

A collection of juvenile holoplanktic Mollusca (Gastropoda, Pterotracheoidea and Pteropoda) from the Miocene of Trinidad, with the introduction of the new genus *Chriskingia*

Arie W. Janssen^{1,3} & Brent Wilson²

¹ Naturalis Biodiversity Center, Leiden, The Netherlands; ariewjanssen@gmail.com

² Petroleum Geoscience Programme, Department of Chemical Engineering, The University of the West Indies, St. Augustine, Trinidad, Trinidad and Tobago, West Indies; Present address: Cedar Lodge, Maenygroes, Ceinewydd, Ceredigion, Wales, UK; brentforam@gmail.com

³ corresponding author

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Holoplanktic gastropods isolated from Miocene rock samples collected for foraminifer research at two localities in central Trinidad consist predominantly of juvenile specimens. Nine samples from the Nollis Tunnel section near Tabaquite, from the Langhian (N8 Zone), yielded 12 species (three Pterotracheoidea, eight Pteropoda, one unidentified). From nine samples of the Brasso gorge section at Brasso Village, from the Serravallian (Zones N11–12), four species (all Pteropoda) were isolated, one of which was not represented in the Nollis Tunnel section. Most species could only be identified to genus level. A new genus in the Atlantidae, *Chriskingia* gen. nov., is introduced. The pterotracheid genus *Firoloidea* Lesueur, 1817 is recorded for the first time from Miocene deposits. The pteropods *Limacina valvatina* (Reuss, 1867) and *Creseis roesti* Janssen, in Cahuzac & Janssen, 2010 represent new species for the American Miocene. The numerical occurrence of the species demonstrates considerable differences that are discussed in the context of the oxygen minimum zone occurring in these sections, as discussed by Wilson & McLean (in press).

KEY WORDS: Pterotracheoidea, Pteropoda, Miocene, Trinidad, systematics, new genus, numerical occurrence, palaeoecology, oxygen minimum zone.

Introduction (BW)

The ~2500 m thick, Miocene Brasso Formation of central Trinidad comprises a series of calcareous, blue-grey clays and silty clays with minor limestones, conglomerates and sands (Renz, 1948). Previous workers have determined the ages of the Brasso Formation and its members using planktic foraminifera. Bolli *et al.* (1994) suggested the entire formation to range between the early to middle Miocene (Burdigalian to Serravallian) *Globigerinatella insueta* and *Globorotalia fohsi robusta* Zones of Bolli (1957). In the more modern, alphanumeric schemes, this range is equivalent to Zones N7 through the very earliest N13 of Blow (1969), and Zones M4A through M10 of Berggren *et al.* (1995) and Wade *et al.* (2011). By including the Los Atajos Conglomerate Member at the top of the Brasso Formation, Wilson *et al.* (2017) extended the Brasso Formation as high as the *Globorotalia mayeri* Zone (N14, M11). Erlich *et al.* (1993) and Wilson *et al.* (2010, 2011) have demonstrated that the Brasso limestone members were typically deposited during the early middle Miocene *Globorotalia fohsi fohsi* Zone (N10, M7). Although these limestone members incorporate some

conglomerates (Erlich *et al.*, 1993) they mostly mark intervals and locations of sediment starvation.

The Brasso Formation was deposited near the eastern edge of the eastward-advancing Caribbean tectonic plate, on an eastward-facing palaeo-shelf and slope (Rohr, 1990). The Brasso palaeoenvironment was sandwiched between a subaerially-exposed proto-Northern Range to the West, and the open ocean of the Cipero Formation to the East. The palaeo-shelf has subsequently been rotated and is now oriented approximately SSW–NNE.

Wilson (2003, 2007) has demonstrated that the Brasso Formation was deposited during two transgressive-regressive (T–R) cycles that were tectonically induced by the advancement of the proto-Northern Range allochthon. The eastward to south-eastward progression of the allochthon twice pressed downwards on the crust locally, inducing the transgressions. The depressed areas were subsequently filled by material eroded from the allochthon, forcing the regressions. The first T–R cycle ended during the *Globorotalia fohsi fohsi* Zone (N10; M7), its termination being marked by limestones such as the Tamana, Guaracara and Concord Members (Wilson, 2012). The second cycle ended during the *Globorotalia mayeri* Zone (N14, M11),

its termination being marked by the Los Atajos Member. Continual upwelling of nutrient-rich, cold water throughout these T-R cycles induced the development of a strong, permanent oxygen minimum zone (OMZ; Wilson, 2004, 2007; Wilson & McLean, in press).

This paper presents the taxonomy of the holoplanktic gastropod assemblages from two sections: the Nollis Tunnel Section near Tabaquite was deposited during the older T-R cycle (Zone N8, M5; Langhian), and the Brasso gorge section at Brasso Village during the younger T-R cycle (Zones N11–N12, M8–M9b; Serravallian). During both cycles, pteropod and ‘heteropod’ (= Pterotracheoidea) remains were especially concentrated in rocks deposited where the OMZ abutted the seafloor.

Material and methods (BW)

Wilson (2007) collected 20 samples (BV1–BV20, oldest to youngest) from the middle Miocene, massive blue-grey clays of the Brasso Formation at the type locality, along the upper Caparo River (Brasso gorge), Brasso Village, where the rocks crop out intermittently in the cut banks of meanders between the bridges at GR 0683382/1151439 and GR 0683814/1151035 (Figure 1). The exposures comprise the planktic foraminiferal Zones N11–N12 of Blow (1969) (= Zones M8–M9b of Wade *et al.*, 2011; Serravallian) and vary from ~1–8 m long. Samples were collected at 1 m stratigraphic intervals within each outcrop. Twenty samples (BV1–BV20) were taken in all, of which nine were used for this study (Figure 2). From a map provided by Kugler (1996) it appears the N11–N12 boundary lies a few metres below sample BV6.

Two hundred grams from each sample were soaked in water until disaggregated, washed over a 63 μm mesh, and air dried. Foraminifera >63 μm indicated that the section was deposited during a regression. The stratigraphic sequence of foraminiferal assemblages reflects changes in palaeodepth and dissolved oxygen concentration and indicates that the fall in sea level brought the seabed into contact with an oxygen minimum zone (OMZ) – a layer of water with a low dissolved oxygen content formed by the oxidation of organic matter raining down from the photic zone (Levin, 2003). Foraminifera in rocks deposited below the OMZ (*Uvigerina quisqueyana* Bermudez, 1949, *Siphonina pulchra* Cushman, 1919) indicate moderately oxygenated water, while those at the OMZ core (*Bolivina subaenariensis* Cushman, 1922, *U. subperegri-na* Cushman & Kleinpell, 1934) indicate pronounced oxygen depletion. Rocks deposited above the OMZ contain middle neritic species (*Elphidium nautiloideum* Galloway & Heminway, 1941, *Pseudononion pizarrensis* Berry, 1928) that may indicate seasonal hypoxia (*cf.* Osterman *et al.*, 2005; Sen Gupta *et al.*, 1996).

The nine samples from the gorge at Brasso Village yielded 252 pteropods (Table 1). All were juveniles and most could be identified only to genus level. Total recovery was dominated by *Creseis spina* (Reuss, 1867), which has been recorded from the middle Miocene of the

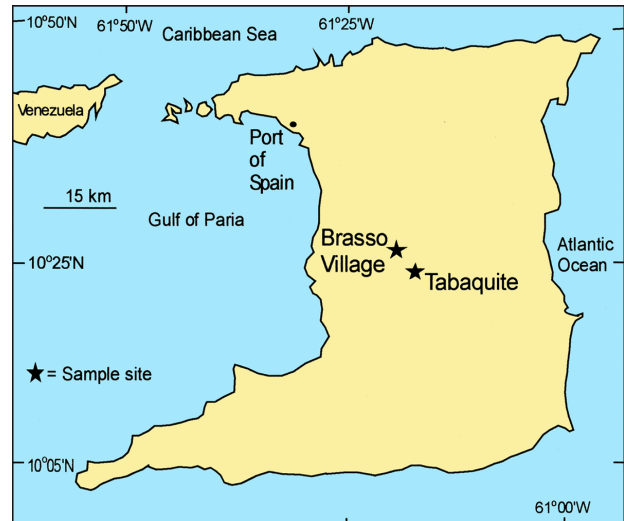


Figure 1. Trinidad, showing the locations of Brasso Village and Nollis Tunnel, Tabaquite. (After Wilson & McLean, in press).

