

THE MORPHOLOGY OF THE NUDIBRANCH GENUS HANCOCKIA

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SIX PLATES (TWENTY-TWO FIGURES)

INTRODUCTION

The genus *Hancockia* was established by P. H. Gosse in 1877 for the reception of a new species of nudibranch, *Hancockia eudactylota* Gosse, of which a single specimen had been taken in dredging in Tor Bay, near Torquay, England. Though brief, his paper so clearly describes the external peculiarities of this singular mollusk, that it is difficult to understand the disregard of the new genus by Bergh ('92) in favor of *Govia*, created by Trinchese nine years later to include two new species found in the Bay of Naples, since the two genera are undoubtedly the same. As pointed out by Eliot ('06), the name *Hancockia* has undoubted priority, and *Govia* must be canceled in its favor. Of this rare genus but nine specimens appear to have been recorded, the original one by Gosse ('77), one by Gamble ('92), and three by Eliot ('06), from the Plymouth region, and the four described by Trinchese ('85, '86) as representing two new species, *Govia rubra* Tr., and *Govia viridis* Tr. from the Bay of Naples. Garstang ('93) has shown that the doubtful *Doto uncinata* of Hesse ('72) from Brest is really a *Hancockia*, and possibly identical with *H. eudactylota* Gosse. Eliot ('06, '10) shares this opinion and indicates the possible specific identity of *Hancockia eudactylota* Gosse, *Doto uncinata* Hesse, and *Govia viridis* Tr., also tabulating the three species as synonymous. It is evident, however, if the above identity be accepted, that the specific name *uncinata*, having priority, must replace the other two, and that the type of the genus should be designated *Hancockia*

uncinata (Hesse). The few specimens thus far studied have been in the main in poor condition, and have left many points in their anatomy doubtful or entirely unknown.

It has been my good fortune to discover a representative of this genus in Monterey Bay at Pacific Grove, California, where it is not at all rare, and the study of this new species has enabled me to clear up many details in its anatomy, which are the subject of this paper. The genus diagnosis following is amended from that given by Gosse, and modified by Eliot in the light of these results.

HANCOCKIA, Gosse, 1877

Hancockia, Gosse, P. H., Ann. Mag. Nat. Hist., Series 4, XX, 1877, p. 316, Pl. XI.

Govia. Trinchese, S., Rend. R. Accad. Sci. fis. mat. Napoli, 1885, 6; —Mem. R. Accad. Sci. Ist. Bologna, Ser. IV, T. VII, 1886, p. 183, 1 Tav.

Hancockia, Norman, A. H., Ann. Mag. Nat. Hist., Ser. 6, VI, 1890, p. 79.

Hancockia, Gamble, F. W., Ann. Mag. Nat. Hist., Ser. 6, IX, 1892, p. 378, Pl. 17, f. 3.

Hancockia, Eliot, C., Jour. Marine Biol. Assoc. VII, 3, 1906, p. 353, Pl. XI-XII, f. 10-13; —Monog. British Nudibr. Moll. (Alder and Hancock) VIII (Supplementary), 1910, p. 163.

Animal elongate; foot narrow, linear, truncate in front, bluntly pointed behind; head with an oral veil bearing palmate processes at the sides; rhinophores with perfoliate clavus retractile into campanulate sheaths. Dorso-lateral margins bearing a series of lobed processes, the cerata. Liver in three divisions, ramifying to the cerata and to the rhinophores. Cnidosacs present in cerata and in rhinophore sheaths. Labial disc armed with chitinous rodlets. Masticatory margin of mandibles denticulate. Radula triseriate, similar to that of Galvina, the median tooth denticulate, the laterals broad and smooth. Genitalia unarmed.

Hancockia californica, sp. nov.

Body elongate, compressed, the highly arched body set off from the foot by a well defined longitudinal groove. Tail short, rapidly tapering to a blunt, slightly notched tip.

Head rounded, bearing on either side a broad, palmate velar lobe, with six to ten or more fingerlike subdivisions of unequal length, the longest one half the length of the whole lobe, the shortest mere tubercules.

Dorso-lateral margins with a single series of four to seven non-caducous cerata on each side. The first pair opposite, in front of the prominent cardiac elevation of the dorsum, the remaining ones becoming progressively less directly paired, until the posterior ones are alternately placed, those of the right side being shifted posteriorly in each case. Each ceras arises from a stout base and expands into a palmate, distal portion, strongly concave on its outer face, and bearing on its margin a series of from four to sixteen digitiform projections, arranged in a horse-shoe shaped grouping, a median, dorsal one above, the others along the anterior and posterior margins of the ceras. The largest of these may bear irregular nodular tuberosities on their margins, those on the anterior cerata being larger, more numerous, and even forming short branches, while on the posterior ones the whole structure becomes smaller and less complex.

Rhinophores nearly erect, divergent, inclined slightly forward, arising from the dorso-lateral margin of the head. The stalk is slender and bears a vertically perfoliate bulb, terminated by a blunt apex, and is surrounded by a large, funnel shaped or calyciform sheath, into which it is deeply retractile. The thin margins of the sheaths bear six to nine slight, blunt elevations, irregularly spaced, the terminations of ridges along the outer surface of the calyx, which approach and merge into each other, and into the stalk of the rhinophore below. The vertical leaves of the rhinophore clavus are few in number, and narrow gradually below, but pass abruptly above into the stalk. They may be simple, or longitudinally cleft along the free margin. Beyond the leaves of the clavus the stalk is prolonged distally as a cylindrical, blunt tip, one-fourth the length of the perfoliate portion. The ridges of the sheath bear a series of minute nodosities on the outer surface, each one of which contains a cnidosac, while the space between the ridges is web-like, thin and smooth.

Foot narrow, linear, bluntly rounded in front, with a slight, median notch, the posterior end relatively broad and rounded, slightly notched, and usually folded into a deep, longitudinal groove along its ventral surface.

General body color reddish brown, in some individuals light, in others dark, or tending to greenish, but in general closely resembling the brown sea-weeds, such as *Laminaria* and *Deleseria* upon which it is usually found, and from which it can be distinguished only by close scrutiny. The tubercles of the rhinophore sheaths and cerata appear usually as opaque white dots, the stalks of the rhinophores and the cerata are often thickly sprinkled with white, which in some individuals becomes aggregated into a series of irregular, larger white spots along the dorso-lateral region of the body back to the third pair of cerata. Foot a clear, translucent pinkish brown. The prominent, pericardial area is usually of a clear, uniform brown color, or may bear a few, small, white or bluish white spots, while in front and behind it, the remaining dorsum may be uniform, or more frequently show irregular, darker, indistinct blotchings of brown. The outline of the vascular ramifications to the cerata is frequently strongly evident in life, more so in preserved specimens, as elevated ridges dividing the dorsum into irregular, rhombic areas, mainly evident behind the heart area, as is shown in figure 1.

The mouth is a longitudinal slit with moderately thin lips. Immediately in front of the opening into the inner mouth cavity the thin cuticle of the mouth tube is thickened into a strong lip disc, or labial armature, encircling the opening, and bearing a band of closely set blunt rodlets, the individual elements of which may reach an altitude of 0.033 mm., and a diameter of 0.006 mm.

Mandibles elliptical, thin and delicate, except the portion near the hinge, which is somewhat thickened. The masticatory margin bears a series of minute serrulations, more or less irregular in form.

The radula is long, moderately wide, triseriate, and but slightly tapering, the teeth from 50 to 62 in number, the last thirty of which are included in the sheath. The median tooth (figs. 8, 9, 10) is massive, horse-shoe shaped as seen from above, and is prolonged into a strong median cusp, with from three to five, usually four, well developed lateral spines or denticles on either side. The laterals are thin and transparent, and not easily seen.

Each lateral tooth (fig. 10, *l*) is a thin, broad, flattened plate, the inner, posterior margin of which is prolonged obliquely upward in a broad, lancet shaped cusp, but slightly elevated above the plane of the plate. The inner margin of this cusp rises abruptly to the tip, the outer margin is more sloping, and bears a variable shoulder, or even denticle-like elevation near its outer end. The inner, anterior angle of each lateral tooth is bifid, being divided into two nearly equal, rounded projections (fig. 10, *e*). Typical median teeth vary in width from 0.021 mm., to 0.052 mm., and from 0.024 mm., to 0.054 mm., in length, including the median cusp, while laterals vary from 0.030 mm., to 0.036 mm., in height of inner cusp, and from 0.044 mm., to 0.090 mm., in width, such differences in measurements being found between the oldest and youngest teeth in the same radula.

Total length of large individual, 21 mm.; diameter of body at thickest region, 3.0 mm.

Habitat, Monterey Bay, California, near extreme low-tide level, in tide pools and channels off exposed rocky points.

Hancockia californica is found near the low-tide limits, usually upon the brown sea weeds such as *Delesseria* growing in the tide pools between the granitic rocks most exposed to the dash of the surf. It has been taken mainly along the outer reefs of Cabrillo Point (Point Alones, Chinatown Point), and along the ocean side of Point Pinos, at the southern end of Monterey Bay, but has not been found in the more sheltered coves. At dead low tide, when the water is exceptionally smooth, it has been found floating, foot uppermost, at the surface of the water, along with other minute species of Aeolids. Ordinarily, however, it frequents the brown algae, to which it clings with great tenacity by means of the mucous secreted by the foot. In captivity it is at first very active, continually creeping around the sides of the aquarium and upon algae by a method entirely different from the smooth gliding movement of other Nudibranchs. The anterior third of the body, i.e. the portion in front of the heart region and the second pair of cerata, is stretched forward to its full extent, the anterior end of the foot and the lip region are closely applied

to the surface and adhere tightly while the rest of the body is pulled forward, a distance of 1 or 2 mm. at a time, the posterior end of the body taking but little active part in the process. When crawling the fingerlike tips of the velar lobes are kept in constant motion as tactile organs, feeling about in every direction in a strikingly characteristic manner. The processes of the cerata are also alternately extended in a plane, and folded together toward the vertical axis of the ceras more or less continually, though more slowly. In captivity the animals often float upside down at the surface of the water, in which position the foot is usually, but not always, expanded flat with the surface. They do not stand confinement well, become sluggish, and die after a few days. Pairing and egg laying take place in the aquaria, but are usually noted soon after capture if at all.

