A cladistic analysis of *Lithasia* (Gastropoda: Pleuroceridae) using morphological characters

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ABSTRACT

The classification of pleurocerid snails and other freshwater mollusks has historically been based on morphological characters. Despite years of taxonomic work on pleurocerids, no single work includes all recognized taxa from a given group and only a few systematic treatments of the family or individual genera exist. Modern methods of phylogenetic systematics have shown that some morphological traits do not support historically accepted mollusk classifications. If analyses of morphological characters do support current taxonomic hypotheses, then the classification of these groups can be considered as stable. If not, our approach regarding diagnostic characters for these groups must change. This paper uses 25 shell and radular characters in a cladistic analysis of the pleurocerid genus *Lithasia*, and compares the findings to previously suggested classifications of the group. Cladistic analyses do not support any current or historical classification of *Lithasia*. However, these morphological characters are found to roughly delineate *Lithasia* and other extant pleurocerid genera, challenging previous works that suggest such characters have limited utility.

INTRODUCTION

Historically, the classification of freshwater mollusks has relied heavily on morphological features such as shell, soft anatomy, and reproductive structures (e.g., Tryon, 1873; Heard and Guckert, 1970; Davis and Fuller, 1981; Burch and Tottenham, 1980). This is particularly evident for pleurocerid snails, where shell features account for the majority of diagnostic characters used in the taxonomy and classification of the group. One group of pleurocerids that has been classified on the basis of shell characters is *Lithasia* Haldeman, 1840, a genus of large river snails found throughout the Cumberland, Ohio, Mississippi, and Tennessee River drainages.

Species of *Lithasia* possess conic to ovate-conic shells with fusiform apertures, a posterior callus on the parietal wall, and frequently some degree of sculpture on the body whorl (Burch, 1982). Most species were described initially as *Melania*, and classified according to shell characteristics such as shape and sculpture. Haldeman (1840) erected *Lithasia* and designated *L. geniculata* Haldeman, 1840, as the type for the genus and later erected *Angitrema* (1841). Presence of posterior and anterior calluses united *Angitrema* and *Lithasia*. The primary characters separating the genera were that *Angitrema* shells were spinous and had apertures with an anterior sinus, while *Lithasia* shells lacked sculpture and the aperture was not as distinctly channeled in front as the typical *Angitremae* (Tryon, 1873). Goodrich (1921) supported Pilsbry and Rhoad's (1896) reduction of *Angitrema* under *Lithasia*, and *Lithasia* subsequently has stood as a single genus. Goodrich (1940) recognized four separate groups within *Lithasia*, based primarily on peculiarities of shell sculpture. In the 1970s, authors suggested taxonomic revisions of the genus, placing all members in *Io* (Davis, 1974) or *Pleurocera* (Stansbery, 1971; Stein, 1978). Burch and Tottenham (1980) recognized *Lithasia sensu stricto* and *Angitrema* as subgenera of *Lithasia* based on position of sculpture on the body whorl (Burch, 1982), and not according to the original diagnosis, while Turgeon et al. (1998) followed Burch in recognizing *Lithasia* as one genus.

Authors have historically assembled pleurocerid genera based on grouping taxa with shared shell characters. Such is the prevalent approach found in the literature published over a period of 150 years, and no analyses of these characters exists for *Lithasia* or any other pleurocerid genus. This may be a result of the lack of uniform information found in the literature. Different authors rarely provided comparable levels of qualitative or quantitative data in their original descriptions, and seldom used terms and expressions that may or may not have the same descriptive connotations (e.g., tapering versus broadly conic shells), making it difficult for readers to draw comparisons between works. Many descriptions were based on one or a few shells, juveniles, or partial shells given to the author, and radulae were not included in these descriptions. Finally, descriptions were subjective based on the experience of the author, the amount of variation they accepted, and their understanding of the other taxa in the literature. Given the current state of freshwater mollusk taxonomy in general and pleurocerids specifically, and the fact that morphological characters are still used to confirm taxon identity, anal-