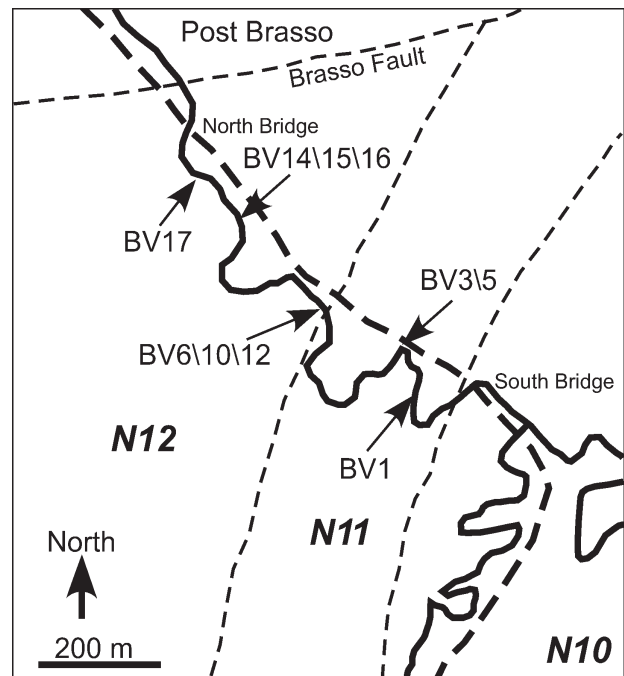


Figure 2. A map of the gorge at Brasso Village, showing the locations of samples used in this study.

European Paratethys Sea (Bohn-Havas and Zorn, 1993; Janssen, 2012a, b), but currently recognised as a very long ranging species (Bartonian to Zanclean; Garvie *et al.*, in prep.). Of the total recovery, 85% came from three samples, BV6 (below OMZ), BV10 (OMZ lower margin) and BV12 (OMZ core). The highest recovery (43% of the total) was from BV10.

A second series of nine samples was taken at Nollis Tunnel, near Tabaquite, central Trinidad (UTM Zone 20 grid reference GR0685141/ 1150386). The samples were taken

at 60 cm intervals and numbered NT1 – NT9 (oldest to youngest). The washed residue from 200 g of rock from each sample was examined for planktic foraminifera, which indicated the early middle Miocene N8 Zone (= Zone M5 of Wade *et al.*, 2011) of Langhian age. The residue was picked clean of molluscs. Most of the specimens yielded were <250 µm maximum dimension. The samples yielded 1448 specimens of planktic gastropods in 11 taxa (Table 2). However, due to the greater number of specimens at Nollis Tunnel compared to Brasso Village, it is not possible to say that the Nollis Tunnel section had greater species richness (*cf.* Hayek & Buzas, 2010). Most specimens from Nollis Tunnel were left in open nomenclature, only *Creseis roesti* Janssen in Cahuzac and Janssen, 2010, *Limacina valvatina* (Reuss, 1867) and *Chriskingia rotundata* (Gabb, 1873) being identified to species level. Total recovery was co-dominated by *Vaginella* sp. and *Heliconoides inflatus*? (d'Orbigny, 1835) (35% each) with subdominant *C. roesti* (16%). No other species formed >4% of the total recovery from this section. All specimens are in pyritic internal mould preservation, now housed in the fossil holoplanktic mollusc collection of Naturalis Biodiversity Center, Leiden, The Netherlands, registered with RGM registration numbers (RGM.777120 to RGM.777210).

Systematics (AWJ)

Phylum Mollusca Linnaeus, 1758
Class Gastropoda Cuvier, 1797
Subclass Caenogastropoda Cox, 1960
Order Littorinimorpha Golikov & Starobogatov, 1975
Superfamily Pterotracheoidea Rafinesque, 1814 (= 'Heteropoda' *auct.*)
Family Atlantidae Rang, 1829
Genus *Atlanta* Lesueur, 1817

Type species – '*Atlanta Peronii*', by subsequent designation of de Blainville (1825, p. 493) = *Atlanta peronii* Lesueur, 1817 (Recent).

Atlanta sp.

Pl. 1, fig. 1

Material examined – Nollis Tunnel, Tabaquite section, 38 specimens from samples 3-7 (Table 2).

Description – Dextral shells of conical shape, with up to c. 3½ rather convex whorls separated by an incised suture and concave spire tangents, the last whorl tumid with a regularly rounded base and a small umbilicus. Aperture lunate, occupying slightly more than half shell height.

Discussion – These tiny shells in internal mould preservation without any information on a possible shell surface ornamentation could easily be taken for larval shells of a benthic gastropod species. However, as the Tabaquite assemblage consists of mainly pelagic species it is as-

sumed that also these specimens belong to a holoplanktic species. They demonstrate a fair resemblance to equally specifically unidentified juvenile shells described from the Miocene (Langhian) of Malta (Janssen, 2012b, pl. 1, fig. 2; pl. 21, fig. 5). Among the present-day atlantids, it are especially the species *Atlanta plana* Richter, 1972 and *A. echinogyra* Richter, 1972 that have a similar shape of the early whorls. Not more than a single species of this genus seems to be represented in the assemblage.

Genus *Chriskingia* gen. nov.

Type species – *Atlanta rotundata* Gabb, 1873, described from the late Miocene of the Dominican Republic.

Diagnosis – Atlantid gastropod in adult state resembling *Protatlanta* Tesch, 1908, but with a strongly different larval shell of spherical shape, almost as wide as high, with a more or less flattened apical side in which only the nucleus sometimes is slightly elevated. Nucleus with a pustulated micro-ornament. Early whorls with spiral ornament of zigzag lines (Figure 3).

Description – Larval whorls attach very high on the preceding whorl and therefore the aperture is just as high as the complete larval shell (Pl. 1, fig. 2). In the type species the protoconch is obliquely positioned with respect to the vertical axis of the adult shell. Therefore, the fourth whorl partly and sometimes even completely covers the third whorl. In a straight apical view, a part of the third protoconch whorl is considerably narrower than the second one or even partly invisible. Nucleus of the protoconch with pustulated micro-ornament, larval whorls with distant spiral lines that in high magnification show a zigzag-shape (Figure 3).

Adult shell planorboid, wider than high, smooth or with vague spiral lines and a peripheral belt on the last whorl indicating the presence of an uncalcified keel in the living state.

Etymology – The new genus is named after Dr. Chris King (1943-2015) in recognition of his important contributions to especially palaeogene (bio-)stratigraphy and his continuous support of the first author's holoplanktic mollusc studies (Janssen, 2016). *Chriskingia* gender feminine.

Discussion – The type species of the new genus has up to now been included in the genus *Protatlanta*, with type species *P. souleyeti* (Smith, 1888) (Recent), in which species, however, the protoconch has a regular naticoid shape with a conical spire (Janssen, 2012a, figs 3, 43C-F) without any ornamentation.

Chriskingia rotundata (Gabb, 1873)

Fig. 3, Pl. 1, fig. 2

v *1873 *Atlanta rotundata* Gabb, p. 201.