Concerning the feeding habits of *Hancockia* but little can be said. In their natural surroundings the brief period of extreme low tide in the dim light of early morning has given but little opportunity for observation, and that period represents a very small portion of the daily life of the animal. It is not to be assumed that the animal confines its wanderings to *Delesseria* and the like, simply because the practiced eye can recognize it then, and it may range more widely among the algae and hydroids of the tide pool. It will feed upon various small hydroids in captivity, and the detritus in the alimentary canal seems to indicate food of that nature.

INTEGUMENT

A marked range of color variation is noticeable in different individuals, ranging from a pale greenish or reddish brown to a dark red in the ground color. The markings upon this background may be entirely absent, few, or abundant, and consist of white, light cream, greenish white, or bluish white sprinklings or blotches of varying size. Such extremes might readily lead to the assumption that more than one species was involved, were it not that further collecting brings intermediate forms to light, and anatomical details are the same throughout. The different color patterns occur together, and the different individuals pair readily

when kept in aquaria. I am inclined to believe that the two species *H. rubra* and *H. viridis*, described by Trinchese ('86), are very possibly but color variations of one species alone.

The epidermis of *Hancockia* consists of a single layer of columnar epithelium containing a vast number of mucous cells. Upon the sole of the foot the epithelium is ciliated, and the unicellular glands of the epithelial layer disappear, their function being assumed by mucous glands made up of crowded cell groups, lying below the epithelium in the dermis, and connected with the external surface by slender ducts. Trinchese ('86) describes cilia as occurring everywhere over the body surface, being especially long on the rhinophores and cerata, shorter on the sides, and shortest on the foot. This statement I am unable to confirm, cilia being limited to the sole of the foot only in *H. californica*. The epithelium rests upon a thin basement membrane followed by connective tissue and muscle fibers, the latter arranged in two illly-defined layers, circular and longitudinal, with numerous oblique bundles interlacing in all directions. The integument thus formed is traversed by irregular blood lacunae, which communicate on the dorsal surface with the venous trunks tributary to the auricle of the heart.

In what may be termed the palmar surface of each ceras, i.e. the face turned outward and concave, is to be found close beneath the epidermis a mass of small alveolar glands, which open externally by slender ducts seen with difficulty, passing between the epithelial cells.

ALIMENTARY SYSTEM

The mouth of *Hancockia* is guarded by moderately fleshy lips (fig. 2), notched slightly in front and behind, surrounding a longitudinal slit which leads into the oral tube. Figure 11 presents a reconstruction of a median section through the anterior end of the animal, in which the mouth, pharyngeal bulb and anterior end of the oesophagus are bisected vertically. The oral tube is here dilated, is short and wide, its sides are folded longitudinally, and the whole is lined by low columnar or cuboidal epithelium through which open numerous oral glands (*l.g.*),

especially on the dorsal surface. Immediately in front of the pharyngeal bulb the tube is dilated by a circular depression, nearly doubling its diameter. At the back of this space and forming the anterior portion of the pharyngeal bulb appears a strong, circular elevation, the labial disc, surrounding the inner mouth opening, the epithelium of which bears a strongly developed ring of closely set cuticular rodlets (fig. 11, *l.a.*) forming a labial armature, used in the prehension of food. Each rodlet, representing the cuticular secretion of the single epithelial cell bearing it, measures approximately 0.003 mm. in diameter, and ranges in length up to 0.033 mm., the shortest rodlets being found on the outer and inner borders of the band (fig. 19, *l.r.*). A labial armature of this form is not uncommon among the Dorids, but, so far as I am aware, has never been found previously among Aeolids save in the case of the Dironidae. In the latter (MacFarland, '12) the lip disc is covered with a thick cuticle, which tends to split up vertically into a closely set mass of flexible, hair-like structures with tapering or split ends, while in *Hancockia*, definite, cylindrical, blunt rodlets are found. In *Bornella* a scale-like cuticular armature has been described.

Immediately in front of the lower margin of the labial armature in the median line opens a common duct, formed by the union of three tubes, one from either side, and a third, median one from behind. The lateral tubes (fig. 11, *d.s.*), are the ducts of the anterior salivary glands, the so-called glandulae ptyalinae of Bergh. Since nothing is known of the nature of the possible ferments secreted by these glands, a name expressing anatomical relations rather than physiological character is more desirable, such as pre-bulbar, or oral tube glands. These glands are large organs, extending dorsally around the anterior portion of the pharyngeal bulb (fig. 11, *a.s.*), and prolonged into the rhinophores nearly to the tip of the bulb (fig. 4, *a.s.*). The single, wide, ciliated duct is crowded with closely-set acini on all sides and extends the full length of the gland. Trinchese ('86) describes similar glands for *H. viridis* and *H. rubra*, which extend into the bases of the rhinophore sheaths, and in which the duct is ramified, instead of undivided as in *H. californica*.

The third, median tube (fig. 11, *m.d.*), uniting with the paired ducts of the anterior salivary glands, is lined with clear ciliated cells of a low columnar or cuboidal form. Immediately below and close to it is the anterior end of the cephalic aorta, not shown in figure 11, from which it is at all times easily distinguishable in sections. Below the posterior portion of the region of the radula this duct shifts slightly to the left, and the cephalic aorta assumes the median position. The diameter of the duct is at first about 0.054 mm., its lumen being circular in outline. It soon flattens somewhat and dilates more or less irregularly, forming a blind sack-like organ, extending backward beneath the ovotestis to the region of the third or fourth ceras of the right side, that is, over three-fourths the total length of the animal (fig. 4, *m.s.*). Its lumen widens to a maximum diameter of 0.3 mm., and is somewhat flattened as a rule. The lining epithelium is composed of clear, cuboidal cells with large nuclei, rich in chromatin. Cilia are borne only at the anterior end of the tube for a distance of some 0.45 mm. Its opening lies at the summit of a short, conical elevation projecting into the slightly dilated, median tube, which laterally receives the ducts of the anterior salivary glands and opens into the mouth tube. Below the posterior end of the pharyngeal bulb the sack dilates (fig. 11, *m.s.*) and its epithelium is thrown into numerous longitudinal folds, which soon disappear, however. Well-developed longitudinal and circular muscles and a slight amount of fine connective tissue surround the epithelium, and together make up a structure readily identified in either transverse or longitudinal sections. I have been unable to find anything in the literature of the Opisthobranchia which records the presence of any similar structure. In Eliot's ('96) brief account of the anatomy of *Hancockia eudactylota* there is represented in figure 12 of plate XII, the cross section of a tube lettered *m*, and, in the explanation of the plates, it is designated as 'duct of albumen gland.' This identification cannot possibly be correct. From a comparison with my own sections it is probable that *m* in Eliot's figure represents the ventral salivary sack here described. Eliot makes no mention of it in his text. What the function of this structure may be requires further investigation.

It may possibly serve as a median reservoir for the secretion from the paired anterior salivary glands, the structure of its epithelium not indicating any great secretory activity on its own part.

Hecht ('96, pp. 128-130, pl. III, figs. 39, 40) describes for *Doto* two sorts of salivary glands representing the pre-bulbar or anterior group. These are: 1) a circlet of small, peribucal glands with separate ducts; 2) two glands, corresponding to the unpaired anterior salivary gland briefly mentioned by Alder and Hancock ('45-'55), and by Bergh ('79, '88). These two unpaired glands are situated, the one above the other, behind the pharyngeal bulb, a little to the left of the median line, and open by separate ducts closely united in the median line in front of the bulb. The upper gland appears to be made up of two elongated piriform sacks opening into the duct. The lower gland, much more spacious, has, in addition to cells of the usual salivary type, enormous spherical cells, reaching 0.060 mm., in diameter, which project outward from the wall into the surrounding spaces, being attached only by a narrow pedicle, and covered by a thin layer of connective tissue. Their cytoplasm is finely granular, the nucleus enormous, with abundant granulations surrounding the nucleolus. In other instances Hecht believed that these cells had separated entirely from the salivary epithelium, which had given them origin, and were free in the general tissue spaces of the body.

Brygider ('14) has more recently studied these glands in detail, confirming and extending the descriptions of Hecht, but interpreting the two glands as forming one paired organ.

It is possible that the condition found in *Hancockia* is comparable to that in *Doto*, if we assume that the upper, unpaired gland in the latter species represents the paired, anterior salivary gland of *Hancockia*, the single bilobed gland and its duct having been divided lengthwise, while the lower, unpaired gland of *Doto* represents the unpaired, sack-like gland of *Hancockia*. Only in two young individuals of the latter species have I been able to find any cells at all comparable to those described by Hecht. They are much smaller and are fewer in number, are found in the region immediately behind the pharyngeal bulb, and bear similar relations to the epithelium of the salivary gland. They

are, however, accompanied by another type of cell equally prominent, very deeply staining which project into the lumen of the gland. In an as yet undescribed species of *Doto* from Monterey Bay I find the two glands much as described by Hecht and Brygider, the giant cells being much larger, however, reaching a diameter of 0.135 mm., equaling in a single cell the size of the whole pedal ganglion in the same animal. Further cytological studies are necessary before this suggested interpretation can be taken as anything other than provisional. With the exception of *Doto*, nothing similar to the unpaired median salivary gland of *Hancockia* has been recorded.

In figure 4 a reconstruction of the alimentary system as seen from above is represented. The body wall is cut through at the level of the cerata bases and the contracted rhinophores are similarly laid open. The mouth tube is here concealed from view by the overlying anterior end of the pharyngeal bulb (*p*), and by the integument of the frontal region. The pharyngeal bulb thus exposed is elliptical in outline, the median, longitudinal section in figure 11 shows its cavity, its muscular walls and radula.

The sides of the muscular pharyngeal bulb bear the thin mandibles, somewhat elliptical in shape, and thinning away posteriorly into the usual cuticular lining of the buccal cavity. In front each mandible bears a slender masticatory process (fig. 11, *m*, fig. 19, *m.e.*) the two uniting below in the median line. The anterior cutting edge of each of these processes is armed with an irregular series of some 20 to 30 blunt denticulations, becoming progressively less prominent below and dying away in an undulatory margin. A somewhat similar armature is described by Trinchese ('86) and by Eliot ('06) for the Neapolitan and Plymouth species, the number of denticulations being apparently smaller.

