Brief report   Acta Palaeontologica Polonica 52 (3): 639–642, 2007

Status of the enigmatic fossil vesicomyid bivalve *Pleurophopsis*

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The status of the vesicomyid genus *Pleurophopsis* Van Winkle, 1919, which occurs in chemosynthetic environments, is evaluated based on a redescription of the type material and observations on subsequently collected material. It is concluded that the name *Pleurophopsis* should not be used because the presently known material of its type species, *P. unioides* of middle Miocene age, does not show critical hinge details like nymph, subumbonal pit, and cardinal tooth 3a of the right valve. From the presently known characters, it can be concluded that *Adulomya*? *unioides* is very similar to the type species of *Adulomya* and *Ectenagena*, and it is shown that *Ectenagena* is a synonym of *Adulomya*. However, should better preserved material of *P. unioides* become available and confirm its close relation to *Adulomya* and *Ectenagena*, *Pleurophopsis* would have priority as it is the oldest of the three names.

Introduction

When Boss and Turner (1980) described *Calyptogena magnifica* from hydrothermal vents at the Galapagos Rift, they considered the enigmatic fossil genus *Pleurophopsis* Van Winkle, 1919 as synonym of *Calyptogena* Dall, 1891. Since then, vesicomyids have been described from various chemosynthetic habitats, including many hydrothermal vents in the Pacific and Indian Ocean (Van Dover et al. 2001; Desbruyères et al. 2006), hydrocarbon seeps on continental slopes of virtually all ocean basins (Levin 2005), whale carcasses (Smith and Baco 2003), and from ancient hydrocarbon seeps as old as the Early Cretaceous (Kanie et al. 1993). There is currently little consensus on the use and systematics of vesicomyid genera, not least because several of them are based on poorly preserved fossil species. The scope of this note is to redescribe the type species of *Pleurophopsis*, which is *P. unioides* Van Winkle, 1919, and to show that the generic name *Pleurophopsis* should not be used until better preserved material becomes available.

Institutional abbreviations.—PRI, Paleontological Research Institution, Ithaka, USA; USNM, U.S. National Museum of Natural History, Washington DC, USA.

Material and methods

Pleurophopsis unioides is known only from internal molds (steinkerns) from isolated limestones on Trinidad (Van Winkle 1919). It was first described by Maury (1912) as *Unio* sp., accompanied by the drawing of a specimen that lacked the posterior end, and showed the hollow spaces left by the hinge. Maury's specimen was included in the synonymy of *P. unioides*, but Van Winkle's drawing of her holotype shows a specimen with complete posterior margin, which clearly represents a different specimen than that illustrated by Maury (1912). Van Winkle's holotype is missing from the PRI collection and must therefore be considered lost. Van Winkle's illustration was reproduced in the Treatise (Keen 1969: fig. E136-6). The specimen figured by Maury (1912) as *Unio* sp. is present in the PRI collection (PRI 28452) and is here designated as neotype for *P. unioides*. A silicon rubber cast of the anterodorsal area of the neotype was made to clarify hinge features.

The type locality of *P. unioides* was initially considered Oligocene or Pliocene (see Boss and Turner 1980) and was recently regarded as Miocene (Gill et al. 2005). The label associated with the PRI material states "middle middle Miocene". This note was probably made by Katherine Van Winkle herself, because she often added new information to specimens in the collection (Jennifer A. Hodgson, personal communication 2005).

Systematic paleontology

Class Bivalvia Linnaeus, 1758

Subclass Heterodonta Neumayr, 1884

Family Vesicomyidae Dall and Simpson, 1901

Genus *Pleurophopsis* Van Winkle, 1919

Type species: *Pleurophopsis unioides* Van Winkle, 1919, by monotypy; middle Miocene, Trinidad.

Note: The Treatise (Keen 1969) cited the author of *Pleurophopsis* as "Palmer, 1919", because Katherine Van Winkle (1895–1982) changed her name to Palmer when she married Ephraim Laurence Palmer (1888–1970), Cornell University professor of Nature Study in 1921. However, her account on the fossils from Trinidad that included the introduction of *Pleurophopsis* was published two years earlier under her maiden name Van Winkle.

Pleurophopsis unioides Van Winkle, 1919

Fig. 1.

1912 *Unio* sp.; Maury 1912: 50, pl. 8: 18, 19.
1919 *Pleurophopsis unioides* sp. nov.; Van Winkle 1919: 24, pl. 3: 12.
1969 *Pleurophopsis unioides* Palmer, 1919; Keen 1969: N664, fig. E138-6.
2005 *Pleurophopsis unioides* Van Winkle; Gill et al. 2005: 205, fig. 7A, B.

