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OBSERVATIONS ON THE MORPHOLOGY AND BEHAVIOUR OF *CHILINA FLUCTUOSA* GRAY (CHILINIDAE), WITH A DISCUSSION ON THE EARLY EVOLUTION OF PULMONATE GASTROPODS

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CONTENTS

An account is provided of (i) the general morphology, (ii) the vascular, nervous and feeding systems, and (iii) aspects of the behaviour of a representative species of the pulmonate genus *Chilina*. Examination of this genus has aided in understanding the pattern of early evolution of freshwater pulmonates from their marine prosobranch ancestors and of their divergence from opisthobranchs.

The gross morphology of *Chilina* is adapted to ploughing through the surface layers of soft substrata. Although *C. fluctuosa* was found on rocks, it was nevertheless capable of burrowing into sand, using a stereotyped digging cycle.

Streamlining to facilitate burrowing was achieved by nuchal shortening and by a 'detorsion' of the mantle complex as in opisthobranchs. The nuchal shortening incurred loss of a major vascular pathway which, in monotocardian prosobranchs, drains the head-foot. 'Detorsion', however, provided a substitute which incorporates the anterior roof of the mantle cavity where, in *Chilina*, the precursor of the rich pulmonary plexus characteristic of later pulmonates may be discerned. The suprapallialial vascular system is described in detail. In contrast, it is apparent that increased reliance on burrowing in opisthobranchs brought about loss of the anterior region of the mantle cavity, and thus any potential for development of a plexus in that region.

Enclosure of the mantle cavity, which clearly pre-adapted the mantle complex to function also as a 'lung', was necessary to reduce clogging of the mantle cavity by particulate material. Only water is held in the cavity of *Chilina fluctuosa*, whose habitat is rivers, but both air and water may be held in the mantle complex of other species found in Chile.

The nervous system is extremely similar to that of the primitive opisthrobranch *Acteon*, but the posterior section of the visceral loop is shorter owing to greater nuchal reduction. The loop is uncrossed, though the supraoesophageal ganglion lies only a little right of the suboesophageal ganglion.

The musculature of the buccal mass is extremely similar to that of *Lymnaea* and *Planorbarius*, and is designed for moving and tensing a broad radular ribbon. It is argued that the buccal morphology characteristic of these snails evolved to manipulate quantities of particulate material during the early infaunal phase, and only later was used to great effect in both microphagous and macrophagous feeding.

Collectively, the observations made on *C. fluctuosa* (and also on estuarine species found in Chile) support the contention that the Basommatophora invaded freshwater habitats via estuarine niches. Continuity during this progression was apparently provided by soft substrata, and probably by diatoms as a food source. Previous arguments purporting a terrestrial or semi-terrestrial origin for the limnic basommatophorans are refuted.

1. INTRODUCTION

A detailed study of both the morphology and behavioural ecology of the primitive genus *Chilina*, which is endemic to South America, is considered central to obtaining a fuller understanding of the early evolution of both freshwater and terrestrial pulmonates. This is so since, first, it is the most primitive pulmonate taxon to have penetrated substantially into freshwater habitats, and, secondly, it retains, in common with the estuarine pulmonate genus *Amphibola*, a gross morphology comparable with that of some primitive opisthobranchs which much work suggests shared a common origin with pulmonates from mesogastropod prosobranchs (Boettger 1954; Fretter & Graham 1954, 1962; Fretter 1975; Brace 1977*a*, *b*).

Such similarity of gross structure with that of basal opisthobranchs, notably *Acteon*, should greatly facilitate the recognition and separation of those adaptations that characterized the common ancestral stock and those that were innovations unique to early pulmonates and which in particular, aided their subsequent colonization of freshwater niches and later of land.

This paper forms part of an investigation into the functional morphology, ecology and taxonomy of the Chilinidae, and deals with certain aspects of the structure of a representative species, *C. fluctuosa* Gray, 1837. As an introduction to the gross morphological adaptations that are shared with primitive opisthobranchs, a description of the functional and behavioural specializations that enable the animal to burrow is provided first. Of great significance in reconstructing the exploitation of more ephemeral aquatic habitats is the functioning of the pallial complex, in particular its ability to hold water and air. To this end, its structure is examined, together with that of the vascular supply to and circulation within the mantle cavity roof since, in later forms, the plexus there is a major site for absorbing oxygen from either a water- or air-filled cavity.

Movement of the mantle complex to the right and posteriorly characterized the early evolution of pulmonates (Fretter 1975), though not to the same degree as in opisthobranchs. That process, which was related to the assumption of an infaunal mode of life, has been called 'detorsion' (a term criticized by Brace (1977*a*)) and resulted in untwisting of the visceral loop. Therefore a description of the nervous system is provided, with emphasis on comparing the distribution of ganglia along the visceral loop with that typical of basal opisthobranchs (Brace 1977*b*).

Finally, the structure of the buccal mass is examined: at present no detailed description is available.

The principal papers dealing with the morphology of the Chilinidae are those by Haeckel (1911) and Harry (1964), the latter specifically dealing with *C. fluctuosa* and including a discussion on the origin and early phylogeny of the Pulmonata. Other morphological data are scattered and scant (Pelseneer 1894; Plate 1895; Hubendick 1945).

2. MATERIALS AND METHODS

Specimens of *C. fluctuosa* were collected from the Rio Aconcagua, 7 km inland from its mouth north of Viña del Mar, Valparaiso, Chile. Observations were made of the animals in small tanks containing bottom materials obtained from the collecting site. *C. fluctuosa* is known to survive well for extended periods ($\ngtr 1$ year) under these conditions (J. Stuardo, personal communication).

The addition of Bouin's fluid and methylene blue to dissections clarified the disposition of musculature and nervous structures respectively. The vascular system was investigated by injecting suspensions of borax carmine, also used for tracing ciliary tracts on the walls on the mantle cavity.

3. RESULTS

(*a*) *Behavioural observations*

At the collecting site, most individuals were confined to a narrow (2 m) transverse belt in the river bed (8 m wide; flow rate of $0.3\ \mathrm{m\,s^{-1}}$), characterized by an abundance of small boulders (< 20 cm diameter) embedded in coarse sand. Animals were found principally adhering to these boulders.

In laboratory tanks, the animals displayed a preference for boulders, feeding from the diatomaceous film that they bore, but the animals also not infrequently traversed the sand,

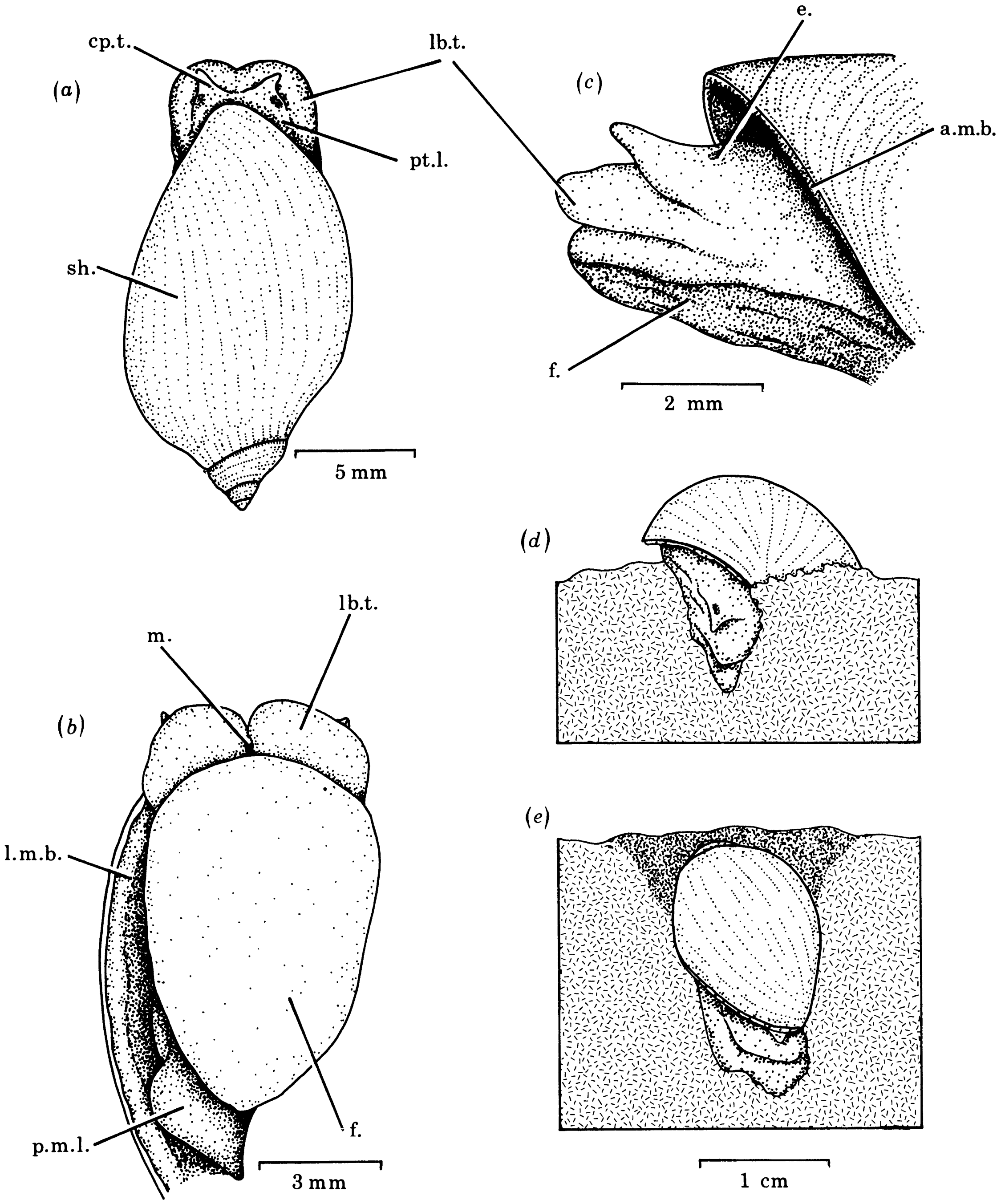

Figure 1. External features and burrowing behaviour of *Chilina fluctuosa*. (*a*) Dorsal view of crawling animal. (*b*) Ventral aspect of head-foot of crawling animal to show the disposition of the labial tentacles and the occlusion of the mantle cavity opening laterally by the posterior mantle lobe. (*c*) Ventrolateral view of parts of the head-foot and shell of an expanded specimen. (*d*, *e*) Burrowing behaviour: note in (*d*) the extended and twisted head-foot, and in (*e*) cephalopedal shortening which draws up the posterior body region and shell after the advancing head-foot. Several cycles of digging activity intervened between the stages in burrowing depicted here.

leaving obvious trails as a result of ploughing through it partially submerged. Progress through sand occurred at speeds of up to 15 cm h^{-1}.

Locomotion over rocks was characterized by side-to-side movements of the anterior portion of the foot (f., figure 1 *b*, *c*) and of the broad labial tentacles (lb.t.) which were held close to the substratum. The cephalic tentacles (cp.t.) were kept raised and the shell (sh.) was maintained horizontally. Forward locomotion was achieved by periodic elongations of the anterior region of the head-foot, each followed by a drawing up of the somewhat truncated, posterior section of the foot, in turn followed by contraction of the columellar muscle which dragged the remainder of the body forwards. Before each anterior extension, a relaxation of the columellar muscle resulted in an obvious though limited backward displacement of the shell relative to the head-foot.

Although found predominantly on boulders in the field, captive animals when placed on sand frequently burrowed, becoming totally immersed within the substratum (figure 1 *d*, *e*). The cyclical movements described above became exaggerated at these times. Anchorage during penetration was facilitated by simultaneous ventral flexions of the most anterior portion of the foot. Observations made on four animals of differing size disclosed that larger animals, not unexpectedly, required more time to disappear from the surface, but that digging (cycle) rate was more or less independent of body size over the range examined (1–2 cm shell height) (table 1).

In the laboratory, animals largely remained on the bottom of tanks and rarely visited the surface. There was no evidence to suggest that animals regularly approached the surface, a feature that was consistent with their benthic position in the field.

(*b*) *Gross mophology*

A detailed description of the shell of *C. fluctuosa*, which is typical of the genus, was provided by Harry (1964). It need only be noted here that it (sh., figure 1 *a*) possesses an extensive last whorl displaying an ovate aperture and flattened columellar area, and a short spire bearing a heterostrophic apex.

The flattened labial tentacles, which are strongly reminiscent of those of *Acteon*, overlap the straight anterior margin of the foot. Each stubby cephalic tentacle incorporates a pigmented eye (e.) at its base. The post-tentacular lappet, reported by Harry (1964) from preserved material to be as large as the tentacle, is in living specimens considerably smaller (pt.l., figures 1 *a*, 2 *a*). The head-foot presents a streamlined profile which facilitates burrowing.

