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THE FAUNA ASSOCIATED WITH THE CRINOIDS OF A TROPICAL CORAL REEF: WITH ESPECIAL REFERENCE TO ITS COLOUR VARIATIONS.

By F. A. Potts, M. A.

INTRODUCTION.

Although so much attention has been devoted to the phenomena of mimicry and protective resemblance displayed by land animals, in only one case has the colour resemblances of a marine animal been exhaustively studied. I refer to the classical instance of *Hippolyte varians*, illustrated by a long series of ingenious observations made by Gamble and Keeble. Briefly stated, the story is as follows: The young *Hippolyte* is free-swimming and colourless, but it becomes virtually a sedentary animal, anchoring itself to a seaweed or hydroid in the Laminarian zone, on which it finds both food and shelter. The prawn has the power of forming red, yellow, and blue pigments and by altering their relative proportions in the chromatophores it can acquire a green, brown, blue, or red ground-colour, and is thus able to adapt itself to the varied colours of the seaweeds and hydroids. The pigment may be laid down in longitudinal stripes or horizontal bars and in this way a colour scheme can be formed matching whatever seaweed the prawn shelters in. In early life a change in habitat is followed by a readjustment of the pigment altering the colour scheme, but this power is soon lost.

There are, however, a great number of cases where species of small marine animals are associated with an environment not varying, as in the case of *Hippolyte*, but definitely fixed for the species—for instance, some particular kind of sedentary animal, sponge, alcyonarian, or crinoid, as the case may be, which it frequents for shelter and commonly resembles in colour. Sometimes the first is definitely a parasite on the second, as in an example of the phenomenon often noted at Murray Island, where the bright blue starfish *Linckia lævigata*, so widely spread on the Indo-Pacific reefs, was a source of food to multitudes of tiny copepods (*Linckiomolgus cæruleus* Stebbing), whose colour exactly matches that of the host, though the pigment is of a different chemical nature.

In the majority of cases the association is of a vaguer nature, and while the associated animal gains protection it obtains its own food-supply. How numerous such cases are in tropical seas may be seen from the following passage:

"We noticed numerous other animal partnerships, which might have been cases of commensalism but were more probably merely one-sided adaptations of one animal standing in need of protection to another animal capable of affording the required protection without any expenditure of effort. For instance, a very common branching zoophyte of this region is *Spongodes pustulosa* (or some very closely related species), a creature near akin to the 'dead men's fingers' of British seas. It looks like a small 'run to seed' cauliflower, of which the individual florets are of a bright pink colour. Hidden among its branches we found no less than four small species of crustaceans (an *Alpheus*, a *Galathea*, a *Porcellana*, and a rare little spider crab known as *Hoplophrys oatesi*), all of which, in life, are greyish white, with bright pink spots, so that they are perfectly invisible so long as they remain quiet in their living refuge. Another zoophyte that we often dredged was *Pteræides elegans* (or a species intimately close to it), one of the seapens, of a grey colour profusely marked with little blackish rings. In its leaves three small species of crustaceans are accustomed to hide, all of which are coloured and spotted exactly like the living citadel in which they dwell. I have already mentioned the sea-lily (*Actinometra*), striped in alternate bands of yellow and purple, on whose fronds similarly striped crustaceans live without fear of detection; here we found the same sea-lily giving secure shelter to sea-worms, banded yellow and purple like itself."—(*A Naturalist in Indian Seas.* A. Alcock, London, p. 112, 1902.)

The association last mentioned in this passage, that between stalkless crinoids and a multitude of smaller invertebrates, forms the subject of this paper. To those who only know the species of *Antedon* found in our own British waters, the wealth of numbers and the riot of colour in the crinoid fauna of a tropical coral reef is a remarkable revelation. In October 1913, during my visit to Murray Island, I was able to observe this fauna under the best conditions. The commonest species there is the form *Comanthus annulatum* (Bell), remarkable for its extraordinary range of colour variation from very light-coloured individuals (in which white, light green, yellow, and grey mingled in the colour scheme) to others which are entirely dark green or black. In the shelter of its arms live commensal forms belonging to many groups of marine invertebrates, and generally speaking they possess a type of colouration which makes them inconspicuous upon the host and so varies with the colour of the host. The fact that such a relation exists between crinoids and such animals as alpheids, galatheids, and worms has been pointed out by Dana, Haswell, and Alcock, but I think the circumstances warrant the publication of a more minute though still very incomplete study of this curious phenomenon.

