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A Synopsis of the freshwater mussels (Pelecypoda, Unionoida)
of New England

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A recent ruling (1992, Opinion 1665, Bulletin Zoological Nomenclature, 49: 81-82) officially recognized Potamilus which has subsequently come to be used in preference to the long established Proptera. The species is found west of the divide in the Lake Champlain drainage.

Leptodea fragilis (Rafinesque, 1820)

Distributed west of the divide in the Lake Champlain drainage.

Ligumia nasuta (Say, 1817)

Distributed east of the divide in southern New England.

Ligumia ochracea (Say, 1817)

(6) Ligumia ochracea is discontinuous in coastal areas east of the divide.

The question of generic affinity of this species was raised by Morrison (1975) and Bereza and Fuller (1975). The major issue regarding the position of L. ochracea concerns the lack of a "mantle flap" which is a feature included in the prevailing definition of Lampsilis (s.s.), the genus to which the species was assigned by many authors (e.g. Reardon, 1929; Johnson, 1947, 1970; Burch, 1973). The generic characters of lampsiline mussels were modernized by Ortmann (1911) who used primarily anatomical and larval features to diagnose the various genera within the assemblage. His definition of the lampsiline genera included features of the mantle margin anterior to the inhalent aperture, the general size and shape of the glochidia, the nature of the marsupial portion of the female gill, and the

degree of attachment of the inner gill to the abdomen. Ortmann (1911) defined a mantle flap, a feature of Lampsilis, as a highly pigmented free lobe extending from the mantle margin anterior to the inhalent aperture with, as indicated by Ortmann (1911), a "lacerated appearance." Papillae are not present in this region of the mantle. The mantle flap is best represented in the female, reduced in the male. Ligumia ochracea clearly does not possess such a structure (Bereza and Fuller, 1975; Morrison, 1975; Kat, 1983, Smith, unpub. observ.). Nevertheless, L. ochracea continued to be placed in Lampsilis, at least provisionally, by several subsequent investigators (Fuller, 1977; Johnson, 1980; Clarke, 1981a; Kat, 1983; Porter, 1985; Strayer, 1987). Certainly part of the reason for maintaining L. ochracea in Lampsilis has been the strong resemblance of the shell to other species of Lampsilis s.s.

Otherwise, following the suggestion of Morrison (1975), the species was placed with Leptodea [Stansbery, unpub. (in Porter, 1985); Turgeon et al., 1988; Smith, 1991; Stiven and Alderman, 1992]. Regarding Leptodea, Ortmann [1911, under Paraptera (=Leptodea)] stated that the mantle margin in females was lamellate with at most marginal crenulations, but without papillae or a flap. The glochidia were listed as "very small" and "suboval." Specimens of Leptodea fragilis from Vermont, carefully relaxed and preserved, comply with Ortmann's (1911) diagnosis. The mantle margin is slightly more lamellate in the female than in the male, but their is

little difference between the sexes. The glochidia are very small and measure on the average 73 um (length) by 94 um (height) and possess a narrow hinge.

Examinations of the mantle and glochidia of L. ochracea from North Carolina and Nova Scotia (Bereza and Fuller, 1975; Porter, 1985; Kat, 1983) clearly show that L. ochracea does not belong to Leptodea either. Fuller (1977) indicated that a new genus name was forthcoming and Clarke (in Porter, 1985) stated likewise. To date, however, no name has been published. Porter (1985) noticed in his study of this species the presence of some papillae along the margin of the mantle of females and males. Reardon (1929), Bereza and Fuller (1975) and Morrison (1975) did not notice these papillae, while Kat (1983a) mentioned the presence of a few papillae.

A close examination of the mantle margin of carefully relaxed preserved male and female specimens of L. ochracea from Massachusetts and North Carolina revealed the presence of a row of small but regular papillae extending from the base of the inhalent aperture anteriorly to the gape of the foot. The mantle edge bearing these papillae is slightly lamellate, there is no indication of a flap and though pigmented, and other than a slight suffusion of darker pigments, no specific pattern of pigment is evident. There is little difference in the morphology of the mantle between the sexes. Furthermore, the glochidia are over twice the

size of those produced by Leptodea fragilis (see also Porter, 1985).