The posterior region of the body, which is composed of the visceral mass and mantle (figure 2), is linked to the head-foot by a nuchal area which, in comparison to that of prosobranchs, is much reduced. Consequently, the entire animal is compact and the proximal portion of the columellar muscle is relatively short, though broad (p.c.m., m.p.c., figures 2 *b*, 4). Internally, the anterior and posterior body regions are separated by a vertical septum (v.s., figure 4) which forms an effective barrier to blood flow between the cephalic and visceral haemocoels. The oesophagus, which passes through it, does so by way of a sphinctered aperture.

The mantle complex lies to the right. The opening of the mantle cavity faces laterally (figure 3) since the anterior mantle border (a.m.b.) is fused (a.m.a.) to the dorsal cephalic wall. Situated contiguous to the mantle attachment on the extreme right is the osphradium (os., see figure 6). Posteriorly, the mantle is folded (p.m.f.) and consequently both the roof and much of the floor of the mantle cavity are, as in tectibranch opisthobranchs (Brace 1977 *a*), formed by

Table 1. Details of burrowing behaviour† of animals of different size (shell height) in sand‡

animal (shell height/cm)...	A (1.65)			B (1.60)			C (1.30)			D (1.10)		
trial no.	time/min	number of cycles	rate/(cycle min⁻¹)	time/min	number of cycles	rate/(cycle min⁻¹)	time/min	number of cycles	rate/(cycle min⁻¹)	time/min	number of cycles	rate/(cycle min⁻¹)
1	23.5	43	1.8	21.5	37	1.7	18	23	1.3	19.5	27	1.4
2	15.5	45	2.9	16	42	2.6	13	37	2.8	10	27	2.7
3	21	38	1.8	15	34	2.3	10	23	2.3	10.5	25	2.4
4	20	40	2.0	19	40	2.1	18	26	1.4	12	22	1.8
5	22	42	1.9	14	34	2.4	9.5	25	2.6	11	22	2.0
mean	20.4	41.6	2.1	17	37.4	2.2	13.7	26.8	2.1	12.6	24.6	2.1

† Observations related to total disappearance from the surface following commencement of digging.

‡ *Details of substratum:*

particle size/mm	percentage dry mass	percentage particle numbers calculated from mean particle volume for size range and mass
> 4	0.1	—
2–4	2·8	negligible
1–2	50.1	negligible
0.5–1	33.7	0.8
0.25–0.5	12.1	6.0
0.125–0.25	0.9	14.2
0.063–0.125	0.3	79.0
< 0.063	negligible	negligible

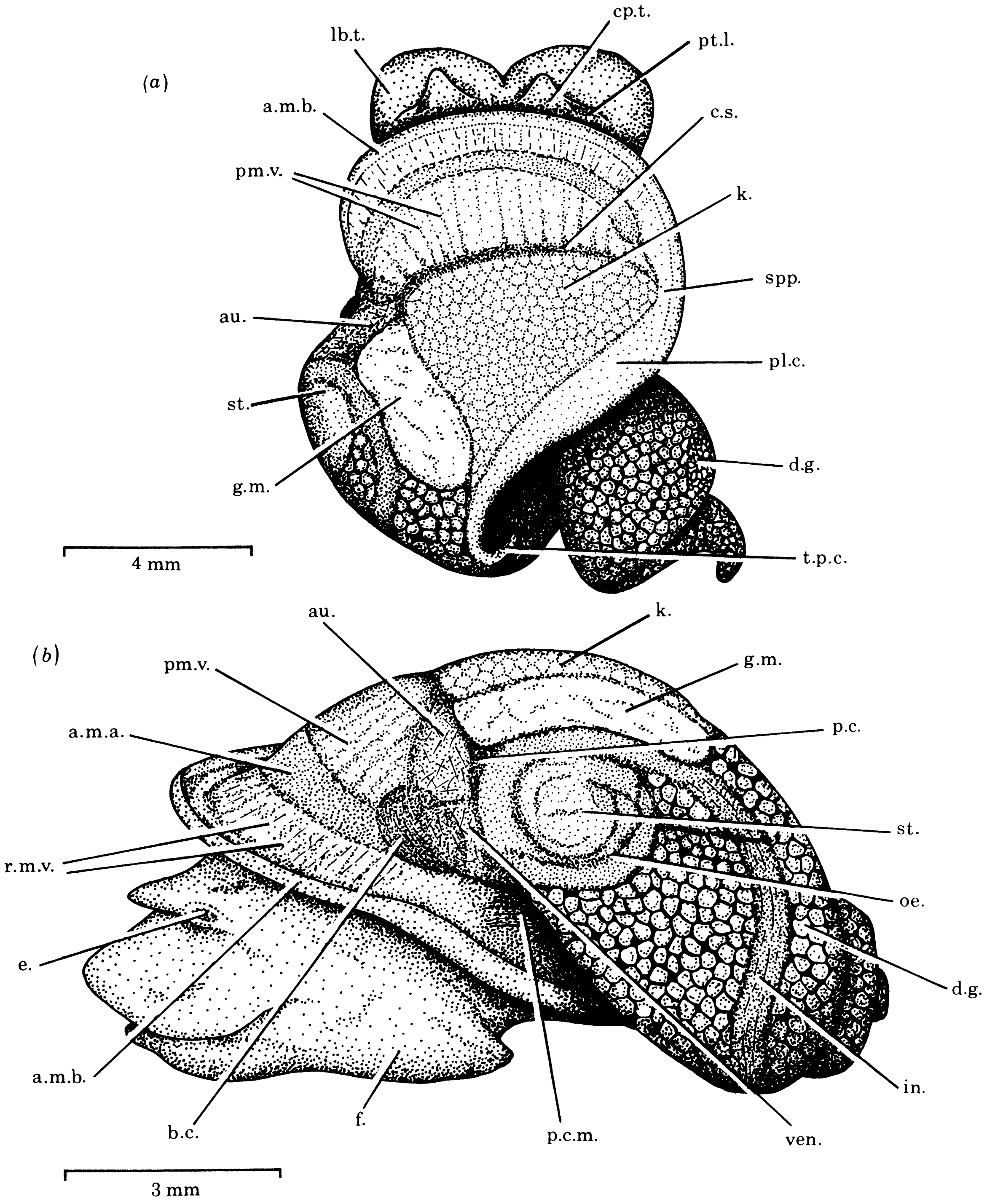

Figure 2. External features of *Chilina fluctuosa* with shell removed: (*a*) dorsal aspect; (*b*) left aspect.

mantle. These two surfaces will be referred to as the suprapallium (spp.) and infrapallium (ifp.) respectively. The thickened portion of the latter, which, to a limited degree, cushions the shell, is termed the posterior mantle lobe (p.m.l.). Such a departure in disposition of the mantle edge from that typical of prosobranchs is easily envisaged as having taken place by a migration (and extension) to the right and posteriorly. Anteriorly, however, the floor of the mantle cavity is still formed by the dorsal cephalic wall.

Reduction of the nuchal area brought about close apposition of the viscera and pallial structures, and both the heart and kidney (k.) overlie the mantle cavity (figure 2), the latter extending within the suprapallium almost to the mantle edge (l.m.b., figure 3*a*) where the kidney opening (k.o., figure 3*b*) is located. The kidney is divisible into two structurally distinct regions (k.l., k.m.). The auricle (au.) and ventricle (ven., figure 2*b*) are transversely orientated. The pericardium abuts the stomach (st.) posteriorly and, anteroventrally to the left, the bursa copulatrix (b.c.). From the bursa, a duct (d.b.c., figure 3*b*) descends to the right to enter the genital mass (g.m.), much of which is accommodated within the infrapallium and posterior mantle lobe. More proximally, the genital structures are sandwiched between the stomach and the medial wall of the mantle cavity.

Posteriorly, the mantle is drawn out into a caecum (pl.c., figures 2, 3*b*) whose short, distal tip (t.p.c.) lies free of the visceral mass. Along the wall of this caecum curve two ciliated bands, dorsal (d.c.b., figure 3*b*) and ventral (v.c.b.), which extend to the lateral limits of the mantle to the right. The ventral band is raised since it runs for much of its length dorsal to the rectum (rec., figure 3*a*) which discharges faeces (f.r.) over the lateral lip of the posterior mantle lobe.

Within the head-foot, the columellar muscle splits up into a number of discrete components (figure 4). There are lateral columellar tracts (l.c.m.), and also a median component (m.c.m.) which, anteriorly, inserts ventral to the oral tube. Each lateral tract gives rise to a buccal retractor muscle (b.r.), the right one additionally providing a penis retractor (pn.r.). Elsewhere, muscle fibre orientations are less organized, though a belt of musculature (t.m.d.) traversing the dorsal cephalic wall at the level of the cephalic tentacles is conspicuous.

A number of tensor muscle strands (t.m.s.) span the cephalic haemocoel posteriorly and stabilize, in particular, that region of the cephalic wall adjacent to the infrapallium and genital mass.

(*c*) *Water flow through the mantle cavity and associated ciliary tracts*

The posteriorly directed flow of water through the cavity is achieved solely by activity of the dorsal and ventral ciliated bands (figure 3). Their ability to transport water efficiently is enhanced by close apposition of the posterior mantle lobe and suprapallial margin so that the water cannot easily leave the cavity laterally at the level of the bands (figure 3*a*). Water is expelled adjacent to the posterior fold of the mantle skirt.

Elsewhere on the walls of the mantle cavity ciliation is weak and serves only to remove particulate material from its recesses. Rejectory tracts which drive particles posteriorly can be discerned on the superpallium beneath the kidney, and also on the floor of the mantle cavity, anterior to and over the genital mass. A further rejectory tract occurs on the infrapallium adjacent to the mantle fold (figure 3*a*); it drives material to the right, along and out of the pallial caecum, an action that is facilitated by the laterally directed water current in this region (see figure 3*a*).

FIGURE 3. To show details of the mantle complex of *Chilina fluctuosa* including the direction of water flow (←) and positions of ciliary rejectory tracts (←- - -). (*a*) Right ventrolateral view: note that the ventral ciliated band overlies the rectum, and as a result only a narrow gap separates the dorsal and ventral bands. Thus the mantle cavity is effectively separated into anterior and posterior chambers. (*b*) Dorsal view with much of the suprapallium reflected to the left to reveal the underlying structures; the pericardial cavity (p.c.) has been opened. Note that the mantle cavity opening faces to the right, that buccal structures (sl.v., b.m.) are visible through the thin, posterodorsal wall of the head-foot, that the kidney is divisible into two regions, that the pericardial cavity partially overlies the mantle cavity and that the ciliated bands continue into the distal region of the pallial caecum.

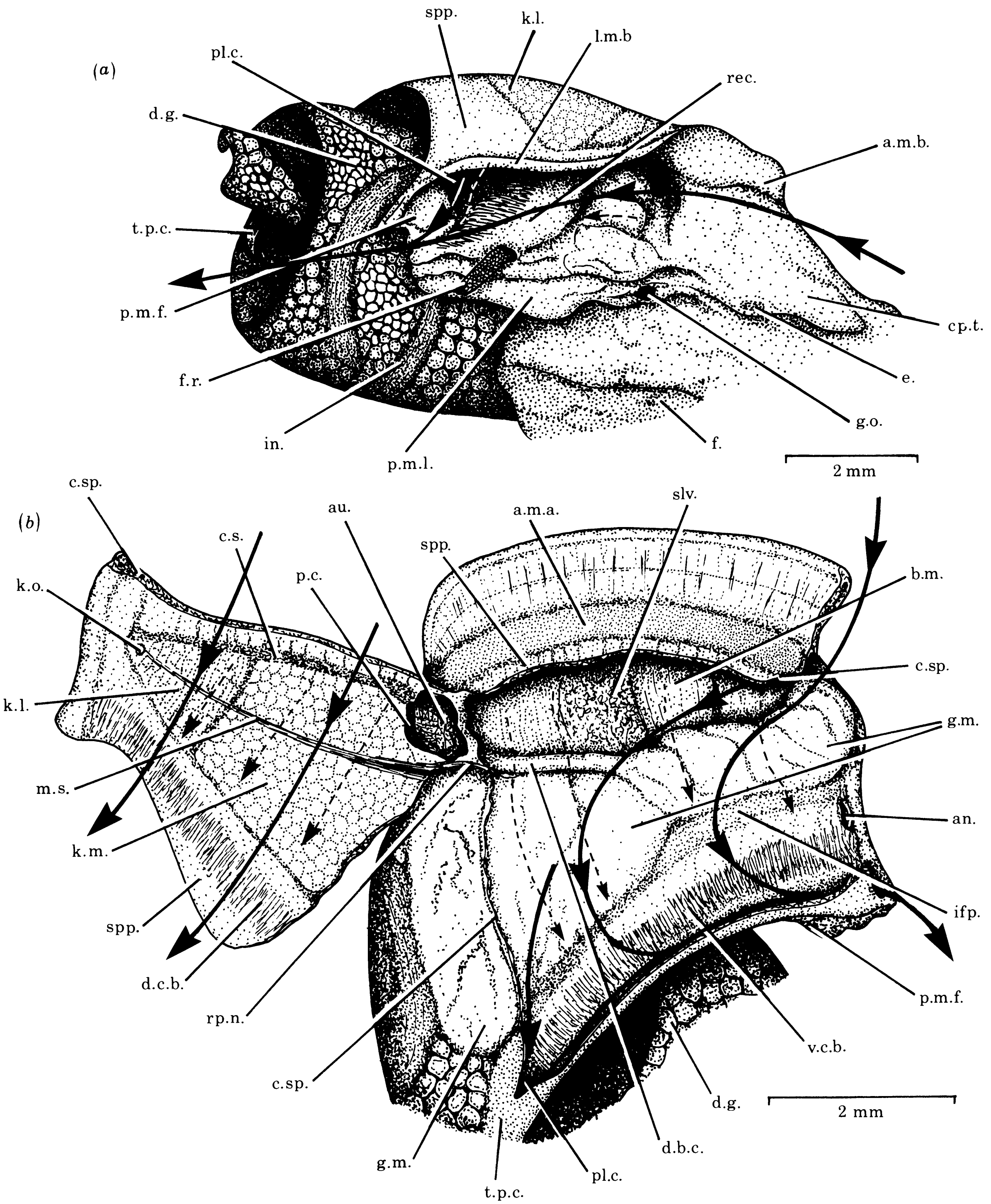

FIGURE 3. For description see opposite.

