. It is the purpose of this paper to describe a new species assignable to this genus.

Hallaxa Eliot, 1909

Of the 3 species of the genus *Hallaxa* known worldwide, none have been previously known from the coasts of North America or the west coast of South America.

On June 10, 1968, we collected 2 individuals of a previously undescribed species of *Hallaxa* from Duxbury Reef, Marin County, California. Additional collections have been made at several other localities, as well as at Duxbury Reef, in California since that time.

Permanent addresses:

Hallaxa chani Gosliner & Williams, spec. nov.

Diagnosis: Body ovoid; body higher in anterior region, more flattened posteriorly. Marginal convolutions of dorsum ephemeral. Ground color light lemon yellow with brownish flecks around margin and with paired, dark subcutaneous maculations on both sides of the hepatic region. Brownish digestive gland visible through central portions of dorsum. Low tubercles most numerous between notal margin and hepatic region. Rhinophores large, mammiform, with pronounced lamellae. Gills 12 - 14, unipinnate. Oral tentacles inconspicuous. Foot corners short and subacute. Radular formula 35 - 36 \times 7-14 · 1 · 1 · 1 · 7-14. Rachidian teeth rudimentary. Lateral teeth dimorphic, tall and denticulated. Spermathecal duct conspicuous. Prostate U-shaped and of uniform, smooth texture. Duct leading from female gland mass to spermathecal duct (the uterine duct) arising between receptaculum seminis and bursa copulatrix.

Type Material: The holotype of *Hallaxa chani* is deposited at the California Academy of Sciences in San Francisco, California where it bears the number CASIZ 674

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in the type series collection. Also deposited are a paratype radula and a whole paratype, designated CASIZ 490 and 675, respectively.

Name: We name this species in honor of Dr. Gordon L. Chan of the College of Marin and Bolinas Marine Station for initially inspiring our interests in marine biology and for his continued enthusiasm in marine science education. We also recognize his instrumental efforts in the establishment of Duxbury Reef as a marine reserve.

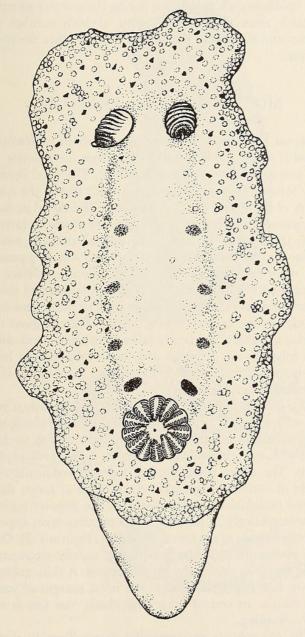


Figure 1

Hallaxa chani Gosliner & Williams, spec. nov.

Dorsal aspect of an 18 mm long animal

Taxonomic Position:

OPISTHOBRANCHIA

NUDIBRANCHIA

Doridacea

ACTINOCYCLIDAE

Hallaxa

Hallaxa chani

WORLD SPECIES LIST

The following is a list of species names at present in use in the genus *Hallaxa* Eliot, 1909 (= *Halla* Bergh, 1878; the name is preoccupied by a genus of polychaete worms):

- 1. Hallaxa apefae Marcus, 1957
- 2. Hallaxa chani Gosliner & Williams, spec. nov.
- 3. Hallaxa decorata (Bergh, 1878)
- 4. Hallaxa indecora (Bergh, 1905)

NATURAL HISTORY

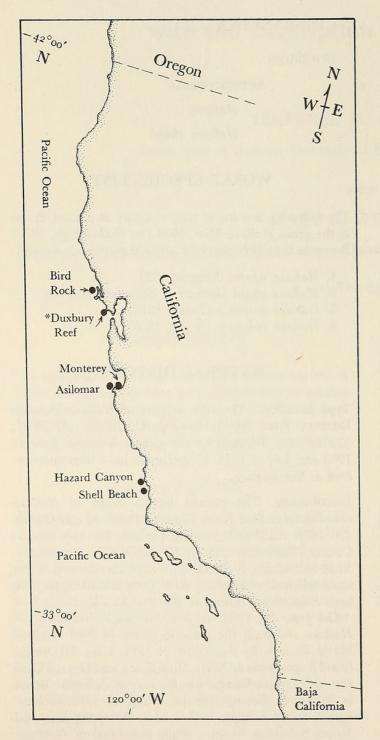
Type Locality: The type locality of *Hallaxa chani* is Duxbury Reef, Marin County, California (37°53′N; 122°42′W). Throughout the period between June of 1968 and July of 1973, 13 specimens have been encountered at this location.