As concluded earlier by Bereza and Fuller (1975), L. ochracea can not be assigned to either Lampsilis or Leptodea as currently defined. In the case of Lampsilis, non-alliance is further supported by recent studies using biochemical techniques (Kat, 1983a; Stiven and Alderman, 1992) which have shown that L. ochracea is quite distantly related to two sympatric species of Lampsilis with mantle flaps. The only recognized lampsiline genus which can accomodate the taxon ochracea is Ligumia. Referring back to Ortmann (1911), a large genus, Eurynia, was diagnosed from other lampsiline genera principally by the presence of papillae, variously developed, along the mantle margin and evident in both the male and female. The glochidia were listed as "subovate, of medium size, or rather large." Other characters, including the nature of the marsupial gill and degree of attachment of the inner gill, were essentially as in Lampsilis. The three subgenera of Eurynia listed by Ortmann (1911) were eventually raised to genus rank and their nomenclature ~~stablized~~ (Ortmann and Walker, 1922). One of these genera is Ligumia and is defined (Ortmann, 1911, as subgenus Eurynia) by having "quite regular, uniform, smaller or larger papillae, reaching about the middle of the lower margin." Ligumia ochracea fits this description and though less developed, the papillae are similar in their external gross morphology to those of Ligumia nasuta, less so to Ligumia

recta which seems to possess mantle features intermediate between Ligumia and Villosa.

The glochidia of L. ochracea are almost identical to those of L. nasuta in size (Fig. 2) but possess a narrower hinge. The surfaces of the glochidial shell of each species are provided with minute pores less than 5 μ m in diameter and the margin opposite the hinge is evenly curved and smooth. Massachusetts L. ochracea glochidia have a mean length of 222 μ m and a mean height of 287 μ m (see Porter and Horn, 1980, for similar values of North Carolina populations) compared to a mean length of 256 μ m and a mean height of 318 μ m for L. nasuta. The ratio of length:height compares favorably as well, 0.77 for L. ochracea and 0.80 for L. nasuta.

It seems unwarranted at this time to erect a new genus for this species in the absence of a more urgently needed critical evaluation of the definitions of lampsiline genera in general.

Ligumia recta (Lamarck, 1819)

Rare west of the divide in the Lake Champlain drainage.

Lampsilis cariosa (Say, 1817)

Historically occurring in large rivers of southern New England east of the divide. Possibly moving into the Lake Champlain drainage west of the divide through the New York (Champlain) canal.

Lampsilis ovata (Say, 1817)

Restricted to the Lake Champlain drainage west of the divide.

(7) The names ovata and cardium (gradually replacing ventricosa, a junior synonym) correspond to separate species or named races of species, depending upon literature consulted. To date no published studies exist demonstrating the limits of variation of characters used to separate L. ovata from L. cardium. The only published study specifically addressing the relationship of these two forms (and the nomen excavata) (Cvancara, 1963) revealed a north-south cline in shell characters.

Traditionally the morphs ovata and cardium are separated by a few features of the shell, the degree of sharpness of the posterior ridge and the distribution and abundance of periostracal rays (e.g. Cummings and Mayer, 1992). Specimens examined by Smith (1982, 1983, 1985a) grade between both forms. While the degree of rayness varies considerably among all ages and populations, an apparent age related gradation exists in which younger individuals within a population demonstrate a sharp ridge characteristic of the ovata morph grading into the low ridged cardium form in older specimens. A study on the pigmentation of the mantle of cardium and ovata morphs (unpublished thesis, D. Stansbery, pers. comm. 1983) revealed differences between the two forms, however, carefully relaxed and preserved specimens from the Lake Champlain and Hudson River drainages show a uniform pigmentation and morphology that differs

little among all specimens examined. Until studies are ~~produced and~~ published that clearly discriminate the two forms, especially in sympatry, the older more established name L. ovata is preferred for New England populations.