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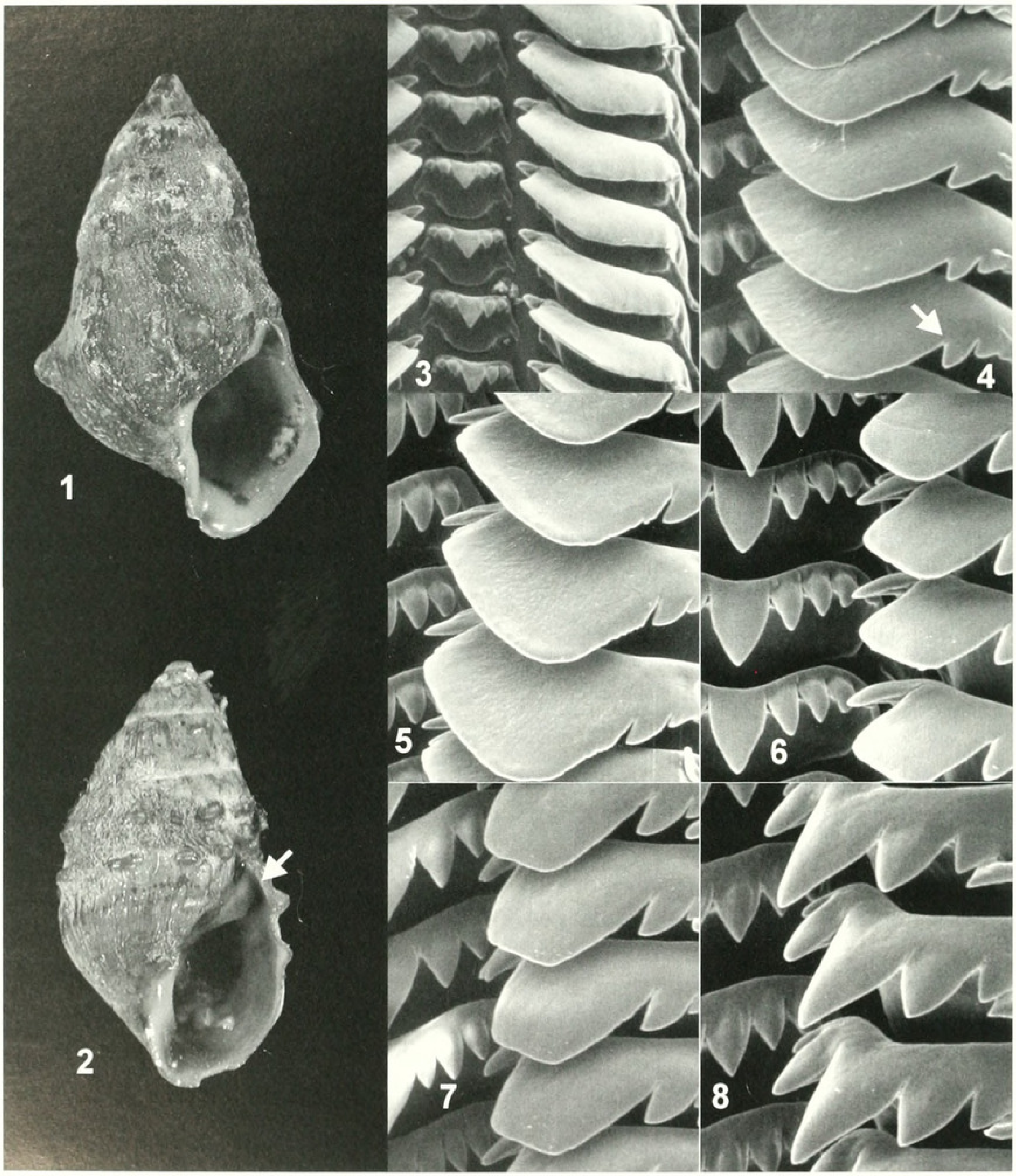

Figures 1–8. Illustrations of selected characters and character states used in the cladistic analysis of *Lithasia*. **1.** *Lithasia armigera* showing fusiform aperture (2:2), and presence of anterior (7:1) and posterior (6:1) calluses on the columella. **2.** *Lithasia verrucosa* showing nodulose body whorl (5:1) and posterior lengthening of aperture (arrow; 10:1). **3.** Absence of cusp next to lateral tooth (13:0). **4.** Presence of cusp next to lateral tooth (arrow; 13:1). **5.** Lamellar main lateral cusp (19:0). **6.** Rectangular main lateral cusp (19:1). **7.** Trapezoidal main lateral cusp (19:2). **8.** Triangular main lateral cusp (19:3).

yses of these characters employing modern techniques is prudent. Modern methods of phylogenetic systematics have shown that some morphological traits do not support historically accepted mollusk classifications (Graf, 2000; Lydeard et al., 2000). If analyses of morphological characters do support current taxonomic hypotheses, then the classification of these groups can be stabilized. If not, our approach to using diagnostic characters for these groups must change. Phylogenetic taxonomies of this kind have been advocated in several studies (e.g., de Queiroz and Gauthier, 1990, 1992, 1994; Bryant, 1996; Sereno, 1999; Lydeard et al., 2000).

Further complicating this problem is that pleurocerids, in a similar fashion to what happens to many other freshwater invertebrate groups, are experiencing declines in their number of species and individuals caused by river impoundment, habitat degradation, and poor land-use practices (Stein, 1976; Bogan et al., 1995; Lydeard et al., 1997). For example, in the Mobile Basin, one genus (*Gyrotoma*) and approximately 31 other species are presumed extinct (Stein, 1976; Bogan et al., 1995; Lydeard and Mayden, 1995; Lydeard et al., 1997). Even with the loss of diversity in the family, only five of 156 recognized pleurocerid species (Turgeon et al., 1998) are listed as either endangered or threatened as of May, 2001 (U.S. Fish and Wildlife Service). If morphology alone is to be used in identification of these imperiled taxa, then analyses of these characters gain even more importance. A lack of such analyses can hinder efforts to recognize, manage, and conserve distinct taxa (Waples, 1991; Mayden and Wood, 1995) within these affected groups.

