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Holotype of *Rahula kleini*
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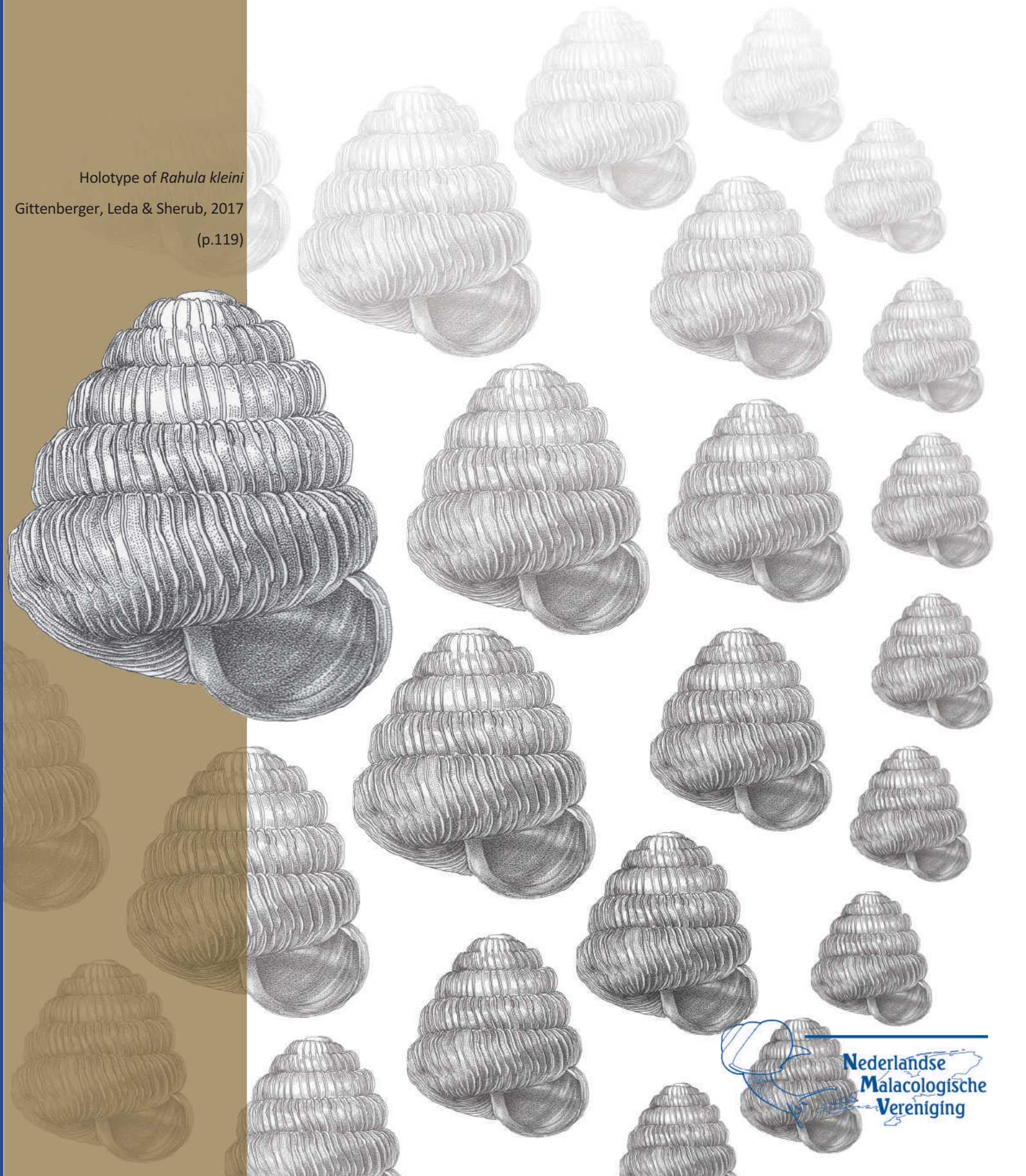

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Inhoudsopgave

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On the anatomy of *Novisuccinea strigata* (L. Pfeiffer, 1855) (Gastropoda, Stylommatophora, Succineidae) from British Columbia, Canada

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Novisuccinea strigata (L. Pfeiffer, 1855) is an arctic-boreal terrestrial mollusc that is both amphiberingian and occurring across a large area of northwestern Canada, including northern British Columbia, Yukon, and the Northwest Territories. The shell, jaw, and reproductive anatomy is described from specimens collected near the Hyland River, on the Liard Plain for northern British Columbia. Reproductive anatomy, and most notably the twisting of the free oviduct around the duct of the bursa copulatrix, indicates that this species properly belongs to the genus *Novisuccinea* as redefined by some American workers.