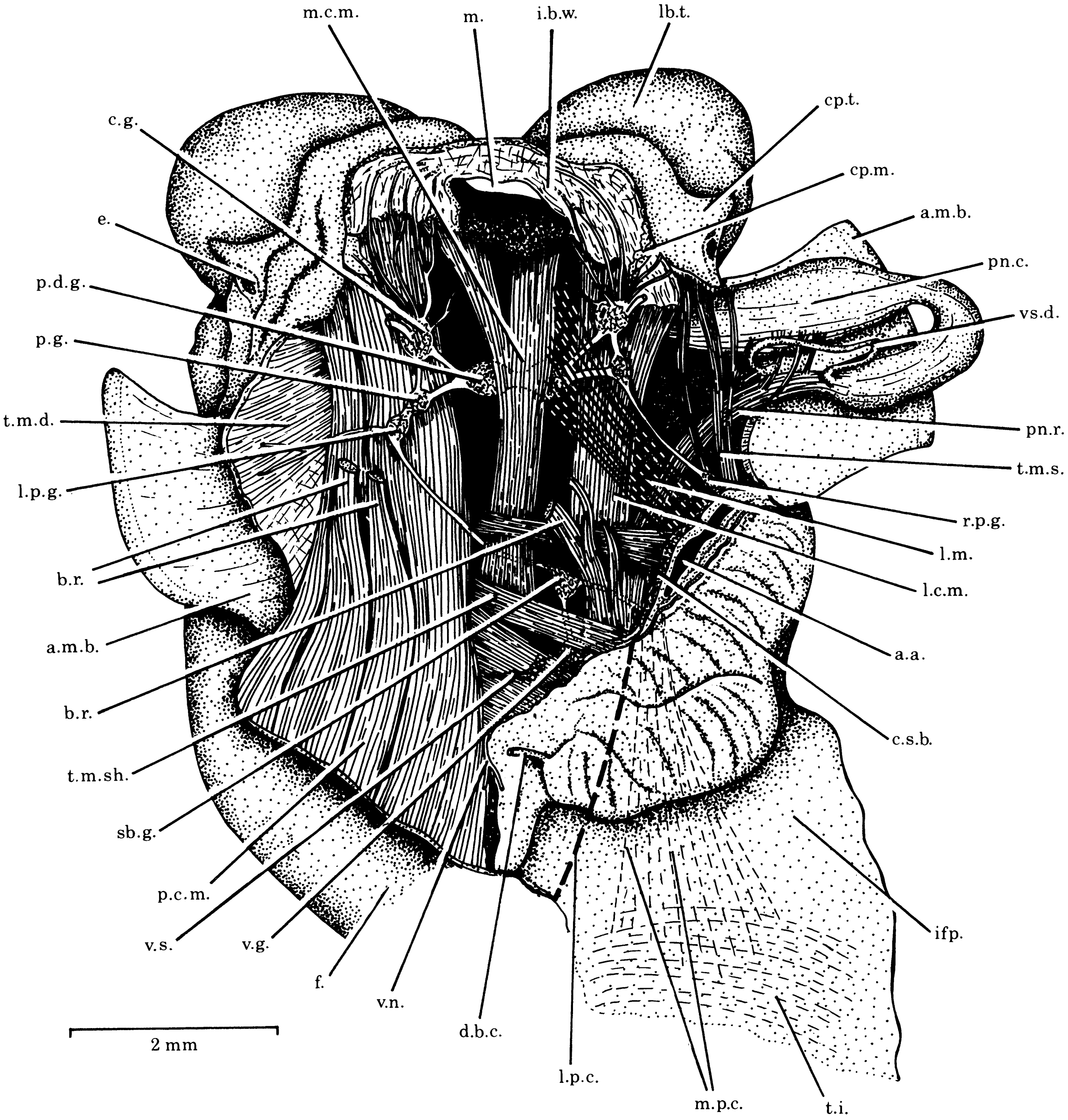

Figure 4. Dorsal dissection of *Chilina fluctuosa* to show the columellar and other musculature of the head-foot and the disposition of the anterior nerve ring and visceral nerve loop. The head-foot has been opened by a mid-dorsal incision, and the flaps pulled laterally. Most of the viscera, many pallial structures and the buccal mass have been removed; the penial complex has been displaced to the right. The cerebral commissure has been cut and the cerebral ganglia pulled laterally; the anterior aorta (a.a.) has been opened adjacent to the supra-oesophageal ganglion (not visible). Note that the proximal section of the columellar muscle is short, but broad, and that anteriorly it is composed of discrete tracts with which it is continuous; it also provides buccal retractor muscles which have been cut close to their origins to enable removal of the buccal mass. The right lateral limit of the proximal muscle, which is here overlain by the genital mass, is indicated (l.p.c.) by a thick dashed line. The thin lateral membrane (l.m.) is denoted by heavy black and pecked white lines; the position of the vertical septum is also indicated (v.s.).

(*d*) *Vascular supply to the mantle complex*

In this section, the circulation of blood within the superpallium, and the routes by which it arrives at that surface, are described. To appreciate the latter fully, it is necessary to describe the major arterial and venous routes within the cephalopedal mass, together with a general scheme of the infrapallial blood flow.

(i) *Suprapallial blood system*

The description that follows is divided into four sections. These are concerned with the following regions: pallial caecum, kidney, anterior roof of the mantle cavity and mantle border. Probable directions of blood flow are inferred only from the overall anatomy of the vascular system; no experimental studies were undertaken to confirm these assumptions.

Blood enters the roof of the pallial caecum through the posterior mantle fold (figures 3, 6) from the infrapallium (if.v., figure 6) and visceral mass. There reside many transverse vessels (p.c.v., pl.v., figure 5), which are interconnected by a vessel (a.s.c.v.) delineating the posterior border of the caecum and one following the posterior border of the kidney. For much of its length, the latter acts as an afferent renal vessel (a.r.v.). To the right, these two vessels connect with those of the lateral mantle border.

The triangular perimeter of the kidney, a structure placed between the pallial caecum and the pulmonary plexus (p.m.v., figures 2, 5), is marked by major blood vessels. Along its anterior edge runs the collecting sinus (c.s.) which delivers blood to the auricle of the heart, while the remaining boundaries are encompassed by afferent vessels (a.r.v., figure 5). In the medial part of the kidney there is a strong anterior convergence of blood vessels (r.v.m.), but laterally the kidney vessels run (r.v.l.) parallel to one another.

The pulmonary plexus receives blood from an afferent vessel (a.p.v.) following the posterior margin of the anterior mantle attachment (a.m.a.). To the right, the afferent vessel is continuous with the afferent renal vessel and indirectly linked to vessels of the anterior and lateral mantle borders; there is little direct confluence with the collecting sinus. To the left, it connects with a plexus (b.v.) on the bursa copulatrix.

There is a complex set of vessels within the mantle border (figure 5), of which two circumferential 'ring' elements (i.r.v., o.r.v.) are prominent; these are connected by numerous radial elements (r.m.v.). Adjacent to the attachment of the mantle to the dorsal cephalic wall is a rich plexus which links the inner (ring) vessel to one (a.m.v.) along the anterior margin of the mantle attachment. To the right, it communicates broadly with the afferent pulmonary vessel and to the left with vessels of the bursa.

(ii) *Blood flow through the head-foot*

Arterial system (figure 6). From its point of separation from the posterior aorta (p.a.), the anterior aorta (a.a.) runs to the right, becoming superficially embedded in the external face of the cephalic wall. It gives off vessels (g.a., g.m.v.) which permeate the distal portion of the genital mass and covering infrapallium. On the right it curves anteroventrally and medially, and penetrates the body wall (see below; figure 4), to become superficially embedded in its inner surface. Here, one vessel is sent off to the supraoesophageal ganglion (sp.g.) and a second to the visceral and suboesophageal ganglia (v.g., sb.g., figure 4). The aorta continues anteriorly,

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ventral to the buccal mass, dividing there to (1) encapsulate (v.r.) the nerve ring (n.r.), and (2) provide a pair of pedal arteries (pd.a.) and a median buccal artery (b.a.). From the blood ring on the right emerges a penial artery (pn.a.) and, to either side, a broad cephalic artery (d.c.a.) which supplies the dorsal wall.

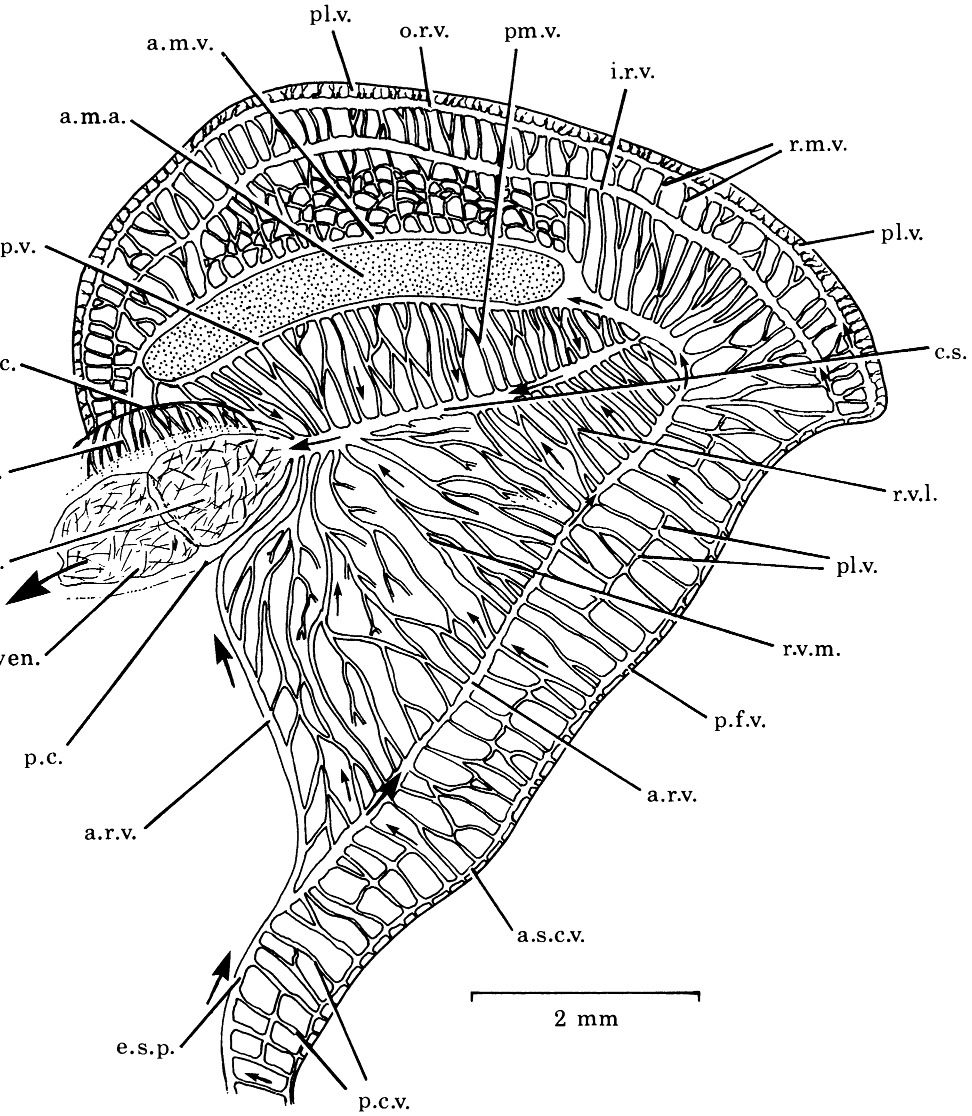

FIGURE 5. Diagram of the suprapallial vascular system of *Chilina fluctuosa*; arrows denote probable directions of blood flow.