Lampsilis radiata (Gmelin, 1791)

Found on both sides of the divide throughout New England. Presently, two concepts of this taxon exist in the northwest region of New England. The first maintains the existence of two subspecies of L. radiata (notwithstanding the status of the taxon L. r. conspicua south of the region), L. r. radiata, the North Atlantic Slope form, and L. r. siligoidea (Barnes, 1823), a Mississippian basin form (Clarke, 1973; Burch, 1973; Johnson, 1980). Clarke and Berg (1959) and Clarke (1973) defined the morphological (shell only) and geographic limits of each subspecies and presented data showing a zone of intergradation in the region west of the New England divide. An examination was made of the index of post-basal expansion of the female shell (B/A of Clarke and Berg, 1959; Hp/Hb of Clarke, 1973) because it provided a quantitative method for comparing populations. "Ray class" was found to be too arbitrary and "nacre class" was not considered reliable because "typical" L. r. radiata specimens from the Atlantic coast streams often have a white or bluish-white nacre (Johnson, 1970).

Application of the "Hp/Hb" method of analysis (sensu Clarke, 1973) to specimens cited in Smith (1985a) from the Lake Champlain drainage revealed extensive intergradation,

more than indicated by Clarke and Berg (1959) for Lake Champlain proper. Many specimens are clearly assignable to L. r. siligoidea (Hp/Hb >1.14).

The other concept considers hybridization between two distinct species, L. radiata and L. siligoidea, as a cause for apparent variation in shell and biochemical features exhibited especially in Lake Champlain animals (Kat, 1986). This consideration is hampered by an imprecise definition of L. siligoidea s.s., however, and nothing is known of the species' reproductive anatomy or morphology throughout its presumed range in the Mississippi basin. Anatomical comparisons (Smith, unpub. observ.) between L. radiata throughout New England and specimens conchologically assigned to the siligoidea form from the Lake Champlain drainage, particularly regarding details of the mantle flap, show no consistent differences relative to conchological differences at end points of Hp/Hb values. It is suggested that at least conchological gradation in L. radiata be treated as simply clinal. Until more information becomes available on the limits of variation of the named forms in question, the use of the trinomen should be discouraged.

Pyganodon cataracta (Say, 1817)

This species and the two following were formerly placed in the subgenus Pyganodon. Recent study by Hoeh (1990) using both morphological and biochemical characters has shown that the traditional subgenera of Anodonta differ at the same

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Dear Dr. Neves:

This letter accompanies a manuscript by D.G. Smith entitled "A synopsis of the freshwater mussels (Pelecypoda, Unionoida) of New England" that I hope you will review for the *Maine Naturalist*. Please return your review to me, not to the author. If you cannot send your review within three weeks, promptly return the unreviewed manuscript. If you must return an unreviewed manuscript, I would appreciate your suggestions for alternate reviewers.

The *Maine Naturalist* is a new regional journal that fills an important need for scientists, natural historians, natural resource managers, educators, and other persons. The fourth issue of the first volume has recently appeared. Although the *Maine Naturalist* is a regional journal, it maintains high scientific, artistic, and editorial standards. That is why we rely on reviewers, like you, who have the knowledge and experience to critically review manuscripts and make recommendations to authors and editors. We shall very much appreciate the time and effort you put into reviewing the enclosed manuscript.

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Ronald B. Davis
Scientific Editor

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The *Maine Naturalist* considers manuscripts, photographs and illustrations on the natural history of the Acadian bioregion encompassing Maine, the rest of northern New England, the Adirondacks, the Gulf of Maine and the Canadian Maritime Provinces. Manuscripts may deal with any aspect of the biology, geology, geography, and anthropology of the region and with any of its terrestrial, wetland, freshwater and marine habitats.