Key words: morphology, reproductive anatomy, dissection, amphiberingian species, Canada.

Introduction

Species of the pulmonate gastropod family Succineidae, in general, are poorly known across large areas of North America. Although the family is conchologically quite distinct from other terrestrial snails, identifications of species (and even genera) by shell characters alone are difficult or unreliable. Identification of succineids usually requires that characters of the reproductive system be examined, but for a number of North American nominal species, anatomical characters remain unknown or poorly described.

Novisuccinea strigata (L. Pfeiffer, 1854) is an arctic-boreal terrestrial snail that occupies a wide variety of mesic to xeric habitats including grassy slopes, coastal tundra, and coniferous, mixed-wood or regenerative forests (Dall, 1905; Kalas, 1981; Forsyth, 2005). It has a broad range that extends from eastern Siberia across the Bering Strait through Alaska and northern Canada (Dall, 1905; Pilsbry, 1948; Likharev & Rammel'meier, 1962). In Canada, this species is known to occur in northern British Columbia (Forsyth, 2005), the Yukon Territory (Dall, 1905; Pilsbry, 1948; La Rocque, 1953) and the Northwest Territories (Dall, 1905; Pilsbry, 1948). However, a record from southern Saskatchewan by Russell (1934) seems very unlikely. Burke (2013) recognised two records of "*N. strigata*" from Washington State but there is little convincing evidence that the identification, made by an unknown malacologist in the form of a personal communication, is correct. The range was also said to extend east to southern Greenland (Pilsbry, 1948) but Waldén (1963) found that the identification was in error.

Novisuccinea strigata (L. Pfeiffer, 1855) was first described as *Succinea strigata* from Port Clarence, Alaska, and over the course of the next 30 years, four

