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STATUS OF THE GENUS *GUNDLACHIA*
(PULMONATA, ANCYLIDAE)

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THE genus *Gundlachia* was described by Louis Pfeiffer (1849) from a small number of septate ancyliiform shells sent to him by Gundlach in Cuba. Although the affinities of the new form (*G. ancyliiformis* Pfeiffer, 1849) were at first in doubt, a study of the soft parts soon established that it was related to *Ancylus* and not to the marine genera *Neritina*, *Navicella*, or *Crepidula*, to which the shell bore a very superficial resemblance. The receipt of a second series of shells from the same locality showed that Pfeiffer's original septate specimens were immature and, therefore, his description was emended (Pfeiffer, 1858) to include the later stage which Parodiz (1957) has called "post-septate." Corresponding septate and post-septate stages of another species collected in Michigan, probably *G. meekiana*, are shown in Figure 1. Since the time of Pfeiffer's original description, septate fresh water limpets have routinely been placed in *Gundlachia*, so that at present some two dozen names, listed in chronological order in Table I, have been embraced by this genus. Since the literature concerning *Gundlachia* is widely scattered and often difficult to procure, this brief review has been prepared to summarize the present state of knowledge about this genus and to facilitate future study.

For over a century the relationships of the various species to each other and of the genus to other groups of ancyliids has been a source of confusion to malacologists. The validity of *Gundlachia* as an actual biological genus has often been challenged, notably by Dall (1904, 1911); Iredale (1944) considered septum formation to be a "curious apparent aberration." Pilsbry (1913, 1924) has defended the concept of *Gundlachia* as a genus. The problem lies in determining whether the septate ancyliid species that are grouped together under the generic name *Gundlachia* actually represent a genetic continuum or whether they are merely independent modifications of other genera of ancyliids.

The genus remained essentially as delineated by Pfeiffer until 1912, when Hannibal divided it into two subgenera, *Gundlachia*, *sensu stricto*, and *Kincaidilla*. The former group included the small septate