The goal of this study is to compile shell and radula characters from *Lithasia*, analyze them using cladistic techniques in order to test historical and modern classifications of the genus and its species composition, and to determine possible relationships of the genus and its taxa to other pleurocerids based on those analyses. Potential changes to the taxonomy of *Lithasia* based on these analyses and the utility of using these characters in pleurocerid classification are discussed.

MATERIALS AND METHODS

Specimens for the study were either collected live or borrowed from museum collections (Appendix 1). Shell characters were taken directly from specimens. Radulae were extracted, cleaned, and prepared according to the method described by Holznagel (1998), viewed using a Hitachi S-2500 scanning electron microscope, photographed, and analyzed. For *Lithasia*, at least one representative from each recognized species and subspecies (Burch and Tottenham, 1980) was included. Specimens of selected taxa representing five other extant pleurocerid genera (*Elimia, Io, Juga, Leptoxis, Pleurocera*) were also included (Appendix 1). Data consisted of a matrix of 25 characters (Appendix 2, Figures 1–8) coded as either binary or multi-state (Appendix 3), and analyzed phylogenetically under maximum parsimony with NONA 2.0 (Goloboff, 1998) using the following settings: unordered data, 100 replicates, with *Juga silicula* and *Melanoides tuberculata* Müller, 1774, as outgroups. *Juga* is basal to the rest of the North American Pleuroceridae (Holznagel and Lydeard, 2000) and *M. tuberculata* was chosen as a more distant outgroup. Jackknife analysis (37% deletion, 1000 iterations of 10 replicates each) was performed in XAC (Farris, unpublished; Farris et al., 1996) to test the stability of the data. A strict consensus tree mapped with characters was produced with Winclada 0.9.99m24 (Nixon, 1999). The analysis was run twice, once using shell characters alone and once with all characters combined. Because most previous classifications (e.g., Tryon, 1873; Goodrich, 1940) were based on shell characters only, they were analyzed separately and combined with radula data.

Once the classification hypothesis was established, it was compared to five different classification schemes proposed by previous authors (Appendix 4):

A. Lithasia represents a single genus. This assumption follows the current (Turgeon et al., 1998) view of the genus.
B. Lithasia represents a single genus comprised of two subgenera, *Lithasia sensu stricto* and *Angitrema*, *sensu* Burch and Tottenham (1980). This classification is commonly used as a starting point in pleurocerid studies (e.g., Lydeard et al., 1997; Holznagel and Lydeard, 2000). Burch and Tottenham's (1980) genera and subgenera differ in species composition from those of Tryon (1873).
C. Lithasia represents a single genus comprised of four species groups based on peculiarities of the nodulous sculpture (Goodrich, 1940). *Lithasia hubrichti* Clench, 1965, had yet to be described and is included in Group 3 based on Clench (1965) allying it to *Lithasia verrucosa* (Rafinesque, 1820).
D. Taxa presently included in *Lithasia* belong to one of three genera: *Lithasia*, *Angitrema*, or *Anculosa*, *sensu* Tryon (1873). In this case, the original descriptions of *Lithasia* and *Angitrema* are used to group taxa based on shell characters. Tryon failed to include *Lithasia curta* (Lea, 1868), and *Lithasia hubrichti* had yet to be described. Both species are included in Tryon's *Angitrema* based on their nodulous shell sculpture. *Lithasia geniculata pinguis* (Lea, 1852) = *Anculosa pinguis*.
E. Taxa presently included in *Lithasia* should be considered species of *Io* based on developmental characters, *sensu* Davis (1974). *Io* Lea, 1831, has precedence over *Lithasia* Haldeman, 1840, and *Angitrema* Haldeman, 1841.

A sixth scheme, Stein's (1978b) recommendation that all *Lithasia* be considered *Pleurocera*, is not treated here as it is nomenclatural, not taxonomic, and has since been resolved by the International Commission on Zoological Nomenclature's decision to make *Pleurocera acutus* the type species of the genus (Melville, 1981; see discussion in Bogan and Parmalee, 1983). Characters supporting relationships in the parsimony analysis were compared to characters that grouped species in the other classifications.

RESULTS

Maximum parsimony analysis of shell characters alone yielded 372 trees of 27 steps (Figure 9). *Lithasia* was rendered non-monophyletic by the placement of *Lithasia geniculata pinguis* in the clade of *Leptoxis* species and the placement of *Lithasia obovata* (Say, 1829) in a polytomy of (*Io* + some *Elimia* + (*pinguis* + *Leptoxis*) + remaining *Lithasia*). Analysis of all characters yielded 20 trees of 107 steps that rendered *Lithasia* non-monophyletic (Figure 10). *Lithasia geniculata pinguis* specimens were basal to a clade of *Leptoxis* species supported by a teardrop-shaped aperture, and *Lithasia obovata* was nested between clades of *Pleurocera* and *Elimia* species near the base of the tree. The remaining *Lithasia* taxa formed a clade with *Io* supported by three characters:

