

# Early Cretaceous gymnolaemate bryozoans from the early to middle Albian of the Glen Rose and Walnut formations of Texas, USA

Silviu O. Martha,<sup>1</sup> Paul D. Taylor,<sup>2</sup> and William L. Rader<sup>3</sup>

<sup>1</sup>Senckenberg Forschungsinstitute und Naturmuseen, Sektion Marine Evertbraten III (Bryozoologie), Senckenberganlage 25, 60325 Frankfurt am Main, Germany ([silviu.martha@senckenberg.de](mailto:silviu.martha@senckenberg.de))

<sup>2</sup>Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom ([p.taylor@nhm.ac.uk](mailto:p.taylor@nhm.ac.uk))

<sup>3</sup>8210 Bent Tree Road, #219, Austin, Texas, USA ([raderw66@gmail.com](mailto:raderw66@gmail.com))

**Abstract.**—Gymnolaemate bryozoans are common encrusters on bivalve shells from the early to middle Albian parts of the Glen Rose and Walnut formations of southcentral and northcentral Texas. Here, we report for the first time the presence of seven gymnolaemate bryozoans, all of which represent new species. They include the bioimmured ctenostome *Simplicidium jontoddi* n. sp., and the cheilostomes *Rhammatopora glenrosa* n. sp., *Iyarispora ikaanakiteeh* n. gen. n. sp., *Iyarispora chiass* n. gen. n. sp., *Charixa bispinata* n. sp., *Charixa sexspinata* n. sp., and *Charixa emanuelae* n. sp. The Glen Rose bryozoans slightly antedate the commencement of an explosive bryozoan radiation and the first appearance of neocheilostomes in the late Albian. Although the diversity of cheilostomes in the Glen Rose and Walnut formations is similar to that of cyclostomes, cheilostomes are more abundant and produced larger colonies. These formations therefore yield the oldest known bryozoan assemblage dominated in terms of biomass by cheilostomes. The genus concept of *Charixa* is discussed and amended.

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## Introduction

Cheilostomata, the dominant group in modern bryozoan assemblages, were sparse and poorly diversified for the first 50 Ma after their first appearance in the fossil record during the Late Jurassic (Taylor, 1994). However, they experienced a rapid diversification during the late Albian and early Cenomanian, with many evolutionary novelties appearing in a relatively short time interval (e.g., Cheetham, 1954; Martha and Taylor, 2016, 2017). Compared to the Eurasian fauna, the known North American Albian fauna of cheilostome bryozoans is more diverse (Ostrovsky et al., 2008) and several key innovations in cheilostomes, including the evolution of defensive polymorphs (avicularia) and of skeletal chambers for brooding of embryos (ovicells) were first reported in species from the late Albian of Texas (Cheetham, 1954; Cheetham et al., 2006). The North American Cretaceous bryozoan fauna described so far is highly endemic (Cuffey, 1994) and shows only a few, if any, species in common with the better known and more diverse Eurasian faunas. Still, the almost simultaneous appearance of key novelties in North American and European cheilostomes suggests some exchange between the two faunal provinces at least during the Albian.

The late Aptian to middle Albian Glen Rose Formation (Trinity Group) and Walnut Formation (Fredericksburg Group) contain frequent bryozoans encrusting bivalve shells. The cyclostome bryozoans from these formations are described elsewhere (Martha et al., 2019). Here, we describe the gymnolaemate bryozoans from the same deposits.

The Glen Rose and Walnut bryozoan faunas slightly antedate the commencement of the explosive evolutionary radiation of neocheilostomes (Taylor, 1988), and the cheilostome bryozoans present in these formations consist of simple, encrusting species dominated by malacostegines in the absence of neocheilostomes. Additionally, one bioimmured species of a soft-bodied arachnidid ctenostome is reported from the Glen Rose.

In summary, the main aim of this contribution is to describe the gymnolaemate bryozoan faunas of the Glen Rose and Walnut formations of Texas, USA. In doing so, we introduce a new genus for *Conopeum*-like malacostegines with multiporous closure plates. The diversity of cheilostomes bryozoans in the Glen Rose and Walnut formations is discussed and compared to that of the cyclostomes.

