

Papyridea clenchi spec. nov. and *Papyridea curvicostata* spec. nov., two new Paper Cockles from tropical America (Bivalvia, Cardiidae), with notes on evolution and dispersal

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POORTEN, J.J. TER, 2019. *Papyridea clenchi* spec. nov. and *Papyridea curvicostata* spec. nov., two new Paper Cockles from tropical America (Bivalvia, Cardiidae), with notes on evolution and dispersal. – *Basteria* 83 (4-6): 109-130. Leiden.
Published 9 November 2019

Papyridea clenchi spec. nov. (Cardiidae) is described from Martinique and compared with the related *Papyridea lata* (Born, 1778), *Papyridea soleniformis* (Bruguière, 1789) and *Papyridea semisulcata* (Gray, 1825). *Papyridea curvicostata* spec. nov. is described from Ecuador and compared with the related *Papyridea hiulca* (Reeve, 1845), *Papyridea crockeri* (A.M. Strong & Hertlein, 1937) and *Papyridea aspersa* (G.B. Sowerby I, 1833). Taxonomic relations within the four tropical Atlantic and four tropical eastern Pacific species are analyzed. Distributions of the living species are given. Atlantic-Pacific geminate species pairs are discussed; a predominantly one-way migration (from Atlantic to Pacific) through the Isthmus of Panama is hypothesized. The fossil record of *Papyridea* is reviewed and the taxonomic position of *Profulvia* is discussed.

Key words: Mollusca, Bivalvia, Cardiidae, new species, western Atlantic, eastern Pacific, taxonomy, biogeography, phylogeny.

INTRODUCTION

Members of the genus *Papyridea* Swainson, 1840, known under the vernacular name ‘Paper Cockles’, with their fragile, gaping shells and elongated oval shape, are a characteristic group of tropical eastern Pacific and tropical Atlantic trachycardiines. Unlike all other trachycardiines, the length well exceeds the height, thus providing an immediate accessible marker for taxonomic separation at genus

level. Identification at species level is often more problematic, as several commonly used morphological characters tend to overlap. Some revisionary work on the genus has been carried out. Kafanov (1997) compiled an illustrated checklist of all valid taxa, and summarized the living species and Cenozoic representatives, including those of the extinct subgenus *Profulvia* Kafanov, 1976. The evolutionary radiation of *Profulvia* and *Papyridea* was treated by Kafanov (2001). Furthermore, Watters (2002) discussed the status and identity of an Atlantic *Papyridea* species.

Until the 1970s, two Atlantic *Papyridea* species were recognized, viz. *P. soleniformis* (Bruguière, 1789) and *P. semisulcata* (Gray, 1825). Odé (1975) outlined the diagnostic features of what he considered an undescribed *Papyridea*, differing from *P. soleniformis* and based on material from Texas. Currently this morph is considered to agree with *P. lata* (Born, 1778). Voskuil & Onverwagt (1991) and Kafanov (1997) believed that *Cardium latum* Born, 1778 was the first available name for *P. soleniformis*. Watters (2002), apparently unaware of the study of Odé (1975), considered both *P. soleniformis* and *P. lata* specifically different and stabilised both taxa by lectotype designations. Both species, as well as *P. semisulcata*, are fairly commonplace elements of the Caribbean fauna province, predominantly occurring in shallow water in sandy and muddy bottoms, commonly in association with seagrass (Lamy & Pointier, 2018; Mikkelsen & Bieler, 2007; Redfern, 2013; Zhang, 2012). Additionally, *P. soleniformis* also occurs in the tropical central and East Atlantic (Rosewater, 1975; Watters, 2002). A record of *P. lata* from West Africa (Huber, 2010) is in need of confirmation. In this paper I introduce a fourth Caribbean species, originating from deeper waters up to at least 80 m, with a quite different shell morphology.

Two tropical eastern Pacific *Papyridea* species were traditionally differentiated, viz. *Papyridea aspersa* (G.B. Sowerby I, 1833) and *P. crockeri* (A.M. Strong & Hertlein, 1937), whereas *P. hiulca* (Reeve, 1845) had been neglected (Olsson, 1961), misinterpreted (Fischer-Piette, 1977) or regarded as

a monstrosity (Smith, 1885; Dall, 1901). *P. mantaensis* Olson, 1961, considered valid by several authors (Keen, 1971; Bernard, 1983; Kafanov, 1997), proved to be synonymous with *P. hiulca* (see Voskuil & Onverwagt, 1991). The latter is presently regarded as the third eastern Pacific *Papyridea* (Huber, 2010; Coan & Valentich-Scott, 2012; Paredes et al., 2016). A fourth eastern Pacific species is described herein. Although the gross morphology bears some resemblance with *P. hiulca*, it can be readily differentiated based on a number of shell characters.

MATERIAL AND METHODS

Studied material

The Caribbean material for this study partly originates from two recent large-scale expeditions to two islands in the Lesser Antilles led by the Muséum national d'Histoire naturelle, Paris with material deposited in the collection of MNHN. KARUBENTHOS 2012 to Guadeloupe took place from 2-30 May 2012 and involved 35 participants. Bathymetric range investigated: 0-160 m, once to 258 m. MADIBENTHOS to Martinique took place from 5 September to 11 October 2016 and involved 64 participants. Bathymetric range investigated: 0-90 m, sporadically to 100 m. Altogether, these expeditions produced no less than 782 collecting events (sampling at low tide; sampling by SCUBA with brushing baskets, suction samplers; hand operated dredging and traps).

Another important Caribbean portion results from the 'Snellius' Surinam Shelf Expedition OCPS-1 (Onderzoek van het Continentale Plat van Suriname / Investigation of the Continental Shelf of Suriname) conducted in March-April 1966 and the 'Luymes' Guyana Shelf Expedition CICAR-15 (Cooperative Investigation of the Caribbean and adjacent regions) conducted in August-September 1970 with material deposited in the collection of RMNH. See Veldkamp (1967, 1971) and Knudsen (2005) for station maps and data regarding the shelf environment. The continental shelf dredgings of these surveys reached a depth of circa 200 m.

In addition, supplementary material present in various institutions and in the reference collection of the author has been examined.

Measurements

The length is the greatest distance between the anterior and posterior ends, parallel to the hinge line formed by the tip of the lateral teeth and the height is formed by the maximum dimension measured along an axis perpendicular to the hinge line (Figs 11cc, 12bb – dotted lines). The anterior length is the distance from the anterior margin to the umbo; the posterior length is the distance from the posterior margin to the umbo – both measured along the length

line. For the morphometrics juvenile specimens were excluded and measurements were extrapolated in case of single valves (see Tables 1-2).

Acronyms of institutions and repositories

ANSP: Academy of Natural Sciences of Philadelphia, Drexel University, U.S.A.; FMNH, Field Museum of Natural History, Chicago, U.S.A.; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMUK, The Natural History Museum, London, U.K.; RMNH, Naturalis Biodiversity Center, Leiden, The Netherlands; SBMNH, Santa Barbara Museum of Natural History, Santa Barbara, California, U.S.A.; UF, Florida Museum of Natural History, Gainesville, U.S.A.; USNM, National Museum of Natural History, Smithsonian Institution, (formerly United States National Museum) Washington, DC, U.S.A.; ZMA, Zoological Museum Amsterdam, The Netherlands (now part of Naturalis Biodiversity Center, Leiden, The Netherlands); JJTP, colln J.J. ter Poorten, Hilversum, The Netherlands; PH, P. Hessel collection, Stichting Schepel Schelp (collection associated with Naturalis Biodiversity Center), Rhenen, The Netherlands; SH, S. Hobbs collection, Cape May, U.S.A.

Abbreviations

AL, anterior length; AQ, anterior quarter of the shell; H, height; L, length; LV, left valve(s); MAQ, median-antero quarter of the shell; MPQ, median-postero quarter of the shell; PL, posterior length; PQ, posterior quarter of the shell; PV, paired valves; RV, right valve(s); V, valve(s); W, width.

SYSTEMATIC PART

Class Bivalvia Linnaeus, 1758

Order Cardiida Ferussac, 1822

Family Cardiidae Lamarck, 1809

Subfamily Trachycardiinae Stewart, 1930

Genus *Papyridea* Swainson, 1840

Papyridea Swainson, 1840: 374. Type species by subsequent designation (Gray, 1847: 185): *Cardium soleniforme* Bruguière, 1789 sensu W. Wood, 1815: pl. 56 fig. 3 [= *Cardium latum* Born, 1778]; Recent, Caribbean.

Diagnosis. — Shell small (15 mm) to medium (70 mm), thin shelled, elongate-oval, inequilateral with longer posterior part, anterior and posterior side gaping. Numerous flattened or triangular radial ribs, which are broader on the posterior slope, forming posterior projections that interdigitate when valves are closed. Posterior ribs spinose, anterior ribs with scaly sculpture. Hinge plate and ligament short. Animal with relatively elongate, separate siphons;

foot reduced, much less muscular than that of most cockles. Living relatively deeply infaunal.

Stratigraphic and geographic range. — Early Miocene, Burdigalian to Recent (Vokes, 1977; Schneider, 1998a). Caribbean, Patagonian, West African, Californian, Panamic, Peruvian; littoral-sublittoral on sand and mud bottoms, often in association with seagrass.

Remarks. — The rather deep infaunal life habit of *Papyridea* is described by Stanley (1970). The functional morphology is quite unique for cardiids, with a gaping shell and a short hinge and ligament allowing the shells to rock along an antero-postero axis (Watters, 1993).

Papyridea clenchi spec. nov.

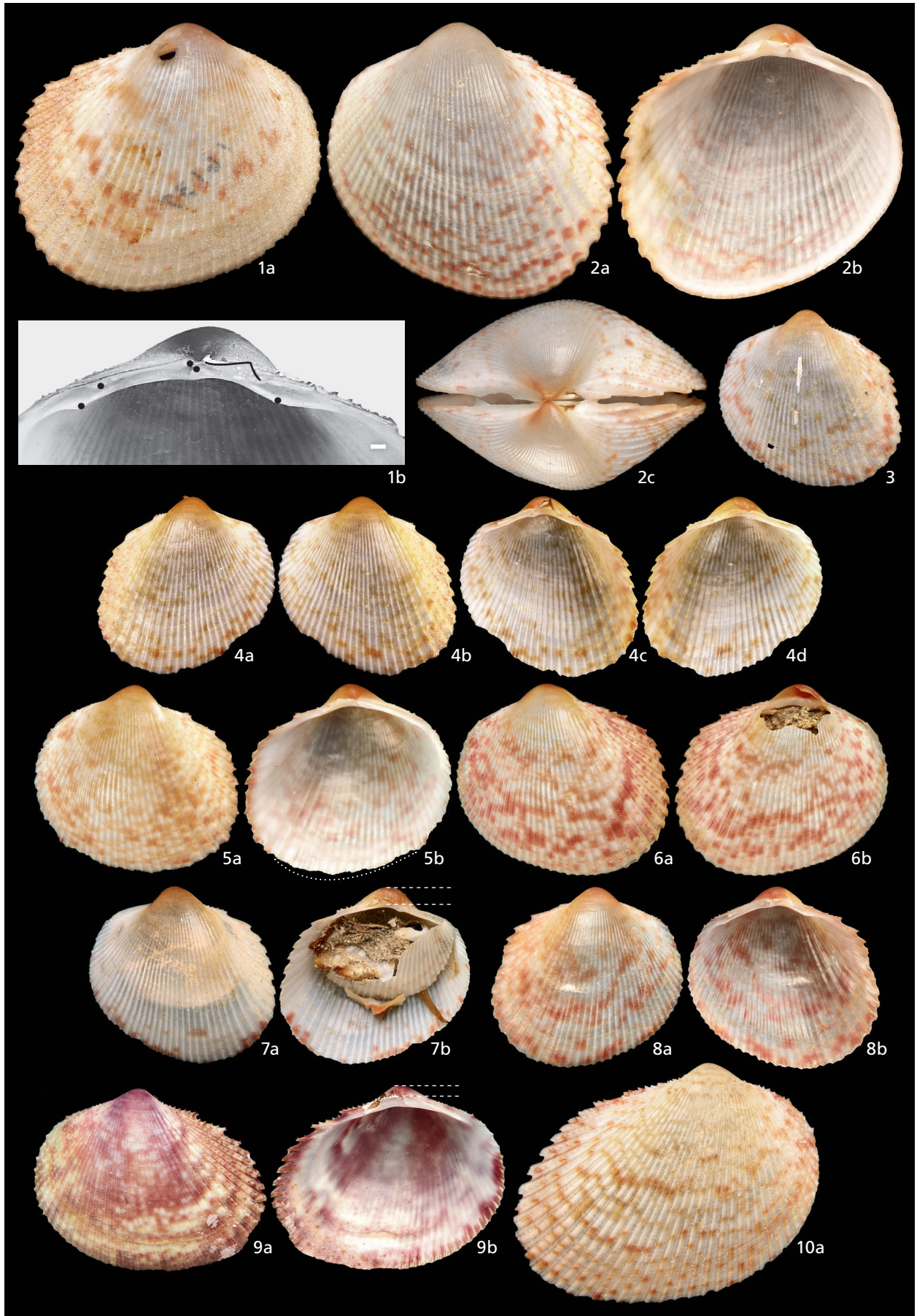
(Figs 1-8, 13, 32, Tables 1, 3)