List of animals commensal with crinoids on the reefs of Murray Island and off Mabuiag, Torres Straits, Australia.

[Other forms described as commensals of crinoids in other areas are included in brackets. Only those forms which show colour resemblance to the host are included.]

CRUSTACEA	Decapoda Macrura Alpheidæ.	Synalpheus comatularum Haswell, S. brucei sp. n. (S. stimpsonii var. maldivensis, Indian Ocean. S. carinatus var. binongeensis, East Indies.)
	Pontoniidæ	Periclimenes commensalis Borradaile. P. pottsi Borradaile. [P. cornutus, ceratophthœlmus, brocketti, Indian Ocean.] [Pontoniopsis comanthi Borradaile.]
	Decapoda Anomura.	Galathea elegans Adam and White (G. deflexipons and longirostris are probably synonyms of this species). G. inflata sp. n. G. minuta sp. n.
	Isopoda	Cirolana lineata sp. n.
	Amphipoda	Cyclotelson gen. n. purpureum sp n.
ECHINODERMATA.	Ophiuroidea	Amphiuridæ. Ophiactis sp.? Ophiotrichidæ. Ophiomaza cacaotica Lyman. Ophiomaza cacaotica var. picta Koehler. [Ophiophthirius actinometræ Döderlein, Torres Straits; Thursday Island. Ophioœthiops unicolor Brock, Amboina. Ophiosphæra insignis Brock, Amboina.
ANNELIDA	Polychæta	Polynoë minuta Potts var. comanthi var. n. [P. crinoidicola Potts, Indian Ocean.]
	Myzostomida.	
MOLLUSCA	Gasteropoda.	

DECAPODA MACRURA.

ALPHEIDÆ.

The species of alpheids commensal with crinoids in Torres Straits are two in number:

Synalpheus brucei sp. n. from *Comanthus annulatum* and *Comatula purpurea* on the reef at Murray Island.

S. comatularum Haswell from *Comanthus annulatum* in shallow water from localities in Torres Straits (Albany Passage, Cape York, and north of Mabuiag).

Coutière has divided the species of this huge genus *Synalpheus* into several groups, each consisting of nearly allied forms. In the *Comatularum* group those species are included which fall in the following diagnosis:

"Supraorbital spines insignificant compared to the rostrum; antennules shorter than the antennæ; spines of the basicerite almost equal, the external always smaller than the stylocerite; external maxillipeds oral, feebly spinous distally; first segment of the carpus of the second pair of feet very long, following feet cylindrical; ventral hook of the dactyl obsolete; telson with an oval median lobe."

nate with dark green or black. There also occurs another variety, in which the green pigment is replaced by yellow and the darker pigment by red or brown. In the specimen figured (pl. 1, fig. 3), which is typical of the species, there were three yellow stripes alternating with two brown of equal breadth. The chela was yellow with a brown line. In this case, however, the commensal, living on a crinoid in which green predominated, was very conspicuous, and I suppose it to have developed its pigment in association with another crinoid of different colour type.

Periclimenes pottsi Borradaile.

This shrimp is comparatively common on the crinoids from the Murray Island reef, but only one or two specimens were obtained at Mabuiag. It is a very transparent creature, and though the general colouration, a beautiful purple, harmonises with the host, there is no distinct arrangement in longitudinal stripes. The low power of the microscopes shows that there is a blue pigment contained in very numerous small cells which are regularly disposed over the body. Also evenly distributed, but much fewer in number, are cells containing red pigment. These may be spherical or branching. The gut is coloured red. The general effect is thus purple.

Periclimenes commensalis Borradaile.

I did not, amongst the living specimens, distinguish this species from *P. pottsi*, so probably what has been said about the latter species also applies to the former. It may be noticed that these are not the only species of the genus *Periclimenes* to be found in association with crinoids. Others are *P. cornutus*, *ceratophthalmus*, and *brocketti*, all found on crinoids from the Maldives, as noted by Professor J. Stanley Gardiner.

