Anatomy of *Alaba* and *Litiopa* (Prosobranchia: Litiopidae): Systematic Implications

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ABSTRACT

Anatomical study of *Litiopa* and *Alaba* shows that these taxa differ from other cerithiaceans by a significant number of synapomorphies. These two taxa have been variously assigned to the Planaxidae, Litiopidae, Diastomidae, Rissoidae, Cerithiidae, and to a number of subfamilies of the latter family. Both genera are highly adapted to algal habitats and have a mesopodial mucous gland on the sole of the foot that produces long, anchoring mucus threads preventing dislodgement from the algae. They share similar taenioglossate radulae; many-whorled, ribbed protoconchs; nearly identical pallial oviducts; egg masses; and planktotrophic larvae. Both genera stand apart from other cerithiacean groups in having long, tapered, epipodial tentacles. The morphological evidence points to a close relationship between the two taxa and also supports their inclusion in the family Litiopidae Fischer, 1885.

INTRODUCTION

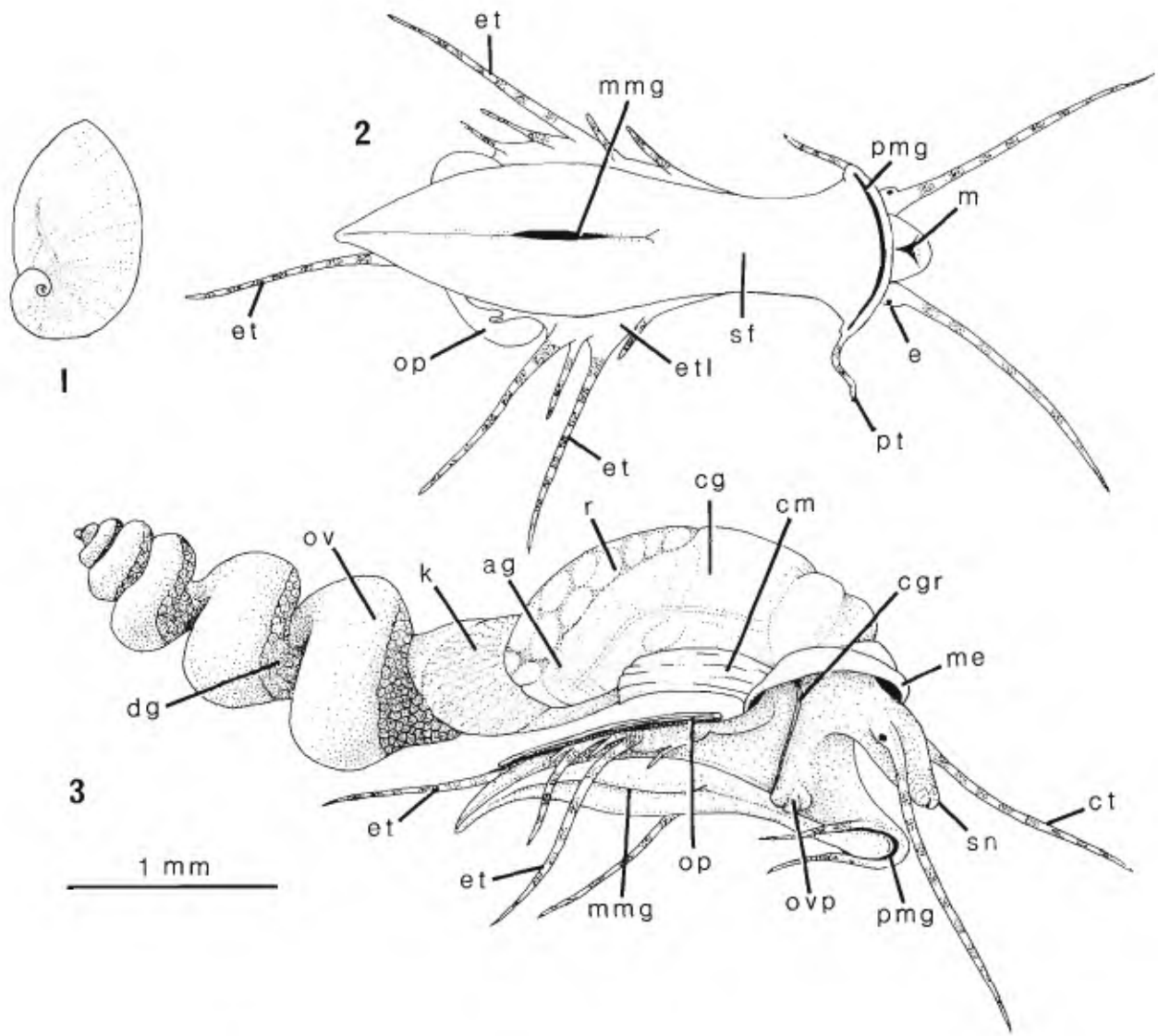
The higher taxonomic assignment of many small species of cerithiacean snails is controversial and frustrating. Convergent shell characters and lack of anatomical knowledge about the various taxa have resulted in an unstable classification. Moreover, many of the published systematic opinions about genera and families of cerithiaceans are based on vague, equivocal, conchological characters. I have discussed the taxonomic problems of small, heterogeneous cerithiacean taxa elsewhere (Houbrick, 1980:4–5, 1981:610–611). This paper deals with the anatomy of *Litiopa* Rang, 1829, *Alaba* H. and A. Adams, 1853, and several related taxa, and presents anatomical data for their natural systematic arrangement. *Litiopa*, while usually assigned to the family Litiopidae, has been thought to be related to the Planaxidae, Rissoidae, or Cerithiidae by various authors. *Alaba* has likewise been referred to the Cerithiopsidae, Planaxidae, Dialidae, Litiopidae, Diastomatidae, Cerithiidae, and to a number of subfamilies of the latter family. Bandel (1984:55) has discussed the confusing literature regarding the placement of *Alaba*. The status of a few other genera such as *Styliferina* A. Adams, 1860, and *Diffalaba* Iredale, 1936 remains uncertain. The genus *Diala* A. Adams, 1861 is frequently considered a close relative of both *Alaba* and *Litiopa* and has been grouped with them (A. Adams, 1862; Smith, 1875:538) or placed in its own family, Dialidae (Hornung & Mermoud, 1928). Dall (1889:258) suggested that *Alaba* was related to *Bittium* Gray and *Diastoma* Deshayes. Other workers, such as Wenz (1938) and Franc (1968), have included *Finella* A. Adams, *Alabina* Dall, and *Alaba* with the Diastomatidae. A summary of the various taxonomic allocations of *Alaba* and *Litiopa* is presented in table 1. Most workers have referred the two taxa to the subfamily Litiopinae and placed this group under the Cerithiidae Bruguière, 1789.