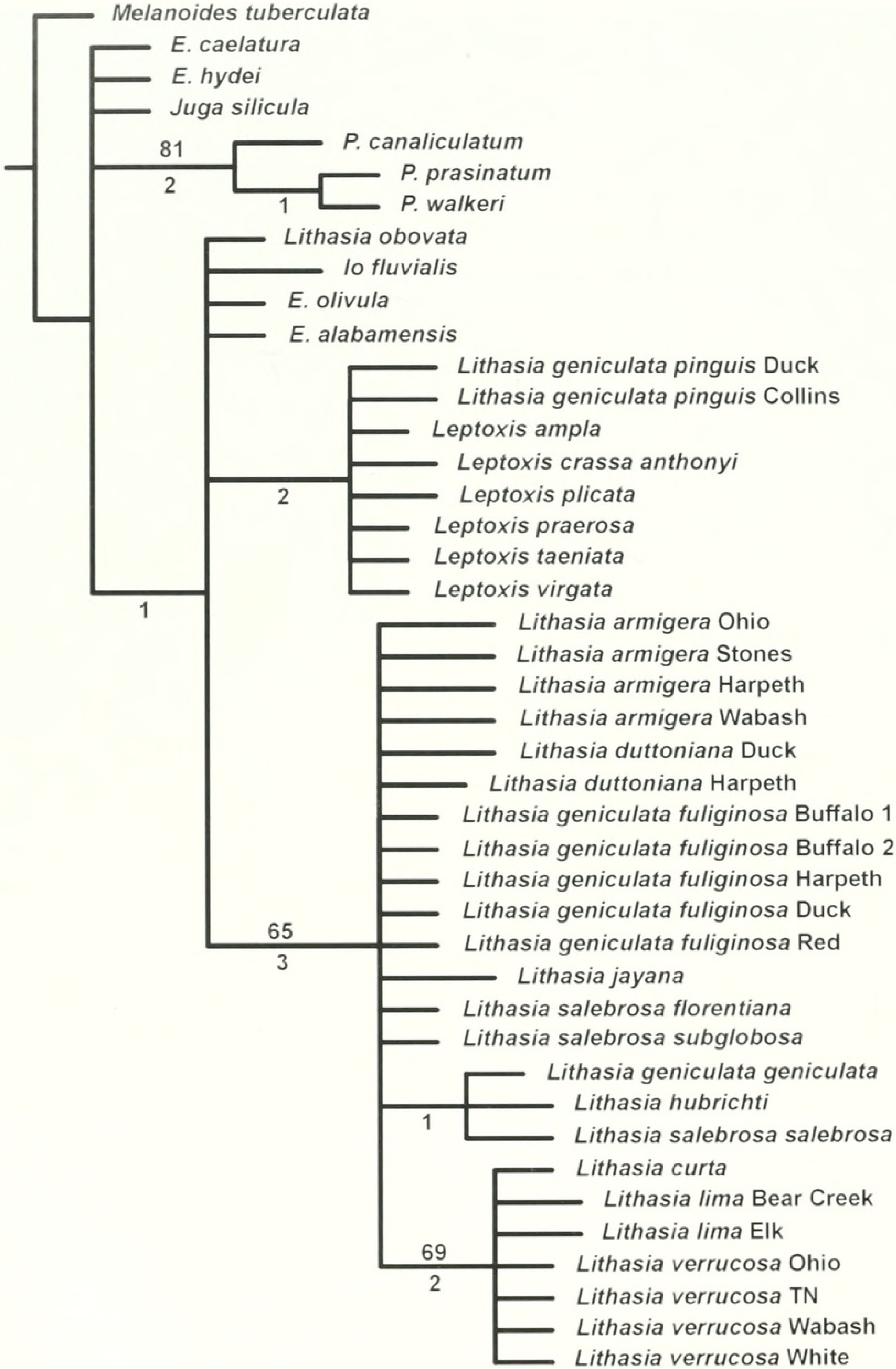

Figure 9. Cladistic analysis of *Lithasia*. Strict consensus of the 372 most parsimonious trees (27 steps; CI = 0.74) generated using shell characters alone. Jackknife values ≥ 63% above nodes, number of unambiguous synapomorphies below nodes.

