

A new species of *Glyphyalus* (Gastropoda, Pulmonata, Oxychilidae) from the Dutch Caribbean island of St. Eustatius

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Glyphyalus quillensis spec. nov. is described from the Caribbean island of St. Eustatius (Lesser Antilles). On the basis of similarities in shell and radula morphology, geographic distribution of the known species, and low similarity with the known CO1 sequences of North American and Palearctic *Perpolita* species, the new species is tentatively attributed to *Glyphyalus*, which we consider an independent genus, rather than a subgenus of *Glyphyalinia*. *Glyphyalus quillensis* spec. nov. appears to be confined to the upper slopes and crater of The Quill volcano, a protected nature reserve with remnants of the original vegetation cover. The species is therefore potentially of conservation value.

Key words: Stylommatophora, Zonitidae s.l., taxonomy, *Perpolita*, *Nesovitrea*, *Glyphyalinia*, Lesser Antilles, Statia, conservation.

INTRODUCTION

In 2015, Naturalis Biodiversity Center (in collaboration with the ANEMOON Foundation, among others) organized both a marine and non-marine expedition to the island of St. Eustatius during which molluscs were collected. The knowledge of the non-marine Mollusca of this small island is summarized in two short reports in Dutch (Hovestadt, 1980; Van der Valk, 1987). The 2015 expeditions, as well as a visit by the third author in 2015, yielded new records and various additions to the Statia list (see e.g. Van Leeuwen & Hewitt, in press), and prompted the re-examination of

the species hitherto reported. Van der Valk (1987) first reported a species as "*Nesovitrea* spec.", the taxonomic status of which has so far remained unclear. Voucher shells of Van der Valk's record could be traced in the Naturalis collection. During the 2015 expeditions new material of this species was collected. Study of the shells, soft parts and the sequence of the Cytochrome C oxidase 1 (CO1) gene with the literature on Caribbean, North and South American land molluscs did not result in a name for this characteristic species. Since it appears to be restricted to the forested upper slopes and crater of the Quill volcano, the least disturbed habitat of Statia, it is potentially of conservation interest and as such it is in need of a name. In this paper we address its taxonomic (family, generic) position and describe it as a new species.

We dedicate this paper to the eminent malacologist Robert G. Moolenbeek, at the occasion of his retirement from the position as curator of Mollusca, formerly at the Zoological Museum Amsterdam, later at Naturalis Biodiversity Center, Leiden. Rob's enthusiasm for malacology in general and his fascination for the Dutch Caribbean malacofauna in particular has been -and still is- an inspiration for the authors.

MATERIAL AND METHODS

Fresh material was collected by the authors using both visual search and leaf litter sifting. Other shell material used in this study was previously collected by Wagenaar Hummelinck (in 1973, unpublished) and by Van der Valk (1987). Shell measurements were taken

from images obtained by a Leica DFC420 digital camera attached to a Leica M165c stereo microscope, using Leica LAS V4.4 software.

DNA.— Of two specimens from the type locality, including the holotype, foot tissue samples were used to extract DNA with the NucleoMagTissues kit (Machery-Nagel, Dueren, Germany). Elution of the DNA was performed with 100 µl elution buffer. The primer sets published by Folmer et al. (1994) were used to amplify the mitochondrial barcoding marker Cytochrome C oxidase subunit1 (CO1). The PCR retraction mixtures contained: 2.5 µl PCR buffer, 0.5 µl DNTP's, 1.0 µl of each primer, 0.3 µl Taq and 18.8 µl

MilliQ. To each reaction mixture 1 µl DNA extract was added as template. Each PCR cycle consisted of 92 C for 5 seconds (denaturation), 50 C for one minute (annealing), and 2 C for one minute (extension). Each cycle was repeated 39 times. Sequencing of both DNA strands was performed on an Automatic Sequencer by BaseClear, Leiden, The Netherlands. The raw sequence data were assembled and edited using Sequencher 4.2 (Gene Codes Corporation, Ann Arbor, USA). Data, including sequence trace files, were submitted to the BOLD database (<http://www.boldsystems.org/>).