Into the pharyngeal, or buccal, cavity projects a strong triangular muscular mass from its posterior wall, the odontophore. This is seen in median section in figure 11. The radula extends forward from the posterior end of the tubular radula sheath (*r.s.*), becomes exposed at its anterior portion, and doubles abruptly back ventrally along the lower face of the odontophore.

Some five teeth are thus free from the sheath behind the anterior angle of the radula, and these, together with those covering the angle and its immediate ventral face, are the functional ones. The epithelium of the dorsal wall of the radula sack is reflected upwards at its opening, and becomes continuous with that covering the upper surface of the odontophore. In this region the cuticle of the epithelium becomes greatly thickened (fig. 11, *c.r.*) and in the median line forms a relatively sharp, longitudinal ridge, shown in transverse section in figures 16 and 17, *a*. Figure 16 represents a cross section of the upper part of the pharyngeal bulb, taken from the region behind the entrance of the oesophagus, while figure 17 is from immediately in front of the opening of the latter, slightly in front of the dotted reference line *c.r.* in figure 11. The epithelium in the median line covers a narrow ridge (fig. 17, *r*) bounded on either side by a deep groove, the whole covered by a strong cuticular thickening which is heaviest in the median line and rapidly thins away laterally. Opposed to this cutting or crushing edge is the thick cuticle of the dorso-lateral walls of the buccal cavity, especially that immediately in front of and lateral to the oesophageal opening, shown in figure 17, *oe.* and in figure 11 in face view, as the whole lateral wall above the odontophore. Nothing similar to this strong, median cuticular ridge has been recorded among the Aeolidiadae. It manifestly forms an additional and effective mechanism for the trituration of food.

The detail of the radula has been given in the preceding specific diagnosis of the animal. It resembles that of *Galvina* in a striking manner, but this resemblance is not borne out in any other anatomical details. Eliot ('06) has figured a typical transverse row of the radula of *H. eudaetylota*, and Trinchese ('86) gives a figure of a single median and two lateral teeth of his species *H. viridis*. A comparison of figures 8, 9, and 10 of the present paper with these shows striking differences. Trinchese ('86) alone gives any measurements, which, of course, vary in different parts of the radula. Since he makes no statement regarding the radula of his other species, *H. rubra*, one may assume that they are practically identical. A tabulation of his data in comparison

with similar measurements taken from *H. californica* is given in the following table.

SPECIES	MEDIAN TOOTH		LATERAL TOOTH	
	Length	Width	Length	Width
	mm.	mm.	mm.	mm.
<i>H. viridis</i>	0.035	0.030	0.020	0.040
<i>H. californica</i>	0.024-0.054	0.021-0.052	0.03-0.036	0.044-0.090

The median cusp of the central tooth in the Californian species is relatively much stronger in proportion to the lateral denticles, than in the European ones, in both of which the lateral denticles are so strongly developed that but little difference in size is found between them and the median cusp. The lateral tooth of *H. californica*, while a thin, nearly transparent plate, seen with difficulty, is proportionately larger also, and, in addition to the sharp pointed, inner, main cusp, has a secondary elevation upon its outer slope, from which the anterior border passes much more abruptly backward to the broad, flattened, plate-like base. The rectangular outline surrounding the lateral tooth of *H. eudactylota* represented in figure 10b of plate XI of Eliot's paper probably has nothing to do with the structure of the tooth or the radula. The anterior margin is deeply indented forming an angle very similar to that of the cusp upon the posterior margin, so that the query naturally occurs as to whether this is actually an anterior margin of the form indicated, or not simply due to an overlapping of the cusp of the following tooth. Such an error can readily be made in studying this difficult radula. Trinchese ('86) represents the posterior margin as straight. In *H. californica* it is curved, as shown in figure 10, l. The anterior inner angle is a simple one in the figures of Eliot and Trinchese, instead of possessing the bifid form seen in figure 10.

The total number of rows as given by Eliot is 31, Trinchese makes no statement in this regard, while in *H. californica*, the number varies from 50 to 62 in the numerous specimens examined. These radula characters alone sufficiently distinguish the Monterey Bay form as specifically distinct from those of European seas.

The posterior salivary glands (figs. 4 and 11, *p.s.*) are branched tubular in form, their many ramifications lying immediately behind the pharyngeal bulb. They unite in a single duct on either side, which passes forward through the central nervous ring, enters the dorso-lateral muscular wall of the bulb, courses laterally forward in it, and open into its cavity on either side, opposite the anterior angle of the radula.

The oesophagus (fig. 4, *oe.*) is a curved tube, passing downward and backward, being displaced to the left by the large anterior genital complex. It is lined by relatively tall, columnar epithelium with small basally placed nuclei, clear, finely granular cytoplasm, and bearing short, fine cilia on the free surface.

A short distance before the oesophagus dilates into the anterior stomach, it gives off dorsally a blind, sausage-shaped diverticulum, the distal end of which is directed forward. This pouch (fig. 4, *d.*) may reach a length of 0.67 mm., and a total diameter of 0.30 mm., the oesophagus, itself, immediately in front of its origin, measuring but 0.15 mm., in diameter. The epithelium of the diverticulum is made up of a single layer of closely packed, slender, cylindrical cells of much the same appearance as those of the oesophagus, but nearly three times as high. The remainder of the wall of both oesophagus and diverticulum consists of a few circular and longitudinal muscle fibers and of connective tissue.

Behind this blind sack, a structure recorded in but few other Aeolids, the oesophagus dilates into the anterior, ventral stomach, relatively thin-walled and roomy. Its posterior end curves upward and forward into the thick-walled, muscular stomach (fig. 4, *st.*). From the left dorsal wall of the anterior division, in the angle formed by the U-shaped gastric bend forward, the roomy, anterior hepatic duct is given off, at once dividing into left and right hepatic ducts (fig. 4, *l.h.*, *r.h.*). Close behind the origin of these the posterior hepatic duct arises, and passes backward in a zig-zag manner, giving off branches to each ceras behind the gastric region in turn (fig. 4, *p.h.*, *h.*).

The epithelium of the first gastric division is composed of low, columnar, ciliated cells, surrounded by a thin layer of connective

tissue and circular and longitudinal muscle fibers. The inner surface is smooth, or but slightly ridged longitudinally. In the dorsal muscular stomach the wall becomes greatly thickened by an increase in the number of circular muscle fibers (fig. 7, *m.*). Within this muscular coat the epithelium and the subjacent connective tissue become raised into ridges, and isolated conical papillae arranged in longitudinal rows. The columnar epithelium is non-ciliated, and bears very strong, tooth-like, cuticular thickenings, forming an efficient gastric mill, or grinding apparatus (fig. 7, *e.*; fig. 20, *t.*). In the depression between these elevations the epithelium bears only a thin layer of cuticle. At the distal end of this division the circular muscle layers are increased, forming a local sphincter, indicated externally by a slight constriction (fig. 4). Beyond this the elevations with their gastric teeth disappear, the epithelium becomes much higher, the nuclei are again basal in position, while the remainder of the cell becomes clearer, and bears distally a border of low cilia. A prominent, low, longitudinal fold of the mucosa is developed along the ventral side of this pyloric division of the stomach, and is continued on into the intestine, into which the stomach now rapidly narrows (fig. 4, *i.*). This typhlosole fold has a somewhat reniform outline in cross section and is connected with the ventral wall of the pylorus and intestine by a very narrow stalk. Its epithelium is of high columnar form with basal, rounded nuclei and clear cytoplasm, and bears quite long cilia. In this region, and throughout the intestine, the general epithelium becomes lower, save along a few, scarcely prominent ridges, in which their elevation is largely due to the increased length of the cells covering them (fig. 21). The intestine forms a loop to the right, approaches the body wall obliquely, and opens externally midway between the first and second cerata on the right side at the level of their bases. Approaching the anus the typhlosole gradually becomes less prominent, and loses its identity among the other longitudinal folds developing in the mucosa of this region.

The liver of *Hancockia* is completely ramified, being made up of the two anterior and the single posterior hepatic ducts, opening into the anterior division of the stomach, and their glandular

subdivisions, contained within the dorsal appendages of the body. The anterior hepatic ducts (fig. 4, *r.h.*, *l.h.*) give off a branch to the first ceras of each side, and then pass forward, and break up into a number of terminal branches in the base of the rhinophores. These subdivisions ascend the stalk and radiate upward and outward in the sheath of the organ, their position being indicated externally by longitudinal ridges, as seen in figures 1 and 3, terminating in the rounded elevations located on the margins of the calyx. The hepatic ducts are lined with a low, cuboidal epithelium, containing relatively few secretion granules. In the cerata and the rhinophore stalks the lumen becomes irregularly expanded into saccular dilatations with short branches, all lined with taller cells, packed with secretion granules of varying sizes. Each of the rounded elevations located at intervals along the ridges of the rhinophore sheaths, incloses an elliptical, or nearly spherical cnidosac, connected with the exterior by a minute pore, and opening into the lumen of the distal hepatic branching by a constricted neck. Each cnidosac is packed full of slightly curved, rod-shaped nematocysts arranged radially, and averaging some 8μ in length. Similar cnidosacs are found in considerable numbers along the subdivisions of the cerata, their presence being usually indicated externally by a rounded elevation or a slight knob.

This extension of the liver branches up into the rhinophores has not been found previously in any of the Aeolids. Trinchese ('86) mentions nothing of the sort for the Neapolitan species of *Hancockia*, and Eliot ('06) states that the anterior hepatic ducts supply the first pair of cerata, and then run straight forward, terminating in the anterior part of the foot. He rather doubtfully records the presence of cnidosacs in the cerata, and traces of similar openings on the anterior margin of the foot. With the limited amount and the poor condition of the material at his disposal, it is quite probable that he mistook a section of a part of the rhinophore for the tip of the foot. Certain it is that in my abundant material there is neither trace of any extension of the hepatic ducts into the foot, nor evidence of cnidosacs in that locality.