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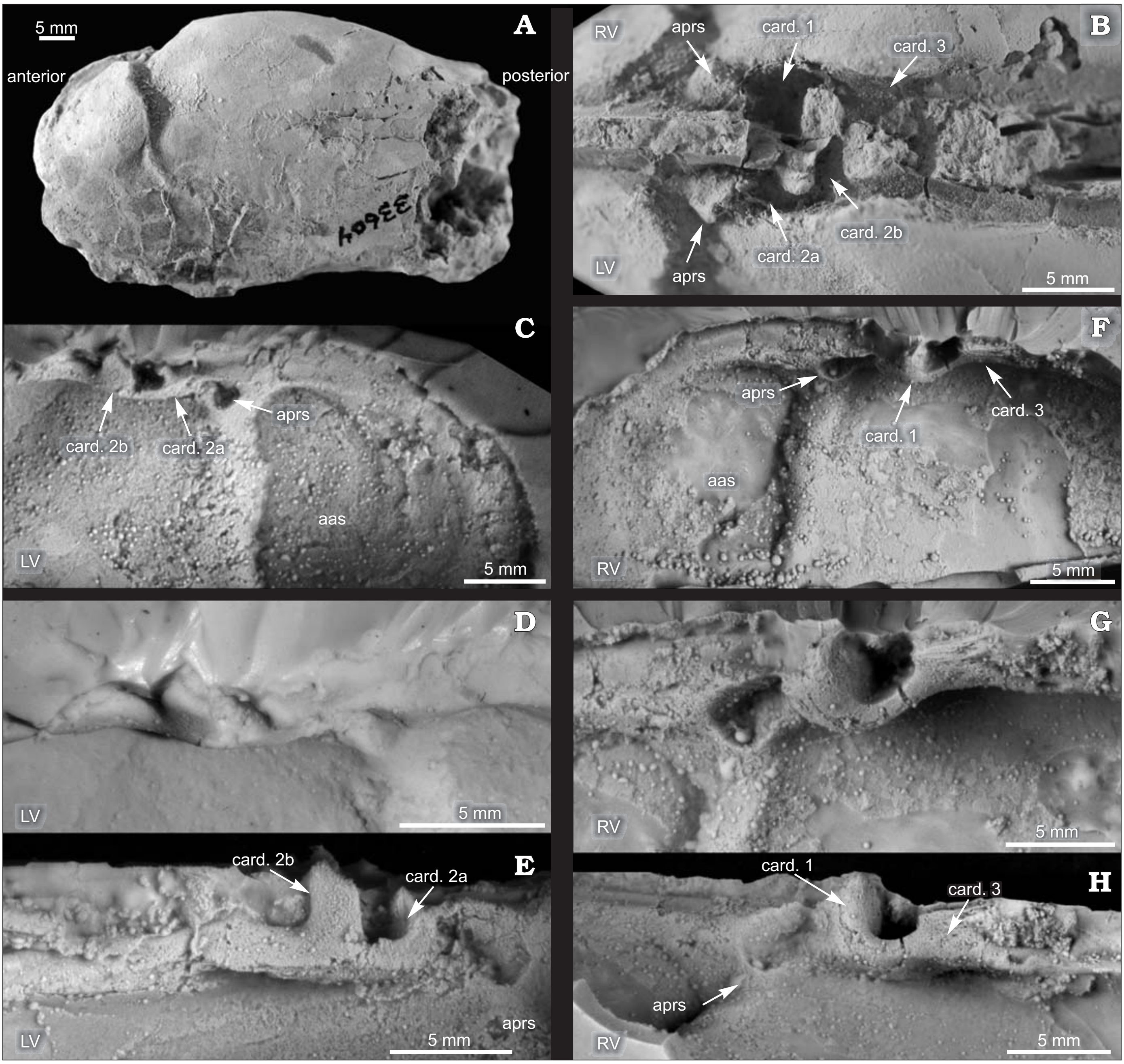

Fig. 1. The vesicomyid bivalve *Pleurophopsis unioides* Van Winkle, 1919 from middle Miocene strata of Trinidad, Neotype (PRI 28452). **A**. Lateral view of left valve, note that the number written on specimen is the former Cornell University number. **B**. Dorsal view of hinge area. **C**–**H**. Silicone rubber casts of neotype illustrating hinge features. **C**. Hinge and anterior adductor scar of left valve in lateral view. **D**. Close-up of C. **E**. Ventral view of left valve hinge. **F**. Hinge and anterior adductor scar of right valve in lateral view. **G**. Close-up of F, slightly tilted ventro-lateral view. **H**. Ventral view of right valve hinge. Abbreviations: aas, anterior adductor scar; aprs, anterior pedal retractor scar; card., cardinal tooth; LV, left valve, RV, right valve.