Abbreviations.— ad., adult; AH, private collection

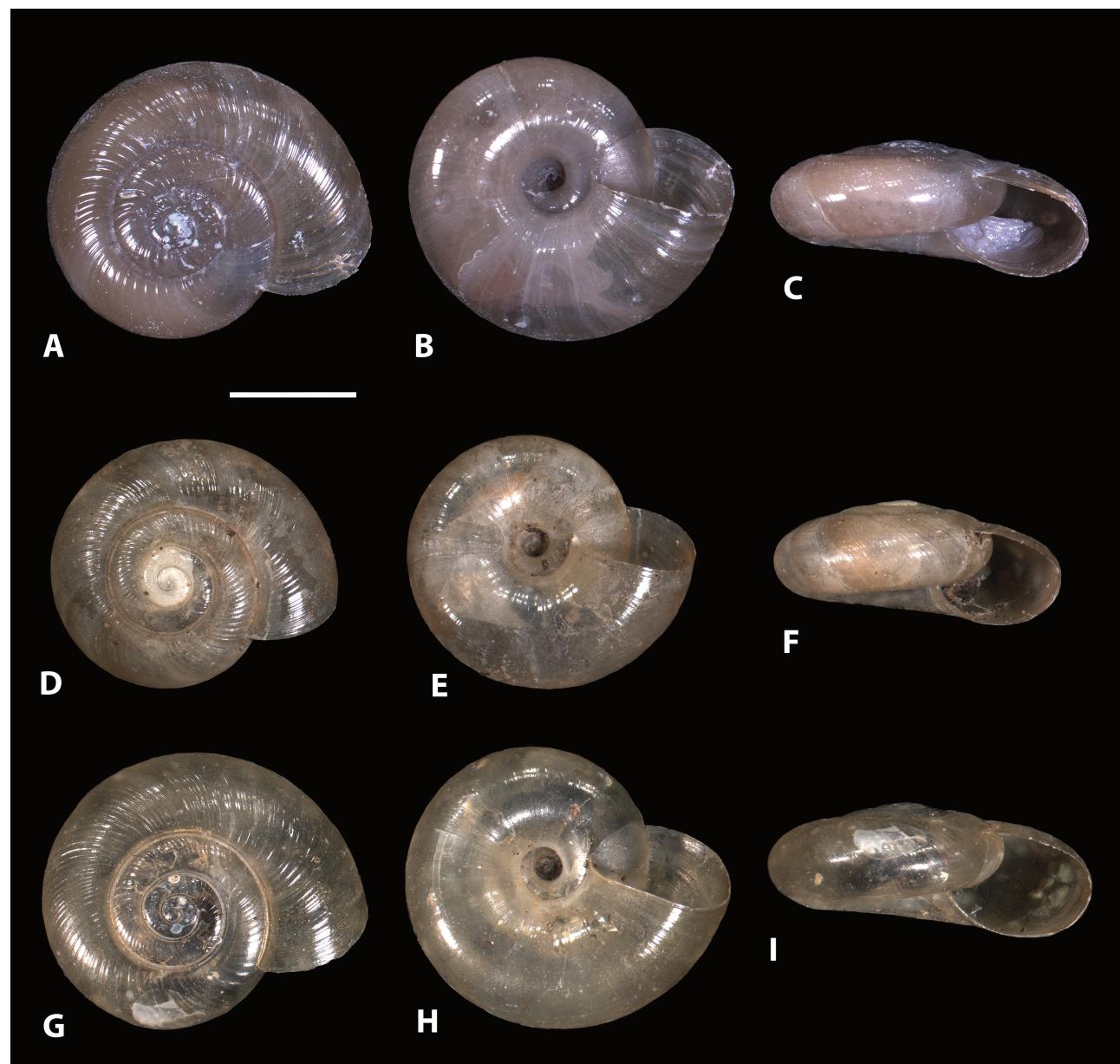


Fig. 1. Shells of *Glyphyalus quillensis* spec. nov. from three localities on The Quill, St. Eustatius. A-C, holotype shell (RMNH.5004017); D-F, specimen from just under crater rim (RMNH.5004166); G-I, specimen from Mazinga (RMNH.280940). Scale bar 2 mm. (photographs A.J. de Winter).

of Ad Hovestadt, Amersfoort; juv., juvenile; RMNH, Collection Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands; SD, shell diameter; SH, shell height; SvL, private collection of Sylvia van Leeuwen, Bilthoven; W, number of whorls following the method described in Kerney & Cameron (1979), rounded to the nearest quarter whorl.

SYSTEMATICS

Family Oxychilidae Hesse, 1927

Genus *Glyphyalus* H.B. Baker, 1928

Glyphyalus quillensis spec. nov. (Figs 1-5)

Nesovitrea spec. – Van der Valk, 1987: 283.

Material (all from St. Eustatius).— Holotype: The Quill, crater bottom, 17.47800° N 62.963444° W, alt. 300 m, 20.vi.2015, S. van Leeuwen leg. (RMNH 5004017/shell, RMNH.5004018/soft parts, radula, jaw, DNA).