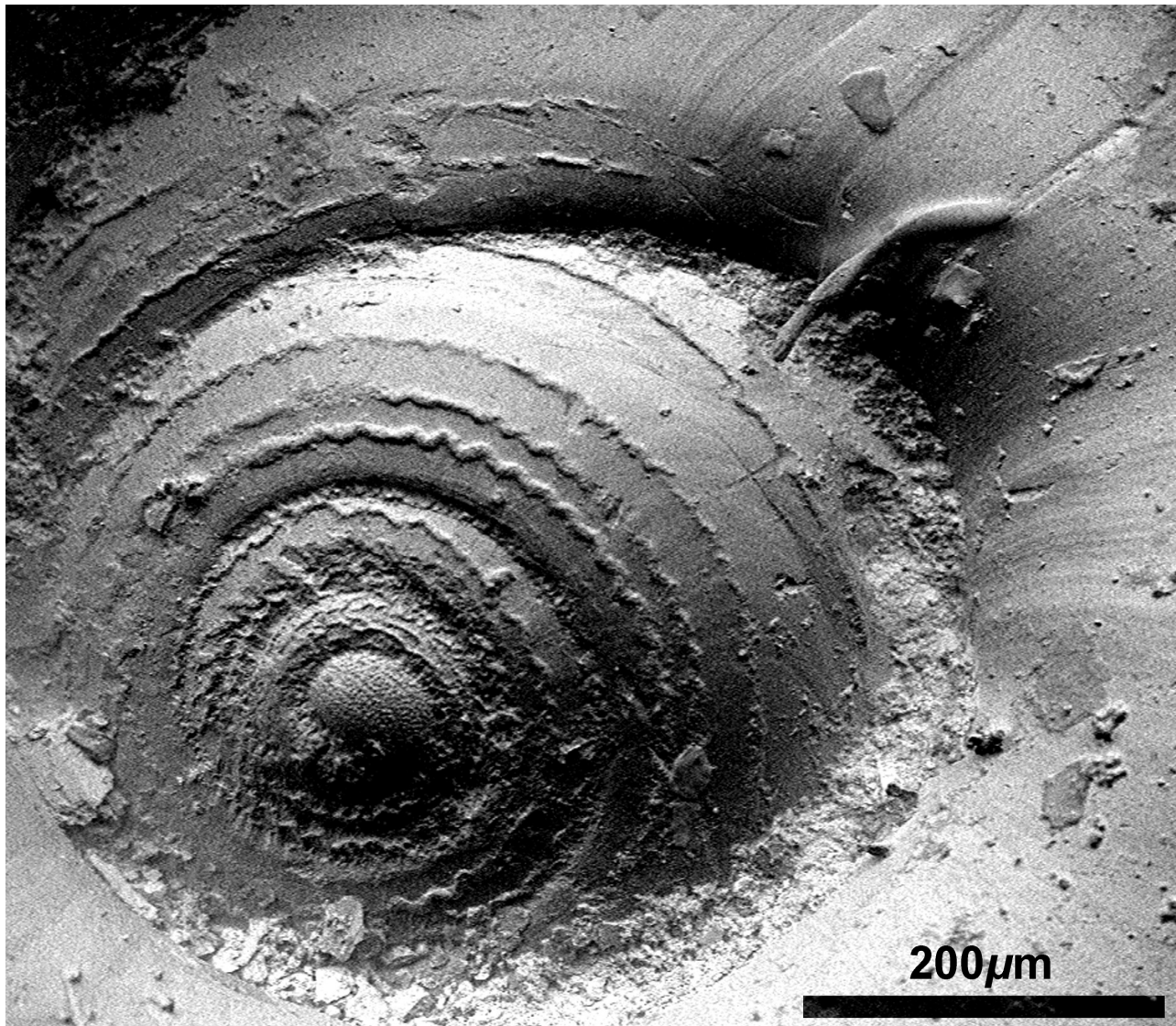


Figure 3. Protoconch of the holotype of *Chriskingia rotundata* (Gabb, 1873), ANSP-IP 2891, showing oblique position, pustulated micro-ornament on nucleus and zigzagged spirals on earliest whorls. SEM image by Paul Callomon.

v. 2012b *Protatlanta rotundata* Gabb, 1873 – Janssen, p. 277, pl. 21, figs 8-10 (with extensive synonymy).

v. in press *Protatlanta rotundata* Gabb. – Wilson & McLean.

Material examined – Two specimens, Nollis Tunnel, Tabaquite samples 3 and 5 (Table 2).

Description – In the few available specimens from Trinidad, larval shell ornament is not preserved, but the shape of the specimens agrees with better-preserved specimens from elsewhere. Well-preserved protoconchs of *Chriskingia rotundata* have an ornament consisting of a finely pustulated nucleus and on subsequent protoconch whorls rather widely spaced spirals with a zigzag structure in high magnification (see Janssen, 2007, pl. 17, figs 1-3; 2012b, pl. 21, figs 8-10, as *Protatlanta rotundata*). This ornamentation can also be recognised in the holotype (Figure 3).

Discussion – The very different protoconch structure of

this species compared to the type species of *Protatlanta* necessitates the introduction of a new genus. In a further fossil species described from the Miocene of Malta, viz. *Protatlanta kbiraensis* Janssen (2012b, p. 275, pl. 1, figs 4-5; pl. 21, figs 11-13), the protoconch has a regular conical shape and is not situated obliquely with respect to the adult shell's axis and for these reasons remains in the genus *Protatlanta*. The single specimen of '*Protatlanta* sp.', also from the Miocene of Malta (Janssen, 2012b, p. 279, pl. 21, fig. 14) resembles *Chriskingia rotundata*, but has a relatively coarse ornament on the last larval whorl and five widely spaced and rather coarsely granulated spirals. Its earliest whorls are missing but the protoconch is also situated obliquely and the earliest preserved protoconch whorl is markedly narrower than the next one. It might be an extreme morph of *C. rotundata*, or another, yet undescribed species.

Adult specimens of these species are very similar in having a planorboid shape, much wider than high and with a

peripheral belt on the last whorl, indicating the presence of an uncalcified keel in living individuals, comparable to *Protatlanta*.

Note – Present-day and quaternary specimens of *Protatlanta* used to be identified as belonging to a single species, *P. souleyeti*, although Issel (1911) had introduced a further taxon, *P. sculpta*, and a variety, *P. sculpta* var. *mediterranea*, giving clear morphological differences. The main distinguishing feature in shell morphology compared to the type species is the presence of a fine spiral ornament on the initial whorls. Later authors, however, considered this intraspecific variability and did not recognise *P. sculpta* as a separate species (Tesch, 1949, p. 13; van der Spoel, 1976, p. 139; Richter & Seapy, 1999, p. 633; Janssen, 2007). Also, specimens from the Pliocene of the Philippines (Janssen, 2007, p. 54, pl. 17, fig. 4; pl. 18, figs 1-2) demonstrate clearly the presence of spiral ornament on the early whorls but were still identified as *P. souleyeti*.

Based on molecular, as well as morphological and biogeographic data, however, *P. sculpta* was revived as a valid separate species (Wall-Palmer *et al.*, 2016). Therefore, most (if not all) of the pliocene specimens from the Philippines, as described in Janssen (2007), belong to *P. sculpta* and not to *P. souleyeti*.

Family Pterotracheidae Rafinesque, 1814
Genus *Fioloida* Lesueur, 1817

Type species – ‘La F. de Desmarest. *F. desmarestiana* [sic] Lesueur’ = *Fioloida desmarestia* Lesueur, 1817, by subsequent designation of de Blainville (1825, p. 492).

***Fioloida* sp.**

Pl. 1, fig. 3

Material examined – 18 specimens, Nollis Tunnel, Tabaguite samples 3, 4, 8 and 9 (Table 2).

Description – Dextral specimens resembling the *Atlanta* sp. specimens in the same samples, but (at comparable size) with one whorl less, a more naticoid shape and a much larger, spherical nucleus.

Discussion – Larval shells of the *Fioloida* type species, the present-day *F. desmarestia* Lesueur, 1817, which is a species without a shell in the adult stage, were recognised rather late and were first described as *Cyclostrema solidum* Di Geronimo, 1974. The true nature of these specimens was first noticed by Grecchi (1984) on quaternary specimens from the Mediterranean. Such larval shells were recorded from Eemian and younger deposits also in the Mediterranean by Janssen (2012a, p. 20).