Venous system (figures 5, 6). Anteriorly a perforated partition, the capitocerebral membrane (cp.m., figure 4) (Carriker 1946), extends radially from the ring to the dorsal and lateral body wall. A number of cerebral nerves course within it. Since the nerve ring surrounds the anterior end of the buccal mass, this partition does not lie behind the feeding structure as it does, for example, in *Lymnaea* in which the anterior ganglia lie more posteriorly. From the chamber anterior to the capitocerebral membrane, much blood obviously percolates posteriorly

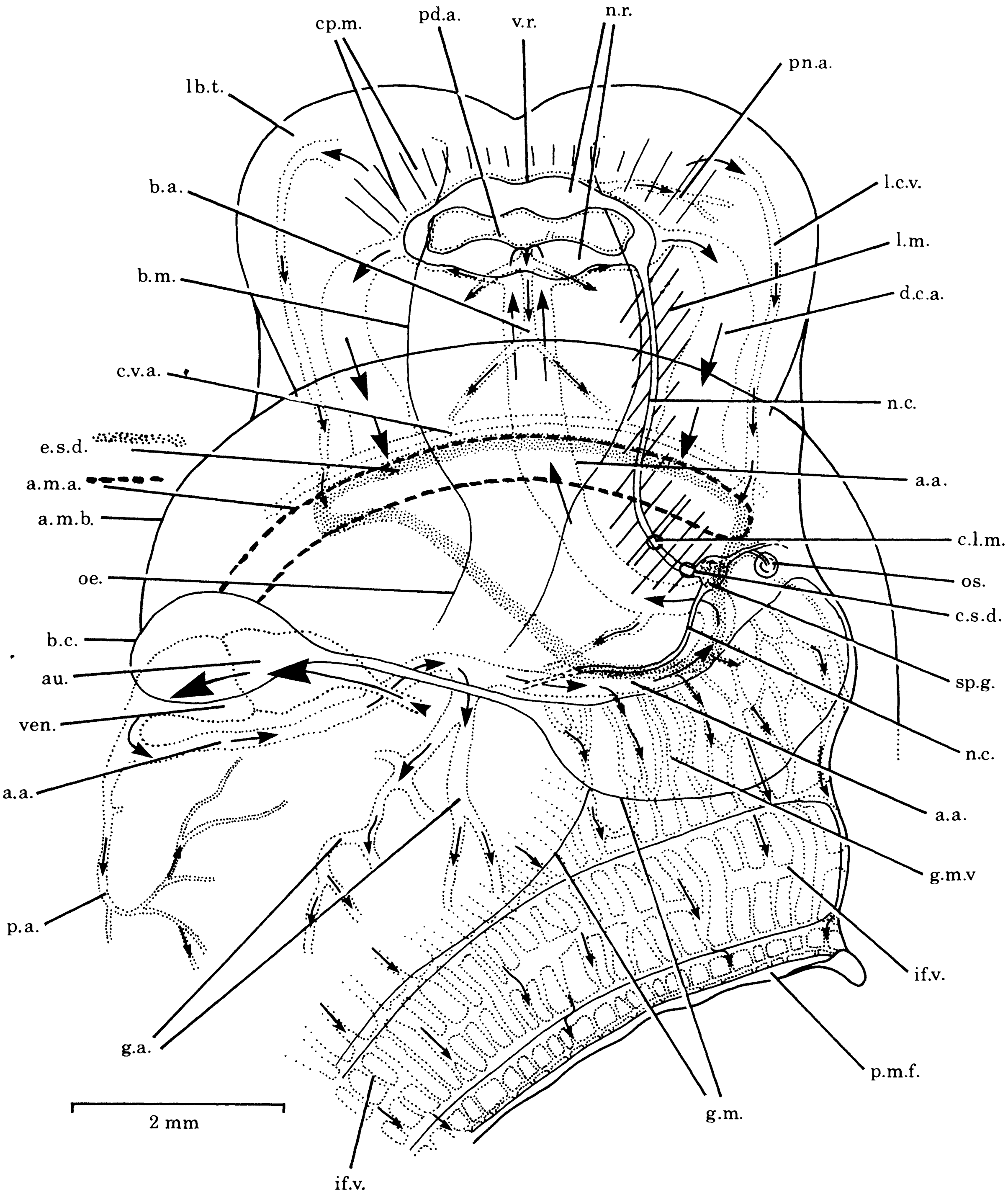

Figure 6. Diagram of the vascular system of the head-foot and infrapallium of *Chilina fluctuosa*. Solid lines indicate the extent of the head-foot and positions of certain structures; dotted lines denote blood vessels. The positions of the capitocerebral membrane (cp.m.) and lateral septum (l.s.) are indicated by series of short parallel lines. The extent of the large sinus (e.s.d.) within the thin, posterodorsal cephalic wall (anterior floor of the mantle cavity) is marked by a narrow band of dots and that of the anterior mantle attachment (a.m.a.) by a heavy pecked line. Arrows denote presumed directions of blood flow.

through the body wall. There are two conspicuous lateral channels (l.c.v., figure 6) which lead to the thin-walled section of the dorsal cephalic wall which constitutes part of the floor of the mantle cavity. That surface obviously contains a large sinus (e.s.d.) which is most extensive on the right, where it contains a supraoesophageal ganglion. Along its floor there runs the anterior aorta. There is no single major exit from this sinus, and thus presumably blood departs by a variety of routes leading into the posterior mantle lobe and infrapallium, and into the mantle border on the left. However, *no obvious communication* is made with the circulation of the anterior mantle border (see below).

Blood within the dorsal cephalic wall can enter the anterior mantle border where a circumferential element (c.v.a.) following its anteroventral margin is an important collecting element. Thereafter, the return route to the heart is provided by the fleshy part of the mantle border (including the vessels, i.r.v., o.r.v., a.m.v.) and the pulmonary plexus.

The vertical septum which separates the cephalic and visceral haemocoels is possibly homologous with the cervical septum (Carriker 1946) of *Lymnaea* and the *membrana transversa* (Kisker 1923) of *Helix*. Within the head-foot on the right is a vertically orientated partition (l.m. figures 4, 6) which extends anteroposteriorly and to which, for a short distance, is attached the visceral loop. It is perforated and blood may freely pass through. There appears, however, to be nothing functionally comparable with the anterior ventral visceral sinus (Nisbet 1973) of prosobranchs and of *Acteon* (Brace 1977*b*), though an incomplete curtain of oblique muscles (t.m.sh.) spanning the haemocoel ventrally (figure 4) is probably homologous with the roof of that sinus. Moreover, no cephalopedal vein was located (see p. 485) and thus the kidney, as in most tectibranchs (not *Acteon*), receives blood solely from visceral and pallial sources.

(*e*) *Nervous system* (figures 4, 7)

The nerve ring encircles the anterior end of the buccal mass and the median columellar muscle, a position apparently retained when the animal is feeding. It is composed of discrete cerebral (c.g.), pleural (p.g.) and pedal (pd.g.) ganglia. The first innervate (t.n., l.n., o.n.) the cephalic and labial tentacles, and the oral region.

The visceral loop is uncrossed, and the supraoesophageal ganglion lies to the right of the midline; the suboesophageal ganglion, in common with the visceral, occupies a median position (see figure 4). There are two pallial ganglia on the loop: one (l.p.g.) situated adjacent to the left pleural ganglion, the other (r.p.g.) partially fused with the supraoesophageal. This is in contrast to *Acteon tornatilis* in which the right ganglion is sited anteriorly rather than posteriorly and the left lies equidistant from the pleural ganglion and the suboesophageal. However, as in tectibranch opisthobranchs (Brace 1977*b*), nerves (pl.n.) originate from them which supply the adjacent body wall and associated mantle border. Innervation by the supraoesophageal ganglion is also conventional, the anterior region of the suprapallium, including the osphradium, and neighbouring body wall being supplied (p.sp.n., figure 7).

One stout nerve departs directly from the suboesophageal ganglion, but two nerves (b.w.n.), which innervate the mantle and ventrolateral body wall, arise from the connective anterior to it. One of these at its point of origin displays a small ganglion (ac.g.). A similar disposition of nerves (Brace 1977*b*) is seen in *Acteon tornatilis* and *Bulla striata*. The major nerve (p.sb.n.) arising from the suboesophageal ganglion passes posteriolaterally to the right, and then posteriorly to innervate the posterior mantle lobe, infrapallium, rectum and the posterior mantle fold.

From the visceral ganglion depart two major nerves; one (gr.n.) passes posteriorly, in

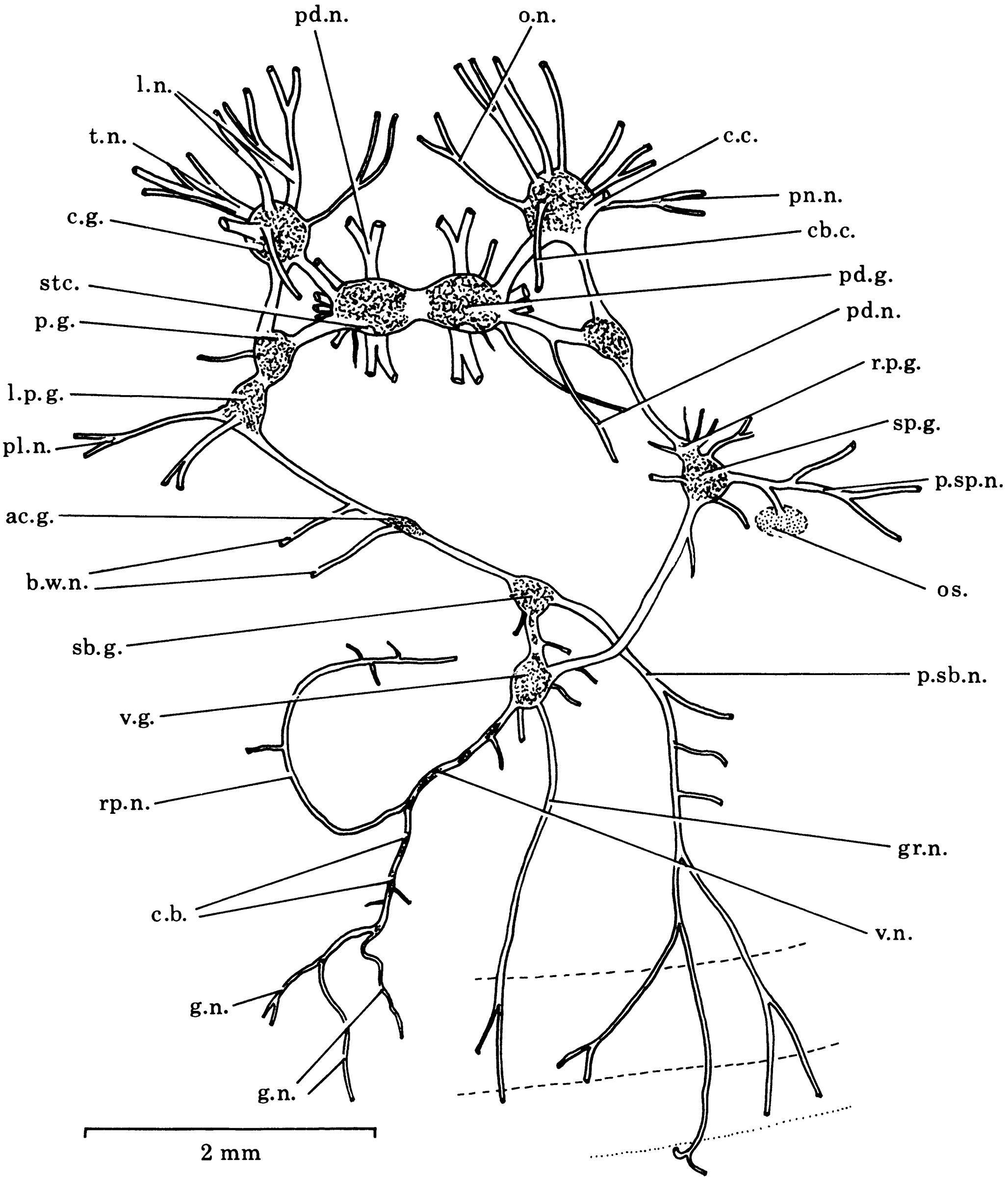

Figure 7. Dorsal view of the central nervous system of *Chilina fluctuosa*. The disposition of the visceral loop approximates to that of an intact animal, though for clarity the supraoesophageal section has been slightly displaced to the right; the visceral loop is euthyneurous. The cerebral commissure has been cut and the cerebral ganglia pulled laterally; the buccal ganglia are not illustrated, though sections of the cerebrobuccal connectives remain. Dashed and dotted lines denote the positions of the ventral ridge (and ciliated band) and posterior mantle fold respectively.

association with the infrapallium, to innervate the genital mass and rectum, while the other travels posterodorsally (v.n., figures 4, 7). The latter bears a number of small cell bodies (c.b., figure 7) along its length and bifurcates, one branch (rp.n.) continuing dorsally and then to the right to innervate the heart and kidney; it extends to the vicinity of the kidney aperture (see figure 3*b*). The other branch (g.n.) quickly divides again, to innervate the proximal section of the genital tract, and other structures within the upper portion of the visceral mass.