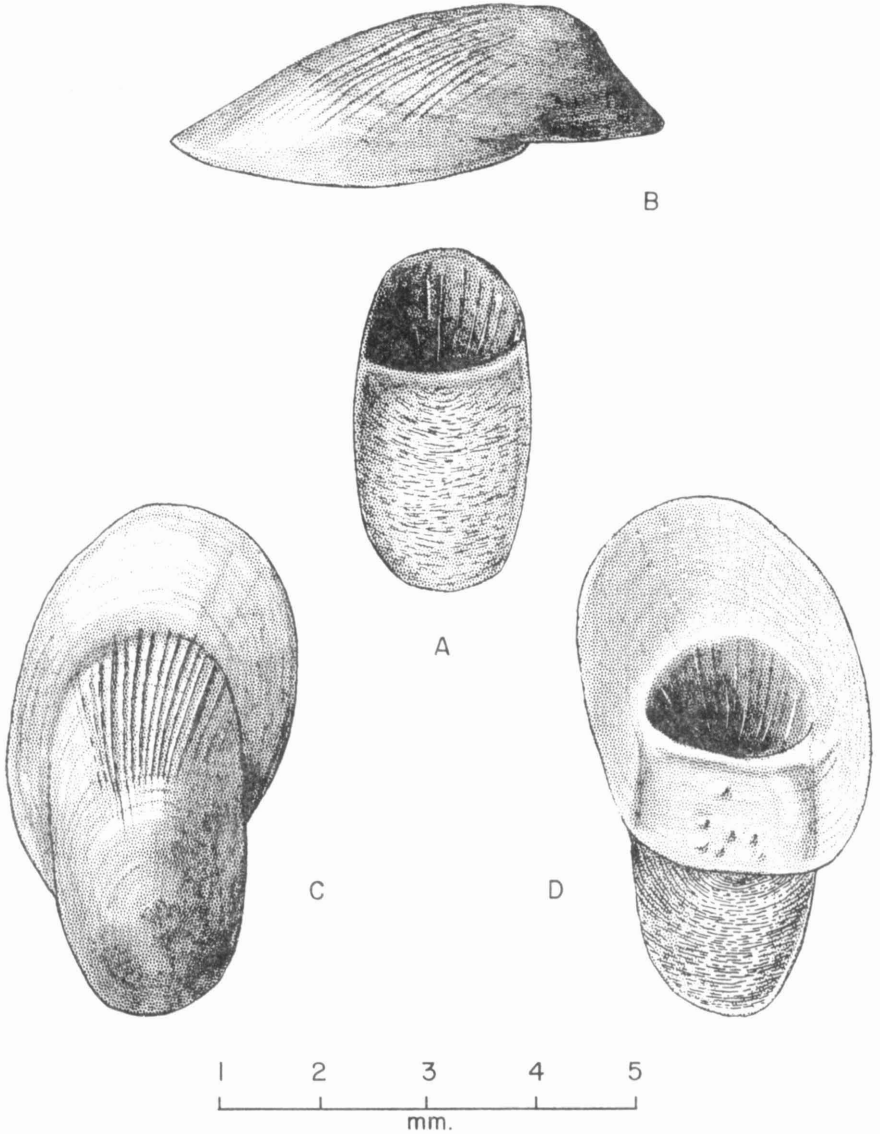


FIG. 1. Shells of the septate form from Ann Arbor, Michigan; presumably *Gundlachia meekiana*: A, young septate shell; B, C, D, left side, dorsal, and ventral views of an older post-septate shell.

forms occurring in various parts of the world, and Hannibal considered that the “. . . several species from New Zealand, Trinidad, etc., referred here, when the apical sculpture and other characters are studied will almost certainly be found to belong to distinct genera which have reached this same stage of specialization.” The latter subgenus included the high-arched shells with striate apices, mainly confined to the Nearctic region. Walker (1917a) maintained that *Kincaidilla* was synonymous with *Gundlachia* Pfeiffer and *Poeyia* Bourguignat, 1862¹, but retained the name (which he always spelled *Kincaidella*) for septate forms with striate apices, including here the Australasian and African forms as well as *G. californica* Rowell, *G. meekiana* Stimpson, *G. stimpsoniana* Smith, and several other undetermined species from the United States. He also characterized the subgenus *Gundlachia, sensu stricto*, as limited to shells possessing smooth apices and occurring in countries bordering the Gulf of Mexico. In addition to the type species, *G. ancyliformis*, Walker included *G. bakeri* Pilsbry, *G. hinkleyi* Walker, and *G. hjalmarsoni* Pfeiffer in this group. The last named species ranges north into Texas and is thus the only representative of the subgenus in the United States. Watson (in Connolly, 1939) further restricted *Gundlachia, sensu stricto*, to those species having, in addition to the above, strongly unequal cusps on the central tooth of the radula.

Walker thought the radulae of North American *Kincaidilla* to be more similar to those of *Gundlachia, sensu stricto*, than to *Laevapex* or *Ferrissia*, the larger North American non-septate ancylids possessing smooth and striate apices, respectively. This is, however, not the case. An examination of the radula of the specimens from Michigan (Figure 2) has shown the central tooth to be quite symmetrical with two large main cusps and two divergent smaller ones. Not all of the rows on the ribbon show the same pattern, and many of the central teeth appear bicuspid, seeming to lack the smaller lateral cusps. The radular formula is normally 16-1-16. The radulae of *Ferrissia* (world-wide?), *Laevapex* (North America), *Burnupia* (South Africa), and *Uncancylus* (Caribbean region and South America) are similar to each other and to the Michigan form illustrated in Figure 2. The radula of *Gundlachia, sensu stricto*, on the other hand, with its asymmetrical central tooth, is more similar to those of *Hebtancylus* and *Anisancylus* from South America than it is to *Kincaidilla*. Good illustrations of these various

¹ Crosse (1890) and others have considered *Poeyia* to be a growth stage of *G. ancyliformis*.

forms of radulae may be found in the papers of Pilsbry (1924), Walker (1925), F. C. Baker (1928), and Connolly (1939).