Information about the surroundings of the animals so seldom accompanies general collections that I fully expect a similar connection to exist in the case of many other species of this enormous genus.

DECAPODA ANOMURA.

GALATHEIDÆ.

There are at least three species of galatheids commensal with crinoids in Torres Straits. These are: *Galathea longirostris* (=*G. elegans*), *G. inflata* sp. n., *G. minuta* sp. n. These are all small forms from 6 to 15 mm. in carapace length and are dark coloured with longitudinal, pigment-free bands, a colour scheme corresponding almost exactly to that of the alpheids. They are not by any means found so commonly as is *Synalpheus*, though *G. longirostris* is not infrequent. My observations do not lead me to suppose that the galatheids occur in pairs on each host, but the absence of evidence on this point may be due to the fact that they are inclined to leave the host whenever disturbed. There is no special modification for clinging to the crinoid

other than the spines on the dactyli of the thoracic legs, but the animals are thigmotropic and swim back immediately to the host when they have been detached.

Galathea elegans Adam and White. (Plate 1, Fig. 5.)

G. elegans, Adam and White, Voyage of the *Samarang*.
G. longirostris, Dana.
G. deflexipous, Haswell, Proc. Linn. Soc. New South Wales, vol. vi; Miers, Zool. Coll. H. M. S. *Alert*.
G. longirostris, Southwell, Anomura, Ceylon Pearl Oyster Rep. Roy. Soc., part V, p. 220, 1906.

In earlier literature there are only three records of the occurrence of galatheids on crinoids. The first is that of Dana, who originally described *G. longirostris* from a crinoid dredged at Fiji; the second is that of Haswell, who founded a new species *G. deflexipous*, associated with *Synalpheus comatularum* on an unidentified crinoid. The third likewise concerns *G. longirostris*, which is mentioned by Southwell as obtained near Ceylon, clinging to *Antedon bella*.

G. elegans Adam and White, *G. longirostris* Dana, and *G. deflexipous* are all very closely related. They all possess a long rostrum with from 5 to 10 small lateral denticles, a very typical dorsal ornamentation, and have a similar colour scheme, with longitudinal stripes of pigment on the dorsum. The first-named species has not been noted as occurring on crinoids, but this may be the fault of the collectors. Balss, in describing a specimen from Japan, which he assigns with some doubt to *G. elegans*, says with regard to its occurrence: "Wahescheinlich an Comatuliden, wie es Haswell von der nahe verwandten *G. deflexipous* und Southwell von *G. longirostris* Dana angeben. Darauf weist die bunte Färbung hin, die wohl als eine mimetische zu deutenist." Probably the whole group of related species are crinoid dwellers. If not, it will be strange that so marked a pattern should occur on a free-living galatheid, when that is a character so definitely associated with crinoid commensalism, both here and in other groups.

The three species are principally defined with regard to the characters of the rostrum; thus:

G. elegans:	*G. longirostris:*	*G. deflexipous:*
Rostrum more than half the length of the rest of the carapace, "with 7 small denticulations on each side" (Haswell). But Balss gives the latter number as 9. But most important of all, the original figure only shows 5 or 6.	Rostrum fully as long as half the carapace "minutely 5–6 serrulate."	Differs from *elegans* only in the fact that the rostrum is entirely deflexed.

With regard to the third species Miers says:

"In more than one of the specimens in the Museum collection the rostrum is slightly deflexed, and I think that *G. deflexipous* Haswell, from Albany Passage, should be regarded merely as a marked variety of *G. elegans*."

In my own specimens the number of denticulations on each side is from 6 to 7; in one individual there were 6 on one side, 7 on the other.

There are also a number of cases in which the rostrum is deflexed. From the comparison here made and the facts stated I think there is little doubt that we are dealing with one very variable species.

I have compared my collection with the full description given by Balss of his specimen (the fullest description given of *G. elegans*) and find the following discrepancies:

(1) In the third maxilliped the merus is armed with three prominent spines on the internal border in the Japanese form, in mine with only two; Henderson and Ortmann both describe *G. elegans* with two spines in this position.

(2) In the ambulatory limbs the merus has a spinose upper angle according to Balss, but is smooth in the Torres Straits forms; the denticulation of the dactylus is weak in the former, but in the latter there is a powerful end claw, succeeded by prominent teeth only gradually decreasing in size.