The posterior hepatic duct (fig. 4, *p.h.*) passes backward to the end of the body cavity, giving off branches to the cerata of either side alternately, the first branch passing to the second ceras of the left side. The duct lies below the lobules of the ovotestis, immediately above the posterior pedal artery close to the foot, instead of in the usual relation above the ovotestis. But few of the Cladohepatica possess this arrangement; Glaucus, Pteraeolidia, Cuthonella, the Janidae, Dendronotidae, and Hermaeidae being listed by Bergh ('92) as showing this relation.

CIRCULATORY SYSTEM

The circulatory system of Hancockia exhibits the usual relations characteristic of the Nudibranchiata. The pericardium forms a very conspicuous hemispherical elevation on the dorsal surface, between the second and third pairs of cerata (fig. 1), and through its thin wall the pulsating ventricle may be readily seen in life. Behind the cardiac prominence a zig-zag ridge may be traced from the posterior end of the animal to the heart. It is alternately directed to the right and left toward points midway between successive cerata of each side, and, at each lateral angle thus formed, receives similar, though smaller, elevations from each of the two adjacent cerata, thus marking off a series of rhombic areas on the dorsum, as shown in figure 1. These elevations correspond to the main venous channels bringing blood from the cerata to the auricle. From the first pair of cerata, in front of the heart a right and left vein, similarly located, open into the anterior ends of the auricle. Into these dorsal venous channels the blood lacunae of the body wall open freely everywhere, so that they collect the blood, which has been aerated in the cerata and the general body integument, and conduct it on to the heart.

The auricle is a U-shaped, thin-walled sack, a lateral lobe on either side extending forward nearly as far as the anterior margin of the spherical ventricle, which is inclosed between them. The auriculo-ventricular opening is guarded by a pair of flap-like, transverse valves. The auricular chamber is lined by flat endothelium and is reinforced by a close-meshed lattice work of

muscle fibers, interlacing at right angles, and supported by a small amount of connective tissue. The wall of the ventricle is similar, but contains stronger and more irregularly arranged bundles, and, in addition, anastomosing trabeculae of strong muscle fibers pass across the lumen, from wall to wall, in various directions. From the anterior, ventral face of the ventricle, slightly to the right of the median plane, a short aortic trunk passes downward, its origin being guarded by a single valve, a flap-like reduplication of the anterior margin. Immediately beyond its emergence from the pericardium the aorta gives off a rear branch, the posterior aorta, which courses backward over the dorsal surface of the hermaphroditic ampulla and accompanies the hermaphroditic duct, usually below it, giving off branches to each follicle of the hermaphroditic gland in turn. The aorta proper curves forward and downward, giving off in succession branches to the stomach and intestine, the nidamental gland, the prostatic portion of the vas deferens, the spermatotheca, the vagina, and the preputium, then, passing downward behind the pharyngeal bulb, sends a branch to the foot, which divides into anterior and posterior pedal arteries. The main trunk, now the cephalic aorta, runs forward in close contact with the ventral wall of the pharyngeal bulb and supplies branches to it, the anterior salivary glands and the mouth region.

The blood thus distributed by the branches of the aorta passes into the tissue spaces and smaller and larger lacunae of the body, finally making its way to the lacunae of the integument and the cerata, where it is aerated, collected in the different veins, and conducted again to the auricle of the heart.

EXCRETORY SYSTEM

The excretory system in *Hancockia* consists of a broad, roomy sack extending nearly the full length of the body along the dorsal surface of the viscera, immediately below the integument, the heart, and its main veins. Laterally this sack is prolonged into numerous blunt, slightly branched diverticula, which extend for a short distance down the sides. The whole structure, however, is relatively simple in its contour, presenting nothing like the

complexity of outline found in most Aeolids. Below the heart the renal sack is prolonged forward on the left side around the aorta, as a blind extension, which does not unite in front with any of the other rami of the organ. The renal sack thus lies on the left side of the aorta. To the right, and behind the passage of the latter vessel through the pericardial wall, the reno-pericardial syrx, or pyriform vesicle, forms the communication between the pericardium and the renal sack. It is a bluntly elliptical or barrel shaped organ, slightly flattened dorso-ventrally, about two and one-half times as long as broad, measuring 0.3 mm., in length by 0.12 mm., in breadth, in an individual of 14 mm., total length. Its wall is muscular and is lined by a layer of high columnar cells, each of which bears cilia, reaching three times the length of the cell itself. These cilia appear to be matted together into a single tuft from each cell, and curve backward in the lumen toward the renal end of the syrx. Aside from a slightly developed ridge on the mid-dorsal and mid-ventral surfaces the epithelium presents a smooth regular surface without the conspicuous folds usually described in this organ. Close to the opening of the pyriform vesicle into the renal sack a short canal is given off, which passes directly upward and to the right, and opens externally immediately above the anal papilla. The kidney is lined everywhere with low cuboidal cells, with clear nuclei, rich in chromatin, and with vacuolated cytoplasm. No evidence of inclosed concretions was seen, possibly due to their solution by fixing fluids.

The simplicity of the renal sack and the lack of inner, longitudinal folds in the syrx in *Hancockia* are characters found also in Doto and Calma (Hecht '96, p. 103).

CENTRAL NERVOUS SYSTEM

The central nervous system presents an extreme concentration of the ganglionic masses, with a maximum shortening of the commissures and connectives joining them. Figure 12 represents the group as seen obliquely from above and behind, figure 13 from the left side, and figure 14 from below and in front. Forced to the left by the pressure of the anterior reproductive

organs, it is decidedly asymmetrical in appearance. The cerebro-pleural ganglia (*c.pl.g.*) form a compactly fused mass of somewhat triangular shape, with a slight, transverse depression vaguely indicating the line of union. Scarcely a trace of the plane of union is shown in the internal structure of the ganglia, however. The median faces of the ganglia are flattened against each other, the cerebral commissure being extremely short and only visible in transparent preparations or in sections. In figure 11, *c.c.* it is seen in section in the median plane. The somewhat smaller, ovoid pedal ganglia located laterally at a lower level are in contact with the lower, outer faces of the cerebro-pleural complex, to the respective portions of which they are united by short cerebro-pedal and pleuro-pedal connectives, seen in figure 13 (*c. p.c.*, *pl.p.con.*) from the side, and in figure 14 from below. Beneath the narrowed oesophagus the pedal ganglia are in contact with each other, and are united by two commissures. The very short and stout pedal commissure is almost obliterated by the contact of the inner faces of the pedal ganglia, being much shorter than that figured by Trinchese ('86) for *Hancockia viridis*. In figure 14 it is seen extending into the ganglia as shown in a transparent preparation, but it is visible externally only after carefully pressing the ganglia apart. The much shortened pedal commissure is a characteristic of the Nudibranch families Dendronotidae, Bornellidae, Heroidae and Dotonidae. The slender parapedal commissure has a longer, external course, and is seen in ventral view in figure 14 (*pp.com.*). Below the oesophagus the cerebral ganglia are united by the sub-oesophageal cerebral commissure, arising from the ventral face of each ganglion near the origin of the cerebro-pedal connectives, and looping ventrally below the oesophagus in front of the pedal commissure. It is seen in ventral view in figure 14 (*s.c.c.*), passing across the ventro-anterior face of the pedal ganglia, and in figure 11 in section in front of the pedal ganglion (*ped.g.*). The buccal ganglia are of good size, and lie in contact with the anterior face of the pedal ganglia immediately below the oesophagus. They are visible in the lateral view (fig. 13, *buc.g.*), projecting forwards from between the pedal ganglia, but have been removed in the

ventral preparation, only the cut ends of the cerebro-buccal connectives laterally (*c.b.con.*) showing their union to the cerebral ganglia. Figure 15 represents the isolated buccal ganglia united by a short and relatively strong commissure. To each ganglion is attached a small gastro-oesophageal ganglion (*g.o.*) by a short connective. In figures 12 and 13 the pleural (or visceral) commissure (*pl.com.*) may be seen arising from the postero-lateral face of each pleural ganglion and looping down around the oesophagus, close to the surface of the pedal ganglia. From its right half is given off the genital nerve (*g.n.*). In figure 11 this commissure appears in section just behind the pedal ganglion (*ped.g.*).

From the cerebral moiety of the cerebro-pleural complex six pairs of nerves are given off, four of them being numbered serially in figs. 12-14. The largest of these (figs. 12 to 14, *c.1*) are those to the rhinophores, terminating in large ganglia at the base of the clavus of each, from which fine nerves are distributed to the leaves and surface of the organ. The second largest nerves, (*c.3*) are distributed to the labial tentacles. The other pairs of more slender nerves (*c.2*, *c.4*) ramify to the mouth region. A distinct oval optic ganglion is borne immediately above the space between the roots of the cerebro-pedal and the pleuro-pedal connectives; as shown in figure 12, *o*, and in figure 13. From this ganglion a slender nerve passes forward to the conspicuous eye (*e.*), situated adjacent to the cerebral ganglia and below their mid-level. Behind the pleuro-pedal connective the conspicuous large statocyst (otocyst) (fig. 13, *s.*) is situated. It is nearly spherical 0.050 mm. x 0.060 mm., and contains a single, rounded statolith 0.022 mm. by 0.0275 mm. in diameter, twice the size of that figured by Trinchese ('86) for *Hancockia rubra*, the statocysts of each species being nearly of the same size. A delicate nerve from the statocyst may be traced with difficulty to the cerebral ganglion in sections.

From the pleural portion of the cerebro-pleural ganglia a single nerve (figs. 12, 13, *pl. 1*) passes backward in a strong trunk, and ramifies to the dorso-lateral body wall and the cerata. From the pedal ganglia the anterior pedal nerve (*p.1*) passes forward to the foot from the ventro-anterior surface of each ganglion,

while the median and posterior pedal nerves arise together as a common trunk (*p. 2*) from the lower posterior margin, almost immediately separating into the two components, which are distributed to the middle and posterior regions of the foot. respectively.