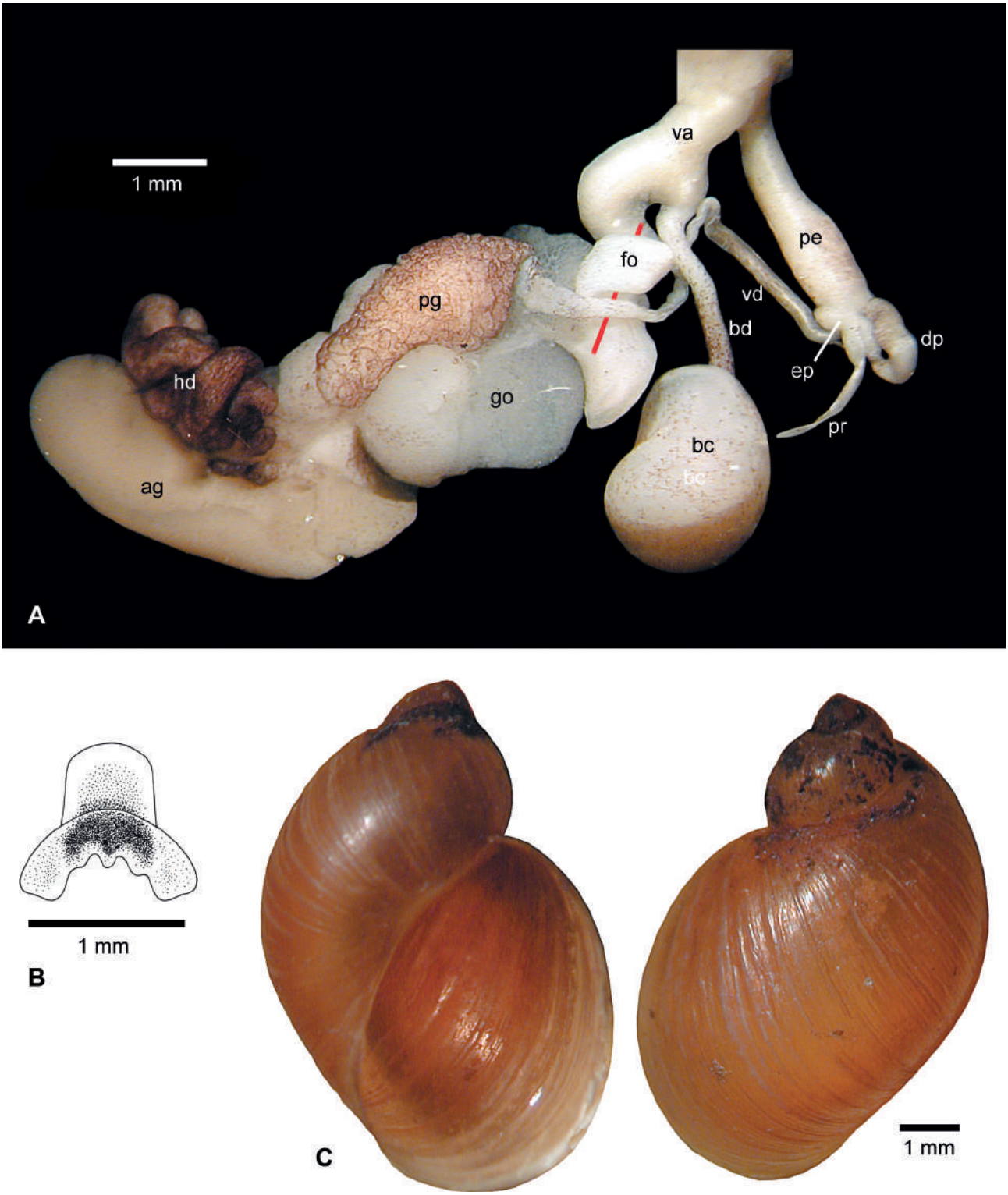

Fig. 1. *Novisuccinea strigata*, west side of Hyland River bridge, Alaska Highway, Liard Plain, Cassiar Land District, British Columbia, Canada; 59°57.54' N, 128°08.96' W (NAD83); leg. R. Forsyth and T. Forsyth, 14 September 2004 (RBCM 004-00132-005). **A**, reproductive anatomy. The bursa copulatrix (bc) and its duct (bd) has been repositioned during the dissection (the red line indicates the approximate position of bd) with the free oviduct (fo) originally wrapping around bd. Other abbreviations: ag, albumin gland; dp, distal penis; ep, epiphallus; go, gonad; hd, hermaphroditic duct; pe, penis; pg, penial gland; pr, penial retractor muscle; va, vagina; vd, vas deferens. **B**, jaw. **C**, shell.

additional specific and subspecific taxa were proposed, all from the same locality: *Succinea rotundata* G. B. Sowerby II, 1872 (not *S. rotundata* Gould, 1846); *S. chrysis* Westerlund, 1883; *S. annexa* Westerlund, 1883; and *S. chrysis* var. *aurelia* E. von Martens, 1885 (Sowerby, 1872; Westerlund, 1883; Martens, 1881-1885). The name most frequently used in older literature was *S. chrysis* Westerlund, 1883, but since the late 1940s (Pilsbry, 1948) this species has usually been referred to by its senior synonym, *S. strigata*.

In this paper, I describe the external pigmentation of the animal, morphology of the shell, jaw, and reproductive system of *N. strigata* from British Columbia and compare these with the previous literature on the species. My examination of the reproductive anatomy of individuals from British Columbia confirms the placement of this species in the genus *Novisuccinea* Pilsbry, 1948, as already done by Russian authors (Schileyko & Likharev, 1986; Gusarov, 1999). Additionally, *N. strigata* appears to fit into the narrower concept of the genus as redefined by Hoagland & Davis (1987).

Materials and methods

I first encountered this species during fieldwork in northern British Columbia in September 2004 for the Royal British Columbia Museum, Victoria (RBCM). This species was collected at six sites along the Alaska Highway, which have been documented and mapped elsewhere (Forsyth 2005). The sites were mesic, with abundant understory, and either mixed forests dominated by spruce or regenerating areas with mostly broadleaf shrubs and trees (Forsyth, 2005). Snails were collected by hand from within leaf litter and from under rocks, logs and other woody debris. Live snails were drowned in carbonated water (Perrier™ brand) and preserved in 70% ethyl alcohol. This material is deposited in the Invertebrate Zoology Collection of the RBCM.

Photographs shells and anatomy were taken through a compound microscope (Russian-built model МбС-10) with a digital camera (Nikon Coolpix 950) hand-held, or mounted, to one eyepiece. The drawing of the jaw was based on photographs.

Results and discussion

In the literature, the shell of this species is said to be highly variable in size and colour (Pilsbry, 1948; Kalas, 1981). The shells of British Columbia and Yukon specimens are ovate, dull, thin, translucent, and reddish horn-brown with lighter and darker colabral streaks. Lighter streaks are associated with very slightly raised or thickened ridges. As for the majority of succineids, there are few whorls, the spire is short, and the aperture is large and ovate, but the suture is not very oblique (Fig. 1C). Altogether, shell characters alone are diagnostic among the succineids of British Columbia. This species has the distinction of being the largest land snail in northern British Columbia and the whole of western boreal and Arctic Canada.