Material.—The description below is based on (i) the neotype PRI 28452, (ii) a rubber cast of the neotype, (iii) Van Winkle's illustration, and (iv) own observations on subsequently collected material (see Gill et al. 2005). Because only the lower portion of the hinge is preserved, characters like nymph and nymphal ridge, escutcheon, and lunule can not be evaluated.

Description.—Shell elongate elliptical, beak small, pointed and slightly prosogyrate, positioned in anterior quarter of shell; anterior margin evenly rounded, ventral margin straight or slightly convex, posterior margin rounded but more pointed than anterior margin, posterodorsal margin almost straight to slightly convex, only slightly inclined ventrally; after slight angulation at about three quarters of total shell length, shell margin slopes gently toward its rounded posterior end. Anterior adductor scar deeply impressed, almost straight on posterior side where bordered by strong vertical ridge; rounded on anterior side. Anterior pedal retractor scar deep, triangular, located directly above strong ridge bordering anterior adductor scar; posterior muscle scars not observed. Pallial line impressed on anterior side of shell, fading away on posterior side of shell; presence or absence of pallial sinus unknown. Interior of shell shows fine radial striations between pallial line and ventral shell margin.

Only lower portion of hinge dentition preserved. Right valve: cardinal tooth 1 strong, triangular in ventral view; cardinal 3b elongate at base, 3a unknown; socket for cardinal 2b of left valve rectangular and deep. Left valve: cardinal 2a thin; cardinal 2b strong, flat on its ventral side. Ligament, nymph, potential escutcheon, and lunule not discernable due to poor preservation. Posterodorsal margin shows some variation in its slope.

Comparisons.—Whereas Van Winkle's (1919) specimen shows a long, inclined and almost evenly convex posterodorsal margin that reaches close to the posterior end without angulation, the angulation is quite pronounced in some better-preserved specimens. Compared to other elongate vesicomyids, *P. unioides* resembles *Calyptogena elongata* Dall, 1916, type species of *Ectenagena* Woodring, 1938, in terms of shell shape, strongly impressed anterior adductor scar and its associated ridge, and hinge dentition. The only discernable difference is the flat base of cardinal 2b in *P. unioides*, whereas cardinal 2b of *C. elongata* has a small indentation (compare fig. 10E of Boss and Turner 1980). Also the Recent Californian *Ectenagena extenta* Krylova and Moskalev, 1996 has a similar deeply impressed anterior muscle adductor scar, pedal retractor scar, and hinge dentition, especially when seen in ventral view (Krylova and Moskalev 1996: fig. 1D). The Recent Japanese *Calyptogena* (*Ectenagena*) *phaseoliformis* Métivier, Okutani, and Ohta, 1986 also has a similar hinge dentition, only its cardinal 2a is more strongly developed than in *P. unioides* (Métivier et al. 1986). Another Japanese species with similar hinge and general shell shape is *C.* (*E.*) *kaikoi* Okutani and Métivier, 1986. Horikoshi (1989) documented some ontogenetic variation in its hinge teeth configuration, but these do not differ significantly from the hinge dentition preserved in *P. unioides*. Horikoshi (1989) also documented an ontogenetic change in the shape of the ventral shell margin of *C.* (*E.*) *kaikoi*, from convex or straight in small specimens, to slightly concave in a larger specimen.

The general shape and hinge dentition of the Miocene Japanese *Adulomya uchimuraensis* Kuroda, 1931 (see Kanno et al. 1998) is very similar to that of *P. unioides*. *Adulomya uchimuraensis* is more elongate than *P. unioides*, has a lower beak, and also the ridge posterior to the anterior muscle-attachment scar is not as strongly developed as in *P. unioides*. The fossil *Pleurophopsis peruviana* Olsson, 1931 from Eocene or Oligocene seep carbonates in northern Peru and southern Ecuador has almost no teeth on its hinge and its systematic position is doubtful (Kiel and Peckmann 2007).

Discussion

There is some consensus in the taxonomic literature on vesicomyids that the presence and shape of the cardinal tooth 3 of the right valve, nymph and nymphal ridge, subumbonal pit, escutcheon, lunule, and pallial sinus are important characters for their classification. Because these characters are not fully preserved in the available material, it is suggested that the name *Pleurophopsis* should not be used until better preserved material becomes available. To further illustrate the taxonomic uncertainties, previous suggestions regarding the systematic position of *Pleurophopsis* and related genera are discussed here.