Distribution: The present known range of *Hallaxa chani* is from Bird Rock, Tomales Point, Marin County (38°14′N; 123°00′W) to Shell Beach, San Luis Obispo County, California (35°12′N; 120°43′W; see map). Most individuals, however, have been encountered in the shale tidepools of Duxbury Reef. Only 8 individuals have been encountered outside of the type locality.

On June 23, 1968 we found a single individual of *Hallaxa chani* on the granitic shores of Bird Rock in Marin County. In the winter of 1971, Gary McDonald found 5 specimens at North Shell Beach and Hazard Canyon in San Luis Obispo County and at Asilomar Beach in Monterey County. In the spring of 1972 Richard Ajeska found a single individual at Monterey Bay and James Nybakken found a single individual at Asilomar Beach.

Habitat: Hallaxa chani is known only from the rocky intertidal shores of lower zone tidepools in Central Cali-

fornia. The animal has not been observed in direct association with any food species. Most individuals have been encountered on algal substrates, particularly the rhodophyte *Iridea* and the angiosperm *Phyllospadix*.



Range Map of *Hallaxa chani* Gosliner & Williams, spec. nov.

(■ = collecting stations; * = type locality)

Duxbury Reef, the type locality, represents a massive shale reef of the Miocene Monterey formation, extending more than 1 km from the Bolinas headland and forming the northern barrier of Bolinas Bay. The seaward edge of the reef supports the greatest diversity of marine life. The leeward side, while more protected, is subject to a greater influx of silt and therefore the substrate is less stable, thus supporting fewer organisms.

Seasonal changes have a dramatic effect on the overall productivity and species composition at Duxbury Reef. The opisthobranch population during the summer months is much more abundant in terms of both number of species and number of individuals than at other times of the year.

MORPHOLOGY AND ANATOMY

External Features: The general body shape of Hallaxa chani is ovoid and generally tapers from the anterior to the posterior region (Figures 1 and 2). The notal border may form temporary convolutions which distort the symmetry of the typical dorid ovoid shape. The dorsal surface is relatively rigid, but not scabrous to the touch. In lateral view, the anterior portion of the animal attains a much higher contour than the posterior region which is generally more flattened (Figure 4b). The dorsal surface is covered with small tubercles. The concentration of these tubercles is greatest around the margin of the notum and scantier in the central hepatic region. The marginal tubercles are characteristically taller than the central ones. The tubercles are yellowish and vary in shape from low. flat-topped forms to taller forms with a rounded subspherical apex (Figure 3c).

The ground color of *Hallaxa chani* is a light lemon yellow with a darker central hepatic region. Individuals less than 12 mm in length are generally light greyish to dull yellow. Larger individuals possess a richer yellow pigment. The entire dorsal surface contains reddish-brown flecks of variable shape and size. A series of larger dark brown maculations is distributed in the hepatic region. Characteristically, 2 prominent subcutaneous spots appear directly in front of the branchial plume (Figures 1, 2). One to 4 other pairs of lighter brown spots usually accompany these on either side of the hepatic region. A thin, goldenbrown line is present around the notal margin of some individuals. In several other individuals, this line is entirely wanting.

The rhinophores are large and mammiform in shape with 8 to 10 pronounced lamellae. The rhinophores may be retracted into translucent yellowish rhinophoral sheaths which extend almost $\frac{1}{2}$ the length of the fully extended