The Trinidad specimens differ only slightly from the Mediterranean ones by a somewhat wider umbilicus. Shells of Recent specimens usually show a distinct boundary between the nucleus of the embryonic shell and

the younger shell part. In some of the Trinidad specimens such a boundary seems to be indicated on the internal moulds as well. This is the first record of neogene specimens of this genus.

Subclass Heterobranchia Burmeister, 1837
Order Pteropoda Cuvier, 1804
Suborder Euthecosomata Meisenheimer, 1905
Superfamily Limacinoidea Gray, 1847
Family Limacinidae Gray, 1847
Genus *Heliconoides* d’Orbigny, 1835

***Heliconoides inflatus* ? (d’Orbigny, 1835)**

Pl. 1, figs 4-5

? *1835 *A[tlanta]* [sic] *inflata* d’Orbigny, pl. 12, figs 16-19.

? 2012a *Heliconoides inflata* [sic] (d’Orbigny, 1834 [sic]) – Janssen, p. 25, fig. 46A-B (with extensive synonymy of mainly present-day occurrences).

? 2012b *Heliconoides inflata* [sic] (d’Orbigny, 1834 [sic]) – Janssen, p. 288, pl. 2, figs 4-6 (with additional synonymy of fossil occurrences).

In press *Heliconoides inflata* (d’Orb., 1834 [sic]) – Wilson & McLean.

Material examined – 14 specimens, Brasso section, samples 1-15 (Table 1); 509 specimens, Nollis Tunnel, Tabaguite section, samples 3-9 (Table 2).

Description – Limacinid larval shells of *c.* three whorls or less, rapidly increasing in diameter. Apical side flattened with the initial whorl only slightly protruding. Aperture large, occupying almost entire shell height. Base gradually rounded, with a small umbilicus.

Discussion – Immature specimens of two species, *Heliconoides inflatus* and *H. tertiaria* (Tate, 1887) cannot with certainty be identified. These species co-occur in late oligocene to late Miocene rocks in southern Europe, but only mature specimens with preserved apertural structures can be recognised with certainty. *Heliconoides inflatus* was described from present-day specimens and its vertical range includes the complete interval from (late Oligocene?) Miocene to present day. It is one of the most common currently living pteropod species.

Heliconoides tertiaria, on the other hand, was originally described from middle to late Miocene rocks in southern Australia (where it co-occurs with *H. inflatus* (Janssen 1990, p. 14, fig. 3) and a closely related, if not identical, species, *H. ferax* (Laws, 1944) is known from the Langhian of New Zealand (Beu & Maxwell, 1990, pp. 169, 391, 424, 506, pl. 57, figs d, e). In Europe *H. tertiaria* was recorded from the Mediterranean and Aquitaine basins. Among the thousands of specimens (Janssen, 2012b, p. 293, fig. 41) collected from Maltese limestones (Langhian) only few could be recognised as belonging to one of these two species and judging from these adult speci-

mens *H. inflatus* is by far the most common.

From the Neogene of the America's *Heliconoides inflatus* was recorded only from the lower pliocene Agueguexquite Formation of Santa Rosa, Vera Cruz, Mexico (Collins, 1934, p. 179, pl. 7, figs 3-5, as *Limacina inflata*; Perrilliat, 1974, p. 34, as *Spiratella inflata*) and from the equally lower pliocene Bowden shell beds of Jamaica (Janssen, 1998, p. 99, pl. 1, fig. 12). Other specimens recorded with the name *Limacina inflata* by Collins (1934, pl. 7, figs 6-8) and by Pilsbry (1922, p. 308, fig. 1) do not belong to that species, but to *Striolimacina imitans* (Gabb, 1873), originally described from the late Miocene (?) of Santo Domingo (see discussion and neoleotype designation in Janssen, 1999, pp. 13-14). A single specimen, however, of *H. inflatus* was recognised with certainty from the upper Miocene Cercado Formation, *Globorotalia humerosa* Zone, of the Dominican Republic (Janssen, 1999, pl. 2, fig. 10a-b). *Heliconoides tertiaria* has never been recorded from the New World.

Here the presence of numerous juveniles is recorded from the Miocene of Trinidad, being especially common in the Tabaquite section. Unfortunately, not one of the specimens demonstrates its adult apertural features and therefore the material is recorded here with a query as *H. inflatus*?, as that species is the most common and most widely spread, and furthermore as the specimens from the Brasso section are dated as Serravallian, from which age the species *H. tertiaria* is not known.

Genus *Limacina* Bosc, 1817

Type species – *Clio helicina* Phipps, 1774 by monotypy = *Limacina helicina* (Phipps, 1774) (present-day).

***Limacina valvatina* (Reuss, 1867)**

Pl. 1, fig. 6

- v *1867 *Spirialis valvatina* Reuss, pp. 32, 146, pl. 5, fig. 11a-b.
- v. 2012b *Limacina valvatina* (Reuss, 1867) – Janssen, p. 301, pl. 4, figs 5-8, pl. 22, figs 12-16, pl. 23, fig. 1 (with additional synonymy).

Material examined – 14 specimens, Nollis Tunnel, Tabaquite section, samples 4-7 and 9 (Table 2).

Description – Sinistral shell with a regularly conical spire, approximately as wide as high, straight tangents along the whorls, a semicircular aperture, an even in adult specimens not reinforced apertural margin and a rounded base with a narrow umbilicus.

Discussion – *Limacina valvatina* is especially common in the Central Paratethys and the North Sea Basin, ranging from late Oligocene (Chattian) to at least the end of the Serravallian. The species reaches its largest dimensions in middle Miocene deposits of Poland (Janssen & Zorn, 1993). From southern Europe (Mediterranean and Aquitaine basins) only smaller specimens are known in low numbers, probably indicating that this species preferred somewhat cooler environments. This is the first American record of *L. valvatina*. A related, possibly identical form is described by Janssen (2016a) from the Cantaure Formation (late Burdigalian to Langhian) of Venezuela. Equally doubtful specimens will be described from the oligocene Lincoln Creek Formation of Washington state, U.S.A. (Garvie *et al.*, in prep.).

Among specimens from the early-middle Miocene of S. Australia, recorded as *Limacina* aff. *gramensis* (Rasmussen, 1968) some specimens have a height/width-ratio approaching *L. valvatina*, but the available material is insufficient for a sound identification (Janssen, 1990).

Superfamily Cavolinioidea Gray, 1850 (1815) = Hyalinea Rafinesque, 1815

Family Creseidae Rampal, 1973

Genus *Creseis* Rang, 1828

Type species – '*Creseis acicula*, Rang' by subsequent designation of Pelseneer (1888, p. 45) (present-day).

***Creseis roesti* Janssen, in Cahuzac & Janssen, 2010**

Pl. 1, fig. 7

- v *2010 *Creseis roesti* Janssen, in Cahuzac & Janssen, p. 57,

Plate 1

1. *Atlanta* sp., sample NT-4, RGM.777121.a; apertural view.
2. *Chriskingia rotundata* (Gabb, 1873), sample NT-5, RGM.777126; apertural view.
3. *Firoloida* sp., sample NT-2; apertural view. (specimen lost).
4. *Heliconoides inflatus* ? (d'Orbigny, 1835), sample NT-2, RGM.777133.a; apical view.
5. *Heliconoides inflatus* ? (d'Orbigny, 1835), sample BV-10, RGM.777196.a-b; apertural views.
6. *Limacina valvatina* (Reuss, 1867), sample NT-3, RGM.777140; apertural view.
7. *Creseis roesti* Janssen, 2010, sample NT-7; RGM.777152.a.
8. *Creseis spina* (Reus, 1867), sample BV-10, RGM.777197.a; frontal view of slightly compressed specimen.
9. *Clio* sp., sample NT-7, RGM.777152.a; frontal view.
- 10-13. *Vaginella* sp., sample NT-7, RGM.777176.a-d, 11-12: frontal views, 13: lateral view.