MATERIALS AND METHODS

Living specimens of *Litiopa melanostoma* Rang, 1829 and *Alaba incerta* (Orbigny, 1842) were studied at the Smithsonian Marine Station at Link Port, Ft. Pierce, Florida during January, February, and April of 1986. *Litiopa melanostoma* was collected offshore on *Sargassum* weed. *Alaba incerta* was collected from intertidal marine grass beds in St. Lucie Inlet, Florida, and on shallow water grass beds around Peanut Island in Lake Worth, Riviera Beach, Florida. Living snails were maintained in petri dishes of sea water and relaxed in a 10% $MgCl_2$ solution for study under a binocular dissecting microscope. Snails were preserved in Bouin's seawater fixative, embedded in paraffin, sectioned at 7 μm, and stained with Alcian blue-PAS and counterstained in hematoxylin (Humason, 1962:269). Critical point dried animals extracted from shells, radular ribbons, and protoconchs were examined under a Novascan-30 scanning electron microscope to determine microscopic anatomical features. Protoconchs of some *Australaba* and *Finella* species were also compared with those of litiopids.

MORPHOLOGY

Shell morphology: Members of both genera are small, not exceeding 25 mm in length, and have moderately turreted, conical, thin, nearly transparent shells. The shell



Figures 1–3. Animal of *Alaba incerta*. **1.** Operculum, showing sinuous attachment ridge, by transparency. **2.** Ventral view, showing sole of foot and disposition of epipodial tentacles. **3.** Side view of female, showing ciliated groove and ovipositor on right side of head-foot (bar = 1 mm). ag = albumen gland; cg = capsule gland; cgr = ciliated groove; cm = columellar muscle; ct = cephalic tentacle; dg = digestive gland; e = eye; et = epipodial tentacle; etl = epipodial tentacular lobe; k = kidney; m = mouth; me = mantle edge; mmg = mesopodial mucous gland; op = operculum; ov = ovary; ovp = ovipositor; pmg = propodial mucous gland; pt = propodial tentacle; r = rectum; sn = snout; sf = sole of foot.

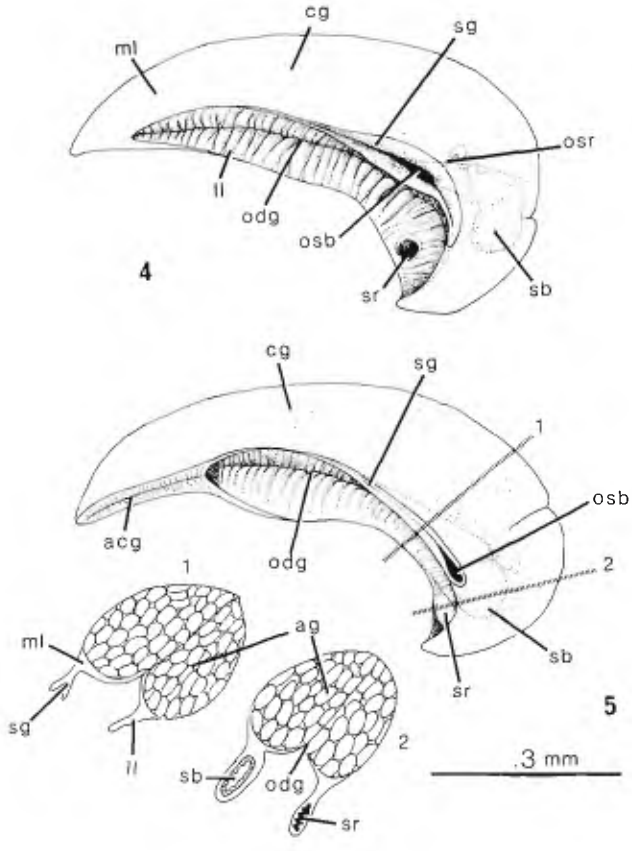
of *Alaba* (figure 11) differs from that of *Litiopa* (figure 9) in being longer and in having irregularly distributed, wide varices and a taller, more turreted apex. In *Litiopa,* the whorls are more inflated and fewer in number than in *Alaba,* and the shell is tan-yellow while that of *Alaba* is vitreous and white. *Litiopa* has a wider aperture and a weak tooth at the base of the columella. Both taxa have tiny brown subsutural spots and flammules, but *Alaba* also has weak, spiral bands of tan spots. *Litiopa* and *Alaba* have nearly identical protoconchs comprising 3.5–4 whorls (figures 8, 10). Protoconch I is smooth (pitted under high magnification) while protoconch II is sculptured with numerous axial riblets divided by a thin spiral thread from a band of subsutural plaits. Microscopic spiral lines lie between the axial riblets in *Litiopa* (figure 8). A good figure of *Litiopa melanostoma* and its protoconch has been given by Okutani *et al.* (1983: 24, figs. 1–5). Robertson (1971:5, pls. 2, 3) presented detailed figures of the protoconchs of *Alaba incerta* and *Litiopa melanostoma*. The periostraca of both taxa are thin and transparent. The ovate, paucispiral opercula are completely transparent and have eccentric nuclei in both taxa. Only the portions of the opercula beneath the nuclei are attached to the metapodia by fine sinuous ridges (figure 1). This opercular attachment scar is clearly depicted by Robertson (1971:pl. 4, fig. 16), who noted