Apart from the radulae, the anatomy of the various species of *Gundlachia* has received little attention. Pelseneer (1901) studied an

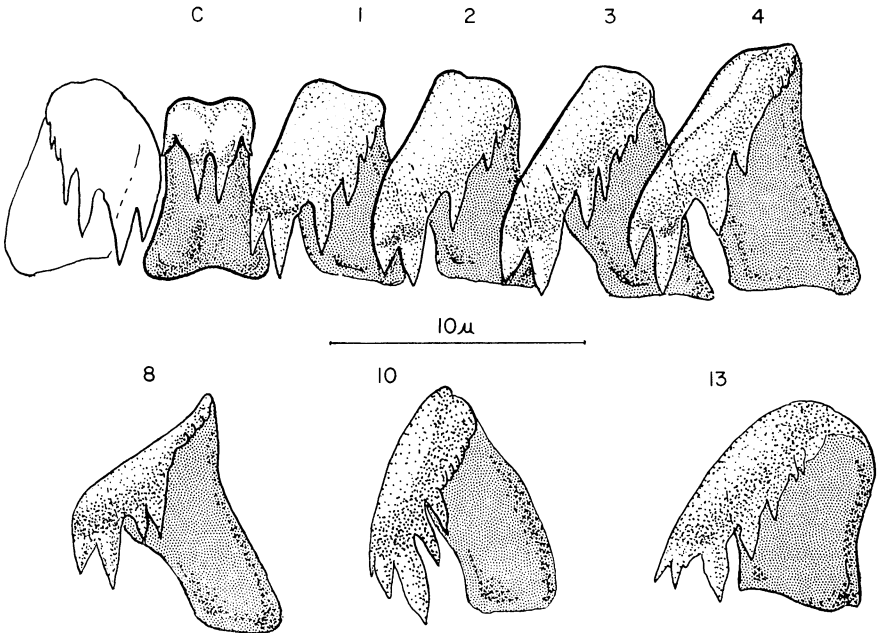


FIG. 2. Radular teeth from the Ann Arbor population whose shells are shown in Figure 1.

undetermined species from New Zealand and found it to be very close to the European *Ancylus* in details of the nervous and excretory systems. The radular pouch is quite short in contrast to the long one in *Ancylus fluviatilis*, where it reaches well back into the body. Several of the American species of *Ferrissia* and *Laevapex* possess similarly short radular pouches, rendering this character of doubtful taxonomic significance.

A study of the anatomy of a *Gundlachia* from South America by Scott (1954) has shown that *G. nordenskioldi* Pilsbry and *Hebetancylus moricandi* (d'Orbigny) are anatomically alike except for those features

incidental to the formation of the septum in the former². Gundlach himself (quoted by Pfeiffer, 1852) compared the external morphology of *G. ancyloformis* with that of *Ancylus* (now *Hebetancyclus*) *havanensis* Pfeiffer, 1839, and could find no difference except for a shorter foot in the septate form. Aguayo (1946) has presumed that these two shell types, which occur together, are merely different forms of the same species. Similarly, Smith (in Smith and Prime, 1870) was unable to find any essential difference between his *G. stimpsoniana* and the species which he found with it and identified as *Ancylus* (now *Laevapex*) *fuscus* C. B. Adams.

Besides the morphological similarity between septate and non-septate ancylicids, the fact that they are often found together has been noted by many authors, whose comments in this regard are summarized in Table I. In addition, associated ancylicid species, other than the non-septate form of a *Gundlachia*, have also been reported in the literature. Walker (1917b) found a species of *Laevapex* (similar to *L. excentricus*) living with *G. hinkleyi*. Calas (1946) stated that the *Gundlachia* which he found in France was accompanied by *Acroloxus lacustris*, and an unspecified ancylicid was discovered together with *G. hjalmarsoni* by Pfeiffer (1858).

The problem of the true nature of *Gundlachia* is rendered more difficult by the observation that reproductive maturity is not necessarily correlated with the septate or post-septate condition (Dall, 1911). Pilsbry (1913, 1924) maintained that the ability to form a septum is a character of taxonomic validity, even though it may not be expressed in all individuals at all times. Such a potentiality is difficult to establish and, as Watson (in Connolly, 1939) has pointed out, we do not know definitely that any species lacks this capability.

The habitat of *Gundlachia* in all parts of the world appears to be restricted to ponds, swamps, and temporary pools in which the water level fluctuates greatly, and standing water may occasionally disappear altogether. It was from just such a swampy area that Pfeiffer's original specimens were collected. The specimens illustrated in Figure 1 were obtained in May, 1957, from a temporary woods pool near Ann Arbor, Michigan. It became completely dry a few months later and remained so throughout the spring and summer of 1958, at which time no

² Nordenskiöld (1903) illustrated this form under the name *Ancylus moricandi* d'Orbigny, 1837. Pilsbry (1924) thought this identification erroneous and called Nordenskiöld's illustrated specimens *G. nordenskiöldi*. Meanwhile he had created the genus *Hebetancyclus* with *A. moricandi* as type species (Pilsbry, 1913). Scott (1954) placed all these names in *G. moricandi*.