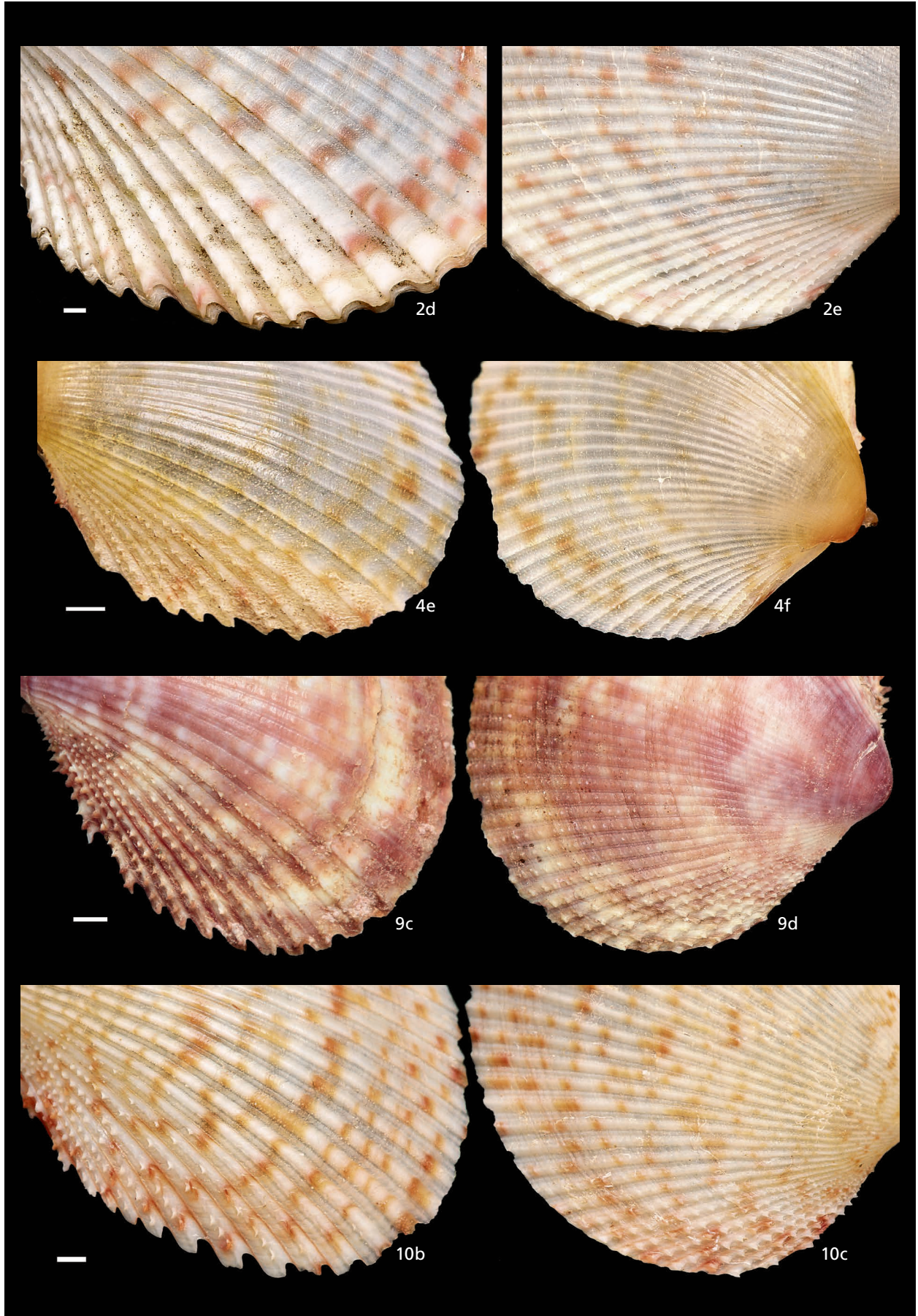
Papyridea lata (Born, 1778) — Watters, 2002: 121 (pars, Bradenton, 30 m depth, R.P.A. Voskuil record [= JJTP 5129]; Boynton Inlet, 55 m depth, UF 168170; West of Naples, UF 461158).

Type series and other material examined. — **U.S.A., Florida**, Palm Beach County, off Briney Breezes, 2 miles below [South of?] Boynton, depth 10 fms [18 m]. Leg. F.B. Lyman, 22.05.1940 (UF 16137, paratype, 1 PV); Palm Beach County, off Boynton, dredged, depth 40 fms [73 m]. Leg. F.B. Lyman, 20.12.1939 (UF 16138, paratype, 1 LV); Palm Beach County, Boynton Inlet, depth 30 fms [56 m]. Leg. McGinty, 01.03.1951, R/v Triton stn 377 (UF 168170, paratypes, 1 PV, 2 RV); Palm Beach County, Palm Beach, Radio Towers (WOE) to Breakers Hotel, 25 fms [46 m]. Leg. McGinty, 14.04.1951, R/v Triton stn 466-477 (UF 219796, 1 PV); Florida Straits, 24°27.4'N, 83°20.2'W, 30' otter trawl, depth 100-104 fms [183-190m]. Leg. G. Burgess, 27.02.2005, stn GHB-2005-11 (UF 355910, 1 RV); Collier County, W. of Naples, depth 190 ft [58 m]. Leg. J. Moore, 30.11.1966 (UF 461158, 1 RV); Manatee County, Bradenton, dredged offshore, depth 100 ft [30.5 m], 12.1970. (JJTP 5129, paratype, 1 PV); off St. Petersburg, 28°11.429'N, 84°48.604'W to 28°10.568'N, 84°48.122'W, otter trawl, depth 93-95 m. Leg. B. Olivar, 29.03.2003, R/v Suncoaster (UF 310729, 1 LV). **Panama**, Atlantic coast [no further data], dredged, depth 24-36 m. (JJTP 1489, paratype, 1 PV). **Guadeloupe**, no data, alive. 05.2012. KARUBENTHOS 2012. (MNHN-IM-2014-6046, paratype, 1 PV, alive). **Martinique**, off Macouba, 14°55.1'N, 61°09'W, dredged, depth 80 m, 24.09.2016. MADIBENTHOS stn AD261 (MNHN-IM-2013-71243, holotype, 1 PV, alive); off Macouba, 14°55.1'N, 61°08.9'W, dredged, depth 80 m, 25.09.2016. MADIBENTHOS stn AD266 (MNHN-IM-2014-6043, 1 LV); Bellefontaine, 14°40.4'N, 61°10.6'W, dredged, depth 70 m, 04.10.2016. MADIBENTHOS, stn AD298 (MNHN-IM-2014-6045, paratype, 1 LV); Baie de Fort-de-France, sw Pointe des Nègres, 14°35.7'N,

61°06'W, dredged, depth 60 m, alive, 30.09.2016. MADIBENTHOS, stn AD276. (MNHN-IM-2014-6044, paratypes, 1 PV, alive, 1 LV). **Guyana**, offshore, 07°45.1'N, 57°30'W, Van Veen grab, depth 69.6 m, 05.09.1970, R/v Luymes CICAR 15 Expedition, stn 106 (RMNH.MOL.341278, paratypes, 2 RV); offshore, 07°34'N, 57°16'W, dredged, depth 59 m, sand, shells, 02.09.1970, R/v Luymes CICAR 15 Expedition, stn 87 (RMNH.MOL.341281, 1 LV); offshore, 07°33'N, 57°05'W, dredged, depth 63 m, sandy bottom, 31.08.1970, R/v Luymes CICAR 15 Expedition, stn 65 (RMNH.MOL.341279, paratype, 1 PV); offshore, 07°34.9'N, 57°04.7'W, Van Veen grab, depth 68 m, sandy bottom, 31.08.1970, R/v Luymes CICAR 15 Expedition, stn 64 (RMNH.MOL.341276, 1 LV). **Suriname**, offshore, 07°35.7'N, 56°52.6'W, rectangular dredge, depth 94-97 m, fragment of calcareous coral rock with some solitary corals, 11.05.1966, R/v Snellius OCPS-I Expedition, stn H57 (RMNH.MOL.119336, 3 LV, 4 fragments); offshore, 07°16.8'N, 56°47.6'W, Agassiz trawl, depth 64 m, 13.04.1966, R/v Snellius OCPS-I Expedition, stn G7 (RMNH.MOL.119337, 1 LV); offshore, 07°15.6'N, 56°40.0'W, van Veen grab/Agassiz trawl, depth 68 m, coarse sand with some mud, shell fragments, 10.05.1966, R/v Snellius OCPS-I Expedition, stn G56 (RMNH.MOL.119340, 1 LV);

> **Figs 1-8.** *Papyridea clenchi* spec. nov. 1. U.S.A., Florida, Palm Beach County, off Briney Breezes, 2 miles below Boynton, 10 fms [18 m]. Leg. F.B. Lyman, 22.05.1940, UF 16137, paratype, L 32.4 mm (a: RV exterior, b: RV interior with hinge details highlighted. Scale bar: 1 mm). 2. Panama, Atlantic coast, dredged, 24-36 m. JJTP 1489, paratype, L 28.9 mm (a: LV exterior, b: LV interior, c: dorsal, d: RV posterior slope, e: RV anterior slope). 3. Martinique, off Macouba, 14°55.1'N, 61°08.9'W, dredged 80 m, alive, 25.09.2016. MADIBENTHOS, stn AD266, MNHN-IM-2014-6043, L 13.2 mm (LV exterior). 4. Martinique, off Macouba, 14°55.1'N, 61°09'W, dredged 80 m, alive, 24.09.2016. MADIBENTHOS, stn AD261, MNHN-IM-2013-71243, holotype (genotyped specimen), L 12.5 mm (a: RV exterior, b: LV exterior, c: RV interior, d: LV interior, e: RV posterior slope, f: RV anterior slope). 5-6. Martinique, Baie de Fort-de-France, sw Pointe des Nègres, 14°35.7'N, 61°06'W, dredged 60 m, alive, 30.09.2016. MADIBENTHOS, stn AD266, MNHN-IM-2014-6044, paratypes. 5. L 16.0 mm (a: LV exterior, b: LV interior). 6. L 16.2 mm (a: LV exterior, b: RV exterior). 7. Guadeloupe, alive, 05.2012. KARUBENTHOS 2012, no data, MNHN-IM-2014-6046, paratype, L 13.3 mm (a: LV exterior, b: LV interior). 8. Martinique, Bellefontaine, 14°40.4'N, 61°10.6'W, dredged 70 m, 04.10.2016. MADIBENTHOS, stn AD298, MNHN-IM-2014-6045, paratype, L 14.0 mm (a: RV exterior, b: RV interior). **Fig. 9.** *Papyridea lata* (Born, 1778). Guadeloupe, Grand Cul-de-Sac Marin, 16°19.65'N, 61°34.26'W, *Thalassia* and patches of coral, 2 m, 21.05.2012. KARUBENTHOS 2012, stn GM28, MNHN-IM-2014-6047, L 17.3 mm (a: LV exterior, b: LV interior, c: RV posterior slope, d: RV anterior slope). **Fig. 10.** *Papyridea soleniformis* (Bruguère, 1789). Guadeloupe, Petite Terre, 16°07.87'N, 61°12.52'W, 50 m, 27.05.2012. KARUBENTHOS 2012, stn GS36, MNHN-IM-2014-6048, L 22.3 mm (a: RV exterior, b: RV posterior slope, c: RV anterior slope). Scale bars: 1 mm.





offshore, 07°00.2'N, 56°26.5'W, van Veen grab/Agassiz trawl, depth 59 m, sand with some fine mud and fine shell fragments, 06.05.1966, R/V Snellius OCPS-I Expedition, stn F40 (RMNH.MOL.119343, 1 RV); offshore, 07°13.8'N, 56°24.4'W, van Veen grab/Agassiz trawl, depth 81 m, sand with shell fragments, 05.05.1966, R/V Snellius OCPS-I Expedition, stn F38 (RMNH.MOL.119339, 1 LV).