Bar represents 100 µm for all specimens.

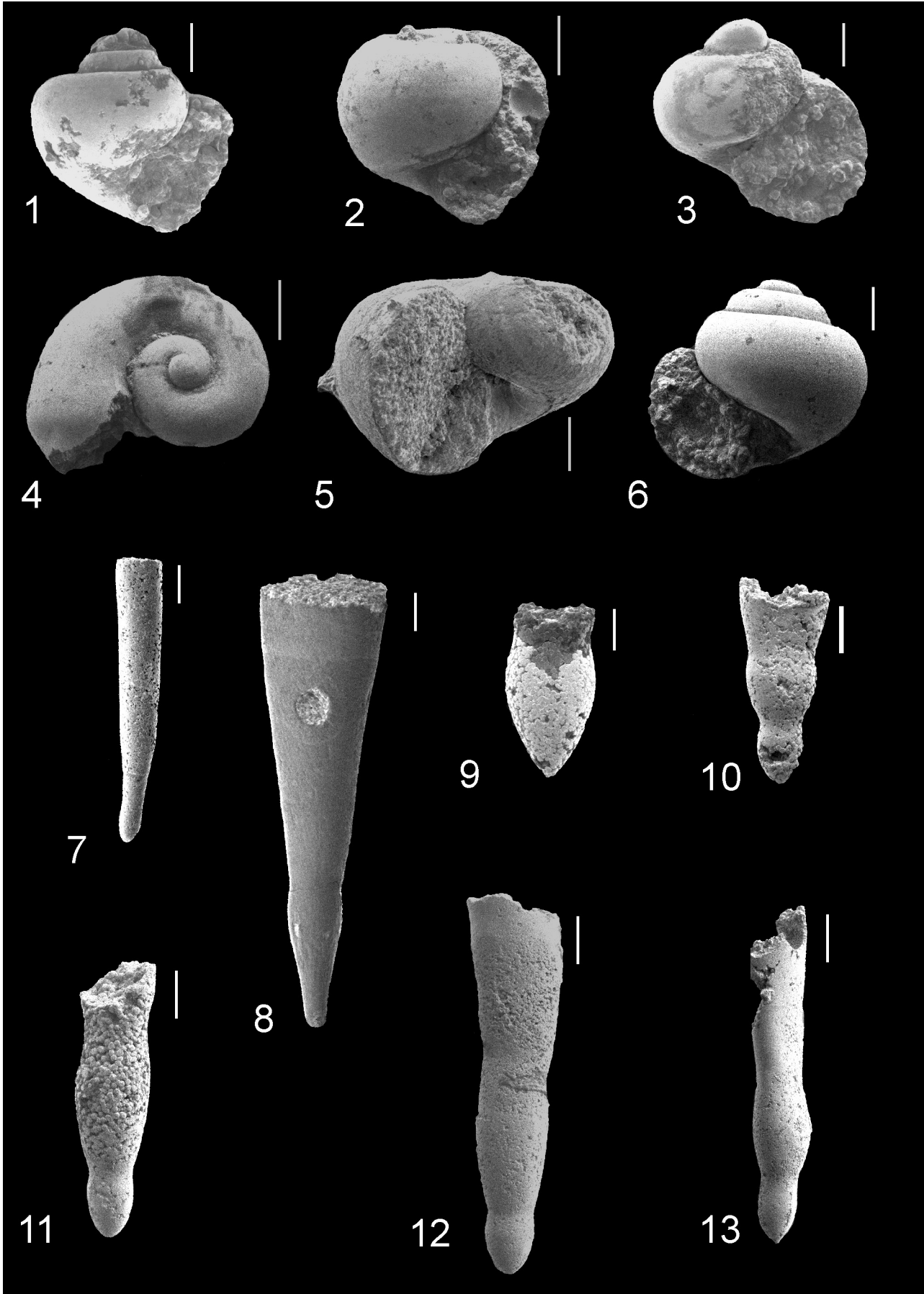


Plate 1.

- pl. 5, figs 8-10, pl. 14, figs 4, 5.
 v. 2012 *Creseis* cf. *roesti* Janssen, in Cahuzac & Janssen, 2010 – Janssen p. 311, text-fig. 42a; pl. 4, fig. 15, pl. 23, fig. 3.

Material examined – 238 specimens, Nollis Tunnel, Tabaquite section, samples 1-9 (Table 2).

Description – Elongated conical shell with a rounded tip. Transverse section circular over the entire shell height, initial part cylindrical, then slowly and regularly increasing in diameter, with protoconch-2 hardly or not indicated.

Discussion – This species was introduced from Aquitanian to Burdigalian sediments in the Aquitaine Basin (France), but was also found to be present in the Langhian of the Maltese archipelago. So far, *C. roesti* has not been reported from other localities. It co-occurs, also in the Trinidad material, with *C. spina* (see below), from which it can easily be separated by its smaller apical angle and the lack of a more swollen protoconch-2.

Creseis spina (Reuss, 1867)

Pl. 1, fig. 8

- v *1867 *Cleodora (Creseis) spina* Reuss, p. 145, pl. 6, fig. 7.
 . 1886 *Styliola hastata* Meyer, p. 78, pl. 3, fig. 11.
 v. 2012b *Creseis spina* (Reuss, 1867) – Janssen, p. 312, Text-fig. 42b; pl. 4, fig. 16, pl. 23, figs 4-9 (with additional synonymy).
 v. 2012d *Creseis spina* (Reuss, 1867) – Janssen, p. 157, pl. 3, figs 11-15; pl. 8, figs 2-6 (with further synonymy).

Material examined – 101 specimens, Brasso section, samples 1, 3, 6-16 (Table 1); 53 specimens, Nollis Tunnel, Tabaquite section, samples 3-9 (Table 2).

Description – *Creseis spina* is easily distinguished from the foregoing species by a more or less clearly separated swelling of protoconch-2 and a slightly wider apical angle of the shell part beyond the protoconch. The illustrated specimen is somewhat flattened by rock compression, so its apical angle seems to be a bit wider than it is in non-deformed specimens.

Discussion – This species was originally described from the Langhian (salt deposits at Wieliczka, Poland), but it is

a long-ranging species, now known from the Bartonian/Rupelian of the U.S.A. (Hodgkinson *et al.*, 1992, as *C. hastata*), the Rupelian to Serravallian of the Aquitaine Basin (Janssen in Cahuzac & Janssen, 2010), Burdigalian to Langhian of the Mediterranean (Janssen, 2012b), Langhian of the Central Paratethis (Zorn, 1991; Janssen & Zorn, 1993, Bohn-Havas & Zorn, 1994) and early Pliocene (Zanclean) of southern France (Janssen, 2012d).

Family Cliidae Jeffreys, 1869

Genus *Clio* Linné, 1767

Type species – *Clio pyramidata* Linné, 1767, by subsequent designation of Gray (1847, p. 203) (present-day).

Clio sp.

Pl. 1, fig. 9

Material examined – Three specimens, Nollis Tunnel, Tabaquite section, samples, 3, 7 and 9 (Table 2).

Description – The few specimens from the Tabaquite section are isolated, droplet-shaped protoconchs resembling those of *Clio pyramidata* Linné, 1767 and related species. Their height is c. 0.75 mm, width 0.20 mm, and the apex is pointed. The constriction between proto- and teleoconch is just preserved and measures c. 0.18 mm.

Discussion – From the Miocene of Trinidad, two species of the genus *Clio* were described by Rutsch (1934). The protoconch of *Clio lavayssei* Rutsch, 1934 is still unknown, but as this species is considered to belong to the subgenus *Balantium* (see Janssen & Zorn, 2001) it is expected to have a spherical larval shell shape, as in the type species of that subgenus, *Clio (Balantium) recurva* (Children, 1823).