REPRODUCTIVE SYSTEM

The ovotestis is made up of some thirty-six or more separate spheroidal lobules, filling something more than the posterior half of the body. Each lobule is composed of a pear-shaped, central portion to which are attached a great number of closely set, smaller peripheral alveoli. These latter are formed by a layer of ovigerous epithelium, the wall of the central cavity being formed by spermatogonia and by spermatozoa in various stages of development. In young, immature specimens of about 5 mm., body length, the lobules are simple spheroids, lined with developing spermatozoa, between the groups of which may be found here and there, young, quiescent ovogonia-like cells; in older animals acini filled with ovogonia push out at intervals from the periphery, and egg development is found in all stages. From the median apex of each central cavity arises a thin-walled duct, which soon unites with the main hermaphroditic duct, coursing forward slightly below the longitudinal axis of the body, as shown in figure 22 at *h.d.* The hermaphroditic duct thus formed passes forward to the median, dorsal surface of the anterior genital complex, where it dilates into the hermaphroditic ampulla (fig. 21, *h.*, *amp.*), a curved, sausage-shaped sack, the proximal end being most anterior. From its distal, posterior end the narrow duct again passes forward, gives off a branch to the left (*ov.d.*), the oviduct, and continuing as the vas deferens (*v.d.*), swells almost at once into a long, thick-walled, glandular tube lying in a number of loops upon the upper, anterior face of the anterior genital complex. This prostatic portion (*pr.*) of the vas deferens enters the basal wall of the preputium (*p.*) a roomy sack lying transversely to the body, retractable by the strong muscle (*m.*) and opening externally at the male orifice on the right side of the body, in front of the base of the first pair of cerata. In figure 22 its dorsal wall has

been removed and the large, somewhat flattened and irregularly plicated glans (*g.*) is shown attached to the inner or basal wall of the preputium. The external opening of the duct is not apical, but about midway of the ventro-anterior surface of the glans.

The oviduct (*ov.d.*) is given off from the anterior portion of the hermaphroditic duct, and passes backward sharply to the left, but quickly makes another abrupt turn forward and opens into the receptaculum seminis, or spermatheca (*spth.*), a small, rounded, ciliated vesicle, whose distal duct passes downward into the thin walled fertilization chamber, close to the entrance of the albumen gland into the latter. Into this flattened, ciliated cavity opens widely the mucous gland (*m.g.*), which makes up the bulk of the anterior genital mass. From it the vaginal, or copulatory duct, leads into the female atrium, a roomy tube with muscular, plicated walls, ending blindly and sending off the vaginal duct from its posterior wall. This duct is crescentic in cross section, and strongly ciliated. The upper horn of the crescent forms a groove leading directly into the duct from the spermatheca, by way of the dorsal portion of the ciliated fertilization chamber, and evidently serves as the channel for the spermatozoa in copulation. The ventral horn of the crescent opens widely into the lumen of the mucous gland, and represents the path of the egg band during oviposition. The diagram shown in figure 18 expresses these relations in a simplified manner, while of course ignoring all details of structure. The sequence of events in the reproduction cycle is probably as follows: As the spermatozoa mature they pass from the central spermathecal chamber of the ovotestis to the hermaphroditic ampulla (*h.a.*), where they are accumulated. During copulation, which is reciprocal, the spermatozoa pass onward from the ampulla through the prostatic portion (*pr.*) of the vas deferens and are deposited close to or within the vaginal canal (*v.*), through the upper groove (*fig. 18a, c.*) of which they are carried by ciliary action, or migrate actively, or both, into the spermatheca (*spth.*). Shortly after copulation the ova pass through the hermaphroditic duct, the ampulla, and the oviduct past the opening of the spermatheca and come into contact with the spermatozoa either here, or in the

fertilization chamber (*f.*). In the system of cavities formed by the accessory glands they first receive a coating of albumen from the albumen gland (*alb.*), then one of mucus from the lobes (*m.*) of the left side, and finally are united into the continuous egg band by the secretion from the larger, nidamental gland (*m'*), on the right, and pass outward through the ventral groove of the vaginal duct (fig. 18a, *ov.*) and through the vestibulum, being fastened in a coil upon the brown alga on which the animal is usually found. From the above it is clear that, while apparently diaulic, the differentiation of the copulatory duct into two longitudinal grooves (fig. 18a, *c.*, *ov.*) makes it functionally, at least, triaulic, i.e. the common hermaphroditic duct divides into three channels: *a*) the vas deferens, *b*) the copulatory duct proper, and, *c*) the duct for oviposition, the latter two in *Hancockia* being incompletely separated by the longitudinal fold, which gives the lumen its crescentic aspect. This is a simpler and more primitive condition than that described by Eliot ('10) for *Aeolidia* in which the triaulic type, characteristic of *Dorids*, is practically reached.

The egg band of *Hancockia* is in the form of a narrow ribbon of a pale greenish color, coiled in two or three turns, and fastened to the fronds of *Laminaria*, *Delesseria*, and other similar brown algae. Copulating individuals have been taken in tide pools during July and August, and even as late as October, and the egg bands may be found during the same period.

SUMMARY AND CONCLUSIONS

The structural characteristics peculiar to *Hancockia* may be summarized as follows:

1. The presence of a labial armature of well-developed rodlets, in addition to the masticatory process of the mandibles.
2. The presence of a median, unpaired, saccular salivary gland, or reservoir, opening into the united ducts of the anterior salivary glands, the short, common tube thus formed leading into the oral tube, in the median line, below and immediately in front of the labial disc.
3. The development of a median, longitudinal, cuticular cutting ridge on the dorsal surface of the odontophore epithelium, above the radula sack.

4. The development of a pear-shaped oesophageal diverticulum in front of the stomach.

5. The presence of well-developed gastric teeth in the muscular division of the stomach.

6. The ramification of the hepatic tubules to the rhinophores, as well as to the cerata, and the presence of cnidosacs in both.

7. The ventral position of the posterior hepatic duct, below the lobes of the hermaphroditic gland.

8. The greatly shortened cerebral and pedal commissures.

9. The digitate character of the velar tentacles and the cerata.

Of the above features nos. 1, 2, 3, 6, and 9 seem to be limited to *Hancockia* alone, so far as our present information extends, while the remaining nos. 4, 5, 7, and 8 have been recorded in but a limited number of forms.

The systematic position of the genus is obscure, and the facts stated in the present paper tend to emphasize differences, rather than to demonstrate affinities with other forms. Bergh ('92) assigned it to the Dotonidae, while Eliot ('10) unites it with the genus *Lomanotus*, in the family Lomanotidae, in virtue of similarities in the origin of the cerata from the mantle margin, the processes of the oral veil, and the perfoliate rhinophores, the family being joined with the Dendronotidae, the Scyllaeidae, the Bornellidae, the Tethymelibidae, and the Phylliroidae into the sub-tribe Dendronotoidea of the Cladohepatica.

Hancockia, however, has no ridge, or 'mantle margin,' along the sides of the back, uniting the bases of the cerata with the rhinophores, as has *Lomanotus*, though a slight lateral expansion of the ceras base might be so interpreted. The dorsum rounds down uniformly into the sides between successive cerata, and the lateral basal expansion is formed by the ridges produced by the divergence of the efferent venous trunks from each ceras, as they pass into the integument of the back. The digitiform processes of the velar tentacles and the cerata resemble somewhat those of *Lomanotus*. The radulae and the internal anatomy of the two genera show great divergences, though our knowledge of the latter form is, as yet, unsatisfactory.

Possible affinities with the Dotonidae are equally, or even more vague, the presence of digitate velar lobes, perfoliate rhinophores, non-caducous cerata, and cnidosacs being the most marked external differences, while, internally, the possible homologies in the anterior salivary glands, and the median, unpaired one, as previously indicated, are the most significant. Other points of resemblance, such as the greatly shortened commissures of the nervous system, are shared with the Dendronotoidea in general.

Taking into consideration the state of our knowledge in general concerning the affinities of the Cladohepatica, it seems to the writer justifiable to recognize the structural peculiarities of *Hancockia* by establishing for it, tentatively at least, a separate family in the group Dendronotoidea, rather than to more artificially unite it either with the Dotonidae, or the Lomanotidae. The arrangement proposed would be as follows:

Sub-tribe DENDRONOTOIDEA

Limaciform animals with oral veils and simple or branched dorsal appendages. Rhinophores usually perfoliate and retractile into sheaths. Liver divided into three portions, which usually ramify into the dorsal appendages. Radula moderately wide, or narrow.

Family 1. Dendronotidae

Family 2. Scyllaeidae

Family 3. Bornellidae

Family 4. Tethymelibidae

Family 5. Lomanotidae

Family 6. Hancockidae

Family 7. Phylliroidae

Family HANCOCKIDAE, Fam. nov.

Body aeolidiform; oral veil prolonged into digitate lobes at the angles; cerata non-caducous, forming digitate lobes. Rhinophores perfoliate, retractile into sheaths; cnidocysts present in cerata and rhinophore sheaths. Liver ramifying to cerata and rhinophores; median unpaired salivary gland present; second stomach with cuticular armature.

Oral disc bearing armature of short rodlets; mandibles with denticulate masticatory process; radula narrow, tri-seriate.

Genitalia unarmed.

Genus HANCOCKIA, Gosse, 1877

The modified diagnosis of the single genus of the family has been given on page 68. If Garstang's ('93) identification of Hesse' *Doto uncinata* be accepted the list of species at present should stand as follows:

1. *Hancockia uncinata* (Hesse), 1872
 Syn. *Doto uncinata* Hesse, 1872
 Hancockia eudactylota Gosse, 1877
2. *Hancockia rubra* Trinchese, 1886
 Syn. *Govia viridis* Trinchese, 1886
3. *Hancockia californica* MacF., 1923

In conclusion I would express my appreciation of the many privileges which I have enjoyed in the Hopkins Marine Station of Stanford University, at Pacific Grove, and to my wife for her invaluable aid in collecting, and her skill in delineating these minute and delicate creatures.

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PLATES

EXPLANATION OF PLATES

All of the figures of plates 1 to 6 were made by Mrs. Olive H. MacFarland from preliminary camera sketches by the author, with the exception of figure 1 of plate 1, which was drawn directly from life.

PLATE 1

EXPLANATION OF FIGURES

1 Dorsal view of *Hancockia californica* MacF. In this specimen an exceptional difference is noticeable in the two rhinophores, the stalk of the left one being much shorter than that of its fellow on the right. No attempt is made to bring out the markings of the body, since they can be adequately represented only in colors. $\times 6$.