the similarity of the opercula of both taxa. A ridge-like attachment scar is also described for *Alaba goniochila* by Kosuge (1964:36, fig. 6).

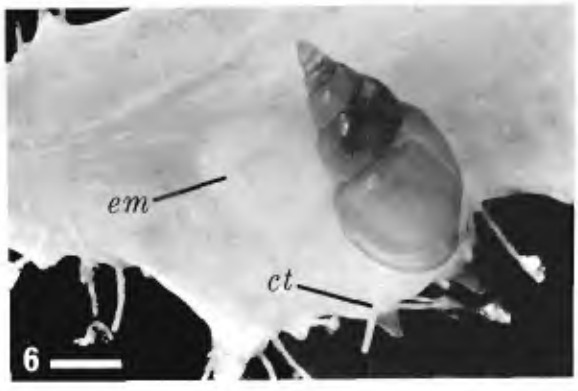
External anatomy: *Litiopa* and *Alaba* are very active snails and move about quickly in the algae or on the underside of the surface film of the water, on which they glide shell down by means of their long foot. Externally, *Litiopa* is yellow with a pale foot while *Alaba* has a whitish base color flecked with olive brown and red spots. The slender cephalic and pedal tentacles are striped with reddish brown in *Alaba*. A conspicuous feature in both genera is the long, narrow, active foot which is used to climb about algal filaments and fronds. A very deep, anterior propodial mucous gland lies at the leading edge of the sole (figures 2, 3, 7, 15, pmg) and a large, mesopodial mucous gland is centrally located at the posterior of the sole (figures 2, 3, 7, 12, 15, mmg). The propodial mucous gland produces a sheet of mucus that moves posteriorly along the sole of the foot. Scanning electron micrographs of critical point dried snails show that the sole of the foot is covered with long, dense, cilia (figure 17). The mesopodial mucous gland is defined by a slit-like groove (figures 2, 3, 7, 12, 15, mmg) that produces a strong mucus thread attaching the snail to the substrate or surface film of the water. If accidentally pulled or dislodged from their algal habitat, litiopids cling to the mucus thread in spider-like fashion, employing the foot and mouth to crawl back and reestablish themselves. The mucus thread is quite strong and tensile. The mesopodial mucous gland occurs in both genera, but is especially well-developed in the pelagic snail, *Litiopa*. Neither of these anatomical features was noted by Kosuge (1964), although he depicted a longitudinal groove on the sole. A. Adams (1862) was the first to note the mesopodial mucous gland in *Alaba*, but his comments on the gland and its use in the spinning of mucus threads have been overlooked by subsequent workers. He also remarked that *Alaba* was similar to *Litiopa* in this respect. A small, median, mesopodial mucous gland that opens by a short duct to the posterior portion of the sole also occurs in the Turritellidae (Randles, 1900:57).

Another conspicuous feature in litiopids, and especially in *Alaba*, is the presence of long epipodial tentacles along the sides of the foot (figures 2, 3, 15, 16, et), as noted by A. Adams (1862). The leading edge of the propodium has a pair of small, short tentacles, one on each side (figures 2, 3, pt). A lobe of epipodial tissue runs along the postero-lateral part of the metapodium, adjacent to the edge of the sole and supports the epipodial tentacles and operculum (figure 2, etl). The major epipodial tentacles are long and tapered. A pair occurs on the left side of the foot and a single one is on the right side. A single tentacle is also at the posterior of the foot. Other smaller tentacles flank the major tentacles. When *Alaba* is viewed dorsally, the long right epipodial tentacle emerges from the exhalant siphon. Epipodial and cephalic tentacles have circular ridges along their lengths (figures 15, 16, et, ct). These ridges are not seen on living snails and may be the result of contraction of the tentacles. A. Adams (1862) described a pair of epipodial tentacles on each side of the foot and a posterior pair in *Alaba picta* A. Adams, 1861. Kosuge (1964:36, figs. 1, 2) illustrated slender epipodial tentacles extending well beyond the shell margin of *Alaba goniochila*. In *Litiopa*, the epipodial tentacles are much shorter and less conspicuous.