The buccal nervous system is described at the end of § 3*f*.

(*f*) *Buccal mass* (figures 8, 9)

(i) *General morphology*

The buccal mass is a pyriform muscular structure (figure 8) which, together with the penial complex, occupies much of the cephalic haemocoel. At rest it lies with its long axis disposed more or less vertically (figure 8*a*) so that the radular sac (r.s.), salivary glands (slv.) and initial segment of the oesophagus (oe.) all lie contiguous to the floor of the mantle cavity, through which they can be seen (b.m., slv., see figure 3).

The buccal mass is joined to the body wall anteriorly where the oral tube is located; elsewhere connections are established by extrinsic muscles (figure 8) which serve to protract, retract or levate it. Within the ventral part is housed the single odontophoral cartilage (figure 9*b*, *c*) upon which the radula (r., figure 9*c*, *d*) is supported, and on which many muscles originate. The muscles described include extrinsic elements, those that manipulate the odontophore, and those that are concerned with moving the radula to and from over the anterior cartilage lip (see figure 9*d*).

The odontophoral cartilage also partially supports the stubby radular sac, which has its own skeletal component, the collostyle, which, as in other pulmonates, bears at its anterior end an epithelial plug or collostylar hood (cs.h.). The cartilage is U-shaped in section, with the concave face uppermost. At each end (figure 9*b*, *c*) it is drawn out, forming posterior horns (p.h.) and anterior flanges (a.f.), the latter overlapping somewhat in the midline. The structure displays a vesiculo-muscular construction (Carriker 1946), being especially muscular in the midline where fibres (intracartilage tensors, ic., figure 9*b*)) are transversely orientated; it is most flexible in this region. At rest, the anterior cartilage lip lies dorsally with the long axis of the skeletal component disposed more or less vertically.

The radular ribbon is broad with a formula of 55 × 60.1.60. A description of the radular teeth was provided by Harry (1964); a comparative treatment of the radular morphology of a number of *Chilina* spp. is in preparation.

Anterodorsally, the inner epithelium of the buccal wall is covered by cuticle which forms a jaw (j., figures 8*a*, 9*d*); less obvious cuticularization is also apparent laterally. The salivary glands (figure 8*a*) resemble those of other basommatophorans and are relatively voluminous.

The terminology of Carriker (1946) and Hembrow (1973), applied repectively to *Lymnaea* and *Planorbarius*, is adhered to in the description of the musculature of the buccal mass wherever possible. This has proved fairly easy since the buccal morphology of *Chilina fluctuosa* closely resembles that of more advanced pulmonates, and most muscles have obvious homologues. Since the anatomy is comparable and since no detailed observations were made on the feeding cycle of *Chilina*, brief comments on the probable functional roles of particular muscles are largely drawn from studies on the other pulmonates.

It is important to note that, in pulmonates, muscles designated as either retractors or protractors may not necessarily be active during or only during the corresponding phase of the feeding cycle (Crampton 1973; Brace & Quicke 1980, 1981); this is especially true of some of those muscles that insert on the radula.

(ii) *Extrinsic odontophoral muscles* (figure 8)

(A) *Muscles active during protraction.*

(1) Dorsolateral protractors (dl.p.). From insertions adjacent to the base of the oesophagus

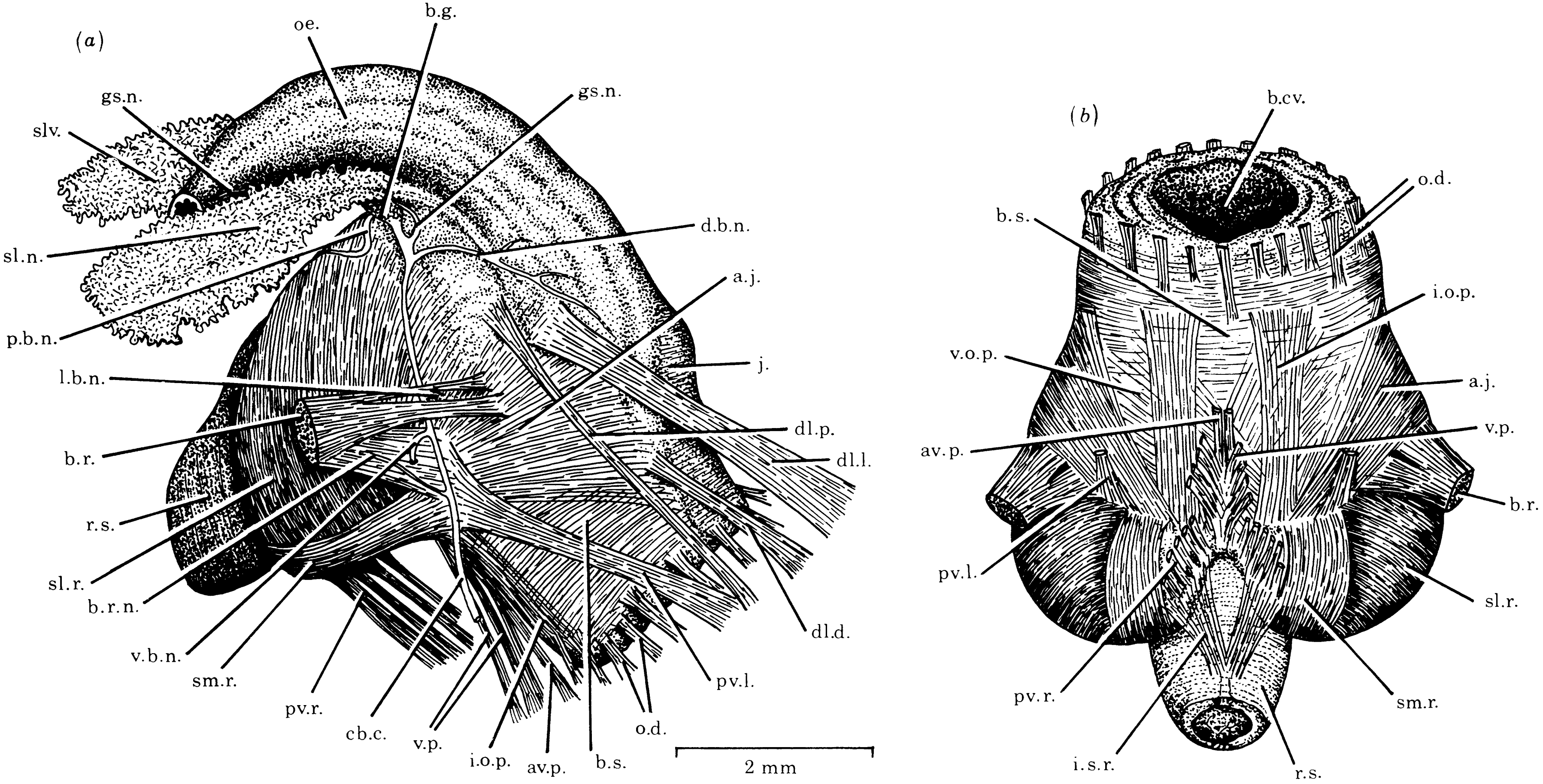

FIGURE 8. Buccal mass of *Chilina fluctuosa*. (*a*) Lateral view from the right, in resting posture. (*b*) Ventral aspect; ventral extrinsic muscles have been cut near their insertions and removed to facilitate the viewing of other muscles.

(figure 8*a*), this pair of slender muscles run anteroventrally to the body wall. They act to draw the upper part of the feeding apparatus forwards and downwards.

(2) Ventral protractors (v.p.). These muscle strands have midventral insertions on the buccal mass, and fan out anteroventrally to the body wall.

(3) Anteroventral protractors (av.p.). These two muscle strands form a continuous series with (2), and extend strictly anteriorly to insert on body wall immediately below the oral tube.

(4) Dorsolateral dilators (dl.d.). This pair of short strands (figure 8*a*) run parallel to the course of the dorsolateral levators, but have more lateral origins on the body wall. They insert immediately lateral to the jaw and act to expand the lumen (b.cv., figure 8*b*) of this region of the buccal mass.

(5) Oral dilators (o.d.). These are short strands radiating to origins on the body wall.

(6) Posteroventral levators (pv.l.). This pair of muscles have broad insertions on the lateral buccal walls, immediately anterior to those of the ventral insertions of the buccal retractors. They undoubtedly tilt the buccal mass into the more vertical position required for rasping. Apparently homologous muscles in *Helisoma trivolvis* have, to the contrary, been reported (Kater 1974) to provide a thrust promoting the return stroke of the buccal mass. Exactly where the relevant fulcrum lies is highly dependent upon activity in other muscles, but, even given variability in this respect, it seems unlikely that Kater's suggestion is at all mechanically feasible in any circumstance.

(7) Dorsolateral protractors (levators) (dl.l.). This pair of muscles run anteriorly from insertions on the dorsolateral buccal walls (figure 8*a*), at the extreme posterodorsal limits of the anterior jugalis muscles, to origins on the wall of the head-foot. These muscles are presumably active during both protraction and rasping.

(B) *Muscles active during retraction.*

(1) Buccal retractors (b.r.). This pair of stout muscles originate (figure 4) from columellar musculature at the end of the head-foot and fasten to the lateral walls of the buccal mass and possibly to the cartilage, there having a number of discrete insertions. They serve to retract the entire buccal mass.

(2) Posteroventral retractors (depressors) (pv.r.). Each member of this pair of muscles consists of a number of separate strands which insert on musculature overlying the ventromedial margins of the posterior horns of the odontophoral cartilage, and possibly on the cartilage itself. They run anteriorly to origins on the body wall, ventral to the oral tube. Although they could effectively draw forwards a section of the feeding apparatus during protraction, electrophysiological work on *Helisoma* and *Lymnaea* (Kater 1974; Rose & Benjamin 1979) has disclosed that the muscles actually participate in retraction when they appear to depress the rear of the buccal mass, in turn causing a retractive rotation of the odontophoral cartilage. The concave nature of the ventral surface of the buccal mass (see figure 8*a*) in *C. fluctuosa* makes this suggestion even more likely.

