

A new species of *Tethocyathus* (Cnidaria: Anthozoa: Scleractinia: Caryophylliidae), a trans-isthmian azooxanthellate species

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Abstract.—A new species of *Tethocyathus* is described, *T. prahli*, characterized by having a tympaniform corallum shape and no fossa. Specimens were found living at 310 m in the Colombian Caribbean, 303–333 m at Cocos Island (Pacific Costa Rica), and from the early Pleistocene of Pacific Panama, suggesting a relictual distribution of a previously more widespread species. *Tethocyathus prahli* is probably unique among the Scleractinia in having a non-cosmopolitan trans-isthmian distribution. The diagnosis of the genus *Tethocyathus* is emended to conform more closely to that of the type species.

The discovery of an undescribed species of *Tethocyathus* from the Colombian Caribbean and the same species from the Pleistocene of Pacific Panama raised interesting zoogeographic questions. In the course of writing the paper, several more specimens were discovered from the Recent of Cocos Island, reinforcing our zoogeographic interpretation. i.e., that living *T. prahli* represent a trans-isthmian relictual distribution of a moderately shallow-water azooxanthellate species that was more widely and continuously distributed in the early Pliocene of both ocean realms. It is one of the very few scleractinian corals to have an trans-isthmian distribution in relatively shallow water.

Abbreviations

BID: Banco Interamericano de Desarrollo.
COLCIENCIAS: Instituto Colombiano para el desarrollo de la Ciencia y la Tecnología, Francisco José de Caldas.
H:D: Ratio of height to maximum calicular diameter of a corallum.
INVEMAR: Instituto de Investigaciones

Marinas y Costeras “José Benito Vives de Andreis” (Santa Marta, Colombia).

SEM: Scanning Electron Microscope.

STRI: Smithsonian Tropical Research Institute, Panama.

USNM: United States National Museum, Washington, DC (now the National Museum of Natural History).

S_x , C_x , P_x : cycle of septa, costae or pali, respectively, designated by numerical subscript.

$S_x > S_y$: in the context of a septal formula, septa of cycle x are wider than those of cycle y .

Methods

Colombian specimens were collected using a bottom trawl of 9 by 1 m in aperture and 16 m length during INVEMAR Macro Fauna cruise 2 (Dec 1998). Pleistocene corals were collected as part of the Panama Paleontology Project. The Cocos Island specimens were collected on the *Johnson-Sea-Link* Galápagos/Cocos Islands Expedition of 1986, sponsored by the Harbor Branch Oceanographic Institute.

The holotype is deposited at INVEMAR,

paratypes at the USNM and INVEMAR. Paratype images were taken at the USNM using SEM; other images were obtained and processed using methods described by Reyes and Navas (in press).

Systematics

Order Scleractinia Bourne, 1900
Suborder Caryophylliina Vaughan and Wells, 1943

Family Caryophylliidae Dana, 1846
Genus *Tethocyathus* Kühn, 1933

Diagnosis (emended).—Corallum solitary, tympaniform to subcylindrical; attached through a polycyclic base. Septotheca costate, but covered with tectura. Paliform lobes before first cycle of septa; discrete pali before all but first and last cycle of septa. Columella papillose.

Type species.—*Theocyathus microphyllus* Reuss, 1871, by original designation.

Remarks.—The emended diagnosis of *Tethocyathus* is narrower than that given by Cairns (1979) in that it requires a polycyclic base and a thecal tectura (sensu Stolarski 1995 and Roniewicz & Stolarski 1999), both characters found in the type species. Of the three Recent western Atlantic species placed in this genus by Cairns (1979), only one fulfills these requirements: *T. cylindraceus* (Pourtalès, 1868). The other two species, *T. recurvatus* (Pourtalès, 1878) and *T. variabilis* Cairns, 1979, have monocyclic bases. Two additional species exist in the western Pacific: *T. virgatus* (Alcock, 1902) and *T. minor* (Gardiner, 1899). The genus is very similar to *Trochocyathus*, differing in having a polycyclic base, a relatively squat corallum, and tectura-covered theca.