Boss and Turner (1980: 164) synonymized *Pleurophopsis* with *Calyptogena* "based on exceptionally large specimens of an unnamed species of *Pleurophopsis* from presumed Oligocene strata of Colombia […]." Examination of the material from this locality in USNM showed that they differ significantly from *P. unioides* by being broadly oval rather than elongate; internal features were impossible to examine due to the poor state of preservation. The systematic position of these specimens is doubtful (Kiel and Peckmann 2007) and they cannot be used to synonymize *Pleurophopsis* and *Calyptogena*.

Based on their redescription of *Adulomya uchimuraensis*, type species of *Adulomya* Kuroda, 1931, Kanno et al. (1998) regarded *Adulomya* as a subgenus of *Calyptogena* and pointed out that the only difference between *Adulomya* and *Ectenagena* is the presence of a subumbonal pit in *Adulomya*, whereas the subumbonal pit is only developed in juveniles of *Ectenagena*, and disappears during ontogeny. This minor difference, however, appears insufficient to justify a subgeneric separation of *Adulomya* and *Ectenagena*. Thus, *Ectenagena* is here synonymized with *Adulomya*. The presently known hinge characters of *Pleurophopsis* are almost identical to those of *Adulomya uchimuraensis*, although the presence or absence of a subumbonal pit is unknown in *P. unioides*. If better preserved material becomes available and a close relationship between *P. unioides* and *A. uchimuraensis* can be confirmed, the name *Pleurophopsis* would have priority over *Adulomya* (and *Ectenagena*), because it is the oldest of the three names.

According to the recent review of genera related to *Calyptogena* (Krylova and Sahling 2006), *Pleurophopsis* lacks a nymphal ridge and the cardinal tooth 3a. A source for this characterization was not cited and could not be verified on the presently available material. These features are lacking due to poor preservation, but whether their absence is a conchological reality is uncertain. Krylova and Sahling (2006: 389) suggested that the "[*Calyptogena*] *phaseoliformis*"-group, which consists of species previously assigned to *Ectenagena*, should be referred to *Pleurophopsis*. These species are indeed similar to *P. unioides*; however, due to the incomplete type of *Pleurophopsis*, and their similarities to *Adulomya uchimuraensis*, these taxa should be better referred to *Adulomya*.

Conclusions

Vesicomyid bivalves play an important evolutionary and ecological role in chemosynthetic environments like hydrothermal vents, methane seeps, and sunken whale carcasses. The rough correlation between the origin of whales and the evolutionary age of vesicomyids estimated from molecular clocks was used by Baco et al. (1999) and Smith and Baco (2003) to suggest that the rise of whales in the Eocene resulted in the radiation of the modern vent and seep fauna. Accordingly, they argued that whale carcasses provided dispersal "stepping stones" for vent and seep taxa, especially vesicomyids, thereby expanding their dispersal capabilities and opening new habitats for them. This hypothesis was challenged by the notion that vesicomyids do not occur at fossil whale falls in the Eocene and Oligocene, but only started to appear in this habitat in the Miocene (Kiel and Goedert 2006).

However, the study of Kiel and Goedert (2006) showed only that the rise of the whales in the Eocene and Oligocene had no significant impact on the evolution of vesicomyids, it did not rule out the possibility that vesicomyids underwent a major radiation once they started to adapt to whale falls in the Miocene. This question may be addressed using a detailed reconstruction of the origin and diversification of vesicomyid species and genera. The clarifications and redescription of *P. unioides* provided here are good steps toward such a consistent taxonomic and phylogenetic assessment of this group.

Due to the lack of data on hinge tooth 3a, nymph, subumbonal pit, escutcheon, lunule, and pallial sinus in all currently available specimens of *P. unioides*, the generic name *Pleurophopsis* should not be used. Instead, the species should be referred to as *Adulomya*? *unioides*. However, should better preserved material become available, *Pleurophopsis* would have priority over both *Adulomya* and *Ectenagena*, because it is the oldest of the three names.

Acknowledgments.—I am indebted to Jennifer A. Hodgson (PRI, Ithaca, USA) for locating the specimen in the PRI collection and making it available; Steve Jabo (Smithsonian Natural History Museum, Washington DC, USA) for his help casting the specimen, Kazutaka Amano (Joetsu University of Education, Niigata, Japan) for critically reading the manuscript and providing hard-to-get literature, Crispin T.S. Little (University of Leeds, UK) for access to additional material, Richard L. Squires (California State University, Northridge, USA) and an annonymous reviewer for their improvements on the manuscript. This study was supported by a Walcott fellowship of the Smithsonian Institution and a Marie Curie fellowship of the European Commission.

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