(iii) *Intrinsic odontophoral muscles* (figures 8, 9*b*)

(1) Anterior jugalis (a.j.). Each muscle forms a noticeable, externally placed sheet of fibres fanning out dorsally and anterodorsally from a compact origin on the ventrolateral face of the cartilage (figure 9*b*). Anterodorsally its fibres interdigitate with those of the buccal sphincter (b.s.). It is generally agreed (Carriker 1946; Crampton 1973; Hembrow 1973) that these

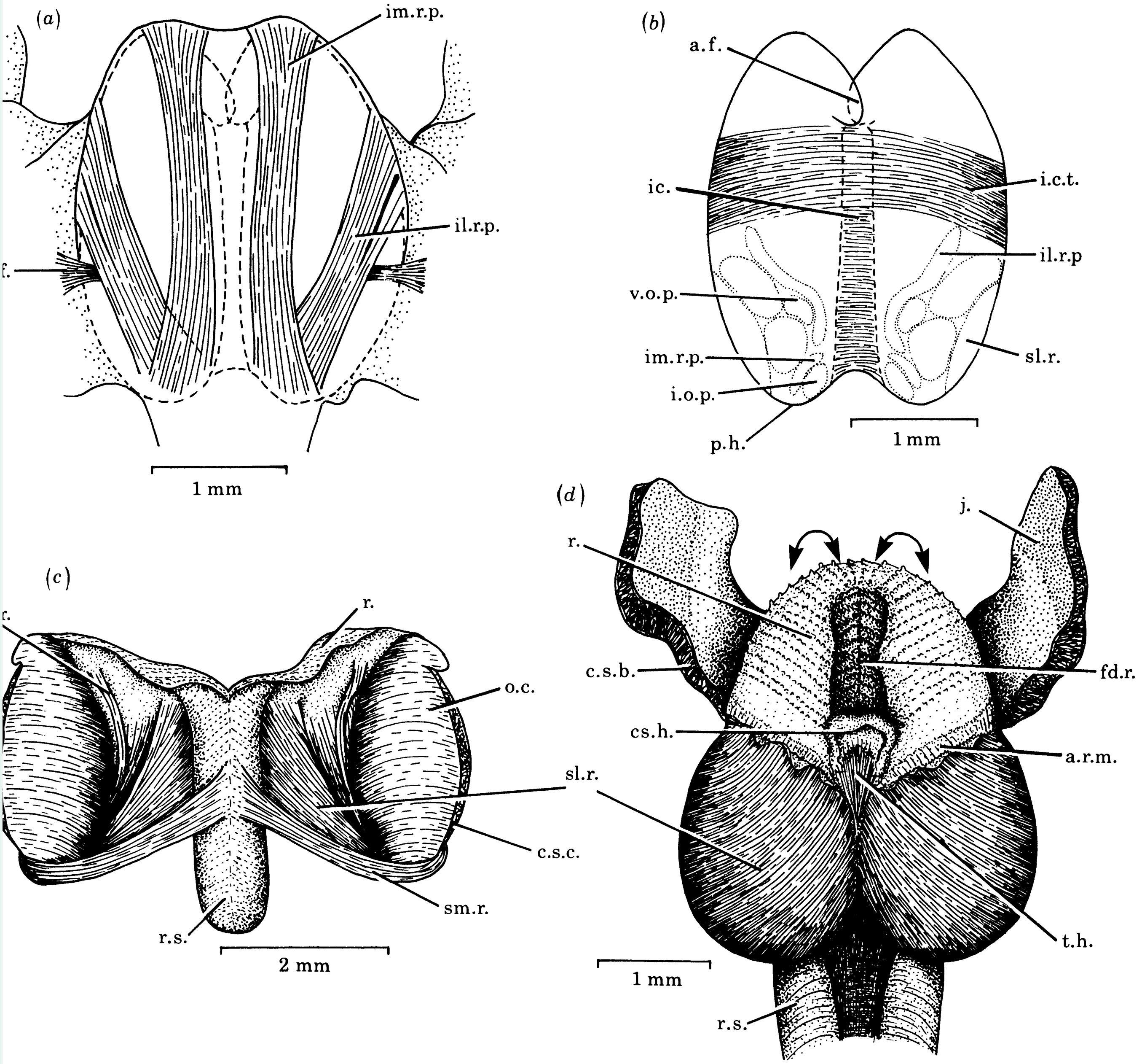

FIGURE 9. Odontophoral morphology of *Chilina fluctuosa*. (*a*) Diagram showing the disposition of radular protractor muscles in ventral view; the outlines of the cartilage 'halves' are shown as dashed lines. (*b*) Diagram depicting the odontophoral cartilage in ventral view to show the extent (dotted lines) of the origins or insertions of the various odontophoral and radular muscles; some musculature is illustrated. (*c*) Ventral view of the insertions of the radular retractor muscles on the radular sac, subradular membrane and buccal epithelium. The cartilage 'halves' have been separated to show the disposition of the radula and insertions of the supralateral radular retractor muscles (sl.r.). (*d*) Dorsal dissection of the buccal mass to show the insertions of the supralateral radular retractors, the anterior cartilage lip and the collostylar hood. Most of the external wall of the buccal mass has been removed, including the thin posterior jugalis muscles which overlie the bulky retractor muscles. Anteriorly the wall remains, but it has been cut mid-dorsally and the parts reflected laterally, thus exposing the jaw; arrows indicate the protractive and retractive movements (and spreading/folding) of the radula over the anterior cartilage lip.

muscles aid odontophoral protraction, but, since they can also be active during rasping in *Lymnaea* (Rose & Benjamin 1979), a second important function may be to steady the odontophore. In contrast to the above, Kater (1974) indicated that they are active during retraction. This observation seems difficult to accept for, even given appropriate positioning of the cartilage fulcrum, it is again impossible to imagine how any mechanical advantage necessary to achieve such a result can be obtained.

(2) Posterior jugalis (not illustrated). This is an extremely thin sheet of musculature overlying the rear of the buccal mass. It helps to suspend the posterior end of the odontophoral cartilage, on which it inserts, during protraction.

(3) Infraventral odontophoral protractors (i.o.p.). Each member of this pair of muscles runs forward from an insertion on the ventromedial face of the posterior horn of the cartilage to an origin among fibres of the buccal sphincter muscle. Anterior to the level of the insertion of the anterior jugalis the muscle is immediately internal to the covering epithelium of the ventral buccal wall.

(4) Ventral odontophoral protractors (v.o.p.). These muscles have more anterior insertions on the cartilage than have (3) and extend anteromedially and dorsally, thus crossing one another to reach contralateral origins among fibres of the buccal sphincter. This pattern is in contrast to that in more advanced pulmonates, in which apparently homologous muscles have a strictly anteroposteriorly directed course. However, some fibres in *C. fluctuosa* do follow this latter type of path, though they appear to fasten primarily to other protractor fibres rather than inserting directly on the cartilage.

(5) Dorsal odontophoral flexors (d.o.f.). These two inconspicuous muscles (figure 9*a*) pass dorsolaterally from insertions on the ventrolateral faces of the cartilage to origins in the buccal wall, internal to the buccal sphincter (posterior part) and anterior jugalis muscles. They presumably help to spread the cartilage halves during protraction.

(6) *Buccal sphincter* (b.s.). A thick muscle band (figure 8) encircling the anterior end of the buccal mass. Its activity undoubtedly forces the odontophoral tip posterodorsally during retraction, as in other pulmonates (Crampton 1973). This conclusion is substantiated by the feature that, in *Planorbarius corneus*, those motoneurons supplying the supralateral radular retractors (see below) which also innervate part of the buccal-sphincter, are primarily active during retraction (Brace & Quicke 1981).

(iv) *Radular muscles* (figures 8, 9)

(1) Inframedian radular protractors (im.r.p.). These relatively broad, though thin, muscle bands originate on the ventromedial margins of the posterior horns of the cartilage (figure 9*b*) and run forwards to insert on the subradular membrane to either side of the midline (figure 9*a*), at a level a little posterior to the anterior cartilage lip.

(2) Infralateral radular protractors (il.r.p.). Each member of this pair of muscles is broader than those described immediately above, and has a long but narrow origin on the cartilage (figure 9*a*, *b*). Each inserts anterolaterally to the subradular membrane and buccal epithelium. These muscles, and the inframedian protractors, serve both to protract and to tense the radula over the anterior cartilage lip, as such acting antagonistically to the radular retractors (see below). Hembrow (1973) noted only one pair in *Planorbarius*, but Carriker (1946) described two pairs in *Lymnaea* whose dispositions closely resemble those found here.

(3) Supralateral radular retractor (tensor) muscles (sl.r.). These muscles, which are the

bulkiest in the bucccal mass, run anteriorly from origins (figure 9*b*) on the lateral and ventrolateral margins of the posterior horns of the cartilage to insertions on the dorsolateral edges of the radular sac, or the subradular epithelium and, more laterally, on the buccal epithelium (figure 9*c*, *d*). The muscles are thickest posteromedially, where they display an obviously curved course from origin to insertion (figure 8). Since the disposition of this pair of muscles is identical to that described in *Planorbarius*, they presumably function in an identical manner. Studies on *Planorbarius* have demonstrated (Brace & Quicke 1980) that they are multifunctional, acting to tense the radula during rasping, to retract it, and also to spread and tense it again after withdrawal, when food is released and conveyed into the oesophagus. Contraction of the medial fibre bundles produces a retreat of the radula over the cartilage lip, while activity in lateral components results in tensing.

(4) Supramedian radular retractors (tensors) (sm.r.). Each of these two compact muscle bands (figures 8, 9*c*) originates on the ventrolateral margin of the radular sac. They undoubtedly tense and retract the radula, presumably with emphasis lying on the latter since they have more posteriorly placed origins than the supralateral radular retractors.

(5) Lateral radular retractors (tensors) (l.r.r.). Although treated by Hembrow (1973) as parts of the supralateral radular retractors in *Planorbarius*, these slender bundles (figure 9*c*) in *Chilina* appear distinct, and thus are considered separately. They are undoubtedly also functionally distinct in *Planobarius* since they may contract independently of their larger neighbours (personal observation). They similarly originate on the posterior horns of the cartilage, but on the medial rather than the lateral faces, and insert on buccal epithelium laterally.

(6) Infralateral cartilage tensor (i.c.t.). These fibres constitute a ventrally positioned muscle band (figure 9*b*) extending in an arc from one side of the cartilage to the other. They counteract a tendency for the cartilage arms to collapse inwards as a result of activity of the radular retractors, thus aiding the maintenance of shape of the cartilage lip, especially important during rasping.

(7) Inferior suspensor of the radular sac (i.s.r.). This pair of small muscles (figure 8*b*) originate on fibres of the supramedian radular retractors, and insert on the ventrolateral surfaces of the radular sac.

(8) Tensor of the hood (t.h.). This aggregation of muscle fibres spread out from origins on the ventral surface of the base of the radular sac to insertions on the collostylar hood (figure 9*d*).

(v) *Buccal nervous system* (figure 8*a*)

With the exception of the posterior buccal nerves (p.b.n.), which originate from the buccal commissure, the buccal nerves arise from the cerebrobuccal connectives adjacent to the ganglia. Four major nerves are given off from each connective (lateral (l.b.n.), ventral (v.b.n.), dorsal (d.b.n.), gastric (gs.n.)), and also a nerve (b.r.n.) supplying the buccal retractor muscle. The pattern of innervation in *Planorbarius* and *Lymnaea* is comparable (Brace & Quicke 1980), with the exception that the nerves largely arise directly from the ganglion rather than from the cerebrobuccal connective, though in those animals the lateral and ventral nerves merge with the connective as it enters the ganglion.

The overall distribution of cell bodies within the ganglia was examined; it appears similar to that of other basommatophorans that have been examined (Benjamin *et al.* 1979; Brace & Quicke 1980).

4. Discussion

This discussion is restricted to considering the significance of those morphological and behavioural features described above in relation to the successful penetration of freshwater niches by basommatophorans. Neither the relationship of the Chilindae to other extant pulmonate families, nor a reassessment of the precise prosobranch origins of pulmonates (and opisthobranchs), is treated in detail since these are topics that have received much attention elsewhere (Boettger 1954; Fretter & Graham 1954, 1962; Fretter 1975; Brace 1977*a*; Hubendick 1978). A monotocardian (and probably common) origin for pulmonates and opisthobranchs is, however, assumed.

It was anticipated that *C. fluctuosa* would be infaunal in common with the morphologically similar opisthobranch *Acteon*. However, most animals were found predominantly on rocks (embedded in sand). Nevertheless, observations in the laboratory clearly demonstrated that the animals are capable of withdrawing completely into the substratum using a stereotyped digging cycle. Moreover, field observations showed that other *Chilina* spp. in Chile were solely associated with soft substrata, through which they ploughed partially submerged, using similar cycles of activity, and thus, as anticipated, this habit is obviously widespread within the family. Therefore, much evidence suggests that a largely infaunal life style was a primitive attribute of the Chilinidae, for which streamlining of the body was an important prerequisite. Significantly, some species were located on mud flats in brackish/marine environments. Such habitats are also characteristic of the related Amphibolidae (*Amphibola*, *Salinator*) (Farnie 1919) which, however, is restricted to this environment.

Although the radiation of the Amphibolidae has been far more conservative, they are essentially amphibious, dwelling at extremely high tidal levels (Watters 1964; Smythe 1975; Shumway 1981). The Ellobiacea, on the contrary, have undergone an explosive radiation and, in addition to occupying mud (mangrove) flats (Morton 1955; see Hubendick 1978), have exploited many other habitats. This may be correlated with their less obvious specialization for burrowing, or could perhaps be related to their generally smaller size. Small size is likely to have been characteristic of all early pulmonates since cogent arguments can be put forward (Fretter & Graham 1962; Fretter 1975; Brace 1977*a*) indicating that the ancestral stock that gave rise to both pulmonates and opisthobranchs consisted of small animals. For example, the fact that the gill, when present, in both early opisthobranchs and pulmonates (*Siphonaria*) is of a different form (plicate) from the prosobranch ctenidium may be satisfactorily explained by assuming that the ctenidium was lost for reasons of small size and a new structure was developed with increasing body size. The two remaining basal pulmonate families, the Siphonariidae and the Gadiniidae, have remained marine, and are adapted for life on rocky shores, having a limpet form (Schumann 1911; Hubendick 1945; Yonge 1952).