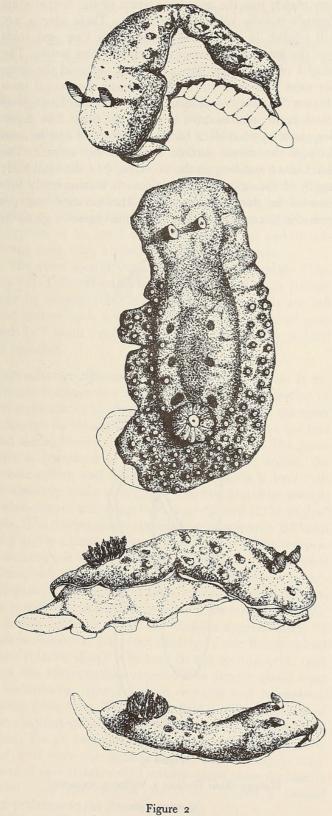
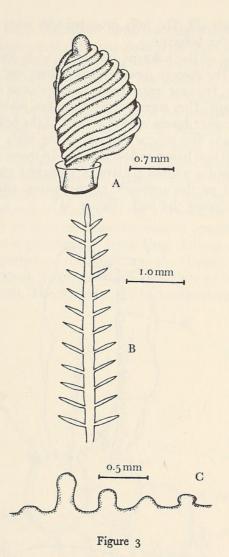


Figure 2

Hallaxa chani Gosliner & Williams, spec. nov.

Various aspects of the living animal



Hallaxa chani Gosliner & Williams, spec. nov.

- A Right lateral view of rhinophore
- B Single gill from branchial plume
- C Variation in dorsal surface tubercles

rhinophore (Figure 3a). The rhinophores are pale yellow in color with darker brownish-maroon pigmentation toward the apices. The extended rhinophores are 2mm long in the holotype.

The body of the living holotype was 18 mm in length and 8 mm in width. Most individuals measured were between 10 and 20 mm in length.

The branchial plume is composed of 12- 14 unipinnate gills. The gills are retractile into the branchial sheath, which is translucent and may attain a height of $\frac{1}{2}$ the length of the extended gills. Each gill is composed of 10- 14 pairs of lateral lamellae on a central stalk (Figure 3b). Small dark reddish-maroon spots are present at the

base of each gill. The fully extended gills were 4mm in height in the holotype.

The foot of the holotype was 4mm wide and 15mm in length. The anterior foot corners are short and subacute at the tips. The oral tentacles are inconspicuous and variable in shape. They surround the outer lips which can be seen in the very antero-ventral portion of the head region (Figure 4a). The ventral surfaces of the body and foot are smooth and lemon-yellow in color. In many individuals examined a whitish pattern of branched venation is distributed on the underside of the notum adjacent to and surrounding the foot (Figure 4a).

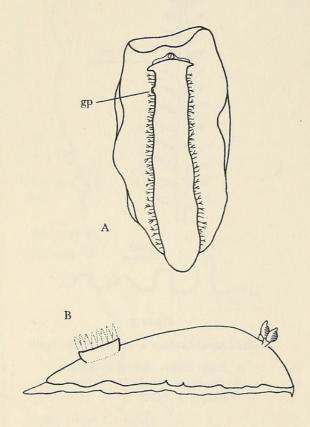


Figure 4

Hallaxa chani Gosliner & Williams, spec. nov.

A Ventral view of body

B Right lateral view of body

gp - gonopore

Digestive System: The digestive system of *Hallaxa chani* is very compact, as it is in the Doridacea in general, and comprises the bulk of the visceral hump.

The buccal mass is located at the very anteriormost portion of the system. The buccal mass is quadrate in shape, but somewhat tapered toward the posterior end where it meets the esophagus. A pair of conspicuous salivary glands join the anterior portion of the buccal mass through narrow tubules (Figure 5). These glands are dull whitish in color. The esophagus is long and folds over the anterior portion of the reproductive system. The ganglia of the central nervous system surround the anterior-most portion of the esophagus near the buccal mass (Figure 5). The esophagus enters the digestive gland which is the most massive organ in the body. The digestive gland appears dark brown in color and can be seen through the dorsal surface of the living animal. The gland was 6 mm long in the holotype, $\frac{1}{3}$ of the total body length of the organism. The stomach is completely surrounded by the digestive gland. The intestine emerges from the latero-ventral portion of the digestive gland in

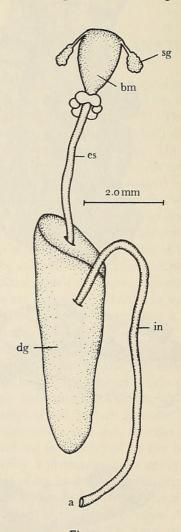


Figure 5

Hallaxa chani Gosliner & Williams, spec. nov.