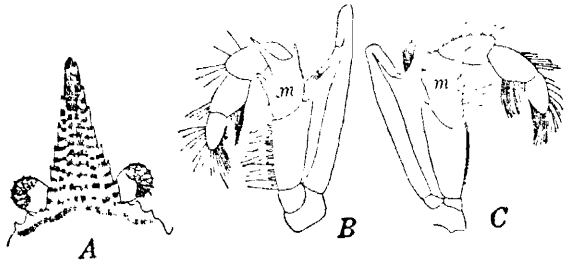

FIG. 4.—*Galathea.*

A. *G. elegans*, Torres Straits, rostrum showing lateral teeth and arrangement of hairs. × 8.
B. *G. minuta*, third maxilliped, showing spines on merus (*m*). × 18.
C. *G. inflata*, third maxilliped. × 4.

But in a variable species we might expect to find such differences. The Japanese form described by Balss is clearly a rather extreme member of the variable series, as shown by the fact that it has the highest number of denticulations on the rostrum recorded. The agreements between Balss's description and my specimens outweigh the differences.

In conclusion, I give the following diagnosis, to embrace all the forms here discussed:

G. elegans: Rostrum rather more than half the length of the remainder of the carapace with from 5 to 9 small denticulations on each side; width about half the length; sometimes deflexed; carapace somewhat pear-shaped; about a dozen indentations on each side; surface traversed by many narrow horizontal furrows, from which spring thick lines of short fine hairs, though these may be absent or nearly so. The rostrum is covered with hairs rather longer than those on the carapace, arranged in distinct crescents posteriorly. Dorsum and limbs covered with dark pigment, but there are generally pigment-free longitudinal bands of variable width. Chelæ long and slender, cylindrical in section, thicker in the male than the female, varying in length in the latter.

Often, if not always, commensal with crinoids.

Measurements of Torres Straits specimens (a female with eggs): Length of carapace 11 mm.; maximum breadth 6 mm.; length of rostrum 4.5 mm.; length of chela 15 mm. (of propodite 7 mm., carpopodite 2.5 mm., meropodite 5 mm.)

Another small male: Length of carapace 6 mm.; breadth 3.5 mm.; length of rostrum 2.5 mm.; of chela, 9.5 mm. (propodite 4, carpopodite 1.5, meropodite 4).

So far as I can find, there is no description of *Galathea elegans* White, but only the figure. From this, however, I think it is possible to assert its community with the other forms under discussion. Balss queries his Japanese individual because its chelæ are more slender and longer than those in White's drawing and because the width of the colour bands is different. In my Torres Straits collection, as I have repeatedly observed, the width of the bands is a variable feature, so the latter point need not trouble us. The discrepancy of the chelæ is likewise to be explained by variation and possibly, to a certain extent, by the draughtsman's error.

I have taken the opportunity of comparing my series with a specimen obtained by Dr. Willey in New Britain and identified by Mr. L. A. Borradaile as *G. elegans*. This certainly differs distinctly from the commensal of *Comanthus* in the following particulars: It has a broader but rather shorter rostrum with more (9) lateral denticles. The eyes are larger, the transverse furrows on the dorsum not so well developed, hairs are almost absent on the greater part of the carapace but present on the rostrum. Here they are arranged in just the manner characteristic of the animals from the Torres Straits. This individual seems to come nearer to that described by Balss from Japan.

Galathea inflata sp. n. (Plate 1, Fig. 7.)

A small galatheid with rather broad and swollen carapace narrowing considerably anteriorly; rostrum of medium length with 3 sharp spines on each side; carapace with very few hairs, gastric region without spines, anterior transverse ridges broken up and surface covered with scales. Merus of third maxilliped with 3 spines internally, 2 externally. Merus of ambulatory limbs with about 9 spines on upper border.

Commensal with crinoids, Murray Island, Torres Straits.

With eggs, length of carapace to tip of middle spine on rostrum, 7 mm.; breadth 5 mm.; length of rostrum 2.5 mm.