TABLE I
CHRONOLOGICAL LIST OF SPECIES OF *Gundlachia*

Species of <i>Gundlachia</i>	Locality	Most Recent Name	Non-septate Form
<i>ancyliformis</i> Pfeiffer, 1849	Cuba	<i>G. ancyliformis</i>	Present (Aguayo, 1946)
<i>hjalmarsoni</i> Pfeiffer, 1858	Honduras	<i>G. hjalmarsoni</i>	Not indicated
<i>adelosa</i> Bourguignat, 1862	Cuba	<i>G. ancyliformis</i>	
<i>poeyi</i> Bourguignat, 1862	Cuba	<i>G. ancyliformis</i>	
<i>californica</i> Rowell, 1863	California	<i>G. californica</i>	? <i>Ancylus fragilis</i> Tryon, 1863
<i>meekiana</i> Stimpson, 1863	Washington, D. C.	<i>G. meekiana</i>	? <i>Ferrissia shimckii</i> (Pilsbry), 1890
<i>stimpsoniana</i> Smith, 1870	Long Island, N. Y.	<i>G. stimpsoniana</i>	Not indicated
<i>textilis</i> (Guppy), 1870	Trinidad	<i>G. textilis</i>	Present (Guppy, 1870)
<i>crepidulina</i> Guppy, 1872	Trinidad	<i>G. crepidulina</i>	
<i>francofurtana</i> Boettger, 1877	Germany (fossil)	<i>G. francofurtana</i>	? <i>Ancylus senckenbergianus</i> Boettger, 1877
<i>petterdi</i> Johnston, 1878	Tasmania	<i>Probancylus petterdi</i> , (Iredale, 1943)	? <i>Ancylus woodsi</i> Johnston, 1878
<i>beddomei</i> Petterd, 1887	Tasmania	<i>Probancylus beddomei</i> , (Iredale, 1943)	Not indicated
<i>lucasi</i> Suter, 1905a	New Zealand	<i>G. lucasi</i>	All arc non-septate (Suter, 1905a)
<i>neozelanica</i> Suter, 1905b	New Zealand	<i>G. neozelanica</i>	Not indicated
<i>equeefensis</i> (Walker), 1912	South Africa	<i>Ferrissia equeefensis</i> , (Connolly, 1939)	Present (Walker, 1912)
<i>bakeri</i> Pilsbry, 1913	Brazil	<i>G. bakeri</i>	Present (Parodiz, 1957)
<i>photellei</i> Walker, 1914	Egypt	<i>G. photellei</i>	Present (Walker, 1914)
<i>hinkleyi</i> Walker, 1917b	Guatemala	<i>G. hinkleyi</i>	Not indicated
<i>farquhari</i> Walker, 1923	South Africa	<i>Ferrissia farquhari</i> , (Connolly, 1939)	Not indicated
<i>nordenskioldi</i> Pilsbry, 1924	Bolivia	<i>G. moricandi</i> (d'Orbigny), 1837	<i>Hebetancylus moricandi</i> (d'Orbigny), 1837
<i>lutzi</i> Walker, 1925	Brazil	<i>G. lutzi</i>	Suggested (Walker, 1925)
<i>burnupi</i> Walker, 1926	South Africa	<i>Ferrissia clifdeni</i> Connolly, 1939	Suggested (Connolly, 1939)
<i>eremia</i> Colton & Godfrey, 1938	Australia	<i>Probancylus eremius</i> , (Iredale, 1943)	Not indicated
<i>sp.</i> , (Calas, 1946)	France		Present (Calas, 1946)

limpets could be found. Boettger (1877) was probably the first to suggest that septum formation in ancyliids is related to the conservation of water during periods of desiccation, an argument amplified by Nordenskiöld (1903) in his well illustrated paper. The types of habitats in which septate forms are found would seem to support this idea.

The status of the genus *Gundlachia* remains unclear. In the Western Hemisphere there are evidently two species complexes, separable on radular characteristics, whose degree of relationship is as yet unknown. If Iredale (1943) is correct, the Australian septate ancyliids are not congeneric with those from the Caribbean. The affinities of the two known European forms, *G. francofurtana* and the undetermined species reported by Calas (1946, 1954), remain a mystery.

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