Type locality. — Martinique, off Macouba, 14°55.1'N, 61°09'W, dredged, depth 80 m.

Description. — Shell length up to 39.5 mm, L slightly exceeds H (L/H 1.00-1.11, mean 1.06, *n* = 14, Table 1), thin-shelled (semi translucent) and fragile, moderately inflated ($W/(L+H/2)$ 0.41-0.69, mean 0.50, *n* = 14, Table 1), obliquely oval, margins rounded, gaping anteriorly and posteriorly, posterior margin with short digitations. Shell equivalve and subequilateral (AL/PL 0.74-0.88, mean 0.82, *n* = 9, Table 1), with rounded, weakly to strongly prosogyrous umbones, placed just in front of the midline and clearly protruding (Fig. 7b, dotted lines). Shell surface covered with a rather dense pattern of microscopic granulations, anteriorly and posteriorly (Figs 4e-f) of a more coarse nature. Shell with 42-49 radial ribs (mean 45.87, *n* = 15, Table 1), low triangular in cross section and gradually becoming wider on the posterior slope where the highest elevation is posteriorly. First dorsal rib posterior of umbo located in RV (Fig. 2c).

Interstices equal to rib width on anterior and median part, about one-half the rib width on posterior part. Rib sculpture of AQ (Fig. 4f) consisting of minute spatulate scales, ribs on MAQ and MPQ unsculptured, ribs on PQ (Fig. 4e) tiny spinose and rather distantly placed.

External ligament small; lunular-like area on antero-dorsal margin elongate, well demarcated and hollowed, unsculptured. Hinge plate small with two cardinal teeth and two anterior and one posterior lateral tooth in RV; LV with two cardinal teeth, of which dorsal one obscure, one posterior lateral and one anterior lateral tooth. Posterior lateral closer to ventral cardinal tooth than anterior ventral lateral (Fig. 1b, black dots). Cardinals separated by a moderately wide socket, not joined dorsally in RV.

External colouration whitish with sparse yellowish or reddish-brown blotches, umbo completely orange-brown or red-brown, interstices on PQ often yellowish. Internal colouration similar by transparency. Periostracum thin, light olive-green, mainly preserved on posterior slope. Animal not observed.

Distribution and ecology. — At present documented from Florida, Panama, Guadeloupe, Martinique, Guyana and Suriname (Fig. 32) with dead records from 30-190 m and live records from 60-80 m. The very thin shell suggests a preference for fine grained muddy-silty sediments and the

Collection, registration number	L	AL	PL	H	W	Ribs	L/H	(L+H)/2	Inflation	AL/PL	Specimen
MNHN-IM-2013-71243, holotype •	12.5			12.1	7.4	43	1.03	12.30	0.60		PV
MNHN-IM-2014-6043 •	13.2			12.7	(7.9)	47	1.04	12.95	0.61		LV
MNHN-IM-2014-6044/1, paratype •	16.0			14.9	(9.9)	42	1.07	15.45	0.64		LV
MNHN-IM-2014-6044/2, paratype •	16.2			14.8	9.2	44	1.09	15.50	0.59		PV
MNHN-IM-2014-6045, paratype •	14.0			13.3	(8.4)	45	1.05	13.65	0.62		RV
MNHN-IM-2014-6046, paratype •	13.3			12.6	(9.0)	49	1.06	12.95	0.69		PV*
UF 16137, paratype •	32.3	14.9	17.4	29.0	19.2	48	1.11	46.80	0.41	0.86	PV
UF 16138, paratype	39.5	17.2	22.3	?	(22.0)	47	?	?	?	0.77	LV
UF 16170/1, paratype	29.4	13.7	15.7	27.4	(17.6)	47	1.07	43.10	0.41	0.87	RV
UF 16170/2, paratype	24.7	10.5	14.2	23.0	16.1	48	1.07	36.20	0.44	0.74	PV
UF 355910	32.8	15.1	17.7	30.1	(20.0)	49	1.09	47.85	0.42	0.85	RV
RMNH.MOL.341278/1, paratype	26.5	12.4	14.1	25.1	(16.1)	44	1.06	39.05	0.41	0.88	RV
RMNH.MOL.341279, paratype	27.3	12.3	15.0	26.7	16.5	43	1.02	40.65	0.41	0.82	PV
RMNH.MOL.119339	23.9	10.7	13.2	22.3	15.3	46	1.07	35.05	0.44	0.81	LV
JJTP 1489, paratype •	28.9	13.0	15.9	28.8	18.6	46	1.00	43.30	0.43	0.82	PV
Mean values						45.87	1.06		0.50	0.82	

Table 1. Shell measurements (mm) of *Papyridea clenchi* spec. nov. Sizes in brackets refer to extrapolated values.

* Broken PV with RV largely missing. Material figured herein indicated with a black dot (•).

large siphonal gape may reflect a relatively deeply burrowed life habit, as has been documented for *Papyridea* by Stanley (1970).

Etymology. — Named after William J. Clench (1897-1984), eminent American malacologist who recognised the present species as new in the early 1940s, based on the presence of a manuscript name in UF 16137 (Fig. 1) and UF 16138. For unknown reasons he did not publish his findings in his paper on the Cardiidae of the western Atlantic (Clench & Smith, 1944) nor in one of his numerous other malacological contributions.

Remarks. — *Papyridea lata* (Born, 1778) (Figs 9, 12, Table 3) differs by a more solid shell, an almost equilateral shell, a more oval shape, a less protruding umbo (Fig. 9b, dotted lines), a higher L/H ratio, a stronger developed rib sculpture, poorly developed ribs on the median part when juvenile, a poorly developed anterior dorsal lateral tooth in the RV and a more vivid and darker colouration with an umbonal area containing two broad orange or purple radial rays. Even in juveniles, the oval shape is apparent, compared to the obliquely oval shape of *P. clenchi* spec. nov. (Figs 11-12).

Papyridea soleniformis (Bruguière, 1789) (Figs 10a-c, Table 3) differs by a more solid shell, a stronger inequilateral shell, a larger adult size, a more elongated oval shape, a higher L/H ratio, a stronger developed rib sculpture, by the absence of microscopic granulations, by the absence of an anterior dorsal lateral tooth in the RV and a whitish-yellowish coloured umbo.

Papyridea semisulcata (Gray, 1825) (Fig. 42, Table 3) markedly differs by a stronger inequilateral shell, a much smaller adult size, a higher L/H ratio, a much lower radial rib number (27-32), strongly protruding rib extensions on the posterior part, by the absence of microscopic granulations, by the absence of an anterior dorsal lateral tooth in the RV and a generally whitish-yellowish coloured umbo.

The pattern of minute granulations recalls comparable precedents in the Miocene *P. multcostula* H.E. Vokes, 1977 and *P. bulbosa* (Dall, 1900). Both species are separated by their more broadly oval shape, lacking the oblique outline of *P. clenchi* sp. nov., and by their more complex tri-partite ribbing with raised marginal areas. Moreover, *P. bulbosa* has broader interstices on the MPQ and *P. multcostula* has much weaker developed ribs on the median part. Based on the present data, the inflation ratio of *P. clenchi* sp. nov. appears to decrease with an increase of size (Table 1).

It appears that *Papyridea clenchi* sp. nov. is occupying a different bathymetric niche than *P. lata* and *P. soleniformis*, generally occurring in deeper water (Fig. 13): a possible explanation for having been overlooked in the past. The combined KARUBENTHOS 2012 and MADIBENTHOS expeditions yielded nearly 200 *Papyridea* samples, of which only five were *P. clenchi* sp. nov. This could imply that suitable habitat has not been adequately sampled or that it occurs in

low densities in the waters around Guadeloupe and Martinique. Watters (2002: 121-123) gives as range 'subtidal to at least 46 m' for *P. soleniformis* and 'subtidal to at least 90 m' for *P. lata*, although the latter depth is based on a poorly documented sample (JJTP 2574, ex Voskuil colln 2203).

Paratype MNHN-IM-2014-6046 from Guadeloupe was labelled with station number GD52 (6 m depth), in a sample together with 8 live collected *Microcardium tinctum* (Dall, 1881) specimens. The latter is a rather well known deeper water cardiid which has been found alive in a depth zone of 45-160 m (based on 81 personally verified live collected samples), hence a mislabeling seems to have occurred and it is considered to originate from unknown depth.

***Papyridea curvicostata* spec. nov.**

(Figs 14-17, 37, Tables 2-3)

Papyridea (Papyridea) mantaense Olsson, 1961 — Kafanov, 1997: 4, pl. 1 figs 4a-b, pl. 2 fig. 3 (pars: pl. 2 fig. 3).

Papyridea hiulcum (Reeve, 1845) — Coan & Valentich-Scott, 2012: 417, pl. 137, middle row (= holotype of *P. curvicostata* spec. nov.), and 1191.

Type series and other material examined. — **Costa Rica**, Guancaste District, Golfo de Santa Elena, 11.0052°N, 85.7952°W, trawled by R/V Urraca [STR1], mud with gorgonians, depth 61-88 m. Leg. K.L. Kaiser, 09.07.2005, stn IMCR-05-T05 (SBMNH 468627, 1 SV); Guancaste District, Islas Murcielagos, Isla San José, 10°51.741'N, 85°54.908'W, gradual slope with turnable scree down to coarse sand, depth 5-12 m. Leg. K.L. Kaiser, 30.06.2005 (SBMNH 630926, 1 PV); Guancaste District, Bahía Panama, in rocky area, dead. Leg. G. Metz, 05.1994 (JJTP 437, paratype, 1 PV); Guancaste District, Playa Hermosa, in rocky area, dead. Leg. G. Metz, 05.1994 (JJTP 5173, paratype, 1 PV). **Panama**, Isla Jicarita, 7°13'0"N, 81°48'18"W, sand and rubble, depth 55 ft [17 m]. Leg. K.L. Kaiser, 18.04.1993 (SBMNH 235043, 1 SV); Isla Uva, 7.8169°N, 81.7602°W, shallow reef of *Pocillopora* & *Porites*; silty sand, scuba, depth 4-7 m. Leg. K.L. Kaiser, 04.05.2003, stn ICP-03-011 (SBMNH 630932, 1 SV); Golfo de Chiriquí, NW Isla Coiba, Isla Santa Cruz, 7.6313°N, 81.7825°W, massive *Porites* heads, various spp. gorgonians under ledges, depth 10-15 m. Leg. K.L. Kaiser, 06.05.2003, stn ICP-03-015 (SBMNH 630930, 2 PV, 3 SV); Golfo de Chiriquí, Coiba National Park, Fijoles rocks, 7.6558°N, 81.7284°W, large rocks sloping down to rubble sand bottom with occasional turnable rubble, scuba, depth 8-18 m. Leg. K.L. Kaiser, 08.05.2003, stn ICP-03-022 (SBMNH 630931, 2 fragments of PV); Golfo de Chiriquí, Isla Coiba, Canal de Rancheria, Fijoles rocks, 7.6488°N, 81.7181°W, rubble and boulder down to sand, scuba, depth 15-18 m. Leg. K.L. Kaiser, 16.05.2003, stn ICP-03-064 (SBMNH 630929, 2 PV, alive); Medidora Island [= Isla Medidor, 7°45'N, 81°34'W],