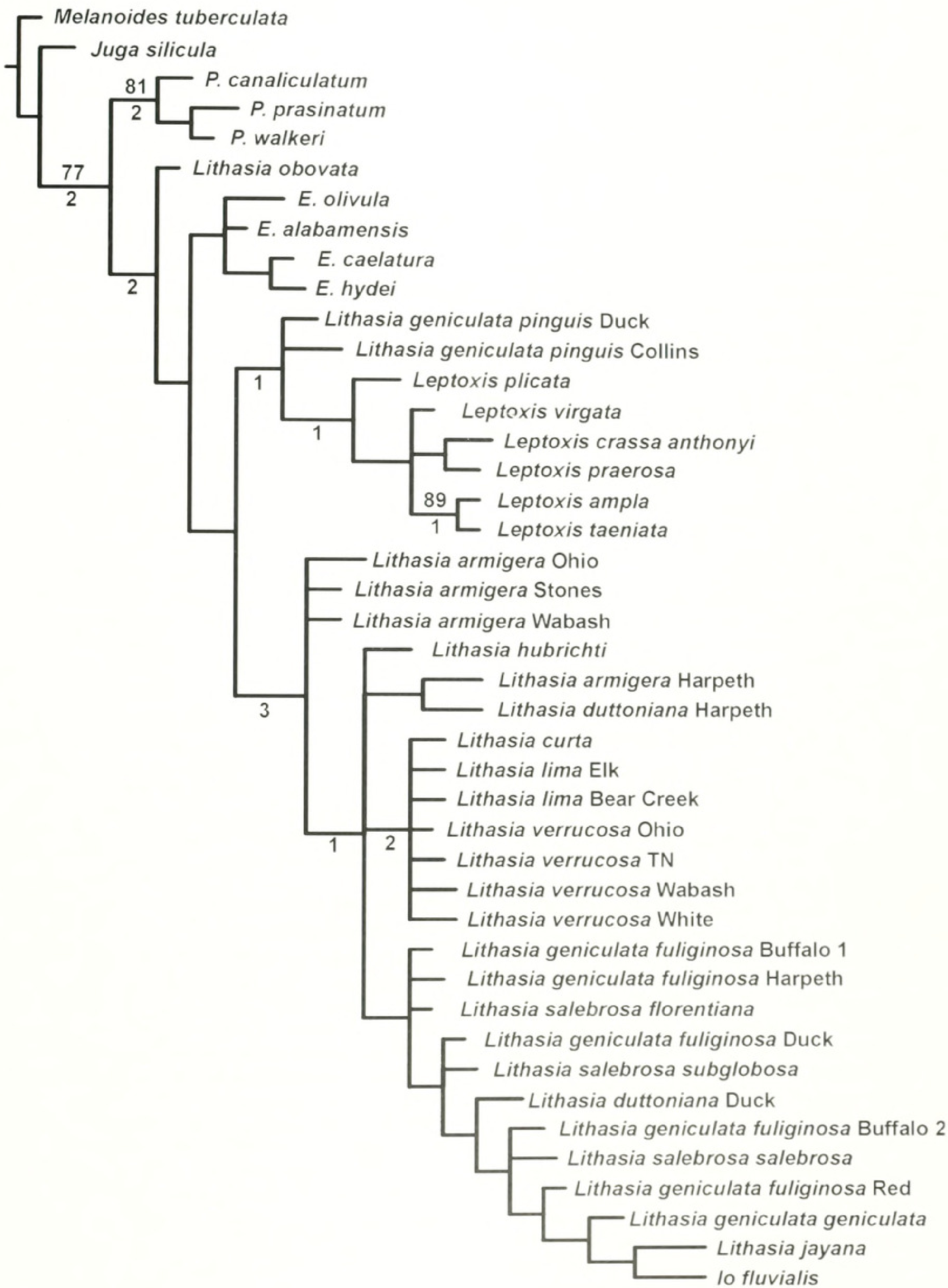

Figure 10. Cladistic analysis of *Lithasia*. Strict consensus of the 20 most parsimonious trees (107 steps, CI = 0.374) generated using shell and radula characters combined. Jackknife values ≥ 63% above nodes, number of unambiguous synapomorphies below nodes.

fusiform aperture (character 2: state 2), posterior callus on aperture (6:1), and slight anterior canalization of the aperture (8:1). Despite being well resolved, little support for any clade existed as evidenced by low jackknife values. Three other pleurocerid genera, *Elimia*, *Leptoxis*, and *Pleurocera*, were all recovered as monophyletic.

DISCUSSION

The current taxonomy of pleurocerids is based on shell characteristics, and most work on the family has focused on these characters. An extensive literature exists for the family, with most works being either wholly descriptive or taxonomic shuffling taxa among groups. This study stands as the first cladistic treatment of all currently recognized *Lithasia* species and their relationships to other pleurocerids based on shell and radula characters.

Neither analysis completely recovered the five classifications being compared. In both phylogenetic treatments *Lithasia* taxa did not form a single group, which refutes the taxonomies of Burch and Tottenham (1980), Goodrich (1940), and Turgeon et al. (1998). Tryon's (1873) groupings of the currently recognized species of *Lithasia* was also not supported, as sculptured and smooth taxa did not group separately. Davis's contention that *Lithasia* species should be considered as members of *Io* was partially supported in the parsimony analysis of all characters, where *Io* was nested deep in a clade containing most *Lithasia* taxa.