The small head has a moderately extensible bilobed snout and a pair of long, tapered cephalic tentacles (figures 2, 3, 6, 15, ct) that are extremely retractile and touch the substrate alternately while the snail is crawling. The black eyes are surrounded by yellow pigment and located on the outer edge of the tentacular peduncle (figures 2, 3, e). The eyes are tiny and the tentacular bases have no peduncular bulge in *Litiopa*. The mantle edge of litiopids is smooth and bifurcate (figures 3, 15, me). Females have a ciliated groove (figures 3, 15, cgr) that emerges from the distal pallial oviduct, runs down the right side of the head-foot, and ends at the foot edge



Figures 4, 5. Litiopid pallial oviducts (distal end on left; bar = 0.3 mm). **4.** *Litiopa melanostoma*. **5.** *Alaba incerta* (dotted lines 1 and 2 represent cuts corresponding to diagrammatic cross sections 1 and 2). acg = anterior ciliated groove; ag = albumen gland; cg = capsule gland; ll = lateral lamina; ml = medial lamina; odg = oviductal groove; osb = opening to spermatophore bursa; osr = opening to seminal receptacle; sb = spermatophore bursa; sg = sperm groove; sr = seminal receptacle.



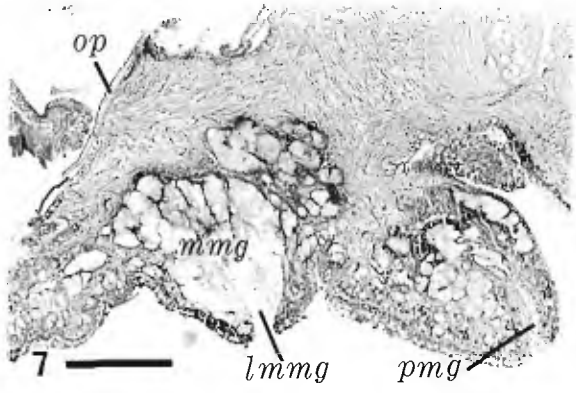


Figure 6. *Litiopa melanostoma* and egg mass on *Sargassum* leaf (ct = cephalic tentacle; em = egg mass). **Figure 7.** Sagittal section through foot of *Alaba incerta*, showing operculum (op), mesopodial mucous gland (mmg), duct opening (lmmg), and propodial mucous gland (pmg) (bar = 0.5 mm). **Figure 8.** Protoconch of *Litiopa melanostoma*, showing sinusigeral notch (bar = 80 μm). **Figure 9.** Adult shell of *Litiopa melanostoma* from off Ft. Pierce, Florida (length 7 mm). **Figure 10.** Protoconch of *Alaba incerta*, showing sinusigeral notch (bar = 80 μm). **Figure 11.** Adult shell of *Alaba incerta* from St. Lucie Inlet, Florida (length 15 mm). **Figure 12.** Transverse section of *Alaba incerta* showing buccal mass (bm), foot (f), large mesopodial mucous gland (mmg), and lumen of duct (lmmg) (bar = 0.5 mm). **Figure 13.** Radula of *Litiopa melanostoma* (bar = 20 μm). **Figure 14.** Details of rachidian, lateral, and marginal teeth of *Litiopa melanostoma* (bar = 16 μm).

adjacent to the sole, where a fleshy glandular pad, the ovipositor (figure 3, ovp), is situated. The ovipositor is especially well-developed in *Litiopa*. Okutani *et al.* (1983:24, fig. 6) depicted the groove but not the ovipositor.

The coils of the body whorl comprise the digestive gland, gonad, stomach, and kidney and are typically cerithioid in groundplan.

Mantle cavity organs: Litiopid snails have a deep mantle cavity dominated by a large ctenidium. A ridge-like monopectinate osphradium extends the full length of the ctenidium. Ctenidial filaments are long, tapered, triangular, and have many long cilia. Similar observations were made by Kosuge (1964:34) on *Alaba goniochila*. The narrow hypobranchial gland is thick, and in *Alaba* secretes an iridescent green substance when the snail is injured or irritated. The rectum is thin walled and produces large ovoid fecal pellets that are tapered at one end. The glandular pallial gonoducts are large and thick in females but small and thin in males.

Alimentary tract: The buccal mass of litiopids is large in relation to the snout size and has a pair of semicircular jaws. The radular ribbon of *Alaba* comprises 35–40 rows of teeth (n = 6) and is about one-fourth the shell length. The large buccal mass of *Alaba* was also noted by Kosuge (1964:34). The radulae of *Alaba* (figures 18–20) and *Litiopa* (figures 13, 14) are taenioglossate (2+1+1+1+2) and typically cerithioid, closely resembling the radulae of Cerithiidae in overall morphology. The rachidian tooth of *Alaba* (figure 19, r) is wider than long, has a straight anterior front, and an hourglass-shaped basal plate with a prominent central triangular buttress. This hourglass shape is also found in some genera and species of the Cerithiidae (Houbrick, 1980). The cutting edge of the rachidian has a sharply pointed central cusp flanked on each side by a pair of smaller denticles. The lateral tooth (figure 19, l) is trapezoidal and has a basal plate with a long lateral basal extension and a strong, ventral, inner buttress. The cutting edge has a long central cusp, one inner denticle, with two outer denticles in *Alaba* (figure 19, l), and two to four in *Litiopa* (figure 13). The marginal teeth of both genera (figures 13, 14, 18–20) are equal in length, scythe-shaped, and have cusped, spoon-like tips. The inner marginal tooth is about twice as broad as the outer and has two inner denticles, a long terminal cusp, and one outer denticle. The narrow outer marginal has 4–5 inner denticles in *Alaba* (figure 20), 8–9 in *Litiopa* (figure 13), a long terminal cusp, and a smooth outer edge. The radula of *Alaba incerta* has been described and figured in detail by Bandel (1984:39–40, fig. 71, pl. 4, figs. 1, 9).