The second species mentioned from Trinidad by Rutsch is *Clio pulcherrima* (Mayer, 1868), a species originally described from the Miocene (Langhian) pteropod marl of Serravalle di Scrivia and Acqui in northern Italy, but known from various other localities in the Mediterranean (see Janssen, 2012b, p. 357 for a long list of references, and distribution). A second Caribbean record of this species is from Carriacou (Jung, 1971, p. 218, pl. 20, figs 8-10). The protoconch of this species has been illustrated just once, by Di Geronimo 1974, p. 189, pl. 1, fig. 2) from the Langhian of Vetto d'Enza (Reggio Calabria, Italy).

Plate 2

- 1a-b. *Diacrolinia* sp. 2, sample BV-6, RGM.777194; a: dorsal view, b: oblique right lateral view.
 2-3. *Diacrolinia* sp. 1, sample NT-7, RGM.777169.a-b; 2: frontal view, 3: lateral view.
 4. *Clione* ? sp., sample TAB-3, RGM.777179.a, frontal view.
 5-6. Veligers of benthic gastropod ?, sample TAB-7, RGM.777186.a-b; 5: apertural view, 6: dorsal view.

Bar represents 100 μ m for all specimens.

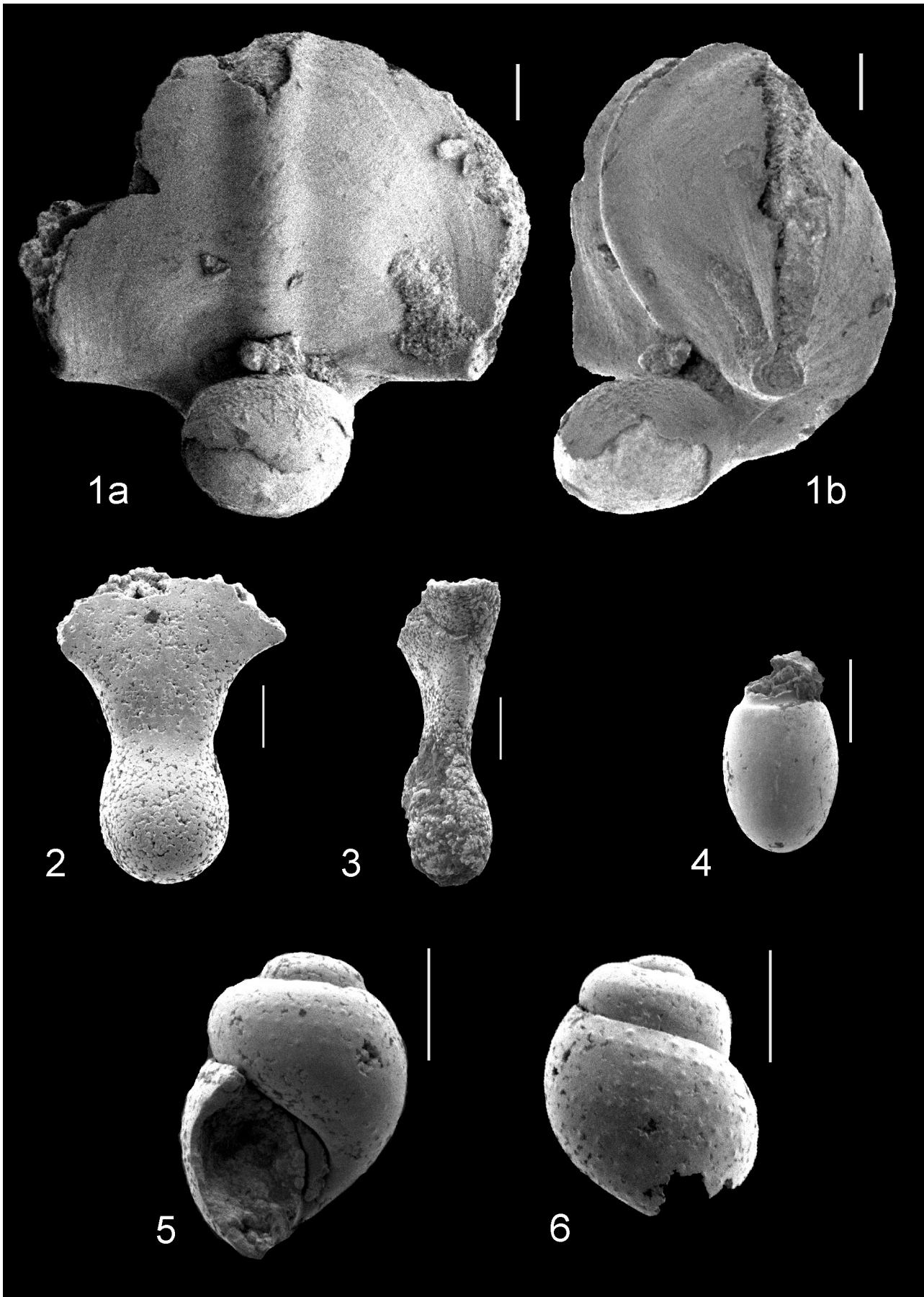


Plate 2.

His illustration resembles the present specimens from the Tabaquite section reasonably well, although the constriction between proto- and teleoconch is narrower. Still, these Trinidadian specimens may belong to *C. pulcherrima* indeed. However, Janssen (in Landau *et al.*, 2016) illustrated three Cliidae from the Cantaure Formation in Venezuela that also resemble the Trinidad specimens to a certain degree. These three specimens remain unidentified to species but do not seem to belong to *C. pulcherrima*. Several further species of the genus *Clio* are known from the Mediterranean Langhian and usually their protoconch morphology is still unknown.

Genus *Diacrolinia* Janssen, 1995

Type species – *Hyalaea aurita* Bellardi, 1873, by original designation = *Diacrolinia aurita* (Bellardi, 1873) (Miocene).

***Diacrolinia* sp. 1**

Pl. 2, figs 2-3

Material examined – One? specimen, Brasso Village section, sample BV12 (Table 1); 45 specimens, Nollis Tunnel, Tabaquite section, samples 3-7 (Table 2).

Description – Most available specimens consist of the protoconch only, with some having just the transition to teleoconch present. Their initial shell part is spherical with a perfectly rounded tip and a width of *c.* 0.20 mm, followed by a clear constriction (width *c.* 0.15 mm) after which the shell widens considerably, representing the transitional part to the teleoconch of which just a few hardly recognisable fragments were found. In lateral view (pl. 2, fig. 3) it is visible that these very juvenile specimens are slightly compressed dorso-ventrally and that there is only a very small angle between the axes of the proto- and teleoconchs.

Discussion – Rutsch (1934, pp. 311-313, pl. 8, figs 7-8) recorded a common cavoliniid species from Trinidad as a new subspecies with the name *Cavolinia audeninoi trinitatis* Rutsch, 1934. *Cavolinia audeninoi* Vinassa de Regny, 1899, was based on specimens from the Langhian at Monte dei Cappucini, in the northern Italian Turin Hills, described by Audenino (1899, p. 101, pl. 2, fig. 2) as *Cavolinia* cfr. *bisulcata* (Kittl, 1886). Specimens from Miocene rocks of Monte della Guardia, near Bologna (Italy) were described by Vinassa de Regny as a variety *bononiensis* Vinassa de Regny, 1899.

Kittl (1886, p. 65, pl. 2, figs 29-32) described *Hyalaea bisulcata* from 'early Badenian' (= Langhian) sediments at Polnisch-Ostrau, nowadays Slezská Ostrava (Czech Republic). As is clear from new illustrations of the type material (Janssen, 1984, pl. 5, figs 4-5) Kittl's illustrations of this species were strongly idealised, what has led to various erroneous interpretations by later authors.

It was found out only much later that the taxon *Hyalaea*

aurita Bellardi, 1873, from Rio de Batteria in the Turin Hills of northern Italy (Langhian) represents the same species and that its larval shell morphology differs basically from that of *Cavolinia*. This has led to a long list of synonyms (Janssen, 2012b, p. 379) and the introduction of the genus *Diacrolinia* in Janssen (1995, p. 110). The genus *Diacrolinia* has a very wide distribution and is known from many localities in the Mediterranean area, the central Paratethys, the Aquitaine and North Sea basins, the Caribbean, New Zealand and Japan.