The dorsal surfaces of the animal are pale grey, and near the edges of the foot there are darker grey streaks. The pale pinkish sole noticed in all British Columbia individuals is undescribed for the species in the accounts of Hanna (1940) and Pilsbry (1948) but observed for this species in Alaska by B. Coles (personal communication). Specimens stored in alcohol lose the pink pigmentation over time. This is also true for the eastern North American *N. ovalis* (Say, 1817), which has pale to vividly orange sole that fades rapidly within a couple of weeks (unpublished personal observation). If working from preserved material, Hanna and Pilsbry would have been unaware of this pigmentation in *Novisuccinea strigata*.

The jaw from the dissected specimen (Fig. 1B) is similar to that shown by Pilsbry [1948: fig. 414(14)]. On its concave edge there is a median projection with an "accessory projection" on either side. Hanna (1940) also figured a jaw; all considered, there appears to be considerable variation in the shape and relative dimensions of this structure, although the median and accessory projections are always strongly indented and clear.

The penis, vagina, and free oviduct are opaque white and nearly without pigmentation. The vas deferens, bursa copulatrix, and bursa copulatrix duct are also opaque white but with fine brown speckles in varying density. The prostate gland is much more densely speckled with brown, particularly between the nodules. The glandular oviduct is white, slightly translucent, and with a very few pigment specks. The albumen gland is beige. The hermaphroditic duct is heavily suffused with dark brown.

The earliest described species of succineids were based on shells alone, without consideration of soft anatomy or ecology. Not until the 1870s were the anatomy of any species of succineids known, but it was only in the 1930s that malacologists realised the importance of the reproductive anatomy (in particular the male genitalia) and developed a new classification (Lee, 1951). Reproductive anatomy became a de facto requirement in determining genera and describing species (e.g., Lee, 1951; Franzen, 1971, 1983; Patterson, 1972), although not always very clearly (e.g., Hubricht in Harris & Hubricht, 1981), and the reproductive system was seen as diagnostic. Some characters are fundamental to the bauplan, such as

the presence of a medial appendix on the penis in *Mediappendix* (Pilsbry, 1948) or the wrapping of the free oviduct around the duct of the bursa copulatrix in *Novisuccinea* (sensu Hoagland & Davis, 1987). Other characters, such as the relative lengths of one organ or structure to another (e.g., Hubricht in Harris & Hubricht, 1981) seem weak, and for these, little consideration seemed to be given to the possibility of variation of such characters, either due to ontogeny or other factors such as artefacts of preservation (retraction). Culver et al. (2013) noted that standardised, repeatable measurements of reproductive organs of *Oxyloma* could not be attained due to the elasticity and flexibility of soft tissues. They found that the organs were packed into the body cavity in various orientations, making measurements difficult, and also noted that up to half of the specimens in some collections were reproductively immature. Coles (cited by Nekola, 2014) observed that a population of a succineid corresponded to multiple described "anatomical species" at various stages of the individuals' ontogenesis. However, ontogenetic variability cannot account for all morphological (or fundamental) differences between succineid genera; natural, well-delimited groups exist that show clear, well-defined morphological patterns. Genera (and/or subgenera) remain largely defined by mostly major differences in their reproductive anatomy.

Pilsbry (1948: xxxiii, 801) originally proposed *Novisuccinea* as a section of *Succinea* and included in it *Succinea ovalis*, *S. strigata*, and most other Nearctic species. He characterised *Novisuccinea* as having the end of the penis and the adjoining part of the epiphallus projecting in a loop free from the penial sheath, the farther end of the epiphallus being usually bound into the junction of the penial retractor and sheath, the vagina of moderate length, and the free oviduct typically very long. Paterson (1971) saw that Pilsbry's *Novisuccinea* included species that seems unrelated and advised avoiding its use, and she noted that the presence of a penial/epiphallal loop occurs in African and Japanese succineids. Although Pilsbry (1948) appears to have considered both *Succinea ovalis* and *S. strigata* to be "typical" in the vernacular sense, he did not explicitly designate a type species contrary to what Schileyko & Likharev (1986) believed; Hoagland & Davis (1987) selected *S. ovalis* as the type species. Some of the characters used by Pilsbry seem difficult to assess; relative lengths and the amount of penis/epiphallus projecting as a loop from the penial sheath could vary.