The first cycle of entosepta (i.e., S_1) of *Tethocyathus* may give off one or two crowns of paliform lobes, pali being found before the succeeding entoseptum. The diagnostic character for *Trochocyathus* and *Tethocyathus* "pali before all but the last cycle of septa" (Vaughan & Wells 1943: 205–206, Wells 1956: F423) does not distinguish pali from paliform lobes; therefore,

we propose the diagnostic character be changed to: paliform lobes before first cycle of septa and pali before all but first and last cycles of septa.

Tethocyathus prahli, new species

Fig. 1

Description.—Corallum tympaniform (H:D usually < 0.5) and firmly attached by an expanded base. Polycyclic base contains up to 5 visible concentric thecal rings; counting from the center of the holotype, rings 2, 3, 4 and 5 measure 1.12 mm, 1.92 mm, 2.42 mm and 2.97 mm in diameter, respectively. Initial ring can not be seen from above because it is covered by the columella; however, in other coralla the first ring is about 0.7 mm in diameter. Calice round to elliptical; calicular edge slightly serrate. Holotype measures 8.1 by 7.7 mm in calicular diameter and 2.5–3.7 mm in height (H:D = 0.46). Theca (tectura) smooth and bears scalloped growth lines. Inner costae (i.e., those not yet encircled by a thecal ring) thin, ridged, and not granular; outer costae (i.e., those occurring on surface of outermost thecal ring) broader and granular. C_{1-3} equal in size; C_4 thinner.

Septa hexamerally arranged in 4 cycles according to the formula: $S_1-S_2 > S_4 \geq S_3$. One paratype (i.e., the complete fossil and largest specimen, calicular diameter 13.8 by 12.0 mm, height 4.5 mm, H:D = 0.33; Fig. 1d) has 54 septa due to the presence of an extra half-system. S_1 and S_2 equal in size and extend 0.75 to columella; each S_1 bears a small paliform lobe and each S_2 bears a small pali. P_{1-2} small (0.34 mm wide) and occur closest to the columella; only one P_2 is wider (0.55 mm) than the others. S_3 slightly smaller or equal in width to S_4 , extend 2/3 width of S_{1-2} , and bear a large pali. P_3 3 times wider (0.9 mm) than P_{1-2} , and are recessed from columella. Therefore, two palar crowns are formed: the inner crown formed by 6 paliform lobes (P_1) and 6 pali (P_2), and an outer crown of 12 P_3 . S_4 fuse by their axial edges to adja-