The mouth (figures 2, 15, m) and oral cavity are large and manipulate long strands of filamentous algae in *Alaba* and large *Sargassum* particles in *Litiopa*. The radula of *Alaba goniochila* is very similar to that of *Alaba incerta* (Kosuge, 1964:36, figs. 7–10).

Litiopids have a pair of tubular, uncoiled salivary glands that originate well behind the nerve ring and pass through it before emptying into the buccal cavity. Salivary gland tubes are thicker in *Litiopa* than in *Alaba*. A large esophageal gland, formed by outpocketing of the lateral walls of the midesophagus, is present in *Litiopa*. This was also found in *Alaba incerta* and was noted by Kosuge (1964:34) in *Alaba goniochila*. The stomach of litiopids has a large central ridge, a gastric shield, and a short style sac. Although not seen in dissections, histological sections show that a crystalline style is present. The stomach of *Alaba goniochila* has been depicted by Kosuge (1964:36, fig. 5), and is similar to *Alaba incerta*. Sections show that the major typhlosole extends well into the proximal intestine.

Reproductive tract: *Litiopa* and *Alaba* are typically cerithiacean in having open gonoducts and aphallate males. The pallial oviducts of both taxa consist of a thick-walled, slit tube attached along its dorsal side to the mantle wall (figures 4, 5). It comprises two laminae, a lateral one attached along its width to the mantle wall (figures 4, 5, ll) and a medial, free lamina (figures 4, 5, ml). Along the longitudinal base of the laminae is the oviductal groove, which is wide and shallow (figures 4, 5, odg). The bulk of the pallial oviduct is dominated by a large swollen, proximal albumen gland (figure 5, ag) and by the adjacent distal capsule gland (figures 4, 5, cg). These glands have a mucus-like consistency and quickly swell with water when cut or injured. The albumen gland is more opaque than the capsule gland and stains a deep blue in section. The free medial lamina has a sperm groove along its median edge (figures 4, 5, sg) that enters into a small, proximal bursa (figures 4, 5, sb). In *Litiopa*, the bursa leads into a small pouch that appears to have a tiny opening on the inner side of the medial lamina (figure 4, osr). In the lateral lamina, immediately adjacent to this opening, is a pit-shaped pouch that is probably the seminal receptacle (figure 4, sr). The seminal receptacle is a round, deep chamber in *Litiopa* (figure 5, sr) while it is a compact pouch in *Alaba*.

Eggs and larvae: The egg masses of *Litiopa* and *Alaba* are similar, forming flattened, gelatinous, clockwise spirals comprising one to four tight turns. Spawn masses of *Alaba* vary in size but average about 4.8 mm in diameter (n = 6). Unwound, an egg mass of this dimension comprises a ribbon 18.5 mm long and 0.35 mm wide. A ribbon has 2–3 layers of very small eggs, about six across the ribbon width, and contains about 4,800 eggs. Each egg is 60 μm in diameter and is enclosed in a clear hyaline capsule about 80 μm in diameter. This, in turn, is enclosed in an irregularly shaped gelatinous chamber about 0.13 mm across. The jelly chambers are covered in a gelatinous sheet forming a ribbon which is wound into a spiral which slightly overlaps the previous spirals. Jelly chambers and their enclosed eggs are tightly packed in the central region of the ribbon. The egg mass of *Litiopa* is deposited on *Sargassum* fronds (figure 6, em) and is similar to but smaller than that of *Alaba*, measuring about 2.5 mm in diameter and having fewer, broader spirals.

Egg masses of *Alaba picta* have been depicted by Habe (1960:122, fig. 4; cited as *Australaba picta*), Amio (1963:306, fig. 26), and Bandel (1976:262). Their figures conform with observations of *Alaba incerta* spawn. The egg mass of *Litiopa* has been poorly figured by Lebour (1945:467–468, fig. 8a) who described it as a flat circular mass. She did not note the spiral arrangement of the jelly ribbon.

Development is rapid in both genera, the trochophore stage being attained in 2 days and early veliger stages within 3 days. Hatching takes place in about 6 days and is preceded by disintegration of the egg mass. Freed veligers are active swimmers and have a large bilobed velum with long cilia and a transparent shell. Lebour (1945:467, fig. 8c) depicted velar lobes of very unequal size in *Litiopa* and stated that it is one of the commonest veligers in open water plankton. The larval shell of *Alaba* has a reddish brown columella. Bandel's (1976:262) observations on *Alaba* from Santa Marta, Colombia, are essentially in agreement with mine. He noted that it takes a female about 90 minutes to produce a 2 cm long ribbon.