Non-type material: 1. Same data as holotype: 1 undissected specimen in alc., used for DNA (RMNH 5004017); > 20 ad. and juv. shells (SvL, AH, RMNH 5004162). 2. The Quill, crater bottom, *Myrcia-Quararibea* forest with large rock boulders on flat terrain, 17.478385° N 62.962086° W, alt. 293m; 10.x.2015; A.J. de Winter leg., 21 specimens in alc. (RMNH 5004163), 12 shells (RMNH.5004164). 3. The Quill, *Coccoloba-Chionanthus* forest just under crater rim on steep, NNW-facing slope, 17.481052° N 62.961964° W; alt. 540 m, 11.x.2015, A.J. de Winter leg., 5 specimens in alc. (RMNH 5004165), 30 shells (RMNH 5004166). 4. De Kant, west rim of The Quill, alt. 400 m, WH 429A, 11.vii.1973, P. Wagenaar Hummelinck leg. (locality in Wagenaar Hummelinck, 1981), 1 shell (RMNH 5004018). 5. The Quill, crater, 20.iv.1986; L. van de Valk leg. (2 juv. shells RMNH 280941). 6. The Quill, Mazinga (alt. ca. 600 m); 20.iv.1986; L. van de Valk leg. (RMNH 280940/19 ad. and juv. shells).

Etymology.— Named after The Quill volcano on St. Eustatius.

Diagnosis.— Shell comparatively small-sized (up to 5.9 mm), strongly depressed with a low body whorl and flattened spire. Umbilicus rather wide, one fifth to nearly a quarter of the shell diameter. Sculpture of teleoconch above periphery with regularly spaced radial furrows, mixed with irregular additional growth lines especially on the last whorl. Sculpture absent on the umbilical side. Spiral sculpture absent. Radula with tricuspid central tooth and three tricuspid lateral teeth.

Shell (Figs 1-3).— Strongly depressed (SH:SD ratio 0.41-0.46, Fig. 3), thin and fragile, diaphanous with a pale brownish-yellowish hue (somewhat darker with the animal inside), consisting of less than 4, extremely

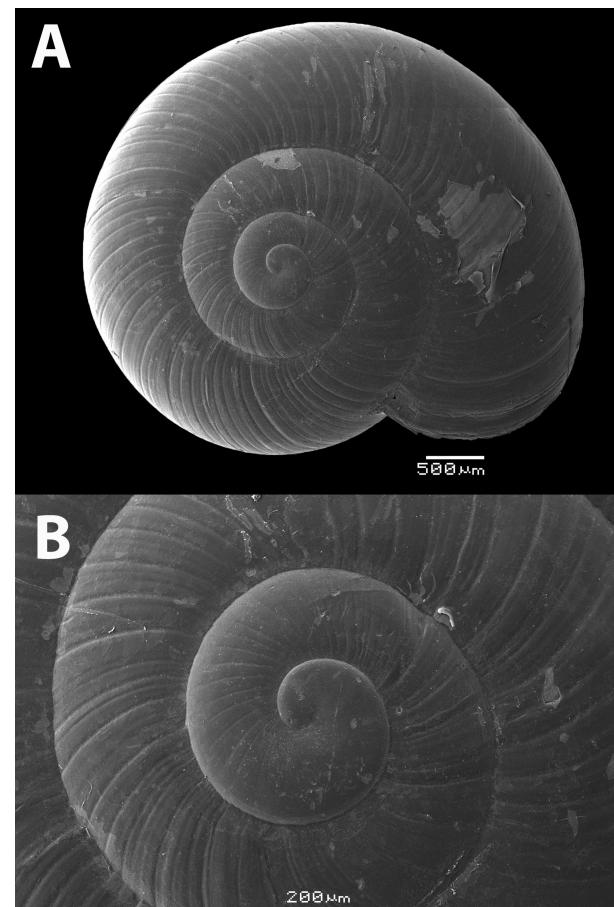


Fig. 2. *Glyphyalus quillensis* spec. nov., SEM photographs of juvenile shell from crater bottom of The Quill (RMNH.5004164).

flattened, whorls. Transition from protoconch to teleoconch not strongly marked. First 0.6-0.7 whorls smooth, thereafter with regularly spaced radial furrows which gradually become more distinct. On later whorls rib-like growth lines mix with the radial furrows, resulting in a more irregular radial sculpture especially on the last whorl. Radial furrows extend not or barely below the shell periphery, and are fully absent from the basal (umbilical) side of the shell. No spiral sculpture discernable anywhere on the shell, even using SEM. Shell diameter up to 5.9 mm (whorl number unknown, damaged apex), usually less (Fig. 3, 10 shells measured), with up to slightly over 4 whorls. Coiling tightness (W/ln SD; Emberton, 2001) ca. 2.3 (range 2.28-2.52). Umbilicus wide, ca. 22% of SD (range 19-23%). Peristome simple and thin, 1.3-1.4 times wider than high.