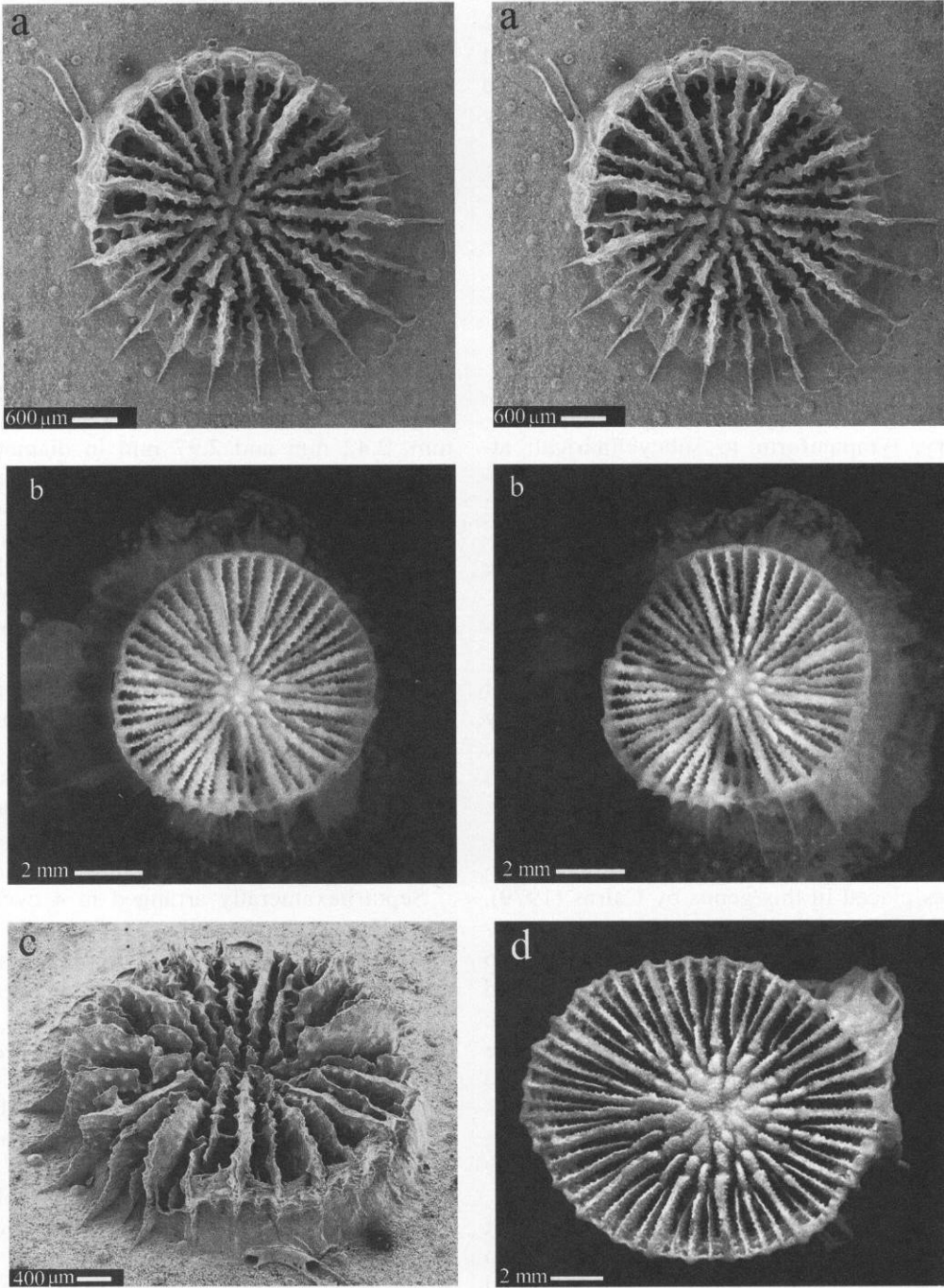


Fig. 1, a–d. *Tethocyathus prahli*. a, c, Recent paratype from Colombia, USNM 100469: a, stereo view of calice; c, oblique calicular view. b, stereo calicular view of holotype. d, Large paratype, Panama Paleontology Project site 148, USNM 95547, calicular view.

cent S_3 or P_3 . Inner edges of S_1 , S_2 and S_4 slightly sinuous; axial edges of S_3 more sinuous. Septal granules numerous, large, and blunt.

Fossa very shallow to non extant. Columella formed of fused papillae: massive and granular, appearing to incorporate part of the P_1 . Each P_{1-2} of fossil corallum have 2 or 3 lobes that extend and fuse to columella.

Discussion.—*Tethocyathus prahli* is quite similar to the type species, *T. microphyllus*, differing from it primarily in shape. *Tethocyathus prahli* has a lower, tympaniform corallum (the H:D ratio of *T. prahli* being between 0.3–0.5), whereas that of *T. microphyllus* is often above 2 and up to 3, i.e., subcylindrical. *T. prahli* also appears to have a larger corallum. *Tethocyathus microphyllus* was most recently described and illustrated by Stolarski (1991). It is known from the Middle Miocene (Badenian) of Poland, Moravia, France, and Morocco. Several voucher specimens from Poland are deposited at the NMNH (USNM 86810 and 96496).

Tethocyathus prahli also differs from *T. cylindraceus* (Pourtalès, 1868) in shape, the latter species being ceratoid to subcylindrical, with a H:D usually over 1. *Tethocyathus cylindraceus* also differs in having a shallow fossa and in having a very thick theca. It is known from the Caribbean (Straits of Florida, Jamaica, Barbados) at 183–649 m (Cairns 2000) and from north-eastern New Zealand (Cairns 1995).