	Digestive system	
a – anus	bm - buccal mass	dg - digestive gland
es - esophagus	in – intestine	sg - salivary gland
	CNS - central nervous	system

the anterior section of its right side (Figure 5). The intestine is long and forms a sharp loop in the posterior part of the female gland mass. The intestine continues along the right side of the body, where it emerges as the anus in the center of the branchial plume.

Radula: The radula is very small, less than $0.5 \,\mathrm{mm}$ in length, and spatulate in shape. The radular formula in one specimen is $35 \times 7 \cdot 14 \cdot 1 \cdot 1 \cdot 7 \cdot 14$. In another specimen the radular formula is $36 \times 8 \cdot 14 \cdot 1 \cdot 1 \cdot 1 \cdot 8 \cdot 14$.

The rachidian teeth are extremely reduced in that the central row is represented by minute vestigial teeth (Figure 7a). The first pleural teeth are stout, conspicuous, and highly variable in form (Figure 7b). Many of these are composed of an inner cusp with pointed tip and an adjacent cusp with several smaller denticulations.

The outer lateral teeth are also highly variable (Figure 7c). Differences between the inner and outer laterals may be considerable. Most of the lateral teeth are tall and narrow with a strongly curved, large terminal cusp and 5-7 small denticles which may be sharply pointed or rounded.

Reproductive System: The reproductive system is extremely compact and is found in the anterior portion of the right side of the body. The hermaphroditic gonopore is located on the right side of the body between the foot and the underside of the dorsum (Figure 4a). The gonopore is composed of 3 openings, the male orifice, the female orifice, and the oviduct. The vagina is long (approximately 3 mm in length). The receptaculum seminis is club-shaped and arises from near the end of the vaginal tube. The receptaculum seminis is approximately 0.75 mm long and is whitish in color. From the base of the receptaculum seminis extends the long, conspicuous spermathecal duct which leads to the bursa copulatrix. The spermathecal duct is approximately 3 mm long. The bursa copulatrix is spherical in shape, pustulose in texture, and is light yellowish-brown in color. The bursa is approximately $1\frac{1}{2}$ mm in diameter. The duct leading to the female gland mass (uterine duct) is located on the spermathecal duct near the receptaculum seminis. The female gland mass is voluminous, light yellowish in color and is approximately 4 mm long. The female gland mass is composed of the albumen gland, mucus gland, and membrane gland which are all very difficult to separate during dissection and thus were not distinguishable. The oviduct is composed of very tightly coiled tubules which enter the female gland mass. The efferent end of the oviduct is located just posterior to the female opening.

The male opening is the most anterior of the genital openings. From the male opening extend the ejaculatory

duct and penis. The penis forms an enlarged portion of the ejaculatory tube. The vas deferens is short and leads from the prostate to the penis. The prostatic segment is horseshoe-shaped and flattened, but similar in texture to the rest of the male system. The prostate is approximately $\frac{3}{4}$ mm long. The tubule leading from the prostate and the tubule leading from the base of the ampulla follow a common duct to the female gland mass (Figure 8). Beginning with the post-ampullar coelomic gonoduct the reproductive system possesses organs common to both sexes in the hermaphroditic system. Arising from the post-ampullar coelomic gonoduct is the conspicuous ampulla which has an uniform brownish-maroon speckling. The ampulla is approximately 2mm long. Arising from the posterior portion of the ampulla is the elongate pre-ampullar coelomic gonoduct which enters the narrow elongate ovotestis. The ovotestes are yellowish-white in color

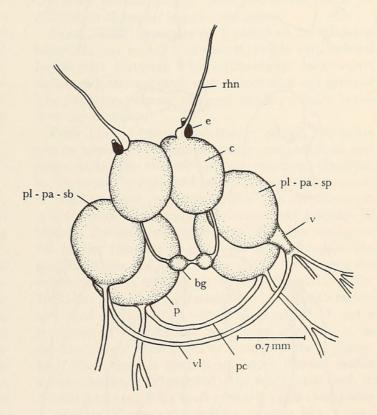


Figure 6

Hallaxa chani Gosliner & Williams, spec. nov.