The consensus trees suggest that shell characters alone do not recover currently or historically recognized groups. However, shell and radula characters combined can be used to recover pleurocerid genera, but do not resolve species level identity well. In the total character analyses, *Elimia*, *Leptoxis*, and *Pleurocera* taxa all grouped in their respective genus. Only two *Lithasia* taxa grouped away from the others, suggesting that these two species may be misplaced. *Lithasia geniculata pinguis* was placed in *Leptoxis* (= *Anculosa*) by Tryon (1864), and subsequently placed in *Lithasia*, where it has represented the headwaters form of the *geniculata geniculata-fuliginosa-pinguis* complex. Based on the morphological characters examined here, *L. geniculata pinguis* should be classified as a species of *Leptoxis*. *Lithasia obovata* is the only species in the genus that occurs in the Green River drainage of Kentucky, and has included many nominal forms that are questionably *Lithasia*. *L. obovata* shells lack the calluses on the aperture, fusiform apertures, and have radulae most similar to *Elimia* species. Though the phylogenetic analysis suggests allocation of *L. obovata* to a separate genus, I believe the addition of more *Elimia* and *Pleurocera* species or more morphological characters to the analysis would resolve its generic designation. The remaining *Lithasia* species would be considered *Io*, as *Io* is the oldest name for that clade. As such, *Io* would be diagnosed by having a fusiform aperture (2:2), posterior callus on columella (6:1), and formation of canal of the aperture (8:1–2). This change would reflect the opinions of Davis (1974) regarding the two genera. Within *Lithasia*, however, individual species were not recovered, and continued analysis is required to elucidate diagnostic characters at the species level. None of the five current and historical classifications of *Lithasia* evaluated in this study are completely consistent with the analysis. Only the diagnosis of Burch (1982) is partially supported. A posterior callus on the columella (6:1) and the formation of anterior canal of the aperture (8:1–2) unite all *Lithasia* (minus *geniculata pinguis* and *obovata* plus *Io*) in the combined character analysis.

This study offers evidence refuting previous notions that shell and radula characters have limited utility in recognizing pleurocerid groups and supports the use of these characters in defining pleurocerid genera. In the most inclusive treatment of pleurocerids to date, Tryon (1873) offered an extensive discussion on the use and validity of shell characters in separating the various genera and species in the group. Tryon recognized that shell characters can vary greatly and looked towards the use of other anatomical characters to separate "natural genera" and discover corroborative shell characters for these groupings. Goodrich (1940: 1) noted that shell characters "once. . .considered immutable have proved to be secondary and more or less evanescent". Tryon (1873: liii–lv) figured some of Troschel's illustrations of radulae and commented on Stimpson's observations that shell and radula characters seem to unite pleurocerids but do little to separate constituent genera and species. It is true that gastropod radulae (Padilla, 1998) and freshwater mollusk shell characters can be plastic, often exhibiting clinal variations (e.g., Adams, 1900, 1915; Ortmann, 1920), and therefore potentially contributing homoplasy to phylogenetic analyses. Adding soft anatomy characters to a study such as this might theoretically improve the resolution of the analyses, but many characters frequently used to delineate taxa vary little among pleurocerids (Dazo, 1965) and in phylogenetic reconstructions shell characters often are less homoplastic than anatomical characters (Schander and Sundberg, 2001).

The results given here are consistent with studies employing molecular methods (Lydeard et al., 1997; Lydeard et al., 1998; Holznagel and Lydeard, 2000) to identify pleurocerid genera. In these works, *Elimia* and *Pleurocera* represent natural groups, and the morphological characters support both genera. However, Lydeard et al. (1997) and Holznagel and Lydeard (2000) showed that *Lithasia* and *Leptoxis* are non-monophyletic, though the combined morphological analysis given here supports the recognition of *Leptoxis* as a natural group. A thorough molecular study of *Lithasia*, including all of its nominal species and forms, will provide valuable information on the species composition of *Lithasia*, and subsequent character analysis will help define the diagnostic features of the genus.

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Appendix 1. Systematic list of taxa used in the cladistic analysis of the genus *Lithasia* (n = 1 for each taxon). Classification follows Turgeon et al. (1998); taxa are named as in Burch (1980). Complete locality information is available from the author. FMNH—Field Museum of Natural History; INHS—Illinois Natural History Survey; NCSM—North Carolina State Museum of Natural Sciences; UAG—University of Alabama Gastropod Collection; UMMZ—University of Michigan Museum of Zoology.