Several further *Diacrolinia* species are recognised or described as new in the meantime from the Mediterranean and North Sea and Aquitaine basins. *Cavolinia regulae* Jung (1971, p. 221, pl. 20, figs 12-13), from the Miocene of Carriacou, apparently also belongs to the genus *Diacrolinia*, but represents a species different from *C. aurita*, by its completely different ornamentation of the dorsal shell part.

The larval shell of *Diacrolinia aurita*, as first described in Janssen (1995, p. 114, pl. 9, figs 8-9) agrees completely with the juvenile specimens here reported from Trinidad and considering Rutsch's observations it might very well be that they do indeed belong to *D. aurita*. Because of their exclusively very juvenile state, I prefer to record them in open nomenclature for the time being.

***Diacrolinia* sp. 2**

Pl. 2, fig. 1

Material examined – One specimen, Brasso Village section, sample BV6 (Table 1).

Description – A single specimen (Pl. 2, fig. 1a-b) from the Brasso Village section, sample BV6, mostly preserving its original shell, differs strongly from *Diacrolinia* sp. 1, not only by a larger and more thickened protoconch, or by preserving a much larger part of its teleoconch, but especially in that its protoconch axis deviates in dorsal direction from the axis of the teleoconch, at an angle of almost 90°. The teleoconch of this presumably not yet fully-grown specimen consists of, for the greater part, separated dorsal and ventral shell parts, both rather convex, and on the dorsal one with a strong longitudinal riblet in the centre. The widening of the post-embryonic shell part is much stronger than it seems to be in the other protoconchs described above, the lower margins of the teleoconch on both sides of the larval shell being in line.

Discussion – The central riblet on the dorsal side of this juvenile shell is known from various other *Diacrolinia* taxa (see Cahuzac & Janssen, 2010, pls 22-24) and seems to be rather characteristic for the genus. Adult or almost adult specimens preserving their larval shell are very rare, but in none of these, the protoconch deviates so strongly from the teleoconch's axis as in the present specimen. It might very well be that it represents an as yet undescribed species. Further, more complete specimens would be needed for a final decision.

Genus *Vaginella* Daudin, 1800

Type species – *Vaginella depressa* Daudin, 1800 by monotypy (Miocene, Burdigalian, SW France).

Note – The oldest species of this genus, *Vaginella gaasensis* Janssen, in Cahuzac & Janssen, 2010 (of which just a single specimen is known), was described from the early Oligocene (Rupelian) of the Aquitaine Basin in France. More species are recorded from the late Oligocene, but especially during the Miocene the number of species increases rapidly, with species described not only from Europe, but also from Australia, New Zealand, Japan, the United States and the Caribbean area. The type species, *V. depressa*, has a very wide distribution, and is a very common species in the Aquitanian/early Burdigalian of the Aquitaine Basin, France, where it occurs abundantly in relatively shallow water deposits. Its successor species, *V. austriaca* Kittl, 1886, is known only from the European late Burdigalian, Langhian and earliest Serravallian, where it locally occurs by the thousands, as for example in the Langhian (Upper Coralline Limestone Member) of Malta.

From the Caribbean Miocene various vaginellids were described. Gabb (1873) introduced *Balantium undulatum*, later included in the genus *Vaginella* by several authors, but nowadays the type species of the genus *Edithinella* Janssen 1995. *Vaginella bicostata* (Gabb, 1881), from the Miocene of Costa Rica, is currently considered to be a probable synonym of *V. lapugyensis* Kittl, 1886.

Dall (1892) described *V. chipolana* from the early Miocene Chipola Formation of Florida. *Vaginella* cf. *lapugyensis* Kittl, 1886 was recorded by Rutsch (1934) from Trinidad. Collins (1934) introduced *V. floridana*, again from the Chipola Formation of Florida, and *V. venezuelana* from the late Miocene La Rosa Formation of Bolivar, Venezuela. Another vaginellid described by the same author is *V. caribbeana* Collins, 1934, which currently is included in the genus *Edithinella*. *Vaginella grenadinarum* Jung, 1971, *V. cf. depressa* Daudin, 1800, *V. aff. undulata* (Gabb, 1873) and *Vaginella* sp. A were described from the Miocene of Carriacou by Jung (1971). Finally, from the Miocene Cantaure Formation in Venezuela, Janssen (2016a) recorded *V. depressa*, *V. lapugyensis* and *V. grenadinarum*. He hesitatingly stated that it cannot be excluded that the species *V. chipolana* and *V. grenadinarum* and even *V. venezuelana* in fact all represent the same taxon for which the name *V. chipolana* would be valid.

***Vaginella* sp.**

Pl. 1, figs 10-13

Material examined – 71 specimens, Brasso Village section, samples 3, 6, 10, 12 and 14 (Table 1); 512 specimens Nollis Tunnel, Tabaquite section, samples 1, 3-9 (Table 2).

Description – Although *Vaginella*'s are the most common pteropods in the material studied here they are exclusively represented by protoconchs. These are easily recognisable as belonging to this genus by their being

subdivided into a protoconch-1, with a slightly pointed apex, and a more swollen protoconch-2, below and above separated by constrictions. Such specimens all demonstrate a dorso-ventral flattening. Of the teleoconch just the most initial part is preserved, and in just a few specimens only.

Discussion – Vaginellid protoconchs were extensively described and illustrated in Cahuzac & Janssen (2012) from the Aquitanian Basin and by Janssen (2012b) from Malta. Although certain differences exist, these are insufficient and unreliable to identify species. Also among the Trinidad specimens there are relatively slender protoconchs (Pl. 1, figs 12-13) and more thickset ones (Pl. 1, figs 10-11). I cannot connect these with a species name. For further discussion on Caribbean vaginellids see Janssen (2016a).

Order Gymnosomata de Blainville, 1824

Note – Thecosomata and Gymnosomata are both pelagic groups of gastropods that, although sharing certain characteristics, for a long time, because of existing anatomical differences, were considered not to be closely related phylogenetically (e.g., von Salvini-Plawen & Steiner, 1995). However, Klussmann-Kolb & Dinapoli (2006) advocated, on the basis of molecular work, a closer relationship than was thought and proposed to re-install the name Pteropoda as a separate taxon in Opisthobranchiata.

One of the more striking differences between Thecosomata and Gymnosomata is that adult individuals with a calcified, aragonitic shell are only known in Thecosomata, whereas Gymnosomata only in the larval stage have a minute aragonitic shell that is shed during metamorphosis.

Gymnosome larval shells were already described as such by Krohn (1860). Lalli & Conover (1973) succeeded in keeping specimens of three gymnosome species alive and to reproduce under laboratory conditions and describe their larval shells. Currently, these are still the only present-day gymnosome larval shells identified to species. Similar specimens from bottom samples had erroneously been described as protoconchs of thecosomes, especially of *Clio polita* (Pelseneer, 1888), but Grecchi (1987) recognised their true nature. Janssen (2012b, pp. 451-455) summarised the various Quaternary-present-day types of gymnosome larval shells from the literature and introduced five new species from the Miocene of Malta. All Gymnosomata larvae, as far as known, have a simple, straight bilaterally symmetric and not a spiralised shell. Specimens illustrated by Wall-Palmer *et al.* (2015, figs 1-3) from the late Quaternary of the Caribbean do not belong to the Gymnosomata, but rather resemble the early whorl of the Cymbulioid species *Gleba cordata* Niebuhr, 1776.

As isolated larval gymnosome shells, although all supposed to belong to the Clionidae, could not be identified to genus level, Janssen (2012b) applied a method frequently used by ichthyologists in otolith systematics, to indicate the various types as 'genus Clionidarum' (*i.e.* 'a genus of

the Clionidae'). This kind of indicating was criticised by various malacologists who considered this a violation of the ICZN regulations. Janssen (2012c) therefore changed the method by using the indication '*Clione* ?' instead. Also for otolith systematics a new nomenclatural indication was proposed in the meantime by Nolf (2013).