The presence of purportedly the same species in two ocean systems (i.e., the Pleistocene of the eastern Pacific and the Recent of the Caribbean) that have been separated for 3.6–3.5 million years (Coates et al. 1992, Collins 1993), suggests both an evolutionary stasis of that species and the existence of that species in both oceanic realms (i.e., the Gatunian Province) before the closure of the isthmus. Indeed, Collins et al. (1996) logically argue that a deep-water species, such as *T. prahli*, would have been restricted from a trans-isthmian dis-

persal since at least 5.3 Ma. Petuch (1981, 1988:156), based on Neogene and Recent mollusk distributions, has shown there to be several relict pockets within the Caribbean, these faunas containing genera or species surviving from an earlier widespread Late Miocene to Pliocene Gatunian distribution that covered the eastern Pacific and Caribbean regions. One of these relict refugia, which he calls the “Venezuelan Secondary Relict Pocket”, contains several mollusk taxa previously thought to be extinct, and appearing “to be most strongly under the influence of temporal stasis”. The type locality of *T. prahli* lies within this region. We therefore suggest that *T. prahli* existed in the Gatunian Province in both the eastern Pacific and Caribbean in the early Pliocene about 5.3 Ma, freely communicating across the future land bridge when there was still a channel of 150–200 m (Collins et al. 1996). Between 5.3 and 3.5 Ma the genetic exchange was terminated due to the shallowing of the sill depth between the oceans. *Tethocyathus prahli* persisted to the Recent (at Cocos Island) and is documented from the early Pleistocene on the continental margin of the eastern Pacific (Panama), as well as surviving to the Recent in a relictual pocket off Colombia. However, based on so few specimens and the apparent lengthy isolation of the Atlantic and Pacific populations of this purported trans-isthmian species, it is not unreasonable to assume that the type material might represent a cognate species pair or components of a subspecies pair.

No reef corals are known to have a trans-isthmian distribution; however, at least seven azooxanthellate species occur in the Caribbean and eastern Pacific (Cairns et al. 1999). But, all of these species are cosmopolitan in distribution and occur at much greater depths than *T. prahli*. Another two azooxanthellate species appear to have a trans-isthmian distribution: *Madracis pharensis* and *M. asperula*. Both species are well known from both sides of the North Atlantic, and have been tentatively reported

from relatively shallow water (i.e., 16–343 m) from the eastern Pacific (i.e., Nazca Ridge, Chile; Galápagos; Colombia; Rocas Alijos; and Baja California), these occurrences reviewed by Bonilla et al. (1995). However, there is doubt about the identity of these two species with the Atlantic forms, the Pacific specimens always being reported as *Madracis* sp. cf. *M. pharensis*. Thus, *T. prahli* and perhaps two species of *Madracis* constitute the only records of non-cosmopolitan Scleractinia with a transisthmian distribution.

Etymology.—This species is named in honor of Henry Von Prah (1949–1989), who made significant contributions to the knowledge of Colombian corals (Ramos & Lemaitre 1991).

Types.—Holotype: INVEMAR Macro Fauna cruise 2, sta. 49, INVEMAR-COR 241. Paratypes: INVEMAR Macro Fauna cruise 2, sta. 49, 1 SEM stub, USNM 10046, and one corallum deposited at INVEMAR-COR 242. *Johnson-Sea-Link I-1943* (5°26'04"N, 87°07'59"W), Cocos Island, Costa Rica, 303–333 m, 2 Dec 1986, USNM 84868. Panama Paleontology Project site 047, 3 fragments, USNM 95546: eastern coast of Punta Burica, Pacific Panama (8°11'24.0"N, 82°52'34.1"W), 1 km south of supertanker dock, 16 Jan 1986 (Charco Azul Group, Armuelles Formation, early Pleistocene). Panama Paleontology Project site 148, 1 complete specimen, USNM 95547: eastern coast of Punta Burica, Pacific Panama (8°11'20.4"N, 82°52'33.5"W), near Q. Melliza, 21 Feb 1987 (Charco Azul Group, Armuelles Formation, early Pleistocene).