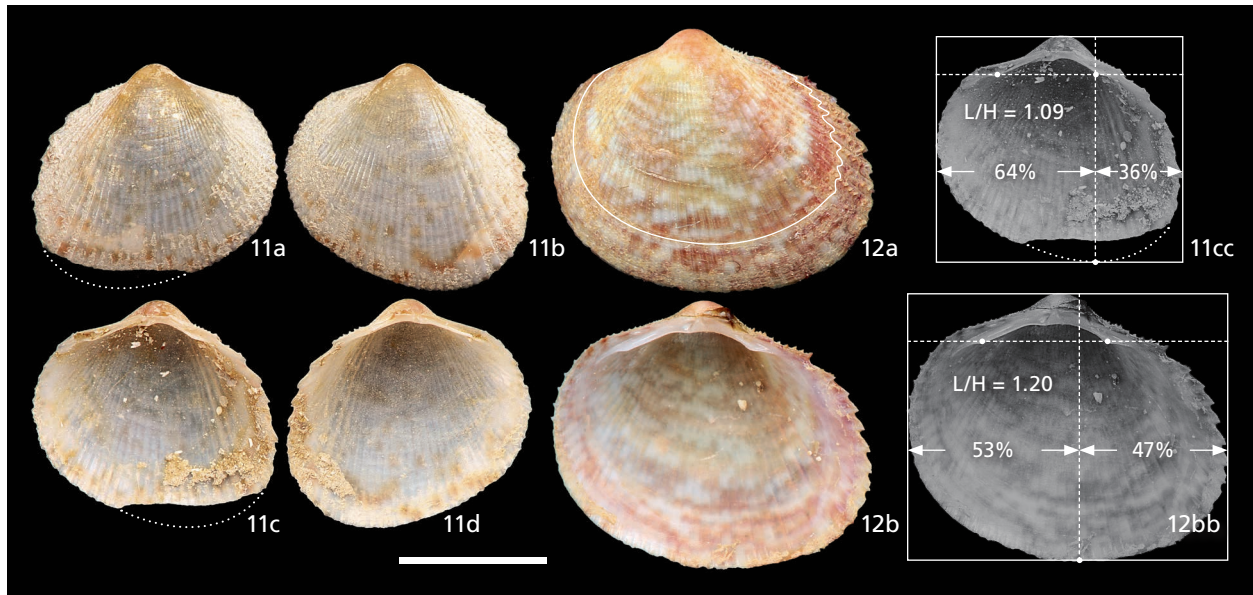


Fig. 11. *Papyridea clenchi* spec. nov. U.S.A., Florida, Manatee County, Bradenton, dredged offshore, 100 ft [30.5 m], 12.1970. JJTP 5129, paratype, L 7.6 mm (a: RV exterior, b: LV exterior, c: RV interior, cc: RV interior with degree of obliquity and L/H visualisation, d: LV interior). **Fig. 12.** *Papyridea lata* (Born, 1778). Martinique, Cap Saint Martin, 14°51.6'N, 61°12.6'W, diving 6-18 m, alive, 02.10.2016. MADIBENTHOS, stn AR380, MNHN-IM-2014-7061, L 9.9 mm (a: LV exterior with juvenile growth interruption highlighted, b: RV interior, bb: RV interior with degree of obliquity and L/H visualisation). Scale bar: 5 mm.

dredged 240 ft. [73 m], 07.1989 (ZMA.MOLL.10010, ex coll. Koekkoek, paratype, 1 PV); Montijo District, Isla del Canal de Afuera, 7°42'12"N, 81°37'20"W, scuba, depth 35-65 ft [11-20 m]. Leg. K.L. Kaiser, 18.04.1993 (SBMNH 238000, 1 PV); Montijo District, Isla del Canal de Afuera, depth 240 ft [73 m] (JJTP 543, paratype, 1 PV); Montijo District, Isla del Canal de Afuera, dredged, depth 72 m, found dead in dead *Spondylus* shell, 1990 (JJTP 2572, 1 PV); Montijo District, Isla Cebaco, 7°31'N, 81°14.8'W, trawled, depth 60-120 ft [18-37 m]. Leg. L. Marr, 01.1997-2001 (SBMNH 630927, 8 PV); Gobernadora Isl., intertidal, 2006 (JJTP 5187, 1 PV); Las Perlas Islands, coral rubble and large coral boulders, sandy bottom, Smithsonian STRI Panama Survey, 06.1979, unknown stn (USNM 1197384, paratype, 1 PV); unknown locality, dredged, depth 20 m (JJTP 1800, 1 PV). **Ecuador**, Manabí District, Isla La Plata, N. side of island, 1.2576°S, 81.0747°W, depth 10-30 m. Leg. D.R. Shasky, 21.06.1979 (SBMNH 461315, 5 PV, 3 SV); Manabí District, Isla Salango, N. side, 1°36'0"S, 80°52'0"W, depth 20-25 ft [6-7.5 m]. Leg. D.R. Shasky, 15-17.09.1978 (SBMNH 348207, holotype, 1 PV; SBMNH 630925, paratypes, 4 PV); Manabí District, Isla Salango, taken by dive, depth 10-15 m. Leg. local scuba diver, 11.2018 (JJTP 5175, 2 PV); Manabí District, Puerto López, under rocks, by dive, depth 2-10 m, 11.2013 (JJTP 4389, 2 PV); Manabí District, Puerto López, on sand, by local diver, depth 5-15 m, 10.2018 (MNHN-IM-2014-7069, paratype, 1 PV; FMNH 344775, paratype, 1 PV; JJTP 5189, paratype, 1 PV); Guayas District, Ayangue, Bajo Copé, in sand bottom, by dive, depth 15-20 m. Leg. G. Medina, 10.2007

(JJTP 3510, 2 PV); Guayas District, Ayangue, Bajo Copé, in sand bottom, by dive, depth 15-20 m. Leg. G. Medina, 10.2009 (JJTP 3878, paratype, 1 PV).

Type locality. — Ecuador, Manabí District, Isla Salango, N. side, 1°36'0"S, 80°52'0"W, depth 20-25 ft [6-7.5 m].

Description. — Shell length up to 69 mm, L well exceeds H (L/H 1.20-1.39, mean 1.29, $n = 20$, Table 2), rather thin-shelled but solid, moderately inflated ($w/(L+H/2)$ 0.35-0.40, mean 0.37, $n = 20$, Table 2), elongated oval, margins rounded, anterior gape rather narrow, posterior gape wide, posterior margin with well-marked digitations. Shell equi-valve and strongly inequilateral (AL/PL 0.56-0.72, mean 0.64, $n = 20$, Table 2), with weakly opisthogyrous umbones, placed in front of the midline and moderately protruding. Shell with 36-45 radial ribs (mean 39.55, $n = 20$, Table 2), rounded in cross section and gradually becoming wider on the posterior slope where the cross section is more triangular with the highest elevation posteriorly. Radial ribbing of a slightly curved nature, flared out in posterior direction (Fig. 17c, dotted line); first dorsal rib posterior of umbo located in LV (Figs 17b, 17d). Ribs on PQ flattened, anterior flank with a narrow groove, separated from the interstices by a tiny ridge and adjacent groove. Interstices equal to rib width on anterior and median part, about one-half the rib width on posterior part, on MPQ separated from ribs by faint radial groove. Rib sculpture on AQ and MAQ consisting of low, irregular sized curved scales, covering the full rib width and diminishing in strength towards MPQ; ribs

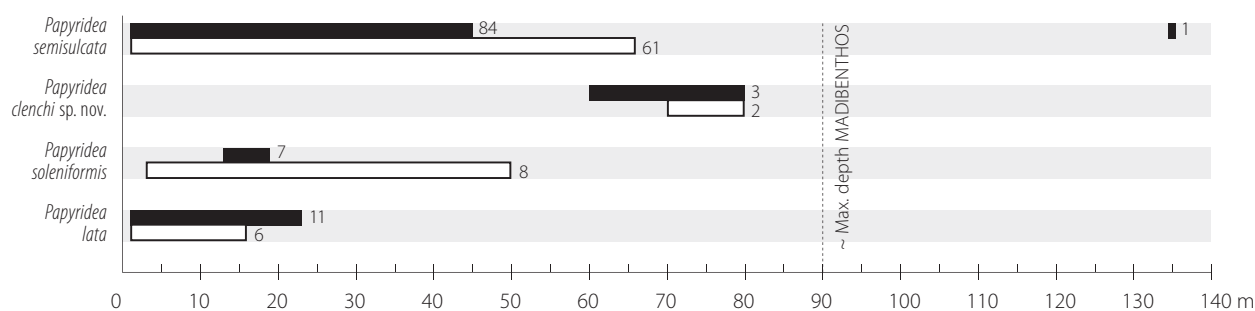


Fig. 13. Bathymetrical range of combined KARUBENTHOS 2012 and MADIBENTHOS recordings of *Papyridea* species (n = 183 samples, based on 782 collecting events). Black bars: live recordings; white bars: dead recordings. Number of samples indicated behind the bars. Covered depth range of KARUBENTHOS 2012 essentially 0-160 m, once down to 258 m; covered depth range of MADIBENTHOS essentially 0-90 m, sporadically down to 100 m.

on MPQ unsculptured; ribs on PQ spatulate and oblique-set, located on posterior slope of ribs.

External ligament small; lunular-like area on antero-dorsal margin very narrow, elongate and hollowed, unsculptured. Hinge plate rather small with two cardinal teeth and one anterior and posterior lateral tooth in RV (Fig. 17e, black dots); LV with one cardinal tooth, one posterior lateral and one anterior lateral tooth. Posterior laterals about equidistant to ventral cardinal tooth. Cardinals in RV separated by a wide socket, not joined dorsally.

External colouration whitish or yellowish with sparse orange-brown blotches, more or less commarginally arranged; umbonal area often completely orange-brown or red-brown. Internal colouration glossy white, umbonal cavity pale orange or yellowish. Periostracum thin, light olive green; thicker, darker and more persistent on posterior slope. Animal not observed.

Distribution and ecology. — At present documented from Costa Rica, Panama and Ecuador (Fig. 37) with one live record from 15-18 m and 24 dead records from 7-73 m.

Etymology. — The epithet is derived from the curvature of the radial ribs: flared out in posterior direction, enhanced by the opisthogyrous umbones. The latin term 'curvus' meaning bent and 'costa', ribs. It is used as an adjective.

Remarks. — *Papyridea hiulca* (Reeve, 1844) (Figs 18-23, Table 3) differs by a more obliquely oval shape with an attenuate anterior end and a higher posterior part, a smaller adult size, by narrower interstices, by the first rib posterior of the umbo located in the RV (Figs 20c-d, 22c), by the 2-3 posterior-most ribs more pointed triangular shaped and dorsally strongly projecting, by the ribs hardly curved in posterior direction (Fig. 20a, dotted line) and by a lower radial rib number (33-38).