Nervous system

bg – buccal ganglion c – cerebral ganglion e – eye p – pedal ganglion pc – pedal commissure pl - pa - sb – pleural - parietal - subintestinal ganglion pl - pa - sp – pleural - parietal - supraintestinal ganglion rhn – rhinophoral nerve v – visceral ganglion vl – visceral loop

and attained a length of 5 mm in the holotype. Areas of granular texture are apparent between the various tubules of the ovotestis. This granular appearance distinguishes the ovotestis from other organs in the reproductive system.

Nervous System: The compact central nervous system of *Hallaxa chani* is concentrated around the esophagus just posterior to the buccal mass. It is composed of 9 ganglionic masses in 4 pairs. The cerebral ganglia are

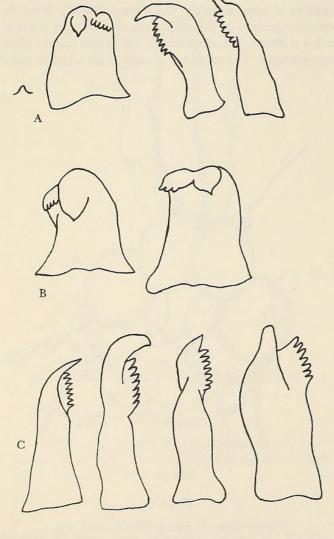


Figure 7

Hallaxa chani Gosliner & Williams, spec. nov.

Radula

- A Vestigial rachidian and first 3 pleural teeth of right half row from central portion of radula
- B Variability of first pleural teeth
- C Variability of outer lateral teeth

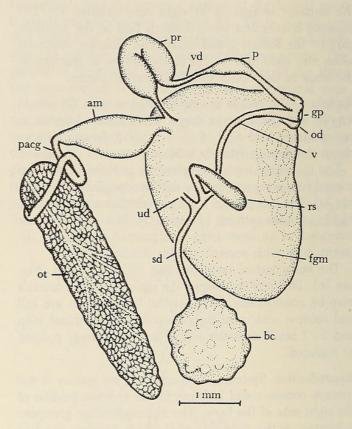


Figure 8

Hallaxa chani Gosliner & Williams, spec. nov.

Reproductive system

am – ampulla bc – bursa copulatrix fgm – 9 gland mass gp – gonopore od – oviduct ot – ovotestis p – penis pacg – pre-ampullar coelomic gonoduct pr – prostate rs – receptaculum seminis sd – spermathecal duct ud – uterine duct v – vagina vd – vas deferens

small (approximately 0.7 mm in diameter). These are connected together by an extremely short cerebral commissure. The optic-rhinophoral lobes of the cerebral spheres are located on the antero-dorsal region of the cerebral ganglia (Figure 6). The eyes are located on the dorsal surface of the optic-rhinophoral lobes. The eyes are black in color and oblong in shape. The lens of each subcutaneous eye can be seen in the distal portion of each eye. From the optic-rhinophoral lobe extend the rhinophoral nerves which lead to the external rhinophores. Directly ventral to the left cerebral ganglion is the ganglionic complex representing a fusion of the left pleural, parietal, and subintestinal ganglia. Extending

from this ganglion are somatic nerves which reach into the visceral and left pleural regions of the body. Attached to the ventral end of the right cerebral ganglion is the ganglion composed of the fused right pleural, parietal, and supraintestinal ganglia. The visceral ganglion is inconspicuous and emanates from the posterior portion of the right abdominal ganglionic complex. Extending from the area of adnation between the visceral ganglion and the right abdominal complex is a series of visceral nerves. The left and right ganglionic masses are basically the same size (each approximately 1 mm in diameter). The pedal ganglia are the largest ganglia in the system and are located directly ventrally to the cerebral and abdominal complexes in the ventral portion of the nerve ring. They are each approximately 1.5 mm in diameter. The pedal commissure is elongate and connects the 2 spheres of the pedal ganglia ventral to the esophagus. From the pedal ganglia extend several extensive pedal nerves (Figure 6).

The paired buccal ganglia are attached to the cerebral ganglia by the cerebro-buccal connective and are attached to the buccal area on the ventral surface of the esophagus. Extending from the buccal ganglia are minute pharyngeal nerves which come in contact with the lateral region of the buccal mass. The buccal ganglia are the smallest ganglia within the nerve ring.