Taxon	Locality	Collection number
Family Pleuroceridae		
Genus *Elimia*		
E. alabamensis (Lea, 1861b)	Coosa River, Coosa Co., AL	NCSM-P-4658
E. caelatura caelatura (Reeve, 1860)	Choccolocco Creek, Calhoun Co., AL	NCSM-P-4659
E. hydei (Conrad, 1834b)	Black Warrior River, Jefferson Co., AL	NCSM-P-4663
E. olivula (Conrad, 1834a)	Alabama River, Monroe Co., AL	NCSM-P-4664
Genus *Io*		
Io fluvialis (Say, 1825)	Holston River, Sullivan Co., TN	NCSM-P-4667
Genus *Juga*		
J. silicula (Gould, 1847)	Oak Creek, Benton Co., OR	NCSM-P-4670
Genus *Leptoxis*		
L. ampla (Anthony, 1855)	Little Cahaba River, Bibb Co., AL	NCSM-P-4671
L. crassa anthonyi (Redfield, 1854)	Sequatchie River, Marion Co., AL	NCSM-P-4672
L. plicata (Conrad, 1834b)	Black Warrior River, Jefferson Co., AL	NCSM-P-4674
L. praerosa (Say, 1821)	Harpeth River, Davidson Co., TN	NCSM-P-4675
L. taeniata (Conrad, 1834b)	Choccolocco Creek, Talladega Co., AL	NCSM-P-4676
L. virgata (Lea, 1841a)	Clinch River, Hancock Co., TN	NCSM-P-4677
Genus *Lithasia*		
L. armigera (Say, 1821)	Wabash River, White Co., IL	INHS 23628
	Ohio River, Massac Co., IL	INHS 23632
	East Fork Stones River, Rutherford Co., TN	UAG 397
	Harpeth River, Cheatham Co., TN	UAG 572
L. curta (Lea, 1868)	Tennessee River, Lauderdale Co., AL	UMMZ 242200
L. duttoniana (Lea, 1841a)	Duck River, Maury Co., TN	UAG 402
	Harpeth River, Davidson Co., TN	UAG 405
L. geniculata geniculata (Haldeman, 1840)	Caney Fork, Dekalb Co., TN	UMMZ 51363
L. geniculata fuliginosa (Lea, 1842)	Buffalo River, Humphreys Co., TN (1)	UAG 406
	Red River, Robertson Co., TN	UAG 398
	Duck River, Maury Co., TN	UAG 403
	Buffalo River, Perry Co., TN (2)	UAG 395
	Harpeth River, Davidson Co., TN	UMMZ 53233
L. geniculata pinguis (Lea, 1852)	Collins River, Warren Co., TN	UAG 407
	Duck River, Coffee Co., TN	UAG 392
L. hubrichti Clench, 1965	Big Black River, Hinds Co., MS	FMNH 137751
L. jayana (Lea, 1841b)	Duck River, Humphreys Co., TN	UAG 573
L. lima (Conrad, 1834a)	Elk River, Limestone Co., AL	UAG 571
	Bear Creek, Colbert Co., AL	UAG 570
L. obovata (Say, 1829)	Green River, McLean Co., KY	FMNH 46219
L. salebrosa salebrosa (Conrad, 1834a)	Tennessee River, Lauderdale Co., AL	UAG 565
L. salebrosa florentiana (Lea, 1841a)	Tennessee River, Hardin Co., TN	UAG 425
L. salebrosa subglobosa (Lea, 1861a)	Tennessee River, Hardin Co., TN	UAG 416
L. verrucosa (Rafinesque, 1820)	Wabash River, White Co., IL	INHS 23629
	Oho River, Massac Co., IL	INHS 23631
	Tennessee River, Hardin Co., TN	UAG 427
	Tennessee River, Lauderdale Co., AL	UAG 568
Genus *Pleurocera*		
P. canaliculatum filum (Lea, 1845)	Duck River, Maury Co., TN	NCSM-P-4686
P. prasinatum (Conrad, 1834a)	Yellowleaf Creek, Shelby Co., AL	NCSM-P-4689
P. walkeri Goodrich, 1928	Shoal Creek, Lauderdale Co., AL	NCSM-P-4692
Family Thiaridae		
Genus *Melanoides*		
M. tuberculata (Müller, 1774)	Drainage ditch, Gainesville, Alachua Co., FL	NCSM-P-4682

Appendix 2. Morphological characters and character states used in the cladistic analysis of the genus *Lithasia*.

1. Shell shape. (0) globose, (1) conic, (2) ovately conic.
2. Aperture shape. (0) teardrop, (1) ovate, (2) fusiform.
3. Sculpture on posterior body whorl. (0) none, (1) carinate, (2) tubercles.
4. Sculpture medially on body whorl. (0) none, (1) sharp angle on body whorl, (2) tubercles.
5. Sculpture on entire body whorl. (0) none, (1) even lateral rows of small nodules, (2) costate.
6. Posterior callus on columella. (0) absent, (1) present.
7. Anterior callus on columella. (0) absent, (1) present.
8. Length of anterior canal of aperture. (0) none, (1) slight, (2) elongate.
9. Twisting of aperture anteriorly. (0) absent, (1) present.
10. Lengthening of aperture posteriorly along body whorl. (0) absent, (1) present.
11. Sculpture limited to body whorl. (0) yes, (1) no, (2) absent.
12. Length of aperture. (0) less than one-half shell length, (1) one-half shell length, (2) more than one-half shell length.
13. Cusp next to lateral tooth exteriorly. (0) absent, (1) present.
14. Shape of upper rachidian margin. (0) convex, (1) straight.
15. Length/width ratio of rachidian. (0) tooth as long as wide, (1) tooth longer than wide.
16. Length/width ratio of central rachidian denticle. (0) length and width equal, (1) longer than wide.
17. Shape of central rachidian denticle. (0) pointed, (1) blunt.
18. Location of cutting edge on main lateral cusp. (0) edge restricted to medial quarter, (1) edge restricted to medial half, (2) edge present on entire tooth.
19. Shape of main lateral cusp. (0) lamellar, (1) rectangular, (2) trapezoidal, (3) triangular.
20. Width of main lateral cusp. (0) less than one-third of cutting edge, (1) less than one-half but more than one-third of cutting edge, (2) greater than one-half of cutting edge.
21. Length/width ratio of main lateral cusp. (0) length and width equal, (1) length greater than width, (2) width greater than length.
22. Shape of leading edge of main lateral cusp. (0) pointed, (1) rounded, (2) straight.
23. Shape of marginal teeth. (0) pointed, (1) round.
24. Number of inner marginal teeth. (0) 1–4, (1) 5–8, (2) more than 8.
25. Number of outer marginal teeth. (0) 1–4, (1) 5–8, (2) more than 8.