Superfamily Clionoidea Rafinesque, 1815

Family Clionidae Rafinesque, 1815

Genus *Clione* ? Pallas, 1774

Type species – *Clione borealis* Pallas, 1774, p. 28, by monotypy = *Clione limacina* (Phipps, 1774, p. 195).

Clione ? sp.

Pl. 2, fig. 4

Material examined – Seven specimens, Nollis Tunnel, Tabaquite section, samples 3, 7 and 8 (Table 2).

Description – Internal pyritic moulds of elliptical shape and a perfectly rounded tip; height of protoconch-1 *c.* 175 μm , width 135 μm , its greatest diameter at mid height, and with a clear constriction (90 μm) at the apertural side. Only the most basal part of protoconch-2 is preserved.

Discussion – The specimens from Tabaquite are quite similar but do not agree with any of the various present-day or fossil types of gymnosomes described and discussed in Janssen (2012b). They resemble *Clione* ? *phosphoritus* Janssen, 2012 but have a more rounded tip and nothing is known about the shape of their protoconch-2.

Gastropoda *incertae sedis*

Veliger larvae of benthic species ?

Pl. 2, figs 5-6

- v. 2007 Veliger larva of unknown gastropod species? – Janssen, p. 165, pl. 24, figs 5-7.
- v. 2012a Veliger larvae of benthic species? – Janssen, p. 72, fig. 57A-F.
- v. 2012b Veliger larva of benthic species – Janssen, p. 515, fig. 69.

Material examined – 113 specimens, Nollis Tunnel, Tabaquite samples 2-7 (Table 2).

Description – Sinistral shells in internal mould preservation of *c.* two convex whorls, total height *c.* 250 μm , width 190 μm , aperture higher than wide, but apertural margin features are not preserved. On the last whorl insignificant, spirally arranged pustules demonstrate that perforations were present in the original shells.

Discussion – SEM images of rather fresh specimens in shell preservation were given by Janssen (2007; 2012a). In

spite of being quite common and described in the meantime from Quaternary-present-day assemblages in the Red Sea, and the Mediterranean, as well as from the Miocene (Langhian) of Malta, its identity remains completely unknown, no doubt because of its small size it will not be noted in standard mollusc research. However, molecular studies are in progress (J.H. de Boer, pers. comm.) on fresh material from, the Atlantic Ocean and it may be expected that this will reveal its systematic position shortly. Also in the Miocene of Trinidad, this appears to be a quite common species. Its apertural structures, as described earlier, seem to indicate that they belong to the Caenogastropoda (C. Hickman, pers. comm.) and might be pelagic protoconchs of some benthic gastropod (see discussion in Janssen, 2012a, p. 72).

Discussion and conclusions (BW, AWJ)

The distribution of planktic gastropods in the various samples is summarised in Tables 1 and 2. The known vertical ranges of the species recorded here do not contradict the ages indicated by foraminifera: Langhian for Norris Tunnel, Tabaquite, and Serravallian for Brasso Village, with the restriction that the genus *Vaginella* is not known to occur later than early Serravallian.

Sample BV	16	15	14	12	10	6	5	3	1
N-zone	11	11	11	12	12	12	12	12	12
<i>Heliconoides inflatus</i> ?	-	2	-	11	33	27	-	2	4
<i>Creseis spina</i>	3	3	17	27	41	4	-	2	4
<i>Diacrolinia</i> sp. 2	-	-	-	1?	-	1	-	-	-
<i>Vaginella</i> sp.	-	-	1	17	35	17	-	1	-

Table 1. Distribution of holoplanktic molluscs in the Brasso Village section.

Sample NT	9	8	7	6	5	4	3	2	1
<i>Atlanta</i> sp.	1	-	18	6	3	5	5	-	-
<i>Chriskingia rotundata</i>	-	-	1	-	1	-	-	-	-
<i>Firoloida</i> sp.	-	-	10	4	-	-	-	3	1
<i>Heliconoides inflatus</i> ?	-	-	218	65	53	60	70	21	22
<i>Limacina valvatina</i>	-	-	7	2	-	1	1	-	1
<i>Creseis roesti</i>	1	-	147	44	17	11	6	7	5
<i>Creseis spina</i>	-	-	12	5	6	5	12	6	7
<i>Clio</i> sp.	-	-	1	-	-	-	1	-	1
<i>Diacrolinia</i> sp. 1	-	-	30	3	6	4	8	1	-
<i>Vaginella</i> sp.	2	-	277	75	46	51	46	9	6
<i>Clione</i> ? sp.	-	-	1	-	-	-	4	2	-
? larva of benth. Gastr.	-	-	61	15	6	13	14	4	-

Table 2. Distribution of holoplanktic molluscs in the Nollis Tunnel, Tabaquite, section (all samples from the N8 Zone).

Wilson & McLean (in press) examined the distributions of abundant species of planktic gastropods examined in samples yielding >40 specimens (BV6, BV10 and BV12). Species were not evenly distributed among these three samples. Simultaneous confidence intervals (Lamboy & Lesnikowska, 1988) show that, while *Vaginella* sp. did not differ in proportional abundance between these samples, *Heliconoides inflatus* ? decreased significantly from 55% of recovery from BV6 to 20% of recovery from BV12 (Figure 4). *Creseis spina* increased significantly in abundance from BV6 (8%) to BV12 (49%), but was proportionally at its most abundant in rocks deposited in waters overlying the OMZ core (BV14, 94%). As concluded by Wilson & McLean (in press), this might imply that the pteropods in the water column were concentrated in and near the OMZ, but were stratified by depth, *C. spina* living above (especially towards the top of the OMZ) and *Heliconoides* sp. below (towards its base). This would limit the flux of *Heliconoides inflatus* to shallower water samples. *Vaginella* sp. was, however, evenly distributed throughout samples BV6–BV12. Modern pteropods show a similar depth stratification; in the Southern Ocean, waters to ~250 m contain *Limacina* sp., while *Clio* sp. live between 200 – 800 m (Lalli & Gilmer, 1989).

Alternatively, however, the abundance of the juvenile planktic gastropods might not reflect the palaeoenvironment in which they lived. Instead, they may have lived mainly above the OMZ, which would not, therefore, have been the direct cause of their abundance in bottom samples. The preservation of the planktic gastropods might instead reflect the rarity of scavengers able to live in the relatively harsh environment of the OMZ. That *Heliconoides inflatus* was replaced stratigraphically by *C. spina* in rocks deposited within the OMZ, might reflect a long-term change in the composition of the fauna living above the OMZ.

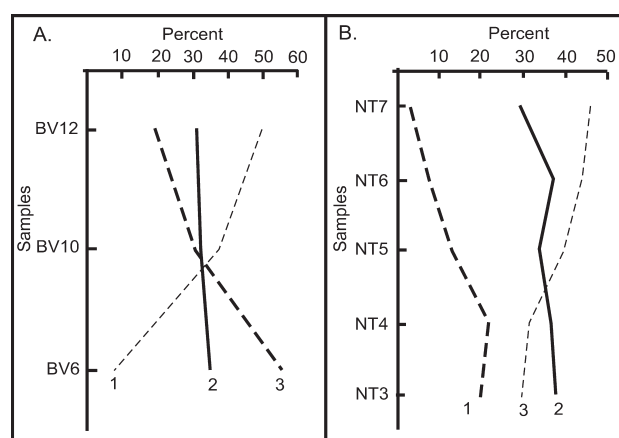


Figure 4. Graphs for species turnover in samples with >40 specimens. **A:** Brasso Village, 1 = *Creseis spina*, 2 = *Vaginella* sp., 3 = *Heliconoides inflatus* ? **B:** Nollis Tunnel, near Tabaquite, 1 = *Creseis roesti*, 2 = *Vaginella* sp., 3 = *Heliconoides inflata* ? (from Wilson & McLean, in press).

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