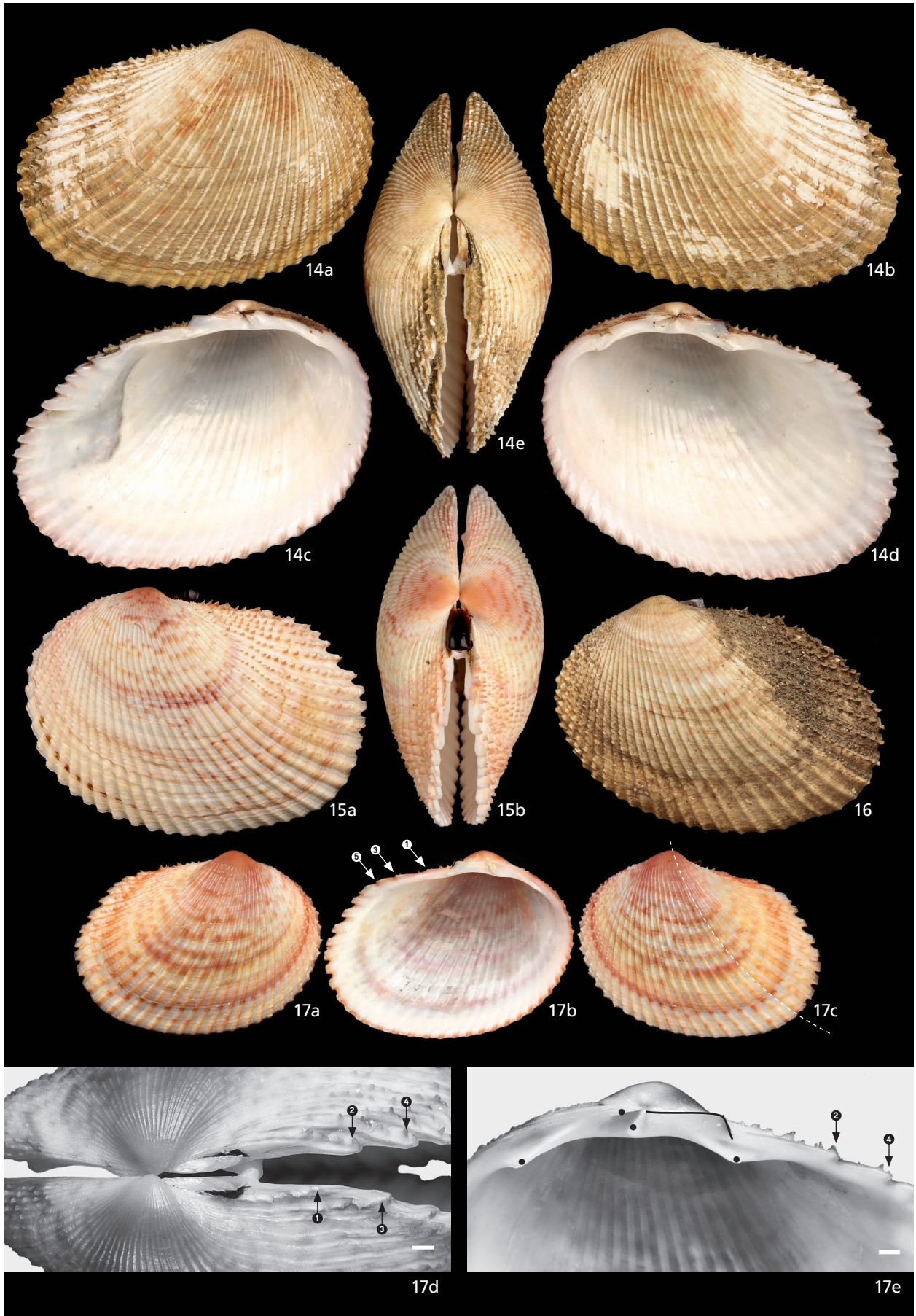
Papyridea crockeri (A.M. Strong & Hertlein, 1937) (Figs 24-26, Table 3) differs by a much more equilateral, rounded-oval shape, a smaller adult size, by a more narrow gape anteriorly and posteriorly, by narrower interstices, by the

first rib posterior of the umbo located in the RV, by a well-defined elongate hollowed area on the antero-dorsal area in both valves (Fig. 24c, arrow), by a well developed dorsal anterior lateral tooth in the RV (Fig. 25b, arrow), by the presence of scattered granulations on the posterior half of the shell (Fig. 26b) and by a higher radial rib number (42-48).

Papyridea aspersa (G.B. Sowerby I, 1833) (Figs 27-30, Table 3) differs by a less inequilateral shell, a smaller adult size, by the first (though poorly developed) rib posterior of the umbo located in the RV or (well developed) in the LV, by the presence of dense granulations on the anterior half of the ribs of the MPQ (Fig. 30c), by a higher radial rib number (41-52) and a more vivid colouration that often consists of purple-brown blotches, a purple-brownish internal margin.

Voskuil & Onverwagt (1991) were the first to consider *P. mantaensis* a synonym of *C. hiulca*, based on the examination of the type material of the latter. Subsequent authors followed this opinion (Watters, 2002; Coan & Valentich-Scott, 2012). The lectotype of *P. hiulca* (Fig. 20), a ventrally distorted juvenile specimen of which the posterior marginal extensions of the RV are partly broken off, is a good match of Reeve's (1845: pl. 21 fig. 123) type figure.

> **Figs 14-17.** *Papyridea curvicostata* spec. nov. **14.** Ecuador, Manabí District, Isla Salango, N. side, 1°36'0"S, 80°52'0"W, 20-25 ft [6-7.5 m]. Leg. D.R. Shasky, 15-17.09.1978, SBMNH 348207, holotype, L 69.1 mm (a: RV exterior, b: LV exterior, c: LV interior, d: RV interior, e: dorsal). **15.** Ecuador, Guayas District, Ayangue, Bajo Copé, taken in sand bottom, by dive, 15-20 m. Leg. G. Medina, 10.2009, JJTP 3878, paratype, L 61.8 mm (a: LV exterior, b: dorsal). **16.** Costa Rica, Guancaste District, Bahía Panama, in rocky area. Leg. G. Metz, 05.1994, JJTP 437, paratype, L 48.4 mm (LV exterior). **17.** Panama, Pacific coast, Canal de Afuera Isl., 240 ft [73 m]. JJTP 543, paratype, L 29.0 mm (a: RV exterior, b: LV interior with numbered ribs, c: LV exterior with marked curvature of radial ribs highlighted, d: dorsal with numbered ribs, e: RV interior with ribbing and hinge details highlighted). Scale bars: 1 mm.





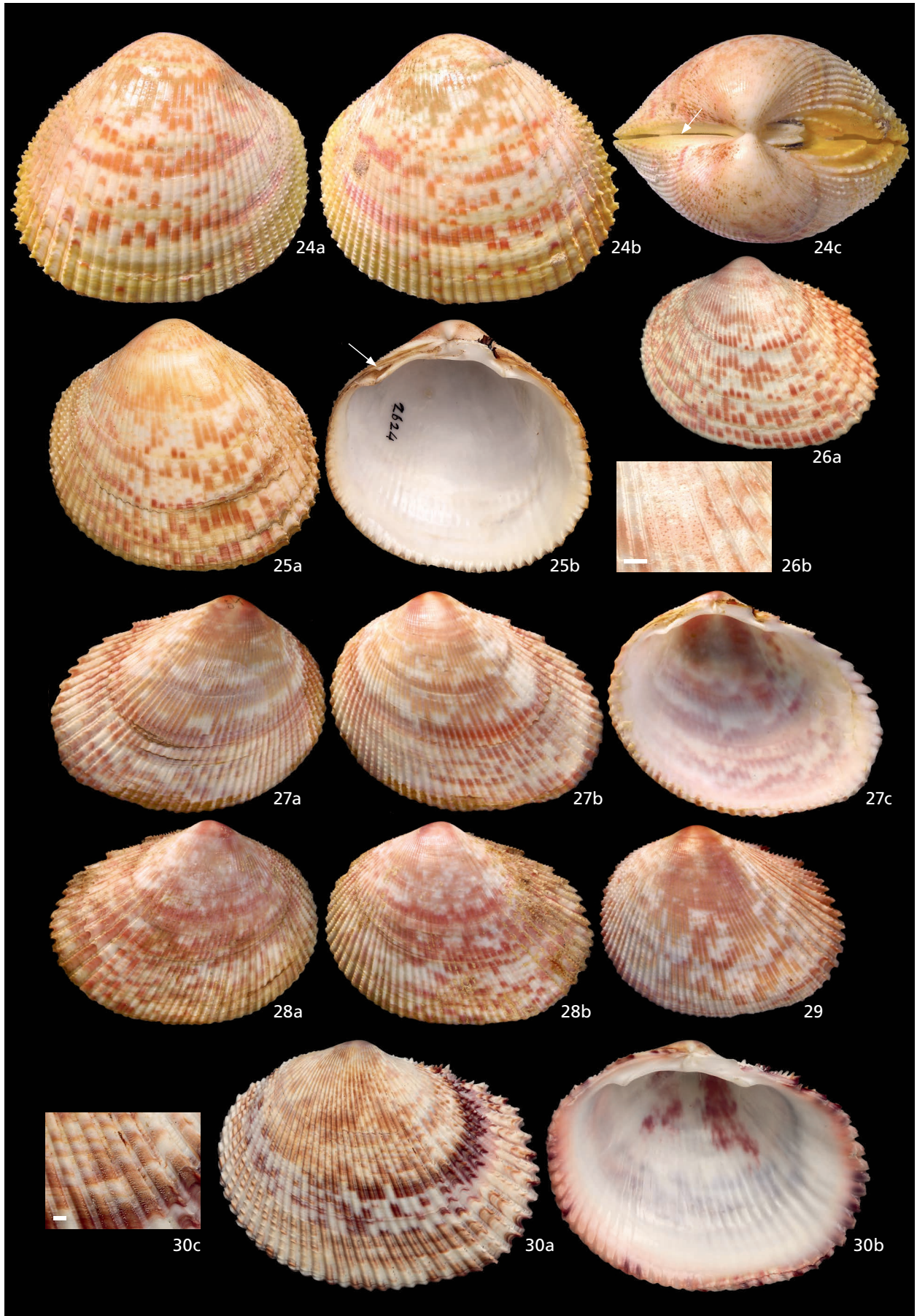
Collection, registration number	L	AL	PL	H	W	Ribs	L/H (L+H)/2	Inflation	AL/PL	Specimen	
SBMNH 348207*, holotype •	69.1	24.7	44.4	52.3	35.2	40	1.32	95.25	0.37	0.56	PV
SBMNH 630925/1, paratype	53.7	21.7	32.0	43.0	28.0	37	1.25	75.20	0.37	0.68	PV
SBMNH 630925/2, paratype	52.4	19.0	33.4	42.6	27.0	41	1.23	73.70	0.37	0.57	PV
ZMA.MOLL.10010, paratype	34.4	13.5	20.9	27.2	17.8	39	1.26	48.00	0.37	0.65	PV
FMNH 344775, paratype	59.2	23.5	35.7	44.8	29.2	39	1.32	81.60	0.36	0.66	PV
MNHN-IM-2014-7069, paratype	55.0	21.7	33.3	43.2	28.7	41	1.27	76.60	0.37	0.65	PV
JJTP 5189, paratype	46.2	16.5	29.7	34.4	22.6	36	1.34	63.40	0.36	0.56	PV
JJTP 437, paratype •	48.4	17.9	30.5	37.9	23.7	38	1.28	67.35	0.35	0.59	PV
JJTP 5173	37.9	15.3	22.6	30.7	19.1	41	1.23	53.25	0.36	0.68	PV
JJTP 543, paratype •	29.0	11.8	17.2	23.0	14.2	36	1.26	40.50	0.35	0.69	PV
JJTP 2572	46.8	18.9	27.9	38.4	25.9	37	1.22	66.00	0.39	0.68	PV
JJTP 1800	61.1	23.4	37.7	44.8	32.9	42	1.36	83.50	0.39	0.62	PV
JJTP 5187	41.3	17.3	24.0	34.3	22.9	38	1.20	58.45	0.39	0.72	PV
JJTP 3878, paratype •	61.8	24.8	37.0	47.6	30.4	41	1.30	85.60	0.36	0.67	PV
JJTP 3510/1	65.3	27.3	38.0	49.9	33.7	38	1.31	90.25	0.37	0.72	PV
JJTP 3510/2	61.3	24.1	37.2	47.0	33.9	39	1.30	84.80	0.40	0.65	PV
JJTP 4389/1	46.6	18.7	27.9	37.3	24.3	40	1.25	65.25	0.37	0.67	PV
JJTP 4389/2	42.0	15.4	26.6	30.3	20.4	45	1.39	57.15	0.36	0.58	PV
JJTP 5175/1	59.0	23.5	35.5	45.8	30.9	43	1.29	81.90	0.38	0.66	PV
JJTP 5175/2	56.9	22.1	34.8	41.6	28.5	40	1.37	77.70	0.37	0.64	PV
Mean values						39.55	1.29		0.37	0.64	

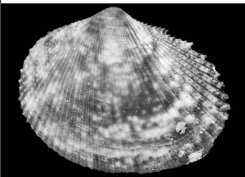
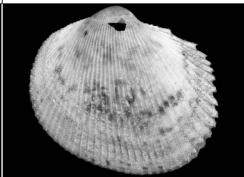

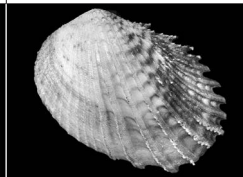
Table 2. Shell measurements (mm) of *Papyridea curvicostata* spec. nov. Material figured herein indicated with a black dot (•).