DISCUSSION

Systematics: THIELE (1931) included the genera Actinocyclus and Hallaxa in the family Glossidorididae, along with such other genera as Cadlina, Chromodoris, etc. PRUVOT-Fol (1934) erected the family Actinocyclidae to include the genera Actinocyclus Ehrenberg, 1831 (= Sphaerodoris Bergh, 1877) and Hallaxa Eliot, 1909. KAY & Young (1969) support this view and state that the genera allotted to the Actinocyclidae differ sufficiently enough from the typical rasping sponge-feeding Dorididae to warrant separate family status. This view separates the Actinocyclidae from the related Chromodorididae and Cadlinidae on the basis of unique features associated with the digestive system, reproductive system, radula, and egg mass. Franc (1968) defines the family Actinocyclidae as follows: Body spherial; anterior side of the border of the foot meets with the slope of the head. Tentacles small; gills unipinnate. Radula without rachidian teeth. First lateral teeth different from outer laterals in shape and denticulation. Prostate absent or more represented by a portion of the vas deferens. We amend this definition as follows: Rachidian absent or vestigial as a spurious row represented by minute rudimentary teeth. Prostate absent or present, undifferentiated, or well differentiated as in the Cadlinidae. Spermathecal duct well defined. Dorsal surface smooth or with variable patterns of low tubercles.

Within the Actinocyclidae there is much confusion with respect to the characteristics which separate the 2 genera, Actinocyclus and Hallaxa. THIELE (1931) states that Actinocyclus has an arched notum more or less tuberculated, a wide foot and a radula with a large plate with small hooks, while the rest of the plates are smaller with a proximal barb which is denticulated. He states that Hallaxa has a body which is smooth, considerably depressed with a narrow foot, and with a wide interior radular plate, smooth on the interior and denticulated on the exterior lobes. The external plates resemble those of Actinocyclus. The gills are unipinnate in both genera.

Marcus (1957), in his discussion of *Hallaxa apefae*, says that "dorsum smooth" must not be diagnostic for *Hallaxa*, as *H. apefae* is quite tuberculate.

Franc (1968) separates the 2 genera on the following bases: *Hallaxa* having back smooth, radula with internal lateral with 2 smooth lobes; *Actinocyclus* back warty, radula with internal tooth with smooth cusp and external lobe pectinate, external marginal small, pectinate below their upper border.

From these 3 views no definitive generic characters can be appraised because of various contradictions and inaccuracies. The exception of foot characters described by Thiele will be explained below. From our observations of Hallaxa chani and investigations into the literature. it is apparent that 3 major distinctions can be made to separate Actinocyclus and Hallaxa. The first applies to the radular formulae in each case. In Actinocyclus the number of rows of teeth in the radula far exceeds the number found in Hallaxa. Actinocyclus japonicus (Eliot, 1913) has 98 rows of teeth while the average in all known species of Hallaxa is 27, with a minimum of 18 and a maximum of 36. Secondly, the degree of variability in the first pleural teeth serves to distinguish the 2 genera. In Hallaxa, the first pleurals are highly variable within a single specimen (Figure 7b). The first pleural teeth in Actinocyclus are similar in all rows of a single radula with a very low degree of variability (Figure 9a). Lastly, characters of the foot serve to distinguish the genera. A narrow, elongate foot is present in Hallaxa, while a broad, rounder foot is seen in Actinocyclus. This character admittedly is not a very reliable one as a diagnostic generic characteristic; however, it does serve as a model for comparison of the 2 genera.

The 4 worldwide species of *Hallaxa* differ significantly in a number of characteristics (Table 1). In reference to external body color, *Hallaxa chani* is dull yellow with

 Table 1

 Comparative Data of Worldwide Species of Hallaxa

	Radular Formula	Gills	Color	Distribution
Hallaxa indecora (Bergh, 1905)	20 x 7-8·1·0·1 7-8 18 x 6·1·0·1·6	10 unipinnate	purplish-red to violet with minute dark dots	Red Sea, East Indies, Japan
Hallaxa decorata (Bergh, 1878)	25 x 14·1·0·1 14	12 unipinnate	grayish-purple with brown-black spots	Ceylon, Philippines
Hallaxa apefae Marcus, 1957	30 x 9-11·1·0·1·9-11	9 unipinnate	yellowish-gray with darker liver	Brazil
Hallaxa chani Gosliner and Williams spec. nov.	35 x 7-14·1·1·1·7-14 36 x 8-14·1·1·8-14	12-14 unipinnate	dull lemon yellow with darker liver and brownish-maroon spots	Central California