The many-whorled, sculptured protoconchs with deep sinusigeral notches (figure 10) seen on the apex of adult snails of both taxa indicate a long planktotrophic phase before settlement. The protoconchs of *Litiopa* and *Alaba* are nearly identical in having many axial riblets. The protoconch of *Litiopa* has microscopic spiral lines between the riblets and comprises about five sculptured whorls (figure 8) while in *Alaba*, there are only three whorls (figure 10). The larger protoconch of *Litiopa* indicates a long planktonic phase that is reflected in the pan-tropical distribution of this pelagic species. Robertson (1971:5) noted the close resemblance between the protoconchs of *Litiopa* and *Alaba* and pointed out that full grown larval shells of *Litiopa* are larger than those of *Alaba*. He also noted the spiral lines ("crests") between the axial ribs on *Litiopa* protoconchs. The litiopid protoconch is distinctive among cerithiaceans and appears to be a good familial taxonomic character.

Nervous system: Litiopids have an epiathroid nervous system. A statocyst occurs on the posterior of each pedal ganglion. The cerebral ganglia are joined by a very short commissure and the pleural ganglia are closely joined to the cerebrals. The subesophageal ganglion, although completely separated from the left pleural ganglion, is only separated from it by a very short connective. Zygoneury does not occur. The supraesophageal ganglion is embedded in the left wall of the cephalic cavity. The RPG ratio (Davis *et al.*, 1976:263) was 0.43 (n = 2) in *Litiopa*, indicating a tightly organized nerve ring. This is the lowest ratio observed among the Cerithiacea, but the low value may be a reflection of the small body size of litiopids, and its significance is questionable.

SYSTEMATIC CONCLUSIONS

Below is a family diagnosis and synonymies suggested for the genera *Litiopa* and *Alaba*. The synonymy for *Alaba* is tentative and needs confirmation by careful conchological and anatomical examination of the type-species of each taxon.

Family **Litiopidae** Fischer, 1885

Diagnosis: Shell small, thin, having weak, shallow anterior canal and protoconch sculptured with numerous axial riblets and subsutural plaits. Animal with epipodial tentacles, smooth mantle edge, mesopodial mucus gland, ridge-like osphradium, large esophageal gland, short sperm gutter, and seminal receptacle in lateral lamina of pallial oviduct.

Genus *Litiopa* Rang

Diagnosis: Shell moderately turreted, yellow-brown in color, with inflated, weakly sculptured whorls and ovate aperture with weak tooth at base of columella. Protoconch sculptured with microscopic spiral lines between axial riblets. Animal yellow with well-developed ovipositor on right side of foot in females. Seminal receptacle a deep round chamber in posterior lateral lamina of pallial oviduct.

Litiopa Rang, 1829:306. Type-species: *Litiopa melanostoma* Rang, 1829, by SD, Nevill, 1884.

Bombyxinus Belanger *in* Lesson, 1835:32. Type-species: *Litiopa melanostoma* Rang, 1829, by OD.

Bombycinus (emend. pro *Bombyxinus* Belanger, 1835) Agassiz, 1846:104.

Genus *Alaba* H. and A. Adams

Diagnosis: Shell vitreous, white, weakly sculptured, with quadrangular aperture and very weak anterior canal; thick varices present on several whorls. Protoconch with numerous axial riblets. Seminal receptacle a compact pouch in posterior lateral lamina of pallial oviduct.

Alaba H. and A. Adams, 1853:241. Type-species: *Rissoa melaneura* C. B. Adams, 1850, by SD (Nevill, 1885).

Gibborissoa Cossmann *in* Sacco, 1895:34. Type-species: *Bulimus costellata* Grateloupe, 1828, by OD.

Diffalaba Iredale, 1936:290. Type-species: *Diffalaba opiniosa* Iredale, 1936, by OD.