Soft parts.— Attempts to study the genitalia of a few of the available alcohol-preserved specimens were not successful, due to insufficient relaxation and fixation in ethanol 96% of the holotype, whereas specimens collected in October proved to be subadult, with somewhat smaller-sized shells (Fig 1 d-f) than those collected in April and June (Fig. 1a-c and Fig. 1g-i).

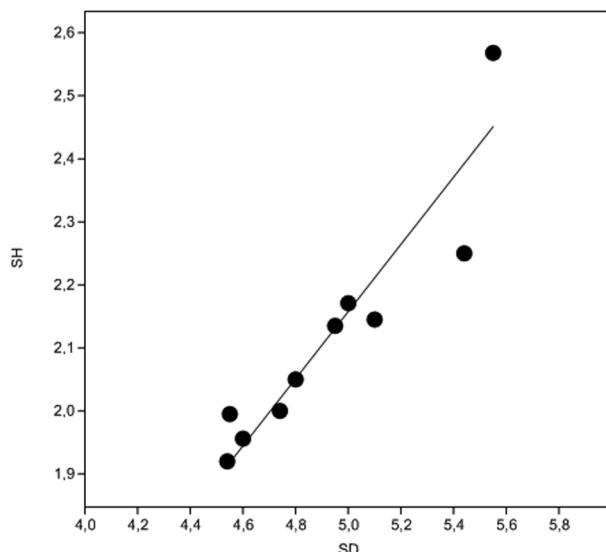


Fig. 3. *Glyphyalus quillensis* spec. nov., shell height (SH, mm) against shell diameter (SD, mm) plot of 10 selected (sub)adult specimens (ex RMNH.5004166, RMNH.5004162, RMNH.280940).

42

Radula (Fig. 4).— Radula of one animal examined. Radula ribbon ca. 1.1 mm long and 0.25 mm wide, with ca. 65 rows of teeth. Central tooth tricuspid with an elongate central cone. Laterals 3, all longer and wider than the central tooth, tricuspid. A single transitional tooth resembles the marginals in shape, but is somewhat wider with a minute endocone. Marginals unicuspids, elongate, distinctly pointed and curved, all rather uniform in size and shape except for the noticeably shorter outer marginals. Marginal teeth positioned at an angle of ca. 25 degrees relative to the row of central and laterals.

Jaw (Fig. 5).— Rather small (ca. 0.5 mm wide) and inconspicuous, oxygnathous, curved, with a median projection.

DNA.— The CO1 sequences of the holotype and one other specimen are identical and are available from <http://www.boldsystems.org/> under accession numbers BOLD: NESQU001-16 (RMNH.5004018, holotype) and BOLD: NESQU002-16 (RMNH.5004017). Comparison of these sequences with those stored in BOLD and GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>) did not yield an identical match. The BOLD identification tool, using released and non-released data, indicated a similarity of 95% with “*Nesovitrea dalliana* (Pilsbry & Simpson, 1888)” from Florida. Similarities with other “*Nesovitrea*” species in BOLD or Genbank were lower, 87% with “*Nesovitrea electrina*”, and 85% or less with “*Nesovitrea hammonis*”. Similarity with *Glyphyalinia* species was 88% or less. Sequences of *Glyphyalus* species were not available from BOLD or Genbank.