The carapace is traversed by only 7 or 8 traverse grooves, but posteriorly incipient grooves make their appearance between the complete ones at the lateral extremities of the segments. The cervical groove is deep and continuous; on each side of it the traverse ridges are broken up into prominent scales. The external border of the cephalothorax has about 7 strong spines on each side.

The rostrum is broad and of medium length. The central spine is long and stout; on each side are two others, almost as well developed, and a third at the level of the eye which is shorter and weaker. The surface is covered with small scales.

The basal joint of the first antenna is provided with 3 spines, the dorsal of which is longer and stronger.

On the merus of the third maxilliped there are internally 3 spines, the middle one being the shortest; externally are 2 very blunt spines; the teeth on the inner border of the ischiopodite are small and numerous.

The chelæ are missing in this specimen. The ambulatory limbs are rather thickly beset with long coarse hairs; spines on the merus not very well developed, but spines on the carpus very prominent. Dactylopodite with strong spine after end claw, others small.

Colouration: Dark-blue pigment on carapace, with two fairly broad longitudinal pigment-free bands.

On *Comanthus annulatum* were a few very small galatheids, white in colour, with rather thin and membranous cuticle. Two which were examined in detail were females with eggs and could not have moulted very recently. In these the form of the rostrum comes very close to *G. inflata*. It is short and broad, armed with 4 spines on each side, of which the 3 anterior are prominent, almost as large as the median spine, and the fourth is much smaller. They differ from *G. inflata* mainly in the fact that the median spine is the same size as those which follow instead of being distinctly larger. The rostrum is covered by coarse hairs. The carapace is traversed by transverse grooves, but in one specimen (the larger) these are broken up at the side into rounded scales, while in the other the lines run interruptedly across. The carapace is not pear-shaped, as in *G. inflata*. In another point the two individuals differ considerably, that is, the development of the third maxilliped, which in the larger form possesses 2 spines on the inner side of the merus and some very small blunt processes on the outer border. In the smaller form (which was parasitised by a bopyrid) there is only a single spine on the inside, while the outside is smooth.

It seems possible that we are dealing with a variable species or possibly a group of species which has the rostrum character described above, while the carapace shape and to a certain extent its ornamentation varies with the size of the individual. The character of the third maxilliped is also variable, the number of spines on the merus increasing with age.

With regard to the strong development of pigment in one and its non-appearance in others, in spite of the fact that all were found on crinoids, I can make no suggestion of any importance. It may be that in a variable species some individuals are incapable of an assumption of pigment. It is not to be supposed, I think, that these unpigmented individuals had but recently taken up their residence in the crinoids, for they were mature females with eggs. However, I can not pretend to explain, on the strength of only three specimens collected, a phenomenon which is of so much biological interest.

For the present, then, I wish to recognize an "*inflata*" group, distinguished by the short, broad rostrum with 3 or 4 spines on each side (of

which the last is the smallest) and the absence of spinulæ on the gastric region. They differ from *multilineata* in having a shorter rostrum and longer spines and in the far less marked sculpturing on the carapace.

Galathea minuta sp. n. (Plate 1, Fig. 6.)

A very small galatheid, with short and broad rostrum, 3 sharp spines on each side; gastric region without spines, carapace with few hairs, traversed by about 12 shallow transverse grooves; chelæ short; merus of third maxilliped with 2 strong spines internally, one externally.

From *Comanthus annulatum*, obtained in about 4 fathoms of water off Mabuiag Island, Torres Straits, Australia.

Measurements: Length of cephalothorax to tip of rostrum 4.5 mm. Length of chela 6.2 mm., of propodite 2.7 mm. Breadth of cephalothorax 3 mm. Length of carpopodite 1.0 mm., of meropodite 2.5 cm.

The carapace is of fairly uniform breadth, narrowing slightly and gradually anteriorly. Its surface is smooth, traversed by only about 12 shallow grooves, in which lie scanty rows of short hairs. There are no spines on the gastric region, but prominent spines (8 in number) exist at the end of the transverse grooves.

The rostrum is rather short and broad. The central spine is very strong and elongated and on each side of it are 3 prominent spines with their bases close together and advanced, also strong and elongated. The surface is smooth.

The basal joint of the first antenna carries 3 anteriorly directed spines; the dorsal one is long, the two ventral smaller and more slender.