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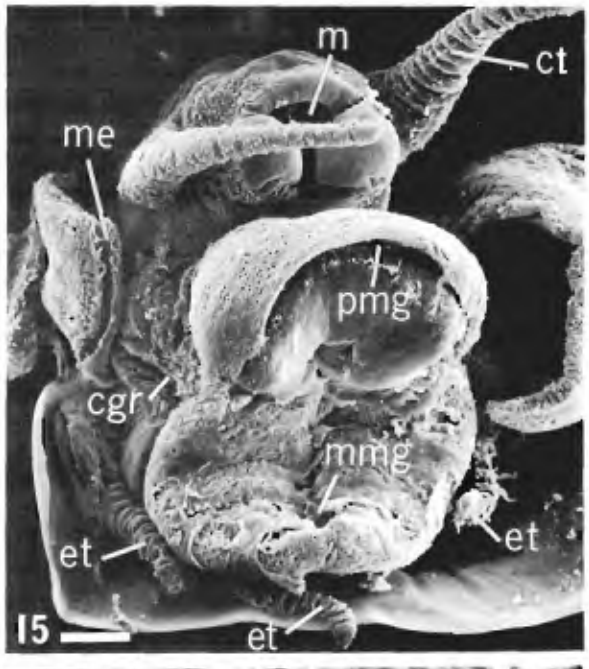
Figures 15–20. *Alaba incerta*, animal and radula. **15.** Critical point dried head-foot, showing sole and mucous glands. ct = cephalic tentacle; et = epipodial tentacle; cgr = ciliated groove; m = mouth; me = mantle edge; mmg = mesopodial mucous gland; pmg = propodial mucous gland (bar = 240 μm). **16.** Detail of epipodial tentacles on critical point dried snail. et = epipodial tentacle (bar = 40 μm). **17.** Dense cilia on sole of foot (bar = 4 μm). **18.** Radula ribbon with marginal teeth spread back (bar = 40 μm). **19.** Detail of rachidian (r) and lateral (l) teeth (bar = 20 μm). **20.** Inner and outer marginal teeth (bar = 20 μm).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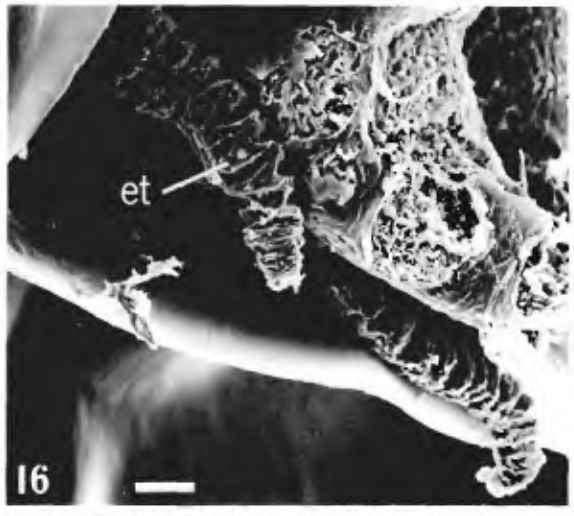
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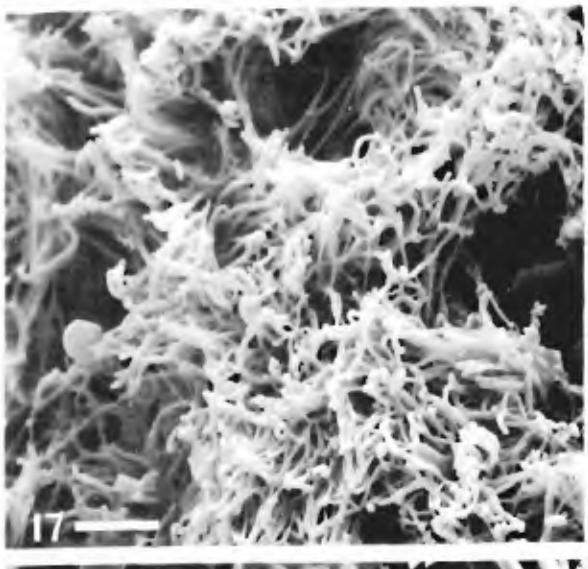
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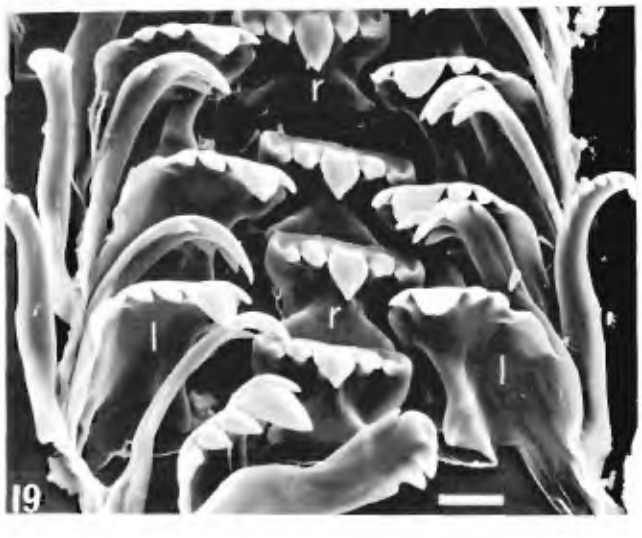
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Table 1. Taxonomic allocations given to *Litiopa* and *Alaba*.

Genus	Subfamily	Family	Citation
Litiopa		Planaxidae	Tryon (1882:246–247)
		Litiopidae	Fischer (1887:718–719)
	Litiopinae	Planaxidae	Cossmann (1906:196–197)
	Litiopinae	Cerithiidae	Thiele (1929:210–211)
	Litiopinae	Cerithiidae	Wenz (1938:753)
	Litiopinae	Cerithiidae	Franc (1968:281)
	Litiopinae	Cerithiidae	Keen (1971:415–416)
	Litiopinae	Cerithiidae	Abbott (1974:108)
		Litiopidae	Iredale and McMichael (1962:43)
Alaba		Planaxidae	Tryon (1882:246–247)
		Cerithiopsidae	H. and A. Adams (1853:239)
	Litiopinae	Cerithiidae	E. A. Smith (1875:537)
	Litiopinae	Cerithiidae	Thiele (1929:210–211)
	Litiopinae	Cerithiidae	Wenz (1938:753)
	Litiopinae	Dialidae	Iredale and McMichael (1962:43)
	Diastominae	Cerithiidae	Keen (1971:415–416)
	Cerithiopsinae	Cerithiidae	Abbott (1974:108)
		Diastomidae	Kilburn and Rippey (1982:537)
		Rissoidae	Laseron (1956:459)

Obstopalia Iredale, 1936:299. Type-species: *Obstopalia lixa* Iredale, 1936, by OD.

Australaba Laseron, 1956:459. Type-species: *Australaba bowenensis* Laseron, 1956, by OD.