Type locality: INVEMAR Macro Fauna project, sta. 49: 11°05.26'–11°05.12'N; 75°15.33'–75°15.74'W, off Bocas de Ceniza, Magdalena, Colombian Caribbean, 310 m.

Distribution and age.—Recent: known only from type locality off Colombia and Cocos Island (Costa Rica); 303–333 m. Fossil: early Pleistocene (Armuelles For-

mation, 1.7–1.5 Ma) of Punta Burica, Pacific Panama.

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Literature Cited

- Bonilla, H. R., E. M. Olguín, & G. A. Reyna. 1995. First record of *Madracis* sp. cf. *M. pharensis* (Heller, 1868) on continental eastern Pacific shores.—*Bulletin of the Southern California Academy of Sciences* 94:172–175.
- Cairns, S. D. 1979. The deep-water Scleractinia of the Caribbean Sea and adjacent waters.—*Studies on the Fauna of Curaçao and other Caribbean Islands* 57(180):341.
- . 1995. The marine fauna of New Zealand: Scleractinia (Cnidaria; Anthozoa).—*New Zealand Institute Oceanographic Memoir* 103:210 p.
- . 2000. A revision of the shallow-water azooxanthellate Scleractinia of the western Atlantic.—*Studies of the Natural History of the Caribbean Region* (in press).
- , B. W. Hoeksema, & J. Van der Land. 1999. Appendix: List of extant stony corals.—*Atoll Research Bulletin* 459:13–46.
- Coates, A. G., J. B. C. Jackson, L. S. Collins, T. M. Cronin, H. J. Dowsett, L. M. Bybell, P. Jung, & J. A. Obando. 1992. Closure of the Isthmus of Panama: the near-shore marine record of Costa Rica and western Panama.—*Geological Society of America Bulletin* 104:814–828.
- Collins, L. S. 1993. Neogene paleoenvironments of the Bocas del Toro Basin, Panama.—*Journal of Paleontology* 67(5):699–710.
- , A. G. Coates, W. A. Berggren, M.-P. Aubry,

- & J. Zhang. 1996. The late Miocene Panama isthmian strait.—*Geology* 24(8):687–690.
- Kühn, O. 1933. Das Becken von Isfahan-Saidabad, und seine altmiocäne Korallenfauna.—*Paleontographica Stuttgart* 79:143–172, 176–221.
- Roniewicz, E., & J. Stolarski. 1999. Evolutionary trends in the epithecate scleractinian corals.—*Acta Palaeontologica Polonica* 44:131–166.
- Petuch, E. J. 1981. A relict Neogene Caenogastropod fauna from northern South America.—*Malacologia* 20:307–347.
- . 1988. Neogene history of tropical American Mollusks. Charlottesville: CERF, 217 pp., 39 pls.
- Ramos, G. E., & R. Lemaitre. 1991. Obituary: Henry Von Prael (1948–1989).—*Journal of Crustacean Biology* 11(3):473–476.
- Reyes, J. O., & G. R. Navas. 2000. El escaner convencional, una herramienta útil para la catalogación de organismos marinos.—*Boletín de Investigaciones Marinas y costeras* (in press).
- Stolarski, J. 1991. Miocene Scleractinia from the Holy Cross Mountains, Poland: Part 1—Caryophylliidae, Flabellidae, Dendrophylliidae, and Micrabaciidae.—*Acta Geologica Polonica* 41(1–2):37–67.
- . 1995. Ontogenetic development of the thecal structures in the caryophylline scleractinian corals.—*Acta Palaeontologica Polonica* 40(1): 19–44.
- Vaughan, T. W., & J. W. Wells. 1943. Revision of the suborders, families and genera of the Scleractinia.—*Geological Society of America Special Papers* 44:363 pp.
- Wells, J. W. 1956. Scleractinia. Pp. F328–F444 in R.C. Moore, ed., *Treatise on Invertebrate Paleontology*, Part F, Coelenterata. University of Kansas Press, Lawrence, Kansas.