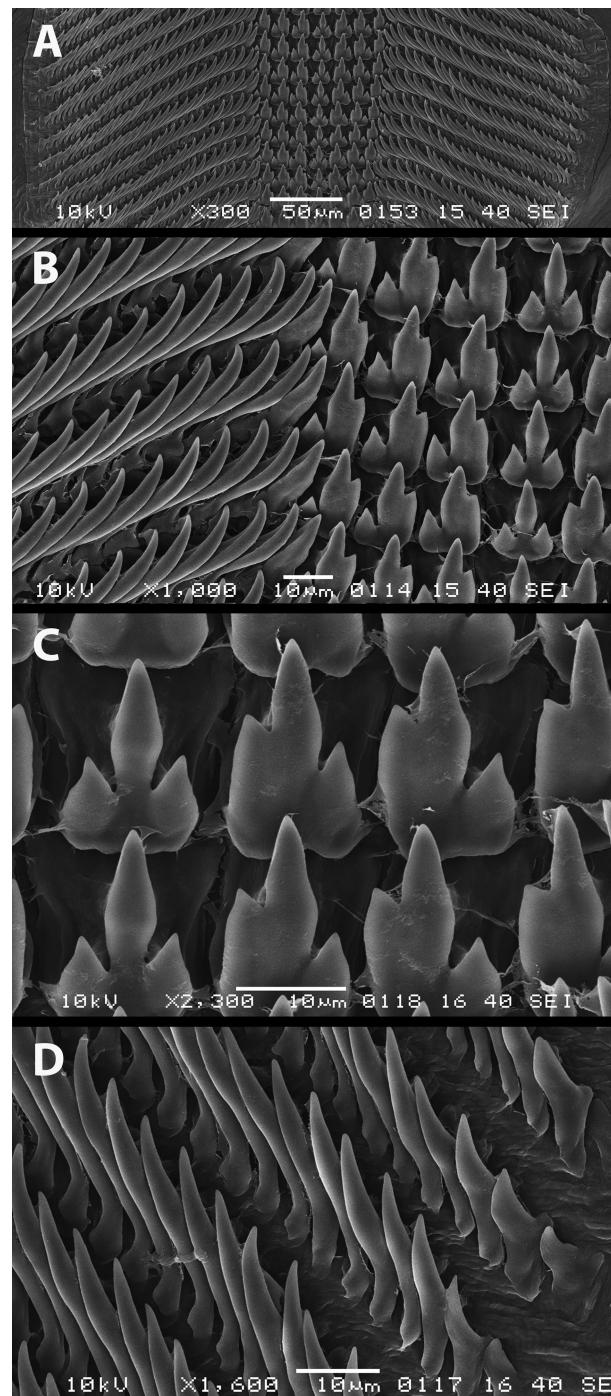


Fig. 4. *Glyphyalus quillensis* spec. nov., SEM photographs of radula of specimen from crater bottom of The Quill (RMNH.5004163). A, entire rows; B, central tooth, laterals and early marginals; C, central tooth and laterals; D, outer marginals.

Distribution.— *Glyphyalus quillensis* spec. nov. was so far only found between ca. 300 and 600 m a.s.l. on The Quill, a dormant volcano with a symmetrical, regular truncated cone, which was formed in the Holocene (Westermann & Kiel, 1961). The crater rim reaches a height of 378 m (western side) up to 600 m (eastern side), and the lowest part of the crater bottom lies at 273 m a.s.l. (De Freitas et al., 2012). The species was

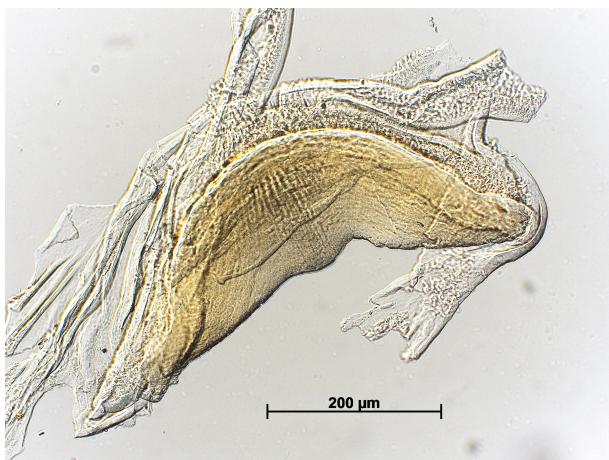


Fig. 5. *Glyphyalus quillensis* spec. nov., jaw of holotype (RMNH.5004017).

not encountered in recent and older collecting campaigns elsewhere on Statia. Its occurrence on other islands is uncertain (see Discussion).

Ecology.— The species was found on the humid forest floor, especially on small and large rocks (Fig. 6). In 2015, it was absent from a sun-exposed calcareous site (the so-called White Wall) as well as from equally intensively sampled plots on lower slopes of The Quill, which may be due to lack of moisture and/or to the absence of cloud forest vegetation. The (closeby) localities where the species was found share *Helicina fasciata* (Lamarck, 1822) as accompanying gastropod species. The climate of The Quill crater floor and rim is more humid due to intercepted clouds and higher rainfall than average on St. Eustatius (De Freitas et al., 2012).

Conservation.— We suggest that *G. quillensis* spec. nov. may be used as indicator taxon for undisturbed and/or recovering natural habitat on Statia. Van der Valk (1987) explicitly considered both *G. quillensis* spec. nov. (as *Nesovitrea* spec.) and *H. fasciata* anthropochorous taxa, possibly based on their absence from (ca. 8000 year old) Holocene deposits on the island. We doubt this conclusion, if only because both species appear to be confined to the least disturbed spots on the Quill volcano, in contrast to the Subulinidae species that were mentioned alongside. This issue requires further study.

DISCUSSION

Determining the taxonomic position of the newly described species was not straightforward. The systematics of the Caribbean and other (sub)tropical New World land snails is still rather confused. Of many taxa the morphology of the soft parts is incompletely known and of only a few species DNA sequences ap-

pear to be published.