Categories of contributions and suggested manuscript page limits

General-interest articles: of interest to amateur as well as professional field naturalists. (10-20 manuscript pp)

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Check lists, taxonomic keys: lists of or keys to species in selected habitats and areas or in the region as a whole. (2-10 manuscript pp)

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Education section: information for educators wishing to bring natural history to the classroom; descriptions of practical exercises for classroom and field experiences; descriptions of field trip sites; etc. (1-6 manuscript pp)

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Form and contents of manuscripts

All manuscripts should be typed double-spaced in their entirety on 8.5" by 11" paper, with 1" margins. Pages should be numbered. Page limits cited above assume 300 words per page and include all text, figures, tables, etc. All manuscripts (except letters and news releases) should have a cover page with the title and name(s) and address(es) of author(s). Multi-authored manuscripts should indicate a primary author for correspondence. The title should be limited to 50 characters including spaces. Research articles should generally have the following sections, in order: Abstract (not to exceed 4 percent of the article), Introduction, Field-Site Description (optional), Methods, Results (or Observations), Discussion, Acknowledgments, and Literature Cited. General interest articles and research summaries can have a variety of formats but should have an Abstract and an Additional Reading or Literature Cited section. A few other specifications follow.

Section headings should be in bold capital letters with the text centered. Subheadings should be in bold lower case letters on their own left justified lines. Sub-subheadings should be in italic lower case letters at the beginning of standard indented paragraphs.

Footnotes should be avoided. Metric units (with English units in parentheses when necessary) should be used. Scientific names should be italicized rather than underlined. With the exception of horizontal lines in tables, bordering of text with lines should be avoided. A few examples regarding commas and quotation marks should be noted: ... a, b, and c. ... "xxx," ... "xxx." ... "xxx?" ... xxx, i. e., yyy. ... "xxx" (Smith 1972).

References to cited literature within the body of an article should follow these examples: ... Gosner (1978) ... (Gosner 1978) ... (Cochran 1985, 1988; Dahl 1969, 1985;

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Please fill out and return this sheet with items (below) checked off, along with the manuscript and any sheet(s) of comments for the author(s) or for me (specify who the comments are intended for). Your review/comments for the author(s) will be sent to her/him/them without your name attached, to protect your anonymity.

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Reviewer: Dr. Richard J. Neves Date: 8/15/94 MS# 81A

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Given the geographic/biogeographic and subject matter coverage of the journal (see *Instructions for Authors*), do you feel that the coverage of the manuscript is suitable for publication in the *Maine Naturalist*?

YES X

NO

The manuscript is

Acceptable in its present form

Acceptable after minor revision

Acceptable after major revision X

Unacceptable

Summary comments:

This manuscript is too long and contains only marginally useful information. Comments on taxonomy should be deleted. Species information is vague. I don't think that this manuscript would be very useful to readers without distribution data that are more definitive, photos, or other useful information to readers unfamiliar with mussels.

For the Author

1. Tighten up the scientific writing in Introduction.
2. If there's no evidence of a species occurrence, then do not include it; "have possibly occurred" = speculation.
3. The lack of a nomenclatorial authority for binomials is unacceptable. Turgeon et al. (1988) is the most often cited source for acceptable binomials; it should be used throughout the manuscript.
4. I see no real value to the narrative descriptions of each family; all of this information is not new, nor has it changed from "recent data". I view this as unnecessary verbiage, really not useful to the readership.
5. Species synopses should include states of occurrence at minimum, if not river basins. The generic descriptions of range ("east of the divide in southern New England") are not user friendly or informative. What about distribution maps or other more useful forms of distribution data? What about a species key? What about photos?
6. Placement of L. ochracea into the genus Ligumia is subjective and inadequately supported in this manuscript. Shell characters of L. ochracea are unlike Ligumia spp.; glochidia (Fig. 2) are unlike L. nasuta in my opinion. The manuscript title does not deal with taxonomy; therefore, attempting to include a contentious taxonomic change is totally unwarranted. This proposed change should not be published as a component of this paper.
7. Reduce the narrative on comparison of L. ovata vs L. cardium and L. radiata vs L. r. siliquoidea. Why give such lengthy deference to these and only 1-liners to other species?
8. I don't find the species synopses to be very informative or useful, over a simple list of species with range maps. Strayer's chapter in Peckarsky et al. (1990) should be referenced or integrated into this manuscript. Therefore, 34 pages for such information is excessive.