2 Ventral view of head region. The mouth appears as a longitudinal slit, surrounded by the thickened lips. The palmate velar processes or anterior tentacles, are asymmetrical as regards their digitations, though a fundamental similarity is evident. $\times 8.5$.

3 Left rhinophore in side view. *s*, stalk, *a*, sheath, *b*, the blunt, apical portion of the bulb rising above the perfoliate part, two leaves of which are seen above the margin of the sheath, or calyx. The external surface of the latter bears a number of ridges, upon each of which is borne a series of rounded nodules, each containing a cnidosac, opening by a minute pore at its summit. $\times 16$.

4 Dorsal view of reconstruction of alimentary system, based on horizontal, serial sections, supplemented by dissections. The body wall is represented as cut through at the upper level of the cerata stalks, the incision passing lengthwise through the retracted rhinophores. *p*, pharyngeal bulb seen from above and behind, its anterior end curving abruptly downward to the mouth, and concealed by the integument of the head region; *a.s.*, anterior salivary glands, compactly racemose in form, extending out axially into the stalk of the rhinophore nearly to the summit of the bulb, the paired ducts curving downward beneath the mouth tube, where they unite in a single median duct; *m.s.*, the unpaired median salivary gland; *p.s.*, posterior salivary glands, branching tubular organs, ramifying freely between the pharyngeal bulb and the stomach, and opening by slender ducts at either side of the exit of the oesophagus, *oe*, from the posterior dorsal surface of the pharyngeal bulb; *d*, oesophageal diverticulum, arising dorsally from the posterior end of the oesophagus and extending forward between it and the overlying pyloric end of the stomach; *st*, the thick-walled grinding stomach below which is seen the thin-walled, ventral, anterior gastric division, giving off in front the two anterior hepatic ducts, *r.h.*, and *l.h.*, and behind the single posterior hepatic duct, *p.h.*, which sends rami to the posterior cerata in succession, where they break up into irregularly branching hepatic tubules, *h*, the first branches of which are here shown. The anterior hepatic ducts, *r.h.*, and *l.h.*, send similar branches to the first pair of cerata, and pass forward into the rhinophores, where they break up into a number of branches, which pass radially upward to the margins of the rhinophore sheaths, and terminate in numerous cnidosacs, *c*; *i*, the intestine, opening externally on the right side at *a*, the anus; *e*, cut edge of body wall. \times ca. 9.

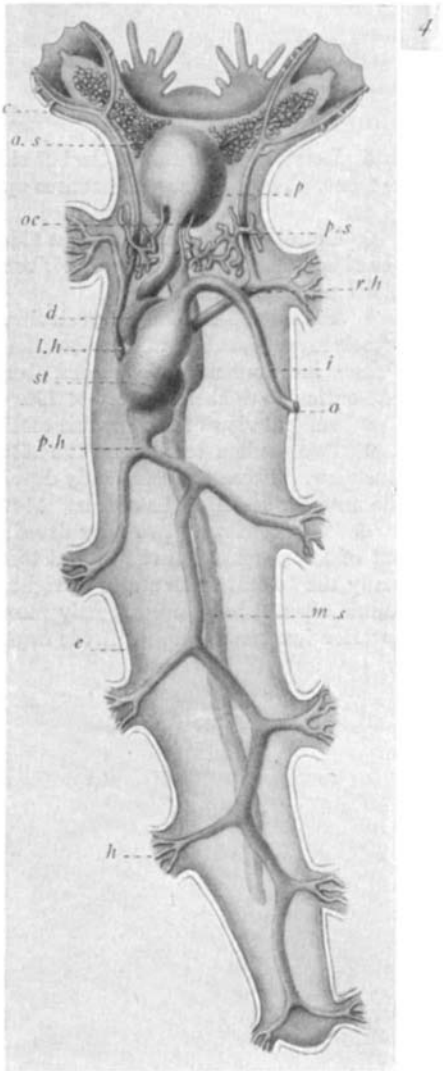
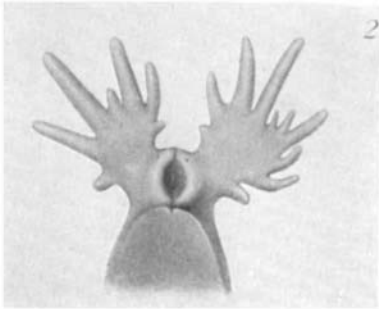
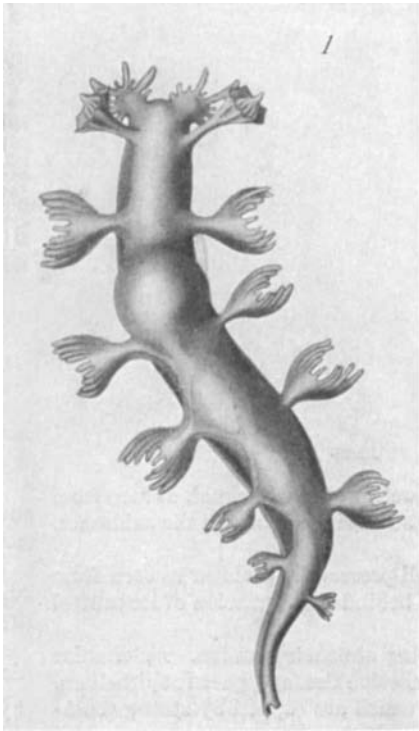


PLATE 2

EXPLANATION OF FIGURES

5 Detail of first ceras of the left side of a well-preserved animal, as seen from in front. The nodular prominences upon the subdivisions contain the cnidosacs. $\times 16$.

6 Detail of first ceras of right side of well-preserved specimen as seen from the side. The stalk of the ceras is concealed behind the expansion of its central distal portion. $\times 16$.

7 Transverse section of posterior, grinding stomach division. *m*, circular muscle layer; *p*, sub-epithelial stratum of connective tissue; *e*, gastric epithelium, thrown into numerous ridges and elevations which are capped by strong tooth-like cuticular thickenings, *c*. $\times 104$.

8 Ventral view of two median teeth of the radula. $\times 520$.

9 Two median teeth from the 25th and 26th rows of the radula, as seen in side view. These represent fully developed functional teeth, and are taken from the anterior angle of the radula. $\times 298$.

10 Dorsal view of two fully developed rows of the radula. In the flattening out of the preparation the lateral teeth, *l*, have been slightly displaced. Normally the lateral teeth stand at right angles to the median ones, *m*, within the radula sheath, becoming slightly more oblique only beyond the sheath at the anterior functioning angle of the organ. $\times 368$.

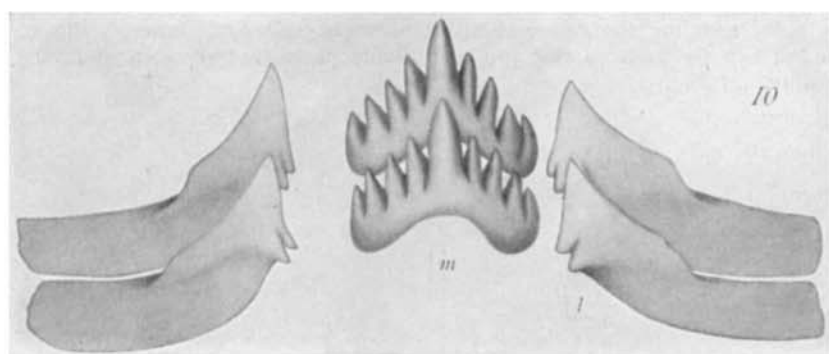
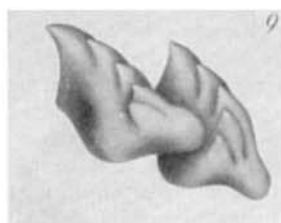
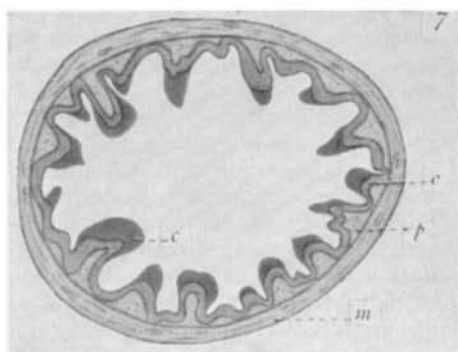
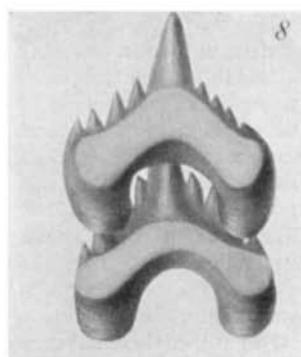
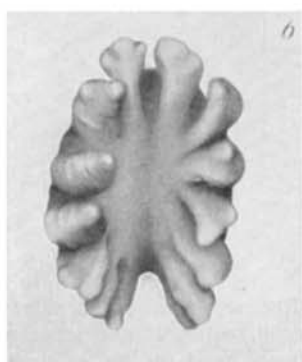


PLATE 3

EXPLANATION OF FIGURE

11 Reconstruction of anterior end of *Hancockia* in median longitudinal plane from serial sections. *e*, external epithelium; *f*, foot; *o*, oral tube; *l.a*, labial armature of blunt rodlets; *m*, denticulate cutting margin of mandible; *h*, hinge of mandibles; the radula is borne upon a median muscular mass projecting into the pharyngeal cavity, and extends forward from *r.s*, the radula sack, to the anterior angle, thence doubling back ventrally to the worn out, oldest portion in the lower part of the cavity. Above the radula the dorsal epithelium, covering the radula apparatus, bears a strongly developed, median, longitudinally thickened cuticular ridge, *c.r*, shown in transverse sections in figures 16 and 17 of plate 5. *oe*, the oesophagus, leading backward from the posterior dorsal buccal cavity; *a.s*, a portion of the left anterior salivary gland, its duct arching downward around the buccal mass and appearing below to join its fellow of the opposite side, *d.s*, and the unpaired duct *m.d*, in a common median tube and opening ventrally into the oral tube immediately in front of the labial armature; *m.d*, duct of the unpaired median salivary gland *m.s*; *p.s*, posterior salivary gland of the left side, its duct passing with the oesophagus through the nerve collar, and opening into the buccal cavity, laterally, opposite the anterior end of the radula its entrance not visible here; *l.g*, labial glands above the mouth; *g*, labial glands below the mouth, and glands of anterior end of the foot; *cer.g*, inner face of left cerebral ganglion, fused behind with the left pleural ganglion, *pl.g*. Near the center of this supra-oesophageal cerebro-pleural ganglionic mass is seen the transverse section of the cerebral commissure, *c.c*. Below the oesophagus is seen the inner face of the left pedal ganglion, *ped.g*; near its center the transection of the large pedal commissure, near its lower border the parapedal commissure in section; close behind it and above the origin of the left posterior pedal nerve, *p.2*, the pleural commissure is likewise seen in cross section; in front of the pedal ganglion in the angle between the ventral wall of the oesophagus and the posterior wall of the buccal mass appears the inner face of the left buccal ganglion, with the buccal commissure in cross section, and between the buccal ganglion and the pedal ganglion the sub-cerebral (sub-oesophageal) commissure is shown. *l.h*, left hepatic duct, passing to the left rhinophore, not represented in the drawing. $\times 56$.