Within a New World context, species with flat, widely umbilicate shells like *G. quillensis* can either belong to the group of families previously included in the Zonitidae, or to carnivorous families like the Scolodontidae (as was done by Van Leeuwen et al., 2015, for a shell from Saba, see below). In the absence of genital characters, we studied the radula and jaw. The presence of tricuspid central and lateral radula teeth precludes the attribution to a carnivorous family, as does the presence of a jaw, which is absent or vestigial in carnivorous snails in this region (Baker, 1925).

The generic attribution is somewhat uncertain due to the confusing – incomplete and partly contradicting – information in the literature on the various New World zonitoid taxa. The species was first addressed to as a *Nesovitrea* Cooke, 1921 (Van der Valk, 1987), a genus commonly used for both Nearctic and Palaearctic species, but the type species is from Hawaii. The genus *Perpolita* Baker, 1928, was introduced as a subgenus of *Retinella* P. Fischer, 1877. As type species Baker designated *Helix hammonis* Strøm, 1765, although later on this turned out not to be the “real” *Helix hammonis*, but a misidentified *Helix electrina* Gould, 1841 (Baker, 1930; Pilsbry, 1946; Riedel, 1980). Baker (1941) questioned the validity of *Perpolita* but maintained both *Nesovitrea* and *Perpolita* as subgenera. Riedel (1966, 1980) treated *Nesovitrea* as the preferred senior name, and this opinion was widely accepted since. Schileyko (2003) restricted *Nesovitrea* to the Hawaiian species, and maintained *Perpolita* as an independent genus for the Holarctic species. In the present paper we follow Schileyko (2003) in preferring *Perpolita* over *Nesovitrea* for the Non-Hawaiian taxa. *Perpolita* would seem to be a likely genus to accommodate the new species, since at least some of the attributed species share similarities in shell morphology with *G. quillensis*, including the radial sculpture and wide umbilicus. However, there are additional Nearctic (sub)genera that potentially qualify as generic umbrella for the new species. According to Riedel’s (1980, and references therein) authoritative overview of the World-wide Zonitidae s.l., species of *Glyphyalinia* Martens, 1892 subgenus *Glyphyalus* Baker, 1928, and subgenus *Glyphyalops* Baker, 1928, strongly agree with species of *Nesovitrea* sensu Riedel in shell size, shape, umbilical development and sculpture. Of these, the (sub)genus *Glyphyalus* particularly resembles *Perpolita* in radula characters, notably the similarly-sized tricuspid central and lateral teeth and the long and slender mesocone of the central tooth (Riedel, 1980: 80). These characters also apply for *G. quillensis*.

We searched for a matching species description in



Fig. 6. Type locality of *Glyphyalus quillensis* spec. nov. (photograph A.J. de Winter).

the above mentioned (sub)genera using especially Pilsbry's (1946) monograph of North American land snails. Various *Perpolita* species have a rather northern distribution, and the occurrence of such species in the tropical Caribbean climate may be less likely. Nearctic species attributed to *Perpolita/Nesovitrea* generally possess less flattened and smaller shells with a less open umbilicus [e.g. *P. electrina*, *P. binneyana* (Morse, 1864), *P. b. occidentalis* (Baker, 1930)]. Judging from Pilsbry's (1889, 1946) descriptions and illustrations, *Retinella dalliana* (Pilsbry, 1889), the species with the greatest similarity in the CO1 gene sequence, has a rather small shell (2.7 mm at 4 whorls), and sculpture of "delicate growth lines", thus rather unlike *G. quillensis*.

Species of *Glyphyalus* appear to be distributed especially in the southern U.S.A. states. Also the shell descriptions of at least some *Glyphyalus* species fit better than those of *Perpolita/Nesovitrea* species. For instance, description and photograph of *Glyphyalus virginica* (Morrison, 1937) in Pilsbry (1946: 265, fig.

130) strongly concurs with *G. quillensis*, but *G. virginica* appears to have half a whorl more at the same size. *Glyphyalus burringtoni* (Pilsbry, 1928), *G. cumberlandiana* (Clapp, 1919), *G. lewisiana* (Clapp, 1908) and *G. raderi* (Dall, 1898) possess smaller shells, whilst *G. specus* (Hubricht, 1965) is a cave-dwelling species that was only tentatively attributed to *Glyphyalus*; *G. vanatai* (Pilsbry & Walker, 1902) and *G. clingmani* (Dall, 1890) both appear to be more narrowly umbilicate.