Thus the evolutionary 'picture' that emerges is one of a range of primitive pulmonate families, many of which at some stage had or still have infaunal types. Within these the Chilinidae are a predominantly freshwater group, with many species dwelling on hard substrata but still containing a number of infaunal representatives.

A radically different picture of basommatophoran evolution is commonly favoured in the literature. This purports that the 'higher limnic' basommatophoran families are derived from stocks that were basically terrestrial. Such a scheme has also been promulgated by Morton (1958), a fact that seems surprising in view of his extensive work on the Ellobiidae, a group that, although having semi-terrestrial and terrestrial representatives, has many estuarine members associated with soft substrata. The evidence brought forward to support a terrestrial origin of most basommatophorans, that amphibious types display more primitive reproductive and nervous systems than fully aquatic forms (which often possess secondary gills), and also show partial uricotely, can be used with equal weight (see, for example, Machin 1975) to support an estuarine ancestry in which animals (lacking a gill because of small body size) were subjected to fluctuating water levels. Moreover there is a wealth of other features, including the presence of free veligers in *Amphibola*, *Salinator* and *Siphonaria*, and an open sperm groove in *Phytia* (Ellobiidae), that support an aquatic rather than a terrestrial origin.

Features that are linked to the assumption of a burrowing mode of life (Brace 1977*a*) are: (1) ploughshare-shaped head-foot (which promoted the production of pallial ganglia (Brace 1977*a*)); (2) reduction of the nuchal region and spire height to aid streamlining; (3) migration of the mantle complex to the right and posteriorly (which, since the supraoesophageal ganglion followed this movement, resulted in uncrossing of the visceral loop), and concurrent fusion of the mantle border to the dorsal cephalic wall (which helps to avoid clogging of the mantle cavity by particulate material during forward progression).

In comparison to *Acteon*, the mantle cavity aperture of *Chilina* lies further to the right, but is similarly partially occluded by fleshy mantle excrescences. In both, the ventilatory flow relies upon the activity of ciliated bands. The long pallial caecum, so characteristic of *Acteon*, is also present in *Chilina* but is much less well developed. The kidney in both animals resides within the suprapallium, its migration from the visceral mass presumably having been prompted by a lack of space accruing from nuchal shortening. Unlike *Chilina*, *Acteon* possesses a gill (plicate), though the primitive opisthobranch *Ringicula*, which is acknowledged to be more closely related to pulmonates (Boettger 1954; Fretter 1960), does not, presumably for reasons of small size (see above).

With regard to the degree of confluence between anterior and posterior body regions, the nuchal area of *Chilina* is further reduced from the condition noted in *Acteon*, and the dorsal cephalic wall does not extend posterior to the vertical septum as it does in *Acteon* (see Brace 1977*b*, fig. 1*b*). As proposed by Hubendick (1978), a comparison of the relationship of structures at the base of the visceral mass has shown that the anterior floor of the mantle cavity of later pulmonates (diaphragm) is undoubtedly formed by the dorsal cephalic wall. Moreover, the suboesophageal and visceral ganglia of *Chilina*, as in more advanced tectibranchs, have approached one another, and the proximal columellar muscle is reduced in length, though broad, supporting the infrapallium on the right.

What is of particular significance to the evolution of the pallial vascular system is that nuchal reduction in pulmonates has not been so extreme as in opisthobranchs, in which streamlining for burrowing was all-important. This difference permitted the exploitation of anteriorly sited (pulmonary) plexuses (incipiently developed in the opisthobranch *Acteon*) in the roof of the mantle cavity in pulmonates alone, whereas the emphasis in opisthobranchs lay with more posterior plexuses (gill, pallial caecum).

As in tectibranchs, migration of the kidney into the suprapallium resulted in loss of a direct connection with the cephalic haemocoel via the anterior ventral visceral sinus and cephalopedal vein (Brace 1977*b*) characteristic of prosobranchs (Nisbet 1973). This route, which still remains in *Acteon*, was looked for in *Chilina*, but not found (see below). Emphasis in both groups has thus shifted to the kidney receiving blood from pallial sources (in turn partially drawn from the visceral haemocoel). The kidney passes blood directly to the heart. It is tempting to suggest that the efferent renal vessel (collecting sinus) partially represents the one-time efferent gill vessel, but, since in prosobranchs a direct connection between the kidney and heart already exists in the form of the efferent nephridial (gland) vessel, this interpretation may well be incorrect. It is in this context that it should prove instructive to compare and contrast the morphologies of the two regions of the kidney in *Chilina* with that of the kidney and nephridial gland of prosobranchs.

Lack of drainage of blood from the cephalic haemocoel into the kidney, which constitutes a major return route to the heart from the head-foot of prosobranchs, undoubtedly necessitated the enhancement of other routes. One such pathway runs from the body wall of the head-foot into the mantle border. Although of minor importance in prosobranchs, reduction of the nuchal area and fusion of the mantle border to the dorsal cephalic wall probably facilitated the development of this route which, with retention of the mantle cavity anteriorly, has been seized upon by pulmonates and the anterior (pulmonary) plexus subsequently elaborated. Departure of blood from the cephalic haemocoel in tectibranchs is also, apparently, partially achieved by the passage of blood through apertures in the diaphragm, but the homologous vertical septum of *Chilina* seemingly constitutes a total barrier to blood flow.

In addition to the pulmonary plexus, the floor of the mantle cavity (dorsal cephalic wall) of *Chilina* presumably also acts as an important site of oxygen uptake since it contains a large blood sinus, and since, in common with its homologue (diaphragm) in more advanced pulmonates, it is sufficiently thin to permit much direct uptake into the cephalic haemocoel.

Vascular arrangements within the roof of the mantle cavity of both *Amphibola* and *Siphonaria* (Farnie 1919; Cottrell 1911, 1912; Fretter 1975) are similar to those of *Chilina*, though the pattern of vessels in *Siphonaria* is more complex since it possesses a gill (plicate), and the kidney, presumably in association with the patelliform body, extends onto the floor of the mantle cavity.

It is instructive now to compare and contrast the vascular systems of *Chilina* and *Lymnaea*. A detailed account of that of the latter has been provided by Bekius (1972); as in *Chilina*, lateral cephalic vessels are important in draining the cephalopedal haemocoel. The dorsal arterial and venous systems are, however, far less conspicuous, an understandable difference since *Lymnaea* is not a burrower and thus presumably does not require, to the same degree, vascular control over local movements or inflations of the head-foot. The lateral vessels in *Lymnaea* converge, forming a cephalopedal vein (vena cephalopedalis) which leads to the kidney. It was initially tempting to homologize this vessel with the cephalopedal vein of monotocardian prosobranchs (and *Acteon*), but its course is sufficiently different, especially in entering the kidney on the right rather than on the left, not to warrant such a conclusion. More difficult is the task of relating it to the vascular pathways of *Chilina*: the most likely explanation is that it is at least partially equivalent to the large sinus within the thin floor of the anterior section of the mantle cavity. Indeed, Bekius describes the vena cephalopedalis as penetrating connective tissue that binds together organs located in this very region in *Lymnaea*.

Bekius divided the pulmonary plexus into a number of regions, the small posterior one of which is clearly homologous with vessels of the pallial caecum of *Chilina*. The extent of the anterior plexus appears, however, to have been under-estimated, but it is apparent that its afferent vessel draws primarily on blood emerging from the vena cephalopedalis. This is in contrast to the situation in *Chilina* in which, presumably since the dorsal cephalic system is better developed, the anterior plexus directly drains cephalic spaces. Comparison with *Helix* demonstrates that, with formation of an extensive afferent 'ring' vessel, the pulmonary plexus can directly drain both cephalic and visceral haemocoelic spaces.

Once the anterior region of the mantle cavity had become established as the prime site for respiratory exchange, it is apparent that it not only could act as a recess within which water could circulate, but also had great potential for aerial respiration. This results from occlusion of the mantle cavity aperture anteriorly and its partial occlusion on the right, providing a largely enclosed chamber which could easily retain water (or at least remain humid), a valuable feature in the exploitation of freshwater habitats which frequently demand an amphibious mode of life. Little evidence was found to suggest that the mantle cavity of *Chilina fluctuosa* is used for holding air, but observations on other species in Chile, particularly those occurring in estuaries, indicate that is is not uncommon within the genus. It has also proved to be of great potential in the colonization of the upper littoral zone. In both *Gadinia* (Yonge 1958) and *Siphonaria* (Yonge 1952; Fretter 1975) the mantle cavity may be used as a lung, circulation of air in the latter genus apparently being encouraged by rhythmic pumping movements of the floor of the chamber. Interestingly, these movements foreshadow the forced ventilation characteristic of some stylommatophorans (see Ghiretti 1966).

Evidence from developmental studies has prompted some workers (Ghose 1963; Regondaud 1964) to suggest that the mantle cavity of pulmonates is not homologous with that of prosobranchs. In view of the continuous evolutionary thread followed here between these two taxa, this possibility seems remote, and I am in total agreement with Fretter (1975), who concluded that the initially separate development of the lung rudiment and pallial groove (*Lymnaea*, *Achatina*, *Helix*) is most likely to be a consequence of yolk in the early development of pulmonates.

The feeding behaviour of pulmonates, which provides for the powerful rasping of surface films and for the ingestion of relatively large pieces of vegetation, is highly dependent upon the efficient manipulation of a broad radular scoop. It is suggested that primitively the broadening radula, which necessitated the development of bulky musculature to manipulate it, was used to ingest copious quantitities of mud and sand; food items ingested were crushed by a bilobed muscular stomach. Since diatoms would appear to be the major food item of *Amphibola crenata* (Farnie 1919) and of several *Chilina* spp. (personal observations), such items are likely to have been utilized by the earliest pulmonates, and have provided a continuing food source during the transition from an infaunal estuarine niche to living on hard substrata.

The powerful buccal musculature, which initially had to deal with large quantities of particulate material, proved subsequently to be eminently suitable for the forceful rasping of rock surfaces, and later for macrophagous feeding (for which a jaw is essential).

The buccal morphology of *Chilina* is virtually identical to that of later pulmonates (*Lymnaea*, *Planorbarius*), and thus does not exhibit the annectant morphological state that characterizes other bodily structures, but is typically pulmonate. Although behavioural observations were not made, the extreme similarity of construction implies that the sequence of movement associated with feeding is very similar to those of more advanced representatives. This being so, it is presumed that the crucial feature of the buccal behaviour of those animals, namely the combined forward movement of the odontophoral lip and radula over the substratum (Hubendick 1957), is also characteristic of *Chilina*. Of great importance to this movement is tensing of the radular membrane by the supralateral radular retractor muscles. Additional pulmonate specializations are also present in *Chilina*: for example, the muscular odontophoral cartilage, and the collostyle and collostylar hood. The last, which serves in *Lymnaea* to direct food from the rear of the buccal cavity into the base of the oesophagus, probably evolved in connection with the need for the effective conveyance of large amounts of particulate material.

In conclusion, this study of the Chilinidae, as illustrated by an examination of some features of the anatomy of *Chilina fluctuosa*, has aided the appreciation of early pulmonate evolution. In particular, adaptations occurring during the early infaunal period (nuchal shortening, and resulting modifications to the mantle complex and its vascular supply) appear to have 'pre-adapted' this gastropod stock for the later exploitation of estuarine and freshwater niches.

Other papers in preparation on the Chilinidae of Chile are concerned with the ecology and taxonomy of the group.

First and foremost I wish to thank Professor José Stuardo for formally inviting me to Chile, and for providing continuous encouragement and hospitality during my stays in Viña del Mar. Without his knowledge of the Chilinidae, which was freely given, much of the research that was successfully completed would not have been possible. I wish also to acknowledge the kindness of Professor Miguel Padilla in putting at my disposal all of the facilities of the Marine Station at Montemar, including the transport necessary for collecting *Chilina fluctuosa*. Professor Fernando Alcazar and other members of the staff of the laboratory continually provided assistance for which I am extremely indebted.

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REFERENCES

Bekius, R. 1972 The circulatory system of *Lymnaea stagnalis* (L.). *Ned. J. Zool.* **22**, 1–58.

Benjamin, P. R., Rose, R. M., Slade, C. T. & Lacey, M. G. 1979 Morphology of identified neurones in the buccal ganglia of *Lymnaea stagnalis. J. exp. Biol.* **80**, 119–135.

Boettger, C. R. 1954 Die Systematik der euthyneuren Schnecken. *Verh. dt. Zool. Ges., Zool. Anz. Suppl.* **18**, 253–280.

Brace, R. C. 1977*a* The functional anatomy of the mantle complex and columellar muscle of tectibranch molluscs (Gastropoda: Opisthobranchia), and its bearing on the evolution of opisthobranch organisation. *Phil. Trans. R. Soc. Lond.* B **277**, 1–56.