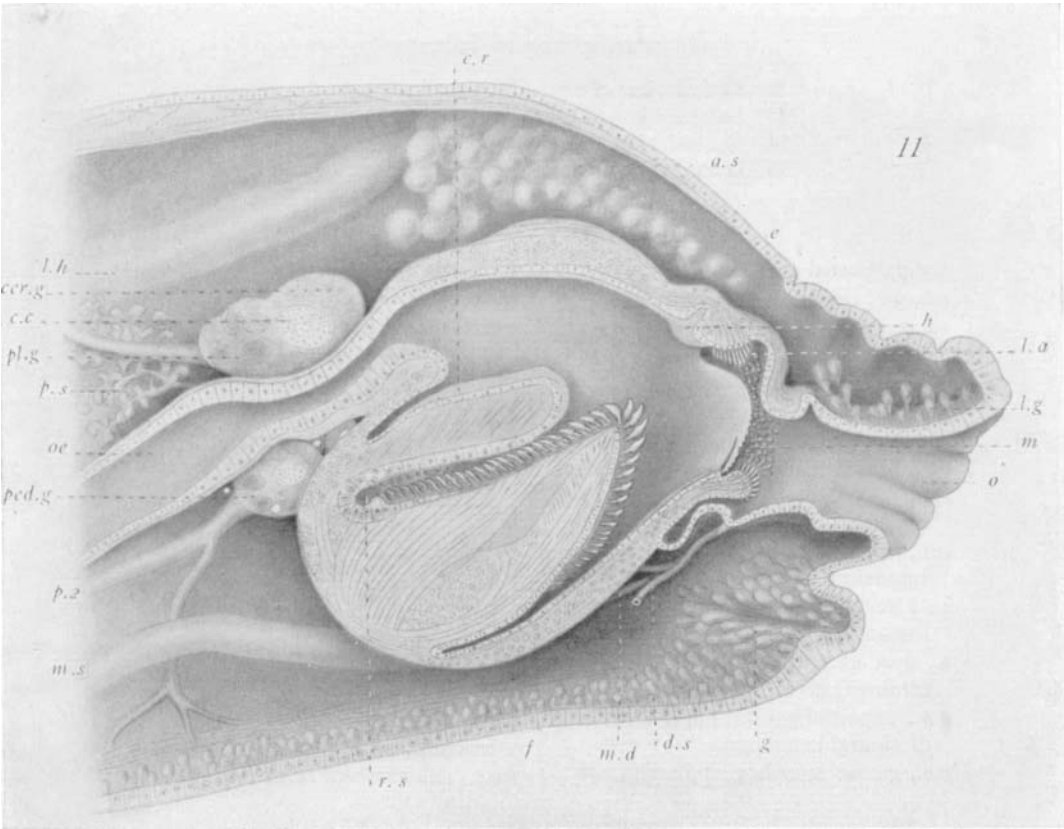


PLATE 4

EXPLANATION OF FIGURES

- 12 Dorsal view of central nervous system. × 60.
- 13 Lateral view of central nervous system. × 60.
- 14 Ventral view of central nervous system. × 60.
- 15 Dorsal view of buccal ganglia. × 60.

ABBREVIATIONS

- | | |
|---|--|
| <i>buc.g.</i> , buccal ganglion. | <i>o.</i> , optic ganglion, at origin of optic nerve. |
| <i>c.b.con.</i> , cerebro-buccal connective. | <i>ped.g.</i> , pedal ganglion. |
| <i>cer.g.</i> , cerebral portion of cerebro-pleural ganglion complex. | <i>pl.com.</i> , pleural commissure. |
| <i>c.p.c.</i> , cerebro-pedal connective. | <i>pl.g.</i> , pleural portion of cerebro-pleural ganglion complex. |
| <i>c.pl.g.</i> , cerebro-pleural ganglion complex. | <i>pl.p.con.</i> , pleuro-pedal connective. |
| <i>c.1.</i> , first cerebral nerve to rhinophore. | <i>pl.1.</i> , pleural nerve to dorso-lateral body wall and cerata. |
| <i>c.2.</i> , second cerebral nerve to mouth region. | <i>pp.com.</i> , parapedal commissure, in front of it in figure 14, the faint outline of the pedal commissure. |
| <i>c.3.</i> , third cerebral nerve to anterior tentacles. | <i>p.1.</i> , first pedal nerve, to anterior end of foot. |
| <i>c.4.</i> , fourth cerebral nerve to mouth region. | <i>p.2.</i> , second pedal nerve, dividing into median and posterior pedal nerve trunks. |
| <i>e.</i> , eye, at end of the optic, or fifth cerebral nerve. | <i>s.</i> , statocyst, its nerve, the sixth cerebral, only visible in sections. |
| <i>g.n.</i> , unpaired genital nerve from loop of pleural commissure. | <i>s.c.c.</i> , sub-cerebral commissure. |
| <i>g.o.</i> , gastro-oesophageal ganglia. | |

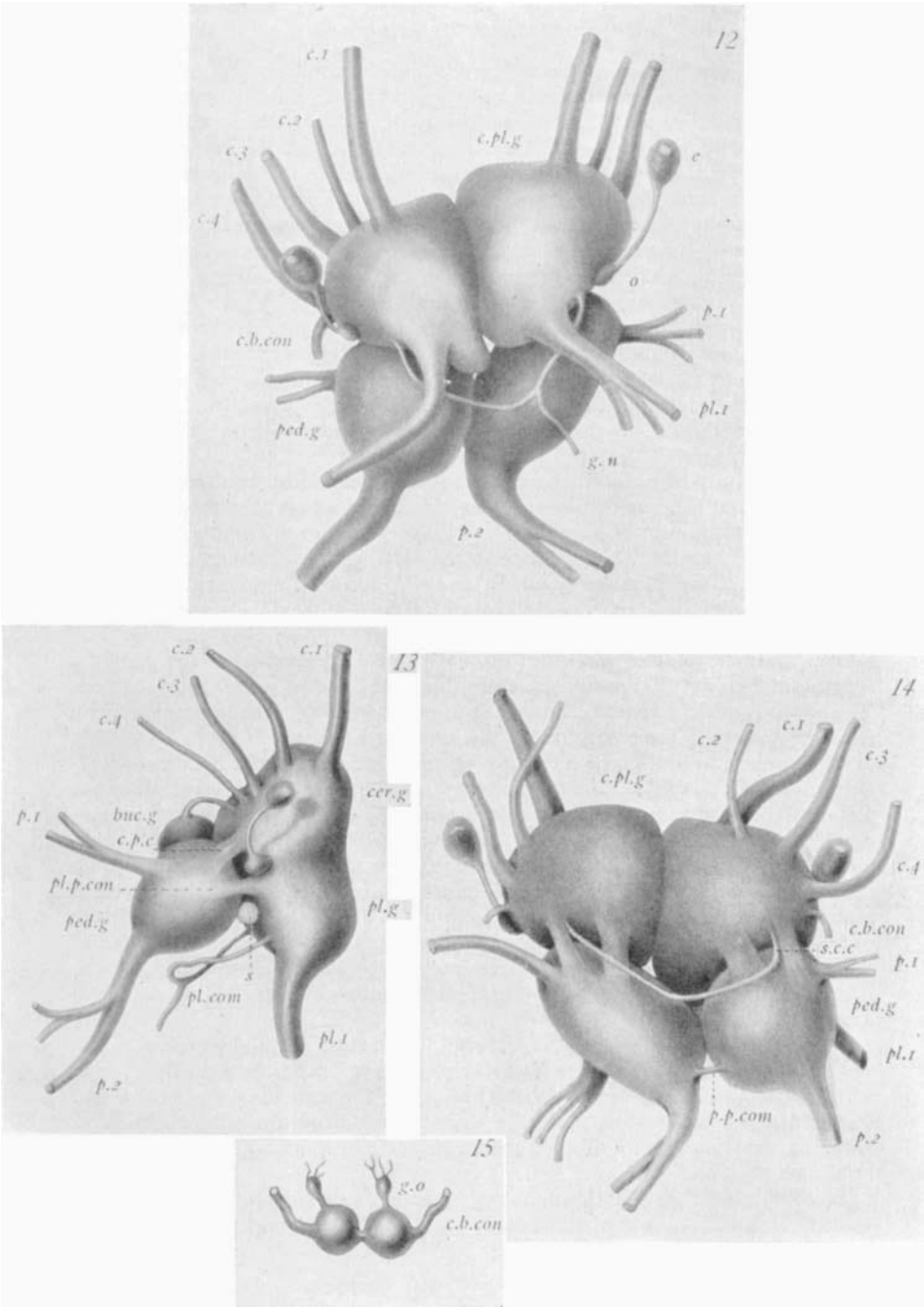


PLATE 5

EXPLANATION OF FIGURES

16 Transverse section of the upper portion of the pharyngeal bulb immediately behind the oesophagus, showing the epithelium of the cavity in the region above the radula sheath. The buccal cavity, *c*, is here reduced to a flattened cleft, bounded above by the epithelium of the roof, *d.e*, and the epithelium covering the dorsal surface of the muscular mass forming the radula mechanism. In the median line this epithelium forms a narrow longitudinal ridge, which is sunken into the subjacent connective tissue and muscle, so that its summit is but slightly above the surrounding level. The cuticula is strongly developed in this region, reaching its greatest thickness in the median line, *a*, and forming a sharp longitudinal ridge. (Compare fig. 11 of pl. 3, *c.r.*). $\times 560$.