The CO1 sequence of *G. quillensis* matched best with that of "*Nesovitrea dalliana*" (95%) of all sequences stored in BOLD and Genbank (accessed Feb 9, 2016). Apart from CO1 sequences, no further details were available, so the identification could not be verified. *Glyphyalus quillensis* and "*Nesovitrea dalliana*" together stand somewhat apart from a group of North American "*Nesovitrea*" species (including the type species of *Perpolita*, *P. electrina*). Both species are also not part of a clade consisting of *Glyphyalinia* species. Since the anatomy of "*Nesovitrea*" *dalliana* appears to be unknown (Riedel, 1980), it seems well possible that both

quillensis and the sequenced “*Nesovitrea dalliana*” belong to *Glyphyalus*. DNA sequence data of other *Glyphyalus* species as yet appear to be unknown, and research on more taxa from a wide geographical range is necessary to warrant definite conclusions.

CO1 sequence data in BOLD suggest that Palearctic “*N.*” *hammonis* and “*N.*” *petronella* (L. Pfeiffer, 1853) form a clade distinct from the group of Nearctic “*Nesovitrea*” species. This raises the question whether “*N.*” *hammonis* is indeed a member of the same genus as the New World taxa. If *Nesovitrea* is restricted to the Hawaiian taxa, a new name might be necessary for the Palearctic species.

Glyphyalus quillensis is so far only known from St. Eustatius, but the occurrence on other islands in the region is not unlikely. The species is as yet unknown from the neighbouring islands of St. Kitts and Nevis (Breure et al., 2016), but can be expected there as the three islands are in close proximity, separated by shallow water only, and offer the same habitat. The species may have been recorded as *Hyalina incisa* by Rush (1891) from St. Kitts. Chase & Robertson (2001) renamed *Helix incisa* L. Pfeiffer, 1866 (non *Helix incisa* Gmelin, 1791) from Barbados as *Glyphyalinia barbadensis* Chase & Robinson, 2001. Baker (1930: 209) referred to *Helix incisa* material from Barbados as “two bleached shells from the Swift Collection (ANSP. 48818, paratypes?) so closely resemble *R. carolinensis* in form, that I am suspicious of the locality given”. Since *Glyphyalinia carolinensis* (Cockerell, 1890) possesses a narrowly umbilicate shell with both radial and fine spiral sculpture, *Glyphyalinia barbadensis* is unlikely to be conspecific with *G. quillensis*.

Van Leeuwen et al. (2015) recorded a *Happia*-like specimen from Saba near the top of Mount Scenery. Two additional specimens were found on Saba along the Crispeen-trail (Hovestadt, unpublished data). These weathered shells are rather similar to *G. quillensis* and we suggest that these specimens might be closely related if not identical to *G. quillensis*, rather than a species of *Happia* (Scolodontidae).

Van der Schalie (1948) reported a “*Retinella* sp.” near *R. subhyalina*, from Puerto Rico. *Helix (Hyalinia) subhyalina* L. Pfeiffer, 1867 was originally described from Mexico. Riedel (1980) included the species without reservation in *Nesovitrea*, but we have been unable to find a published description of the soft parts. Pfeiffer’s (1867) original description concerns a much smaller species, and Strebel & Pfeiffer’s (1880) interpretation of the taxon refers to a species quite different from Pfeiffer’s species. Alvarez & Willig (1993) report *Nesovitrea subhyalina* as a Puerto Rican species that occurs on the forest floor. Although this is potentially the same species as *G. quillensis*, the name *subhyalina* cannot be applied.

Based on these considerations, we describe the species from Sint Eustatius as a new species of *Glyphyalus*. We consider *Glyphyalus* sufficiently distinct in both shell and soft parts morphology (see Riedel, 1980) to consider it an independent genus, rather than a subgenus of *Glyphyalinia*. We suggest that the sequenced material addressed to as *N. dalliana* in BOLD may in fact not be a species of *Perpolita/Nesovitrea*, but a species of *Glyphyalus*, to which genus at least one more species from Florida has been attributed.