* Sizes slightly deviate from those given by Coan & Valentich-Scott (2012) due to minor differences in the way of measuring (see Material and methods section).

< **Figs 18-23.** *Papyridea hiulca* (Reeve, 1845). **18-19.** Ecuador, Manta. Leg. A. Olsson, 1958. **18.** ANSP 218895, holotype of *Papyridea mantaensis* Olsson, 1961, L 40.5 mm (a: LV exterior, b: LV interior). **19.** ANSP 218896, paratype of *Papyridea mantaensis* Olsson, 1961, L 33.6 mm (RV exterior). **20-21.** Unknown provenance. Coll. H. Cuming. **20.** NHMUK 197837, lectotype, L 22.9 mm (a: LV exterior with weak curvature of radial ribs highlighted, b: RV exterior, c: LV interior with numbered ribs, d: RV interior with numbered ribs). **21.** NHMUK 197837, paralectotype, L 22.7 mm (a: LV exterior, b: RV exterior). **22.** Panama, Pacific coast, Bahía de Chiriquí, Gobernadora Island, dredged, 20-30 m. Leg. J. Ernest, 05.2010, JJTP 4388, L 28.5 mm (a: RV exterior, b: LV interior, c: dorsal with numbered ribs, d: RV interior with ribbing and hinge details highlighted). **23.** Panama, Veraguas, Montijo District, Isla Cebaco, 7°31'N, 81°14.8'W, trawled, 60-120 ft [18-37 m]. Leg. L. Marr, 01.1997-2001, SBMNH 630928, L 29.5 mm (LV exterior). Scale bars: 1 mm.

> **Figs 24-26.** *Papyridea crockeri* (A.M. Strong & Hertlein, 1937). **24.** Mexico, Sonora District, by shrimpers working out of Guaymas, SH, no. reg. no., L 52 mm (a: RV exterior, b: LV exterior, c: dorsal). **25.** Mexico, Sonora District, Guaymas, offshore, trawled by shrimpers, 12.1976, JJTP 2624, L 41.2 mm (a: LV exterior, b: RV interior). **26.** Mexico, Baja California Sur, Isla Danzante, N.E. end, 25.804°N, 111.249°W, 200-300 ft [61-91 m]. Leg. C. Norrid, 1995, SBMNH 213403 (a: LV exterior, b: MPQ with minute granulations). **Figs 27-30.** *Papyridea aspersa* (G.B. Sowerby 1, 1833). **27-29.** 'ad Sanctam Elenam et ad Montem Christe' [Santa Elena and Monte Cristil], in sandy mud, 7 fms. Coll. H. Cuming, NHMUK 20130521, syntypes. **27.** L 42.6 mm (a: RV exterior, b: LV exterior, c: RV interior). **28.** L 40.7 mm (a: RV exterior, b: LV exterior). **29.** L 37.9 mm (LV exterior). **30.** Panama, Veraguas, Montijo District, Isla Cebaco, 7°31'N, 81°14.8'W, trawled, 60-120 ft [18-37 m]. Leg. L. Marr, 01.1997-2001, SBMNH 167953, L 52.9 mm (a: LV exterior, b: RV interior, c: MPQ with minute granulations). Scale bars: 1 mm.



	TROPICAL ATLANTIC			
Species	<i>Papyridea lata</i>	<i>Papyridea clenchi</i> spec. nov.	<i>Papyridea soleniformis</i>	<i>Papyridea semisulcata</i>
				
Shell shape	Oval, weakly inequilateral	Obliquely oval, moderately inequilateral	Elongated oval, strongly inequilateral	Obliquely oval, strongly inequilateral
Umbones	Orthogyrous or weakly opistogyrous	Weakly to strongly prosogyrous	Orthogyrous or weakly opistogyrous	Prosogyrous or orthogyrous
Shell thickness and solidity	Shell very thin, fragile	Shell very thin, fragile	Shell rather thin but solid	Shell thin, fragile
Common adult size / Maximum size (source)	L 30-40 mm / L 47.5 mm (JTP 5177)	L 20-30 mm / L 39.5 mm (UF 16138)	L 40-50 mm / L 61.5 mm (Huber, 2010)	L 10-15 mm / L 18 mm (Huber, 2010)
Number and nature of radial ribs	43-59 low rounded ribs, in juveniles hardly developed on median part	42-49 low triangular ribs	40-49 rounded ribs	27-32 low rounded ribs, very broad on MPQ, higher and strongly digitate on PQ
Location of first rib posterior of umbo	RV	RV	RV	RV
Microscopic granulations on shell exterior	Scattered granulations present, mainly on MPQ	Scattered to dense granulations present on most parts of the shell	Completely lacking	Completely lacking
Rib sculpture on AQ, median part and PQ	AQ: small scales; median part unsculptured; PQ: spinose, rather close-set	AQ: minute spatulate scales; median part unsculptured; PQ: tiny spinose, rather distantly placed	AQ: small scales; median part unsculptured; PQ: spinose, rather close-set	AQ: minute spatulate scales; median part unsculptured; PQ: spinose scales, more or less interconnected
Lunular-like area on antero-dorsal margin	Elongate and narrow	Elongate, wide and hollowed	Indistinct or elongate and very narrow	Relatively short, often wider in RV; sometimes poorly defined
Anterior dorsal lateral tooth in RV	Poorly developed	Well developed	Lacking	Lacking
External colouration	Whitish with large patches of yellow, orange, pink or purple; umbonal area with two broad orange or purple radial rays	Whitish with sparse yellowish or reddish-brown blotches; umbo orange-brown or red-brown	Whitish or yellowish with reddish-brown or yellowish blotches and flecks; umbonal area sometimes with 1-2 purple radial rays	Whitish with often pinkish or yellowish patches on posterior half. Occasionally pure lemon yellow or orange

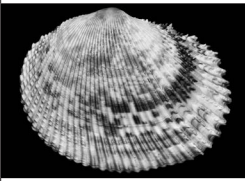
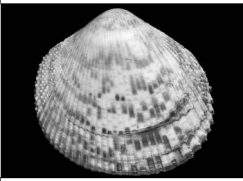
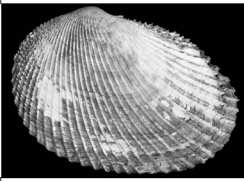
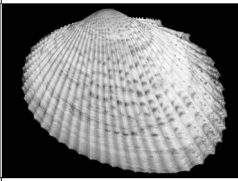
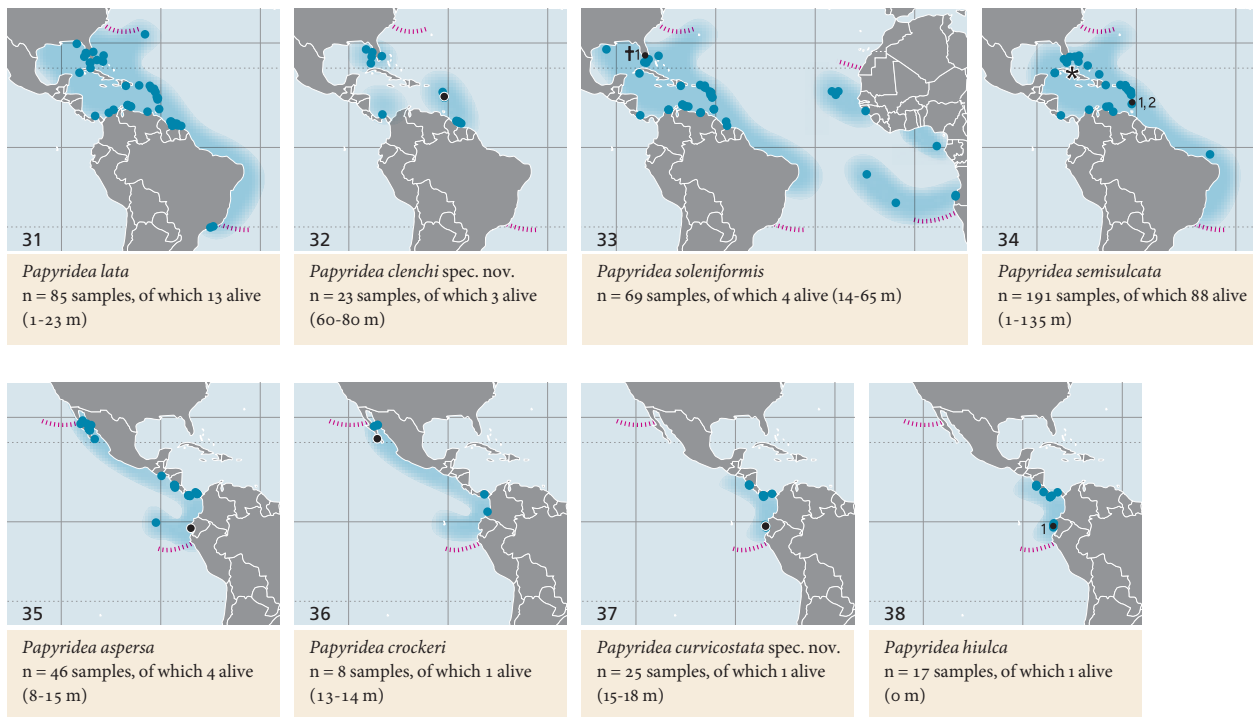
	TROPICAL EASTERN PACIFIC			
Species	<i>Papyridea aspersa</i>	<i>Papyridea crockeri</i>	<i>Papyridea curvicostata</i> spec. nov.	<i>Papyridea hiulca</i>
				
Shell shape	Oval, weakly inequilateral	Oval, weakly inequilateral	Elongated oval, strongly inequilateral	Obliquely oval, strongly inequilateral
Umbones	Weakly to strongly opisthogyrous	Orthogyrous or weakly opisthogyrous	Weakly to strongly opisthogyrous	Weakly to strongly opisthogyrous
Shell thickness and solidity	Shell rather thin but solid	Shell rather thin but solid	Shell rather thin but solid	Shell rather thin but solid
Common adult size / Maximum size (source)	L 40-50 mm / L 64 mm (Coan & Valentich-Scott, 2012)	L 40-50 mm / L 60 mm (Coan & Valentich-Scott, 2012)	L 50-60 mm / L 69 mm (SBMNH 348207)	L 30-50 mm / L 64 mm (Olsson, 1961)
Number and nature of radial ribs	41-52 low rounded ribs	42-48 rounded ribs, flattened on median part	36-45 rounded triangular ribs	33-38 high triangular ribs, posteriormost ribs dorsally projecting
Location of first rib posterior of umbo	RV (poorly developed) or LV (well developed)	RV	LV	RV
Microscopic granulations on shell exterior	Dense granulations present on MPQ	Scattered granulations present on MPQ	Completely lacking	Completely lacking
Rib sculpture on AQ, median part and PQ	AQ: well developed scales; median part: tiny, close-set papillae or unsculptured; PQ: twisted spatulate scales	AQ: scales, not covering the full rib width; median part: close-set papillae; PQ: twisted spatulate scales	AQ: irregularly sized scales; median part unsculptured; PQ: twisted spatulate scales	AQ: irregularly sized scales; median part unsculptured; PQ: twisted spatulate scales, posteriormost projecting and close-set
Lunular-like area on antero-dorsal margin	Indistinct or elongate and very narrow	Elongate, wide and hollowed	Indistinct or elongate and very narrow	Elongate and narrow
Anterior dorsal lateral tooth in RV	Lacking	Well developed	Lacking	Lacking
External colouration	Whitish with large patches of reddish-brown or pink, sometimes predominantly yellowish or orange	Whitish or yellowish, with reddish-brown patches, often confined to the ribs; PQ orange-yellow	Whitish or yellowish with orange-brown blotches; umbonal area often orange-brown or red-brown	Completely whitish or whitish with small purple-pinkish mottlings; umbonal area sometimes uniform purple-brown

Table 3. Comparative summary of shell characters of all living *Papyridea* species (based on adult material). Left page: tropical Atlantic taxa; above: tropical eastern Pacific taxa.