Brace, R. C. 1977*b* Anatomical changes in nervous and vascular systems during the transition from prosobranch to opisthobranch organisation. *Trans. zool. Soc. Lond.* **34**, 1–25.

Brace, R. C. & Quicke, D. L. J. 1980 Neural control of radular retractor muscles of the pulmonate snail, *Planorbarius corneus* (L.): functional anatomy and properties of neuromuscular units. *J. exp. Biol.* **86**, 115–133.

Brace, R. C. & Quicke, D. L. J. 1981 Activity patterns in radular retractor motoneurones of the snail, *Planorbarius. J. comp. Physiol.* B **142**, 259–270.

Carriker, M. R. 1946 Morphology of the alimentary system of the snail *Lymnaea stagnalis appressa* Say. *Trans. Wisc. Acad. Sci. Arts Lett.* **38**, 1–88.

Cottrell, A. J. 1911 Anatomy of *Siphonaria obliquata* Sowerby. *Trans. N.Z. Inst.* **43**, 582–594.

Cottrell, A. J. 1912 Vacular system of *Siphonaria obliquata* Sowerby. *Trans. N.Z. Inst.* **44**, 374–379.

Crampton, D. M. 1973 The functional anatomy of the buccal mass of one opisthobranch and three pulmonate gastropod molluscs. Ph.D. thesis, University of Reading.

Farnie, W. C. 1919 The structure of *Amphibola crenata* Martyn. *Trans. N.Z. Inst.* **51**, 69–85.

Fretter, V. 1960 Observations on the tectibranch *Ringicula buccinea* (Brocchi). *Proc. zool. Soc. Lond.* **135**, 537–549.

Fretter, V. 1975 Introduction. In *Pulmonates*, vol. 1 (*Functional anatomy and physiology*; ed. V. Fretter & J. Peake), pp. xi–xxix. London: Academic Press.

Fretter, V. & Graham, A. 1954 Observations on the opisthobranch mollusc *Acteon tornatilis* (L.). *J. mar. Biol. Ass. U.K.* **33**, 565–585.

Fretter, V. & Graham, A. 1962 *British prosobranch molluscs.* London: Ray Society.

Ghiretti, F. 1966 Respiration. In *Physiology of the Mollusca*, vol. 2 (ed. K. M. Wilbur & C. M. Yonge), pp. 233–248. New York: Academic Press.

Ghose, K. C. 1963 Morphogenesis of the shell gland, lung, mantle and mantle cavity of the giant land snail *Achatina fulica. Proc. malac. Soc. Lond.* **35**, 119–126.

Haeckel, W. 1911 Beiträge zur Anatomie der Gattung *Chilina*. *Zool. Jb.* (*Suppl.*) **13** (*Fauna chilensis* **4**), 89–136.

Harry, H. W. 1964 The anatomy of *Chilina fluctuosa* Gray re-examined, with prolegomena of the phylogeny of the higher limnic Basommatophora (Gastropoda: Pulmonata). *Malacologia* **1**, 355–385.

Hembrow, D. 1973 Observations on the structure and function of the buccal mass of *Planorbarius corneus* (L.). *Proc. malac. Soc. Lond.* **40**, 492–505.

Hubendick, B. 1945 Phylogenie und Tiergeographie der Siphonariidae. Zur Kenntnis der Phylogenie in der Ordnung Basommatophora und des Ursprungs der Pulmonatengruppe. *Zool. Bidr. Upps.* **24**, 1–216.

Hubendick, B. 1957 The eating function in *Lymnaea stagnalis* (L.). *Ark. Zool.* **10**, 511–521.

Hubendick, B. 1978 Systematics and comparative morphology of the Basommatophora. In *Pulmonates*, vol. 2A (*Systematics, evolution and ecology*; ed. V. Fretter & J. Peake), pp. 1–47. London: Academic Press.

Kater, S. B. 1974 Feeding in *Helisoma trivolvis*: the morphological and physiological bases of a fixed action pattern. *Am. Zool.* **14**, 1017–1036.

Kisker, L. G. 1923 Über Anordnung und Bau der interstitiellen Binde-Substanzen von *Helix pomatia* (L.). *Z. wiss. Zool.* **121**, 64–125.

Machin, J. 1975 Water relationships. In *Pulmonates*, vol. 1. (*Functional anatomy and physiology*; ed. V. Fretter & J. Peake), pp. 105–163. London: Academic Press.

Morton, J. E. 1955 The evolution of the Ellobiidae with a discussion on the origin of the Pulmonata. *Proc. zool. Soc. Lond.* **125**, 127–168.

Morton, J. E. 1958 *Molluscs*. London: Hutchinson.

Nisbet, R. H. 1973 The role of the buccal mass of the trochid. *Proc. malac. Soc. Lond.* **40**, 435–468.

Pelseneer, P. 1984 Recherches sur divers Opisthobranches. *Mém. cour. Mem. Sav. étr. Acad. r. Sci. Belg.* **53**, 1–157.

Plate, L. 1895 Bemerkungen über die Phylogenie und die Entstehung der Asymmetrie der Mollusken. *Zool. Jb.* (*Anat.*) **9**, 162–206.

Regondaud, J. 1964 Origine embryonnaire de la cavité pulmonaire de *Lymnaea stagnalis*. Considérations particuliers sur la morphogenèse de la commissure viscérale. *Bull. biol. Fr. Belg.* **98**, 433–471.

Rose, R. M. & Benjamin, P. R. 1979 The relationship of the central motor pattern to the feeding cycle of *Lymnaea stagnalis*. *J. exp. Biol.* **80**, 137–163.

Schumann, W. 1911 Über die Anatomie und die systematische Stellung von *Gadinia peruviana* Sowerby und *Gadinia garnoti* Payraudeau. *Zool. Jb.* (*Suppl.*) **13** (*Fauna chilensis* **4**), 1–88.

Shumway, S. E. 1981 Factors affecting oxygen consumption in the marine pulmonate *Amphibola crenata* (Emelin, 1791). *Biol. Bull. mar. biol. Lab., Woods Hole* **160**, 332–347.

Smythe, K. R. 1975 On the occurrence of *Salinator fragilis* (Lamarck) in the Arabian Gulf. *J. Conch., Lond.* **28**, 335–342.

Watters, P. A. 1964 Distribution of *Amphibola crenata* (Pulmonata) in the Dunedin area with notes on the probable origin of the species. *Trans. R. Soc. N.Z.* **4**, 117–134.

Yonge, C. M. 1952 The mantle cavity in *Siphonaria alternata* Say. *Proc. malac. Soc. Lond.* **29**, 190–199.

Yonge, C. M. 1958 Observations on the pulmonate limpet *Trimusculus* (*Gadinia*) *reticulatus* (Sowerby). *Proc. malac. Soc. Lond.* **33**, 31–37.

LIST OF ABBREVIATIONS

a.a.	anterior aorta
ac.g.	accessory ganglion
a.f.	anterior flap of cartilage
a.j.	anterior jugalis muscle
a.m.a.	attachment of mantle border to dorsal cephalic wall
a.m.b.	anterior mantle border
a.m.v.	vessel (suprapallial) of anterior mantle attachment
an.	anus
a.p.v.	afferent pulmonary vessel
a.r.m.	attachment of retractor muscle to subradular membrane
a.r.v.	afferent renal vessel
a.s.c.v.	afferent vessel of suprapallium of pallial caecum
au.	auricle
av.p.	anteroventral protractor muscle
b.a.	buccal artery
b.c.	bursa copulatrix
b.cv.	buccal cavity
b.g.	buccal ganglion
b.m.	buccal mass
b.r.	buccal retractor muscle
b.r.n.	nerve to buccal retractor muscle
b.s.	buccal sphincter muscle
b.v.	vessels of bursa copulatrix
b.w.n.	nerve to body wall
c.b.	cell body
cb.c.	cerebrobuccal connective
c.c.	cerebral commissure
c.g.	cerebral ganglion
c.l.m.	connective passing through lateral membrane
cp.m.	capitocerebral membrane
cp.t.	cephalic tentacle
c.s.	collecting sinus

c.s.b.	cut surface of body wall
c.s.c.	cut surface of cartilage
c.s.d.	connective entering sinus of dorsal cephalic wall
cs.h.	collostylar hood
c.sp.	cut surface of suprapallium
c.v.a.	circumferential vessel of anterior mantle border
d.b.c.	duct of bursa copulatrix
d.b.n.	dorsal buccal nerve
d.c.a.	dorsal cephalic artery
d.c.b.	dorsal ciliated band
d.g.	digestive gland
dl.d.	dorsolateral dilator muscle
dl.l.	dorsolateral levator muscle
dl.p.	dorsolateral protractor muscle
d.o.f.	dorsal odontophoral flexor muscle
e.	eye
e.s.d.	extent of large sinus in dorsal cephalic wall
e.s.p.	efferent vessel of suprapallium of pallial caecum
f.	foot
fd.r.	folded radula
f.r.	faecal rod
g.a.	genital artery
g.m.	genital mass
g.m.v.	vessels of genital mass
g.n.	genital nerve
g.o.	genital opening
gr.n.	genitorectal nerve
gs.n.	gastric nerve
i.b.w.	inner face of body wall
ic.	intracartilage tensor muscles
i.c.t.	infralateral cartilage tensor muscles
ifp.	infrapallium
if.v.	infrapallial vessel
il.r.p.	infralateral radular protractor muscle
im.r.p.	inframedian radular protractor muscle
in.	intestine
i.o.p.	infraventral odontophoral protractor muscle
i.r.v.	inner 'ring' vessel of mantle border
i.s.r.	inferior suspensor muscle of radular sac
j.	jaw
k.	kidney
k.l.	lateral portion of kidney
k.m.	medial portion of kidney
k.o.	kidney opening
l.b.n.	lateral buccal nerve
lb.t.	labial tentacle
l.c.m.	lateral columellar muscle
l.c.v.	lateral cephalic vessel
l.m.	lateral membrane
l.m.b.	lateral mantle border
l.n.	labial nerve
l.p.c.	limit of proximal columellar muscle (to right)
l.p.g.	left pallial ganglion
l.r.r.	lateral radular retractor muscle
m.	mouth
m.c.m.	median columellar muscle
m.p.c.	muscle bundles of proximal columellar muscle (to right)
m.s.	muscle strand
n.c.	nerve connective
n.r.	nerve ring
o.c.	odontophoral cartilage
o.d.	oral dilator muscles
oe.	oesophagus
o.n.	oral nerve
o.r.v.	outer 'ring' vessel of mantle border
os.	osphradium
p.a.	posterior aorta
p.b.n.	posterior buccal nerve
p.c.	pericardial cavity
p.c.m.	proximal columellar muscle
p.c.v.	vessel within roof of pallial caecum
pd.a.	pedal artery
pd.g.	pedal ganglion
pd.n.	pedal nerve
p.f.v.	vessel of posterior mantle fold
p.g.	pleural ganglion
p.h.	posterior horn of cartilage
pl.c.	pallial caecum
pl.n.	pallial nerve
pl.v.	pallial vessel
p.m.f.	posterior mantle fold
p.m.l.	posterior mantle lobe
pm.v.	pulmonary vessel
pn.a.	penial artery
pn.c.	penis complex
pn.n.	penial nerve
pn.r.	penis retractor muscle
p.sb.n.	pallial nerve arising from suboesophageal ganglion
p.sp.n.	pallial nerve arising from supraoesophagial ganglion
pt.l.	post-tentacular lappet
p.v.	peripheral mantle vessels
pv.l.	posteroventral levator muscle
pv.r.	posteroventral retractor muscles
r.	radula
rec.	rectum
r.m.v.	radial mantle vessel
r.n.	renal nerve
r.p.g.	right pallial ganglion
rp.n.	renopericardial nerve
r.s.	radular sac
r.v.l.	renal vessel (lateral portion of kidney)
r.v.m.	renal vessel (medial portion of kidney)
sb.g.	suboesophageal ganglion
sh.	shell
sl.n.	salivary nerve
sl.r.	supralateral radular retractor muscle
slv.	salivary gland
sm.r.	supramedian radular retractor muscle
sp.g.	supraoesophageal ganglion
spp.	suprapallium
st.	stomach
stc.	statocyst
t.h.	tensor muscle of collostylar hood
t.i.	transverse muscles of infrapallium
t.m.d.	transverse muscles of dorsal cephalic wall
t.m.s.	tensor muscle strand
t.m.sh.	tensor muscle sheet
t.n.	tentacular nerve

t.p.c.	tip of pallial caecum
v.b.n.	ventral buccal nerve
v.c.b.	ventral ciliated band
ven.	ventricle
v.g.	visceral ganglion
v.n.	visceral nerve
v.o.p.	ventral odontophoral protractor
v.p.	ventral protractor muscles
v.r.	vascular 'ring' encapsulating nerve ring
v.s.	vertical septum
vs d.	vas deferens