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REFERENCES

- BAKER, H.B., 1925. Agnathomorphous Aulacopoda. — The Nautilus 38: 86-89.
- BAKER, H.B., 1928. Minute American Zonitidae. — Proceedings of the Academy of Natural Sciences of Philadelphia 80: 1-44, Plates 1-8.
- BAKER, H.B. 1930. The North American Retinellae. — Proceedings of the Academy of Natural Sciences of Philadelphia 82: 193-219.
- BAKER, H.B., 1941. Zonitid snails from Pacific Islands Parts 3 and 4. — Bulletin Bernice P. Bishop Museum 166: 205-370.
- BREURE, A.S.H., HOVESTADT, A., FIELDS, A. & ROBINSON, D.G., 2016. The land Mollusca (Gastropoda) of Saint Kitts and Nevis (Lesser Antilles), with description of a new species. — The Nautilus 130: 27-52.
- CHASE, R. & ROBINSON, D.G., 2001. The uncertain history of land snails on Barbados: implications for conservation. — Malacologia 43: 33-57.
- COOKE, C.M. Jr., 1921. *Nesovitrea* new genus. In: Notes on Hawaiian Zonitidae and Succineidae. — Occasional Papers Bernice P. Bishop Museum 7: 271-272.
- DE FREITAS, J.A., ROJER, A.C., NIJHOF, B.S.J. & DEBROT, A.O., 2012. A landscape ecological vegetation map of Sint Eustatius (Lesser Antilles). IMARES report number C053/12.
- EMBERTON, K.C., 2001. Dentate Gulella of Madagascar (*Pulmonata: Streptaxidae*). — American Malacological Bulletin 16: 71-129.

- FOLMER, O., BLACK, M., HOEH, W., LUTZ, R. & VRIJENHOEK, R., 1994. DNA primers for amplification of mitochondrial cytochrome oxidase subunit I from diverse metazoan invertebrates. — *Molecular Marine Biology and Biotechnology* 3: 294-299.
- HOVESTADT, A., 1980. De landmollusken van Sint Eustatius— Correspondentieblad van de Nederlandse Malacologische Vereniging 195: 1042-1044.
- KERNEY, M.P. & CAMERON, R.A.D., 1979. A field guide to the land snails of Britain and North-west Europe: 1-288. Pparey, London.
- LEEUWEN, S. VAN, BOEKEN, M. & HOVESTADT, A., 2015. De land-slakken van Saba. — *Spirula* 404: 23-30.
- LEEUWEN, S. VAN & HEWITT, S.J., in press. Preliminary Report on the Mollusca of Sint Eustatius. In: B.W. Hoeksema (Ed.). Marine biodiversity survey of St. Eustatius, Dutch Caribbean, 2015. Preliminary results of the Stata Marine Biodiversity Expedition, 2015. Naturalis Biodiversity Center, Leiden.
- PFEIFFER, L., 1867. Neue Heliceen. — *Malakozoologische Blätter* 14: 195-199.
- PILSBRY, H.A., 1889. New and little-known American mollusks. No. 1. — *Proceedings of the Academy of Natural Sciences of Philadelphia* 41: 81-89, pl. III.
- PILSBRY, H.A., 1946. Land Mollusca of North America (north of Mexico). Vol II Part 1: 1-520. Philadelphia.
- RIEDEL, A., 1966. Zonitidae (excl. Daudebardiinae) der Kaukasusländer (Gastropoda). — *Annales Zoologici* 24: 1-303.
- RIEDEL, A., 1980. Genera Zonitarum: 1-197. Backhuys, Rotterdam.
- RUSH, W.H., 1891. List of species collected on the islands St. Thomas, St. Kitts, Barbados, Jamaica and at Pensacola, Florida; with prefactory notes. — *The Nautilus* 5: 65-70.
- STREBEL, H. & PFEFFER, G., 1880. Beitrag zur Kenntniss der Fauna Mexikanischer Land- und Süßwasser-Conchylien. Theil IV: 1-112, 15 plates. Herbst, Hamburg.
- SCHALIE, H. VAN DER, 1948. The land and fresh-water mollusks of Puerto Rico. Miscellaneous Publications, Museum of Zoology, University of Michigan 70: 1-168.
- SCHILEYKO A.A., 2003. Treatise on Recent Terrestrial Pulmonate Molluscs. Part 10: Ariophantidae, Ostracolethidae, Ryssotidae, Milacidae, Dyakiidae, Staffordidae, Gastodontidae, Zonitidae, Daudebardiidae, Parmacellidae. — Ruthenica, Supplement 2, Part 10: 1309-1466.
- VALK, L. VAN DER, 1987. De fossiele en recente malacofauna van Sint Eustatius en het verband met de jongste geologische geschiedenis van het eiland. — Correspondentieblad van de Nederlandse Malacologische Vereniging 236: 280-283.
- WAGENAAR HUMMELINCK, P. 1981. Land and fresh-water localities. Studies on the Fauna of Curaçao and other Caribbean Islands, vol. 63 (192): 1-133, figs 1-27, pls 1-49 excl.
- WESTERMANN, J.H. & KIEL, H., 1961. The geology of Saba and St. Eustatius, with notes on the geology of St. Kitts, Nevis and Montserrat (Lesser Antilles). Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen, Utrecht: i-xiii, 1-175, 33 plates, 6 maps.