Styliferina A. Adams, 1860:335. Type-species: *Styliferina orthochila* A. Adams, 1860, by OD.

Dialessa Iredale, 1955:81. Type-species: *Alaba translucida* Hedley, 1906, by OD.

DISCUSSION

No comprehensive anatomical studies of *Litiopa* or *Alaba* have previously been made. The earliest descriptions of the superficial anatomy and habits of *Alaba* were by A. Adams (1862), who described the animal of *Alaba picta*, a Japanese species living in shallow water *Zostera* beds. Adams (1862) pointed out the unusual features, such as epipodial tentacles and the mesopodial mucous gland, and noted that *Litiopa* shared these characters. He considered *Diala* and *Styliferina* as subgenera of *Alaba* and grouped all three in the family Litiopidae. His paper has been overlooked by subsequent workers. The genus *Styliferina* was originally described by A. Adams (1860:335), who later considered it a subgenus of *Alaba* A. Adams, 1862.

There are two short recent papers on the anatomy of litiopids: one by Kosuge (1964) on *Alaba goniochila*, and a few brief notes on *Litiopa melanostoma* by Okutani *et al.* (1983). Ponder (1985:104) has noted that in Kosuge's (1964) paper, *Alaba goniochila* is incorrectly cited as *Diala goniochila*, and likely to be overlooked in the literature for this reason. Furthermore, this paper may mislead others to include the genus *Diala* with the Litiopidae. There can be no doubt that the species shown by Kosuge (1964) is an *Alaba* and not a *Diala*, for his description and figures unequivocally depict epipodial tentacles. I was previously misled by this paper when I incorrectly stated that *Diala* snails have epipodial tentacles (Houbrick, 1980:4). Living *Diala* species examined in Queensland, Australia, did not have epipodial tentacles. It is thus clear that *Diala* is not closely related to *Litiopa* or *Alaba* and should not be referred to the Litiopidae. In the brief paper by Okutani *et al.* (1983) on *Litiopa*, only a radular drawing and a sketch of the head-foot were presented. The authors did not note the epipodial tentacles or the metapodial mucous gland, and incorrectly stated that there was no modification for pelagic life.

Although only two genera are now unequivocally included in Litiopidae, other species and genera of small cerithiaceans may prove to be members of this group when their anatomy is better studied. The type of *Finella xanthacme* (Melvill, 1904) [= *Obtortio*] has a protoconch like that of *Litiopa*, but no epipodial tentacles (Ponder, personal communication). Ponder (1967:197, pl. 10, figs. 7–9) has depicted the radula and operculum of *Alaba* (*Dialessa*) *translucida* (Hedley), strongly suggesting that the subgenus *Dialessa* is a litiopid. He later considered *Dialessa* to be a litiopid (Ponder, 1985:104) and has stated that *Dialessa* has an *Alaba*-like animal (Ponder, personal communication).

Much of the anatomy of litiopids is similar to that of the cerithiids. The long extensible foot observed in litiopids also occurs in *Bittium* species from similar algal habitats. The ovate, paucispiral operculum with eccentric nucleus is also like that of *Cerithium* species. The ciliated groove and ovipositor on the right of the foot of females occur in Cerithiidae, in the genera *Cerithium*, *Bittium* (Marcus & Marcus, 1964:507), and *Rhinoclavis* (personal observation); in Potamididae, in *Batillaria* (personal observation) and *Cerithidea* (Houbrick, 1984: 3); and in the Modulidae and Thiaridae (Houbrick, 1984: 10). The large esophageal gland is also present in most members of the Cerithiidae (Houbrick, 1985:29) and

Modulidae (Houbrick, 1980:126). Litiopids, however, differ from members of the Cerithiidae in having a smooth mantle edge and in lacking a bipectinate osphradium. Bandel (1984:55), on the basis of radular configuration alone, erroneously placed *Alaba* close to *Cerithium*. However, a number of significant, apomorphic, anatomical characters separate litiopids from other cerithiacean families and define them as a unique group that should be given familial recognition. These include: 1) a median posterior, metapodial mucous gland that produces a strong mucus thread, anchoring the snail to its algal habitat [a mesopodial mucous gland also exists in the Turritellidae (Randles, 1900:57), but does not produce a mucus thread and is probably a convergence]; 2) location of the seminal receptacle in the lateral lamina of the pallial oviduct; 3) an extremely short, distal sperm gutter in the medial lamina of the pallial oviduct; 4) long, retractile epipodial tentacles along the sides and posterior of the foot; and 5) an unusual protoconch sculptured with numerous axial riblets and subsutural plaits. Other distinguishing characters are: 1) a very deep propodial cleft into which the anterior mucous gland empties; 2) extremely long, slender cephalic tentacles; 3) a long extensible, narrow foot; 4) an operculum with a narrow spiral ridge on the attached surface; 5) an hourglass-shaped rachidian tooth with a strong triangular buttress; 6) large, swollen albumen and capsule glands in the pallial oviduct; and 7) mound-shaped egg masses comprised of tightly coiled jelly ribbons.

The hypothesis that *Litiopa* and *Alaba* are closely related had been previously suggested by A. Adams (1862) and Robertson (1971). Anatomical, radular, and conchological evidence resulting from this study supports this hypothesis. The two genera are herein allocated to the family Litiopidae, as defined by the shared, derived characters described above.

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