The merus of the third maxilliped carries 2 large spines internally and one, rather shorter, externally followed by small spinulæ. The teeth on the internal border of the ischiopodite are comparatively few and strong.

Abdomen with two transverse lines to each segment.

Chelæ short, about half as long again as the cephalothorax, beset with long, coarse, scattered hairs and strong spines on the propodite, carpopodite, and meropodite, especially the carpopodite. Dactylopodite little more than a third of the propodite in length.

Merus of ambulatory legs beset on upper angle with about 10 spines, very small proximally, prominent distally. Dactylopodite with strong end claw and one prominent spine succeeded by minute processes.

Colouration: Alternate longitudinal stripes of white and dark blue, as shown in plate, of about equal breadth. On a light-coloured individual of *Comanthus annulatum*.

AMPHIPODA.

A tiny amphipod which occurred very often on the darker crinoids is apparently to be referred to the family *Amphilochidæ*, a new genus of which must be established for its reception.

CYCLOTELSON gen. n.

Rostrum curved, acuminate, lateral angles of head rounded. Side plate 1 not much smaller than 2, rounded, obscured by those succeeding it; 2 to 4 large and deep, 2 and 3 rounded, 4 largest, quadrangular shape (also 5) as in *Amphilochus*. Antenna 1 very short and stout, flagellum particularly so. No accessory flagellum, upper lip bilobed, lower lip with small inner lobes. Mandible with very narrow denticulate cutting edge, molar process absent, third joint of palp very long. Maxilla 1, inner plate absent, outer plate with 8 or 9 spines, the proximal much the largest and forming dentate process

SUMMARY.

The object of this paper is to point out that of the large number of species belonging to many phyla which habitually shelter amongst the branches of the crinoids of tropical reefs, by far the greater proportion exhibit colour resemblance to the host. As the colour scheme of the host is often extremely variable (*e. g.*, *Comanthus annulatum*), that of the commensal, in some cases at least, varies too, but some commensals seem to be restricted in their response to the stimulus which causes this colour resemblance. Thus among the Crustacea, in *Synalpheus* all stages of variation are met with, according to the individual inhabited, between a pale form with very narrow stripes of pigment, to an extreme form totally covered with dark pigment: while in *Cirolana*, on the other hand, the individuals associated with even the darkest crinoids possess only insignificant lines of pigment on the otherwise totally white body. In the latter case there is, then, no protective resemblance, although we witness the incipient stages of its establishment. Other forms like the polychæt, the amphipod, and the brittle-star, *Ophiomaza*, give rise to dark varieties only and occur upon dark-green crinoids.

The following represents in a tabular form the results of the observations:

Commensal.	Pigments developed.	Host and colour variety of host.
Synalpheus brucei	Purple-black	All colour varieties of Comanthus annulatum and some other crinoids.
Synalpheus brucei	Red	Comatula purpurea.
S. comatularum	Brownish purple, purple and white.	All colour varieties of Comanthus annulatum and some other crinoids.
Cirolana lineata	Red or purple in faint thin lines, rest white.	All colour varieties of Comanthus annulatum and some other crinoids.
Cyclotelson purpureum	All purple	Dark varieties of C. annulatum.
Pontoniopsis comanthi	Bright green and black or yellow and red-brown.	Light (green or yellow) varieties of C. annulatum.
Periclimenes spp	Red and blue-purple	Dark varieties of C. annulatum.
Ophiomaza cacaotica	Dark purple, brown or black.	Dark varieties of C. annulatum (one exception).
Ophiomaza cacaotica var. *picta*	Black and white	Dark varieties of C. annulatum.
Ophiomaza obscura	Dark brown and dull yellow.	Dark varieties of C. annulatum.
Polynoë minuta	Dark brown or black	Dark varieties of C. annulatum.