In redescribing *Novisuccinea*, Hoagland & Davis (1987) made valuable anatomical observations and pointed out nine characters of the reproductive system by which the genus differs from *Succinea* sensu stricto. They included in the genus *N. ovalis*, *N. chittenangoensis* (Pilsbry, 1908), and an undescribed species from Minnesota. Their main contribution in general is that anatomy should be viewed in situ, that is, without manipulation of structures, as is often done and including my dissection (Fig. 1A). For practical reasons, it is easier to make traditional dissections, and in my case, the organs were rearranged before I realised the taxonomic value lies in how they are positioned. In *Novisuccinea*, according to Hoagland & Davis (1987), the free oviduct as wraps 360° around the duct of the bursa copulatrix. No other succineids for which anatomical data exists appear to have this character (Pilsbry, 1948; Schileyko, 2007).

The genitalia of *Novisuccinea strigata* was first described seven decades ago by Hanna (1940: plate B, lower right), whose illustration show a straight free oviduct, without a twist around the duct of the bursa copulatrix. Pilsbry (1948) republished Hanna's figure, but also added two figures of his own. Pilsbry's figure 429c also does not show the free oviduct twisting around the duct of the bursa, but his figure 429d does. However, it is easy to imagine that in figure 429c the S-curved free oviduct is a "flattened" rendition of the twists and the duct of the bursa has been "untangled" from it. In these cases some uncoiling and rearrangement of the ducts seems likely, as I had done myself. The advantage of doing this is to better show the relative sizes and forms of the various ducts and glands, but this comes at a loss of the actual relationship of the structures to one another and may obscure one of the key and most remarkable characters that distinguish *Novisuccinea*. Neither Pilsbry (1948) nor Hanna (1940) made any special mention of this character.

Some of the other characters used by Hoagland & Davis (1987) to diagnose *Novisuccinea* were observed. These include: the vas deferens twists about midway along its length; proximal to this twist, the vas deferens is an even, circular and well-muscularised tube, but distal to this twist, it is flaccid; the penis sheath encases only the proximal and a portion of the distal penis; the epiphallus is bound tightly to the distal penis; and the loop of the distal penis/epiphallus is free of the penial sheath. Hoagland & Davis (1987) also found that in *Novisuccinea* the bursa copulatrix duct is massive near its junction with the vagina and continues as a wide tube for half its length before narrowing, whereas in *Succinea* the bursa copulatrix duct is slender at its junction with the vagina, or if swollen, then it abruptly becomes slender close to the vagina. The published figures by Pilsbry (1948: fig. 429C, D) and Hanna (1940: plate B, lower right) both show that the bursa copulatrix duct swollen at the vagina then gradually tapering. The dissection of the British Columbia material likewise shows this, although the extent of this enlarged section is less than half the length of the whole duct (Fig. 1A).

Until quite recently North Americans had overlooked a monograph of the succineids of the USSR (Schileyko & Likharev 1986). A later publication by Gusarov (1999), which presents much the same information but in a shorter form, is more accessible for most North Americans because it is in English. These Russian authors utilised *Novisuccinea* as a full genus, but their concept of it is broader than that of Hoagland & Davis (1987), and they included in it *S. ovalis*, *S. strigata*, and five other Russian species (Schileyko & Likharev, 1986). Two of these five species, *N. lyrata* and *N. diserta*, would seem not to belong to *Novisuccinea* (sensu Hoagland & Davis 1987), if having the distinctive 180° twist of the oviduct around the duct of the bursa copulatrix is diagnostic of the genus.

It is a little unfortunate that Hoagland & Davis (1987) did not include *N. strigata* in their work, but doing so would clearly have been outside of their project's scope. By omission from that work, *S. strigata* was effectively removed from the *Novisuccinea* group and its generic position unresolved, at least in the North American literature. As a result, Turgeon et al. (1998) continued to use regard this species as a *Succinea* (sensu stricto), where it remained at least into 2005 (Forsyth, 2005). *Novisuccinea*, as the correct genus for this species, has been gradually gaining acceptance in the United States and Canada (e.g., Burke, 2013; NatureServe, 2016), and at least in the case of NatureServe, the basis for this was my comment in the online database "E-fauna BC" (http://linnet.geog.ubc.ca/efauna/Atlas/Atlas.aspx?sciname=Novisuccinea%20strigata). The present study supports the premise that *S. strigata* is indeed a member of the *Novisuccinea* in the sense of Hoagland & Davis (1948). It is rather fitting that this species is restored to *Novisuccinea* in which Pilsbry originally placed it.

Acknowledgements

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