17 Section similar to figure 16, but more anterior, passing through the entrance of the oesophagus. *oe*, cavity of oesophageal opening, its epithelial lining bearing a strong cuticula which is continuous forward over the roof and sides of the pharyngeal cavity; *r*, the median epithelial ridge, bearing the longitudinal cuticular armature, *a*, reaching its greatest development in the median line. $\times 560$.

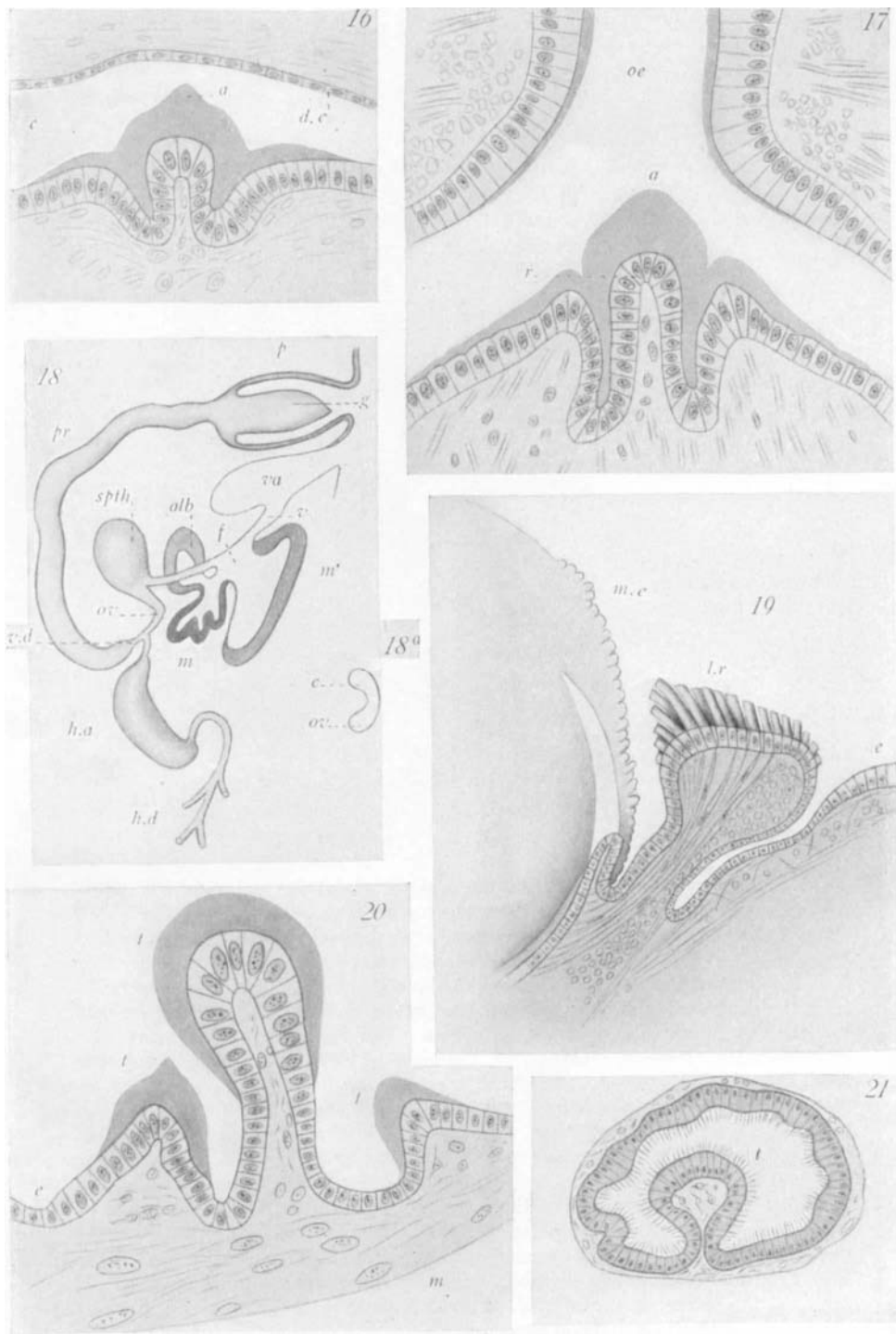
18 Diagram of reproductive system. *h.d*, hermaphroditic duct; *h.a*, hermaphroditic ampulla; *v.d*, vas deferens, enlarging at once into *pr*, the prostate gland; *p*, the preputium cut open to show the glans penis, *g*; *ov*, oviduct; *spth*, the spermatheca; its duct leading into *f*, the fertilization chamber, close to the entrance of *alb*, the albumen gland; *m*, and *m'*, the two divisions of the mucous gland; *va*, the vagina, connected with the fertilization chamber by the vaginal duct, *v*.

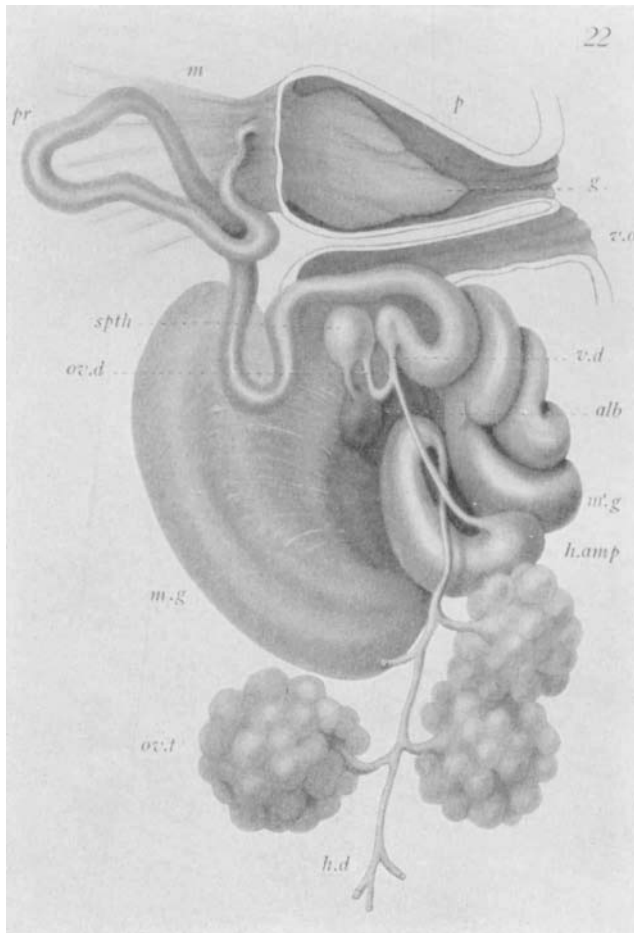
18a Diagram of cross section of the vaginal duct, incompletely divided by a longitudinal ridge into *c*, the copulatory duct, and *ov*, the duct for oviposition. The copulatory channel leads into the spermatheca, while the lower egg-laying channel opens into the cavity of *m'*, the nidamental gland.

19 Transverse section of labial armature on ventral side of mouth. *e*, epithelium of mouth tube; *l.r*, labial rodlets, borne as cuticular differentiations on the oral tube epithelium, arranged in a complete circle surrounding the inner mouth opening, immediately in front of the mandibles. These rodlets are borne on a prominent muscular ridge, here shown in cross section. The outer group of muscles of this ridge form the constrictor oris muscle, and is seen here in cross section; immediately within it is found a group of radial fibers, forming a dilator oris muscle, some of the fibers of which are here shown. The anterior portion of the mandible is shown in perspective, its irregularly dentate masticatory margin, *m.e*, extending downward to the tip of the masticatory process behind the labial armature. $\times 312$.

20 Detail of transverse section of wall of muscular grinding stomach. The tunica mucosae is elevated into irregular papillae and longitudinal ridges, upon which are borne strong tooth-like thickenings of the cuticle of the epithelium. In the depressions between these the cuticle thins away to a very slight layer only. *m*, muscular gastric wall; *e*, gastric epithelium; *t*, gastric teeth formed by thickened cuticula. $\times 560$.

21 Transverse section through the intestine showing the typhlosole, *t*, a ventral, longitudinal fold of the mucosa extending throughout nearly the whole length of the organ. $\times 200$.





22 Reconstruction of reproductive system of Hancockia, combined from several series of sections in the three body planes, and from dissections. *ov.t.*, three of the numerous lobes of the ovotestis; *h.d.*, the hermaphroditic duct, formed by the union of the ducts from the individual lobules of the ovotestis, and dilating into *h.amp*, the hermaphroditic ampulla, here displaced slightly to the right; from the distal end of the ampulla the duct again leads forward and divides into *v.d.*, the vas deferens, and *ov.d.*, the oviduct. The vas deferens dilates at once into the thick, prostatic segment, *pr*, the loops of which have been folded over forward and to the left to show the relations of the underlying organs. At its distal end the prostatic portion of the vas deferens narrows and passes into the broad basal end of the preputium, *p*, a roomy sack, the dorsal wall of which has been cut away to show the large, flattened, triangular glans penis, *g*, attached at its basal inner end. The preputium and glans penis, *g*, when everted, form the intromittent organ, retracted by the retractor penis muscle, *m*, the inner end of which is inserted on the left wall of the body. The oviduct, *ov.d.*, forms a sharp bend and passes into the spermatheca, *spth*, from which a short duct leads into the roomy fertilization chamber, close to the opening of the albumen gland, *alb*, into the latter; *m.g.* and *m'.g.* the left and right divisions of the mucous glands, respectively; *v.o.*, the external opening of the female channel. Compare with diagram figure 18. $\times 24$.