Figs 31-38. Distributions of *Papyridea* species as currently known. Borders of fauna provinces with red striped lines. Black circle: type locality; black asterisk: type area (in case no specific locality is given); blue circles: verified samples; dagger (†): extinct. Number of samples (n) given, including number of live samples and depth range based on live samples. Material mainly originating from FMNH, MNHN, RMNH (ex ZMA), SBMNH, UF, and JTP. **33.** No. 1: type locality of *Cardium* (*Papyridea*) *spinosum* var. *turtoni* Dall, 1900 (†), junior synonym of *Cardium soleniformis* Bruguière, 1789. **34.** No. 1: type locality of *Cardium ringiculum* G.B. Sowerby II, 1834; no. 2: type locality of *Cardium petitianum* d’Orbigny in Sagra, 1853. Both: junior synonyms of *Cardium semisulcatum* Gray, 1825. **38.** No. 1: type locality of *Papyridea mantaensis* Olsson, 1961, junior synonym of *Cardium hiulcum* Reeve, 1845.

The undistorted paralectotype of *P. hiulca* (Fig. 21) even more closely agrees with the juvenile stage of the holotype of *P. mantaensis* (Fig. 18). It appears that *P. hiulca* is rather vulnerable to shell damage, as shown by commonly occurring shell malformations, especially affecting the ventral margin.

DISCUSSION

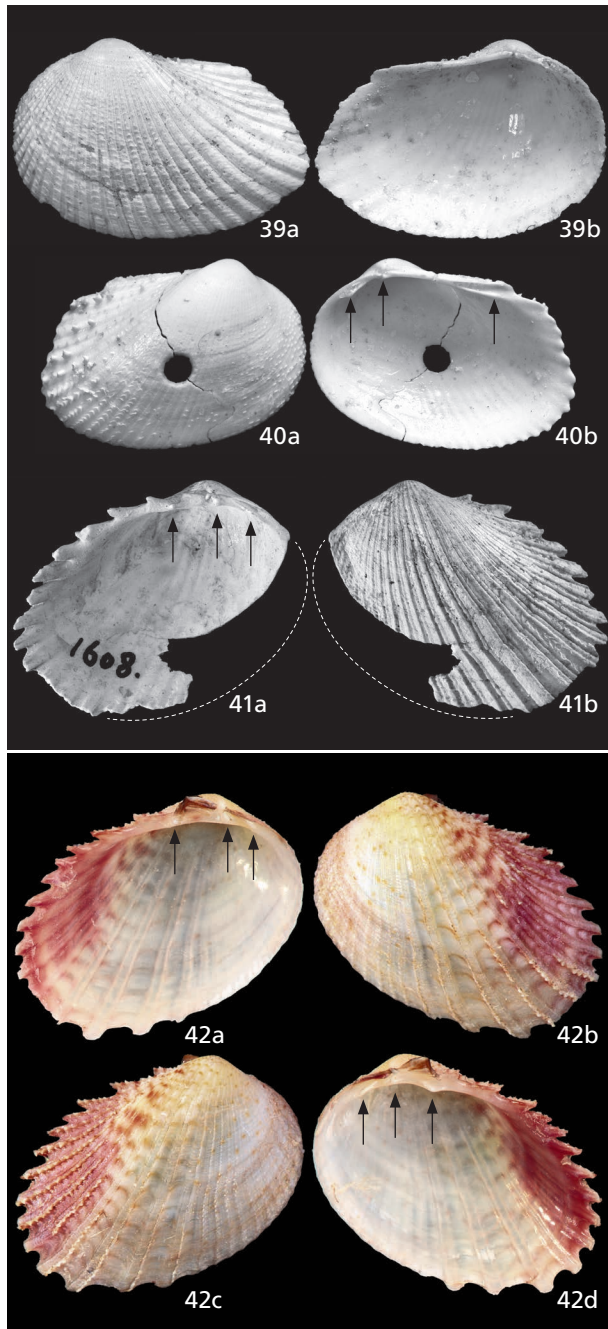
Evolution and dispersal of *Papyridea*

Several authors, including Cossmann (1886), Glibert & Van de Poel (1970) and Kafanov (1997, 2001) include *Cardium capsoides* Bayan, 1873 from the Paris Basin, France (Middle Eocene, Upper Bartonian) in *Papyridea*. Indeed, at first sight this species (Figs 39-40) has an overall appearance that is roughly similar to *Papyridea*. However, it considerably differs by the following characters: an elongated quadrangular shape, a rather well-marked umbonal keel with an angular postero-ventral margin, a weakly crenulate posterior margin, rather narrow interstices on the median part of the shell, reduced cardinal teeth, very long posterior lat-

eral teeth with the tip of the posterior lateral much further away from the cardinals than the tip of the anterior lateral (Fig. 40b, arrows), a rather long nymph plate and a rib sculpture consisting of crescent-shaped or chevron-shaped scales.

If that assignment is rejected, the next oldest unequivocal representatives are *P. multicostrula* H.E. Vokes, 1977, *P. bulbosa* (Dall, 1900) and *P. miocica* H.E. Vokes, 1977, all from the Late Early Miocene, Chipola Formation, Florida., U.S.A. A Miocene age of *Papyridea* is also advocated by Keen (1980) and Schneider (1998a: 60), the latter considering all alleged Eocene *Papyridea* records species of *Parvicardium*. Rib sculpture and hinge characteristics of “*Cardium*” *capsoides* indeed point at a closer relationship with *Parvicardium*, though the elongated quadrangular shape is different. Two *Parvicardium* species, *P. vroomi* van Aartsen, Menkhorst & E. Gittenberger, 1984 and *P. trapezium* Cecalupo & Quadri, 1996, do have a shell shape that is rather similar to *C. capsoides*.

Western Atlantic and eastern Pacific taxa have been regarded as species pairs or “cognate species” (Radwin, 1969; Vermeij, 1978; Bernard et al., 1991) resulting from the emer-



Figs 39-40. “*Cardium*” *capsoides* Bayan, 1873. **39.** France, Paris Basin, Val d’Oise, Le Guépelle. Eocene, Bartonian. PH 495, L 11.7 mm (a: LV exterior, b: LV interior). **40.** France, Paris Basin, Oise, Hadancourt. Eocene, Bartonian. PH 25886, L 10.5 mm (a: RV exterior, b: RV interior). **Fig. 41.** *Papyridea ponteleviense* (Mayer, 1868). France, Loire Basin, Vienne, s. of Mirebeau, Amberre, disused sand quarry. Middle Miocene, ‘Helvetian’ [Langhian], faces Pontilevian. JJTP 1698, L 17.9 mm (a: LV interior, b: LV exterior). **Fig. 42.** *Papyridea semisulcata* (Gray, 1825). Martinique, Le Prêcheur, s. Pointe Lamare, 14°46.8’N, 61°12.7’W, 17 m, by brushing, alive, 04.10.2016. MADIBENTHOS, stn AB386, MNHN-IM-2014-7068, L 9.4 mm (a: LV interior, b: LV exterior, c: RV exterior, d: RV interior). Arrows indicating the tip of the main cardinal and lateral teeth.

gence of the Central American Isthmus (CAI) and the closure of the Central American Seaway in the Pliocene, that ended the wide-scale and mostly one-way (from Atlantic to Pacific) migrations of marine biota (Kafanov, 2001). The final separation of planktotrophic molluscs on the two coasts of tropical America by uplift of the CAI occurred at about 2 Ma (Beu, 2010, from the evidence of tonnoidean gastropods), at the Plio-Pleistocene boundary. A recent study pinpoints the formation of the Isthmus of Panama at around 2.8 Ma (O’Dea et al., 2016).

Traditionally, *Papyridea aspersa* was recognised as the eastern Pacific counterpart of *P. soleniformis* (Odé, 1975; Vermeij, 1978; Bernard et al., 1991; Vermeij & Rosenberg, 1993; Watters, 2002). Additionally, Watters (2002) considered *P. crockeri* the eastern Pacific counterpart of *P. lata*. Based on gross morphological similarities and including the two new *Papyridea* species of this paper, the following Atlantic-Pacific geminate species pairs could be recognized, with the most notable shared characters added in brackets (Atlantic species listed first):

1. *Papyridea lata* – *P. aspersa* (subequilateral, shell relatively flattened, anterior + posterior granulations)
2. *P. soleniformis* – *P. curvicostata* sp. nov. (strongly inequilateral, elongated oval, large size, no granulations)
3. *P. clenchi* sp. nov. – *P. crockeri* (rounded shape with comparable L/H ratio, well defined lunular-like area, granulations)

Powell (1986, 1988) discusses a species, as ‘*P. crockeri* new subspecies’, from the Imperial Formation (currently interpreted as an unnamed lower member, Late Miocene; pers. comm. C.L. Powell, II, 06.2019) at Super Creek, southern California, U.S.A. Based on the figures (Powell, 1986: pl. 12 figs 3, 6), the most closely related species are *P. bulbosa*, *P. clenchi* sp. nov. and *P. crockeri*. Lacking any further pre-Pleistocene eastern Pacific data of *Papyridea*, this record seems to be the only evidence of a pan-tropical American occurrence of the genus before the closure of the CAI. Contrarily, several Pleistocene records are known, involving the following eastern Pacific species:

1. *P. aspersa*: Hoffstetter (1948), from the Pleistocene Third Terrace at Santa Elena, Guayas Province, Ecuador; Aguilar (1987), as *P. aff. aspera* [sic!], from the Montezuma Formation (Pleistocene: Beu, 2010), South Costa Rica; Ashby & Minch (1987) from the late Pleistocene of Baja California Sur, Mexico.
2. *P. hiulca*: García-Talavera (1993), as *P. cf. mantaensis*, and Ragaini et al. (2002), as *P. mantaensis*, from the Pleistocene of the Galápagos Islands. It is not listed as part of the living fauna of the Galápagos Islands (Hickman & Finet, 1999; Coan & Valentich-Scott, 2012).