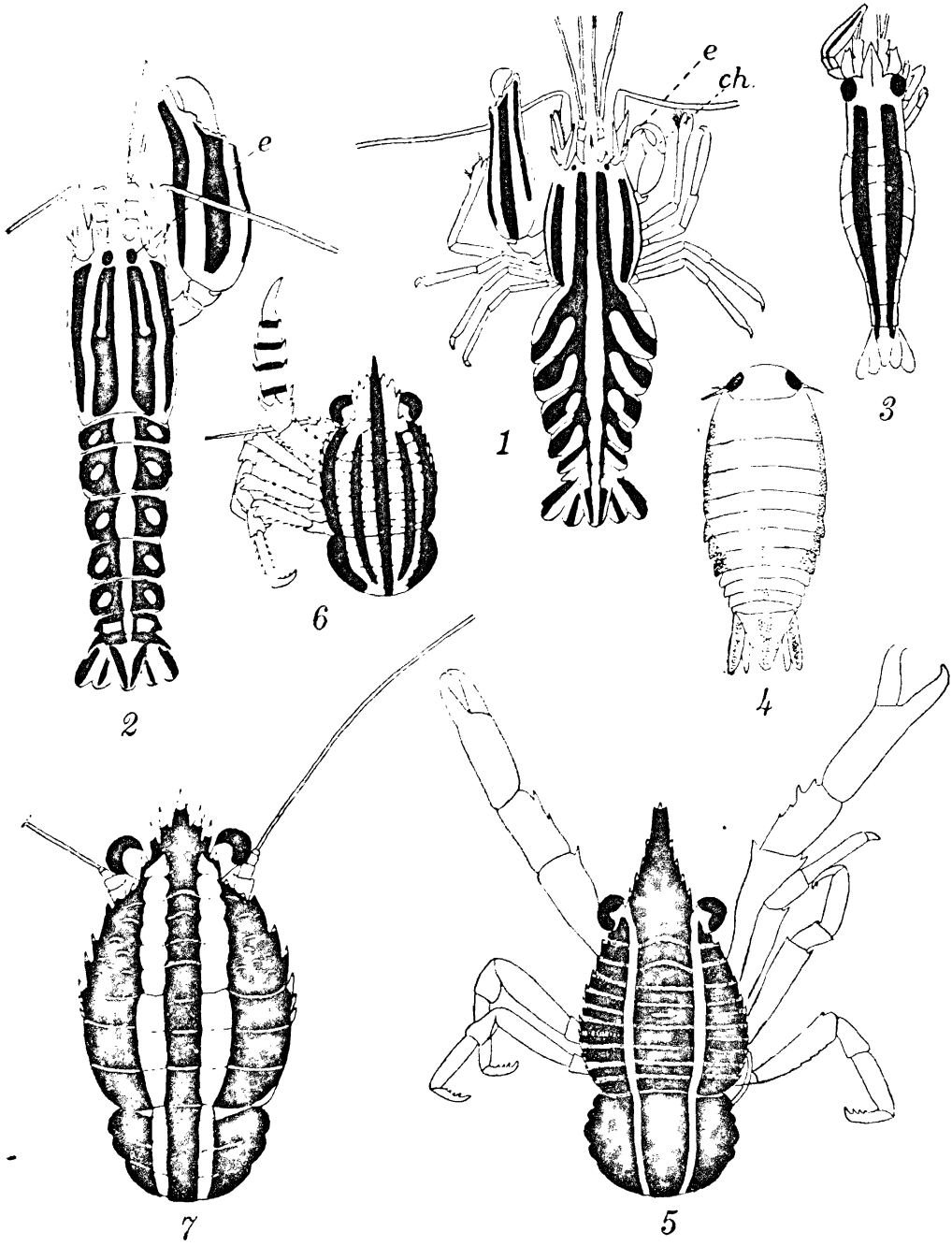

FIG. 1 *Synalpheus comatularum*. ×1.5.

FIG. 2. *S. brucei*. *e*, eye; *ch.*, small chela with its incurved thumb. ×3. Only a single example of *S. comatularum* and another of *S. brucei* is figured, so no idea of the variation in extent of pigmentation is shown, but only the type of arrangement. But both the type and variation are alike in the two species, that of *S. brucei* having rather deeper pigmentation, the bands being wider and the lateral unpigmented areas in the abdominal segments being completely enveloped by pigment.

FIG. 3. *Pontoniopsis comanthi*. ×6. FIG. 4. *Cirolana lineata*. ×7.

FIG. 5. *Galathea elegans*. ×4. FIG. 6. *G. minuta*. ×5. FIG. 7. *G. inflata*. ×6.