Appendix 3. Cladistic analysis of the genus *Lithasia*. Data matrix of taxa and character states. River names follow appropriate taxon names where needed.

Lithasia armigera Ohio	2202010100011011002101112
Lithasia armigera Stones	2201010100011011012102112
Lithasia armigera Harpeth	2202010100011011001012101
Lithasia armigera Wabash	2202010100011011001102112
Lithasia curta	2200111010110110101112112
Lithasia duttoniana Duck	2201010100011010020212112
Lithasia duttoniana Harpeth	2200010100011011013020102
Lithasia geniculata fuliginosa Buffalo 1	2200011100011011020211112
Lithasia geniculata fuliginosa Buffalo 2	2200011100011011021212112
Lithasia geniculata fuliginosa Duck	2200011100011010021212112
Lithasia geniculata fuliginosa Harpeth	2200011100010011021212112
Lithasia geniculata fuliginosa Red	2200011100011010120211112
Lithasia geniculata geniculata	2220011100011010110111112
Lithasia geniculata pinguis Duck	0000000000001011011102112
Lithasia geniculata pinguis Collins	0000000000011010111202112
Lithasia lubrichti	2220011000011011011112112
Lithasia jayana	2202010100011110011111111
Lithasia lima Bear Creek	2200110101011011011112112
Lithasia lima Elk	2200110101011011011112112
Lithasia obovata	2100000000011011001021112
Lithasia salebrosa salebrosa	0220011100011010020211112
Lithasia salebrosa florentiana	2200011100011011021212112
Lithasia salebrosa subglobosa	2200011100011010121212112
Lithasia verrucosa Ohio	2200111010110110111112112
Lithasia verrucosa TN	2200111010110110111212112
Lithasia verrucosa Wabash	2200111010110100111212112
Lithasia verrucosa White	2200111010110110011102112
Io fluvialis	2200000200011010110100111

Appendix 3. Continued.

Leptoxis ampla	0000000000020101020212101
Leptoxis crassa anthonyi	0100000000021110120212111
Leptoxis plicata	0010000000021111011002101
Leptoxis praerosa	0000000000021110120212102
Leptoxis taeniata	0000000000020101020212101
Leptoxis virgata	0000000000021110021212101
Elimia alabamensis	2100000000011011001001111
Elimia caelatura	2100200000111011001001111
Elimia hydei	2100200000111011001002111
Elimia olivula	2100000000011010101001101
Juga silicula	2100200000101011003020011
Pleurocera canaliculatum filum	1101000010101011001011122
Pleurocera prasinatum	1100000010201011003010122
Pleurocera walkeri	1100000010201011001011122
Melanoides tuberculata	2100200000101111103020022

Appendix 4. Genus *Lithasia*. Classification schemes used in comparison to cladistic hypotheses. Taxa marked with a (*) were not treated by the original author but are included in the groups based on their works (see text for explanation).

Turgeon et al., 1998	Burch and Tottenham, 1980	Goodrich, 1940	Tryon, 1873	Davis, 1974
Genus *Lithasia*	Genus *Lithasia*	Genus *Lithasia*	Genus *Anculosa*	Genus *Io*
L. armigera	Subgenus *Lithasia*	Group 1	*L. geniculata pinguis*	*Io fluvialis*
L. curta	*L. geniculata geniculata*	*L. armigera*	Genus *Angitrema*	*L. armigera*
L. duttoniana	*L. geniculata fuliginosa*	*L. duttoniana*	*L. armigera*	*L. curta*
L. geniculata	*L. geniculata pinguis*	*L. jayana*	*L. curta**	*L. duttoniana*
L. hubrichti	*L. obovata*	*L. lima*	*L. duttoniana*	*L. geniculata geniculata*
L. jayana	*L. salebrosa salebrosa*	Group 2	*L. geniculata geniculata*	*L. geniculata fuliginosa*
L. lima	*L. salebrosa florentiana*	*L. geniculata geniculata*	*L. hubrichti**	*L. geniculata pinguis*
L. obovata	*L. salebrosa subglobosa*	*L. geniculata fuliginosa*	*L. jayana*	*L. hubrichti*
L. salebrosa	Subgenus *Angitrema*	*L. geniculata pinguis*	*L. lima*	*L. jayana*
L. verrucosa	*L. armigera*	*L. salebrosa salebrosa*	*L. salebrosa salebrosa*	*L. lima*
	L. curta	*L. salebrosa florentiana*	*L. verrucosa*	*L. obovata*
	L. duttoniana	*L. salebrosa subglobosa*	Genus *Lithasia*	*L. salebrosa*
	L. hubrichti	Group 3	*L. geniculata fuliginosa*	*L. salebrosa florentiana*
	L. jayana	*L. curta*	*L. obovata*	*L. salebrosa subglobosa*
	L. lima	*L. hubrichti**	*L. salebrosa florentiana*	*L. verrucosa*
	L. verrucosa	*L. verrucosa*	*L. salebrosa subglobosa*	
		Group 4		
		L. obovata		