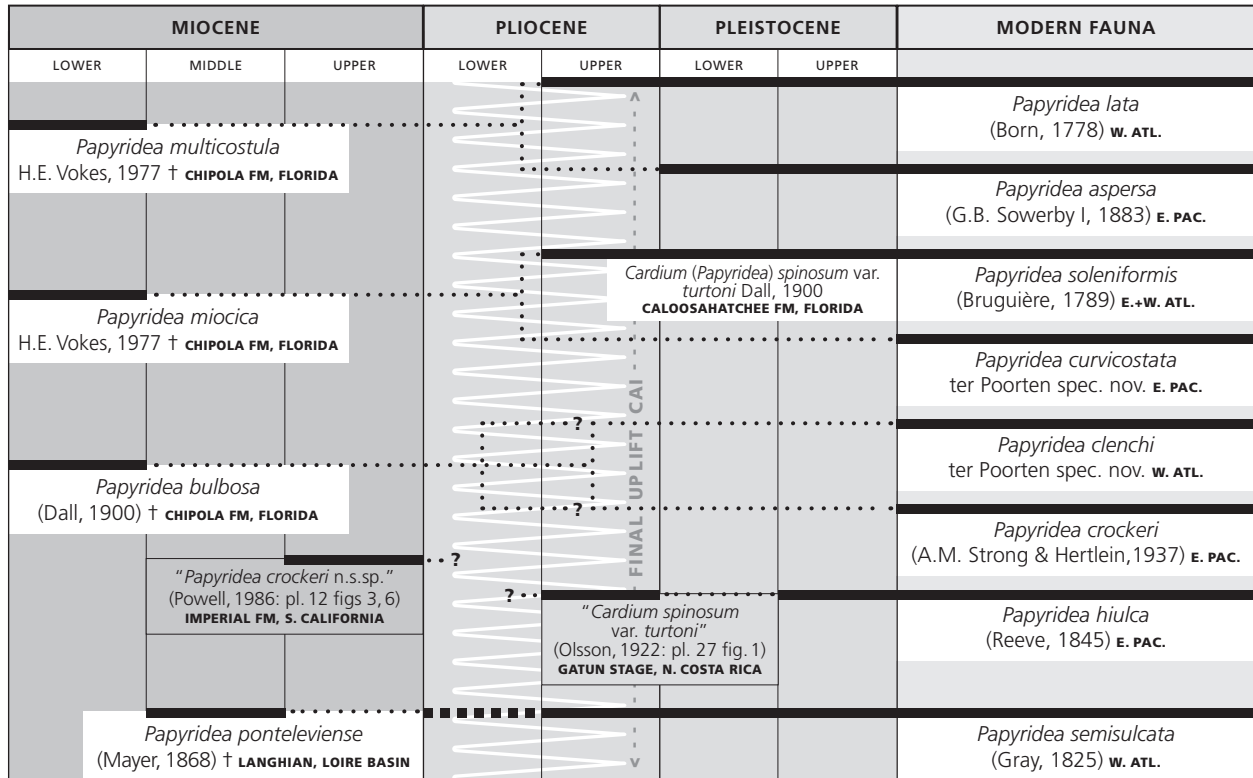


Fig. 43. Hypothetical phylogeny of *Papyridea*. Indicated references are discussed in the text. Time span of the latest uplift of the Central American Isthmus (CAI) denoted by a white zigzag line.

Based on the fossil record, a predominantly one-way migration (from Atlantic to Pacific) through the Isthmus of Panama is hypothesized. The available data suggest that at least species pairs 1-2 are the result of allopatric speciation after the uplift of the CAI. Regarding the third species pair, *P. clenchi* sp. nov. – *P. crockeri*, there is more uncertainty. The Late Miocene record of *P. crockeri* sensu Powell (1986) could also indicate a scenario of a Miocene or early Pliocene speciation event long before the final uplift of the CAI. This has been inferred for other bivalve lineages in the region (e.g. Marko, 2002; Marko & Moran, 2009).

Papyridea hiulca, with its projecting posterior-most ribs and attenuate anterior part, does not easily fit with a modern Caribbean congener. A rather similar and possibly ancestral specimen is figured by Olsson (1922: pl. 27 fig. 1) from North Costa Rica, Limón, ‘Gatun Stage’ (late Pliocene; Beu, 2010), misidentified as *Cardium (Papyridea) spinosum* var. *turtoni* Dall, 1900 (junior homonym of *Cardium turtoni* G.B. Sowerby III, 1894; junior synonym of *Cardium soleniforme* Bruguière, 1789). Hence a scenario in which *P. hiulca* or its ancestor lived in both the Atlantic and the Pacific side of tropical America during the Pliocene, followed by a regional extinction in the Atlantic and with the eastern Pacific serving as a refuge, is not unlikely. It would represent an evolutionary pathway typical for many tropical American taxa (Vermeij & Petuch, 1986).

The Caribbean *Papyridea semisulcata* (Fig. 42) lacks an eastern Pacific counterpart and forms a different lineage, with a different biogeographic history. It is much smaller, has a considerably lower radial rib number (27-32) and ribs on the MPQ that are much broader than on other parts of the shell. Olsson & Harbison (1953: pl. 15 fig. 7) illustrate material from the Pliocene of St. Petersburg, Florida, U.S.A. Dall (1900: 1109) records material from the ‘Miocene of the Natural Well’, which is the Duplin Formation ‘Natural Well biota’, from Natural Well, Duplin Co, North Carolina, correlated by Campbell (1993) with the Yorktown Formation (lower to middle Pliocene). Unfortunately, Campbell et al. (1995) do not list the species. Portell & Kittle (2010) record the species from the Bermont Formation, middle Pleistocene, Florida, U.S.A. The ancestor of *P. semisulcata* appears to be *P. ponteleviense* (Mayer, 1868) (Fig. 41; also extensively figured by Dollfus & Dautzenberg, 1913: pl. 27 figs 1-6), from the Loire Basin, France (middle Miocene, lower Helvetian; now considered as Langhian). This species has a shell morphology that is so remarkably similar to *P. semisulcata* that an inference of close relationship seems warranted. In the phylogenetic tree of Herrera et al. (2015) *P. semisulcata* has a very long branch, suggesting a relatively long, unmodified evolutionary history. A hypothetical phylogeny of *Papyridea* is given in Fig. 43.

Profulvia Kafanov, 1976 was introduced as a genus, and

later ranked as a subgenus of *Papyridea* and placed in subfamily Cardiinae (Kafanov, 1997). Apart from the more reduced rib sculpture, '*Profulvia* hardly differs from the typical *Papyridea*' (Kafanov, 1997: 3). This high-latitude North Pacific group of cardiids has as oldest representative *P. utchokense* (Slodkewitsch, 1938) from the Middle Eocene (Upper Lutetian) of W. Kamchatka (Kafanov, 2001) and as youngest *P. kurodai* (Hatai & Nisiyama, 1952) from the Sawane Formation, Lower Pleistocene of Sado City, Japan (see also Amano & Tanaka, 1992). The Eocene "*Cardium*" *capsoides* not only considerably differs from *Papyridea*, but is also unrelated to *Profulvia*. Hence the predominant Paleogene / Early Neogene Tethyan evolutionary pathway as sketched for *Profulvia* by Kafanov (2001) is not supported. Phylogenetic analysis (Schneider, 1998b) led to placement of *Profulvia* in Clinocardiinae, sister to *Ciliatocardium*. The type species, *Papyridea harrimani* Dall, 1904, from the 'Miocene' (now assigned to the Stepovak Formation, Lower Oligocene) of Popof Island, Alaska, has the following characteristics (based on examination of the holotype, USNM MO 164867): oval shell shape, moderately inflated, weakly inequilateral, shell gaping posteriorly and at least 45 countable ribs that are weakly sculptured. These characters clearly indicate a close relation with *Papyridea*. Moreover, *P. kurodai* has ribs that become considerably broader on the posterior slope, a character typical for *Papyridea*. Following the phylogenetic results of Herrera et al. (2015), placement of *Papyridea* in Trachycardiinae is appropriate.

CONCLUSIONS

The recognition of two new species of *Papyridea* in tropical America, and a re-evaluation of some fossil forms sheds light on the origin and diversification of the genus. The rejection of the Middle Eocene *Cardium capsoides* as oldest representative of *Papyridea*, implying that the oldest species are rooted in the Late Early Miocene of the western Atlantic, has major consequences for our understanding of the dispersal of the genus in the Neogene. A scenario as advocated by Kafanov (2001), in which *Profulvia* originated from *Papyridea* due to dispersal from the Paleogene Mediterranean via the Indo-West Pacific to the North Pacific, needs re-evaluation. The same is the case for hypothesized unidirectional Oligocene and Miocene migrations from the Mediterranean to the western Atlantic. Our knowledge of the speciation events and evolutionary pathways of *Papyridea* and *Profulvia* is still fragmentary, as exemplified by a single Miocene tropical eastern Pacific *Papyridea* record and the occurrence of a single species in the European Neogene. More complete sampling and additional taxonomic research is needed to reconsider the above scenarios and address alternative dispersal models. Our current

knowledge of the evolution of *Papyridea* points to multiple instances of local extinction and geographical restriction, with the Caribbean as possible centre of diversification. A scenario in which *Papyridea* evolved in the Late Paleogene from *Profulvia*, rather than the other way around, cannot be excluded, but is hampered by the poor Mio-Pliocene fossil record of *Papyridea* in the tropical eastern Pacific.

ACKNOWLEDGEMENTS

The MADIBENTHOS expedition was spearheaded by the French Agency for Marine Protected Areas (now part of the French Agency for Biodiversity), the Regional Directorate for the Environment (DEAL), and the Martinique Water Bureau (ODE), with support from the Directorate of the Sea (DM) and the Martinique Natural Regional Park (PNRM). It was implemented by Muséum national d'Histoire naturelle (MNHN, Principal Investigator Philippe Bouchet), with funding from the European Regional Development Fund (ERDF), the Territorial Collectivity of Martinique (CTM), Plantations Saint-James et BRED. The expedition was hosted in Fort-de-France on the French Navy Base, and also benefited from the support of Université des Antilles, and the NGOs OCEANVIRONNEMENT and Flabellina.

Philippe Bouchet (MNHN) is kindly acknowledged for sending cardiid material of this and other Caribbean expeditions on loan. Rüdiger Bieler, Jochen Gerber (both: FMNH) kindly searched their holding for both new *Papyridea* species. John Slapcinsky (UF) is thanked for hosting the author at the UF; the u.s. National Science Foundation Grant 1633535 (to David Jablonski) supported travel costs. Paul Callomon and Amanda Lawless (ANSP); Andreia Salvador and KathieWay (NHMUK) and Thomas Waller (USNM) are acknowledged for allowing the author to study their collections.

Harry Lee (UF) kindly checked the collections for the presence of the new Caribbean species. Bram van der Bijl and Jeroen Goud (both: RMNH) searched the collection for *Papyridea* samples. Paul Valentich-Scott and Cara Fuller (SBMNH) kindly sent *Papyridea* material on loan, including the new eastern Pacific species. Piet and Rudi Hessel (Stichting Schepel Schelp, Rhenen, The Netherlands) and Sue Hobbs, Cape May, U.S.A., kindly gave access to their collection. Charles Powell, II (United States Geological Survey) kindly shared information and literature. Henk Menkhorst (Naturalis) kindly gave linguistic advice regarding the specific epithet of one of the new species. David Jablonski (University of Chicago) read an earlier version of the manuscript and kindly made valuable suggestions for improvement. The constructive comments made by the reviewers, Rüdiger Bieler and Paul Valentich-Scott, are much appreciated and attributed to improve the manuscript.

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APPENDIX

Supplementary data

From the following living and fossil species in the paper, a 3D-image with animation (by K.S. Collins, courtesy of the Jablonski Lab, University of Chicago) has been made publicly available by the following permalinks:

- Papyridea curvicostata* ter Poorten spec. nov. Paratype, FMNH 344775: https://www.morphosource.org/Detail/MediaDetail/Show/media_id/46240
- Papyridea clenchi* ter Poorten spec. nov. Paratype, JSTP 1489: https://www.morphosource.org/Detail/MediaDetail/Show/media_id/46242
- Papyridea lata* (Born, 1778), FMNH 182759: https://www.morphosource.org/Detail/MediaDetail/Show/media_id/41095
- FMNH 770532: https://www.morphosource.org/Detail/MediaDetail/Show/media_id/46243

- Papyridea soleniformis* (Bruguière, 1789), FMNH 301980: https://www.morphosource.org/Detail/MediaDetail/Show/media_id/41098
- Papyridea semisulcata* (Gray, 1825), FMNH 189372: https://www.morphosource.org/Detail/MediaDetail/Show/media_id/41096
- Papyridea aspersa* (G.B. Sowerby 1, 1833), USNM 78650: https://www.morphosource.org/Detail/MediaDetail/Show/media_id/46238
- https://www.morphosource.org/Detail/MediaDetail/Show/media_id/46239
- Papyridea bulbosa* (Dall, 1900), UF 43729: http://www.morphosource.org/Detail/MediaDetail/Show/media_id/46304