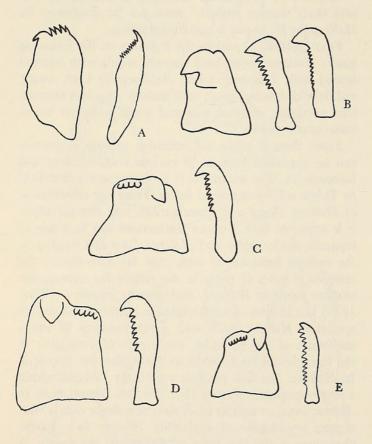


Figure 9

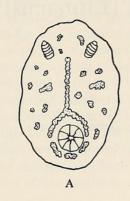
- A 1st and 2nd pleural teeth of Actinocyclus japonicus (after KAY & YOUNG, 1969)
- B 1st to 3rd pleural teeth of Hallaxa indecora (after Baba, 1949)
- C 1st and 2nd pleural teeth of Hallaxa apefae (after MARCUS, 1957)
- D 1st and 2nd pleural teeth of Hallaxa chani Gosliner & Williams, spec. nov.
- E 1 st and 2nd pleural teeth of Hallaxa decorata (after Eliot, 1909)

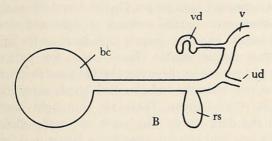
subcutaneous and surface flecks of brownish-maroon to almost black. On the basis of color, H. chani seems closest to H. apefae, which is yellowish gray with a darker liver. These 2 species are also the only 2 species of Hallaxa with tuberculated dorsal surfaces. The patterns of tuberculations differ substantially, however. In H. chani the tubercles are basically similar in shape and size and are distributed around the dorsal surface between the visceral hump and the notal margin. In H. apefae the tubercles are randomly distributed over the dorsum with a ridge of of tubercles between the rhinophores running posteriorly and bifurcating just anterior to the branchiae and then surrounding them (Figure 10a). Of the 2 remaining species, H. indecora is purplish-red to violet with small dark spots, while H. decorata is grayish-purple with dark brown spots.

Characteristics of the radula also differ significantly on an interspecific basis (cf. Figures 9b - 9e). The radular formulae in the 4 species of Hallaxa are similar (Table 1) with the main difference being in the number of rows of teeth. The previously known 3 species of Hallaxa have been recorded as having no rachidian teeth. In our study of H. chani we have observed a minute "spurious plate" or row of vestigial, rudimentary teeth in the rachidian position. Individual teeth of the rachidian row can only be detected by use of the oil immersion under a light microscope. It is possible that this vestigial rachidian is present in the other 3 species of Hallaxa, and may have been overlooked.

All gills in *Hallaxa* are unipinnate and the number of gills differs little from species to species (Table 1).

The reproductive systems of the related species, *Hallaxa chani* and *H. apefae* show several major differences. First, *H. chani* has a well-defined U-shaped prostate as opposed





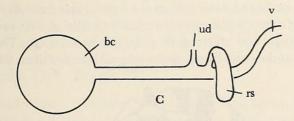


Figure 10

- A Dorsal aspect of Hallaxa apefae (adapted from MARCUS, 1957)
- Partial reproductive system of Hallaxa apefae (adapted from Marcus, 1957)
- C Partial reproductive system of Hallaxa chani spec. nov. bc - bursa copulatrix rs -receptaculum seminis
- ud uterine duct v - vagina vd - vaginal diverticulum

to the condition in H. apefae where the prostate is straighter and shorter and not as distinguishable from the rest of the vas deferens as in H. chani. Secondly, H. chani lacks the vaginal diverticulation of H. apefae as diagrammed in Marcus (1957: fig. 80) (cf. Figures 10b and 10c). Thirdly, in H. chani the uterine duct arises from the spermathecal duct near the receptaculum seminis, but between this organ and the bursa copulatrix. In H. apefae the uterine duct arises from the vaginal duct near the receptaculum seminis (cf. Figures 10b and 10c).

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