## Geological setting

The Glen Rose Formation is a unit of the Trinity Group resting on the Pearsall Formation and at the base of the Paluxy Sands in northcentral and southcentral Texas, USA. The formation was first proposed by Hill (1891) for exposures along the Paluxy River near Glen Rose and comprises a sequence of shallow-water carbonates deposited for ca. 5 Ma on a carbonate platform during the uppermost Aptian to the youngest part of the early Albian (Young, 1967; Scott et al., 2007).

The Glen Rose Formation of southcentral Texas has been divided into a Lower Member consisting of two informal

units, and an Upper Member comprising seven informal units (Stricklin et al., 1971; Ward and Ward, 2007). The two members are separated by ~0.3–1.1 m thick *Eoursivivas harveyi* Marker Bed (Lozo and Stricklin, 1956; Scott et al., 2007). The Aptian-Albian boundary is considered to occur within Unit 1 of the Lower Member. In northcentral Texas, the Glen Rose Formation is much condensed compared to southcentral Texas and subdivided into Lower, Middle, and Upper members, which do not correspond to the Lower and Upper members of the Glen Rose Formation in southcentral Texas. The three members of the Glen Rose Formation in northcentral Texas have been subdivided into several beds (see Bergan and Pittman, 1990).

The Walnut Formation of the Fredericksburg Group overlies the Glen Rose Formation in southcentral Texas. It consists mainly of micritic or sparitic limestone and marlstone, and is divided into six members (e.g., Moore, 1964). For a more detailed account of the geological setting, see Martha et al. (2019).

## Materials and methods

The material used in this study was collected by W.L. Rader, P.D. Taylor, A.B. Smith, and M.A. Wilson over a period of a few decades. Bryozoan colonies were mostly found encrusting bivalve shells in: Unit 2 of the Lower Member and units 1–4, 6, and 7 of the Upper Member of the Glen Rose Formation in southcentral Texas; beds 2–4 of the Lower Member, Bed 10 of the Middle Member and Bed 14 of the Upper Member of the Glen Rose Formation in northcentral Texas; and the Walnut Formation of southcentral Texas. Geographical and stratigraphical details of the collection sites of bryozoan material used in this study are summarized in Supplementary Data Sets 1 and 2 accompanying Martha et al. (2019). Preservation of the material varies from moderate to very good.

Scanning electron microscopy (SEM) was performed at the NHMUK on selected, ultrasonically cleaned specimens using a LEO 1455VP scanning electron microscope equipped with a low-vacuum chamber to accommodate uncoated specimens that were imaged using back-scattered electrons. For morphometry, SEM images were analyzed using the image-processing program ImageJ. Zooid measurements are given as range in  $\mu\text{m}$  and arithmetic mean ( $\bar{X}$ )  $\pm$  standard deviation with coefficient of variation (CV) and number of measurements (N).

*Repository and institutional abbreviation.*—All specimens are housed in the collections at the Natural History Museum, London (NHMUK).

## Systematic paleontology

Phylum Bryozoa Ehrenberg, 1831  
 Order Ctenostomata Busk, 1852  
 Suborder Stoloniferina Ehlers, 1876  
 Superfamily Arachnidioidea Hincks, 1880  
 Family Arachnidiidae Hincks, 1880  
 Genus *Simplicidium* Todd, Taylor, and Favorskaya, 1997

*Type species.*—*Cellaria smithii* Phillips, 1829 from the Cornbrash Formation (late Bathonian or early Callovian) of Scarborough, Yorkshire, England, by original designation.

## *Simplicidium jontoddi* new species

Figure 1.1–1.4

*Holotype.*—NHMUK BZ8165, early Albian, Glen Rose Formation, Lower Member, Unit 2, 765 Astral Point, opposite entrance to White Acres Farm, Mystic Shores Subdivision, Spring Branch, Comal County, Texas.

*Paratype.*—NHMUK BZ8166, same locality and stratigraphical information as for the holotype.

*Diagnosis.*—*Simplicidium* budding daughter zooids that give rise to new branches laterally or proximolaterally; zooid orifice D-shaped.

*Occurrence.*—Only known from the type locality.

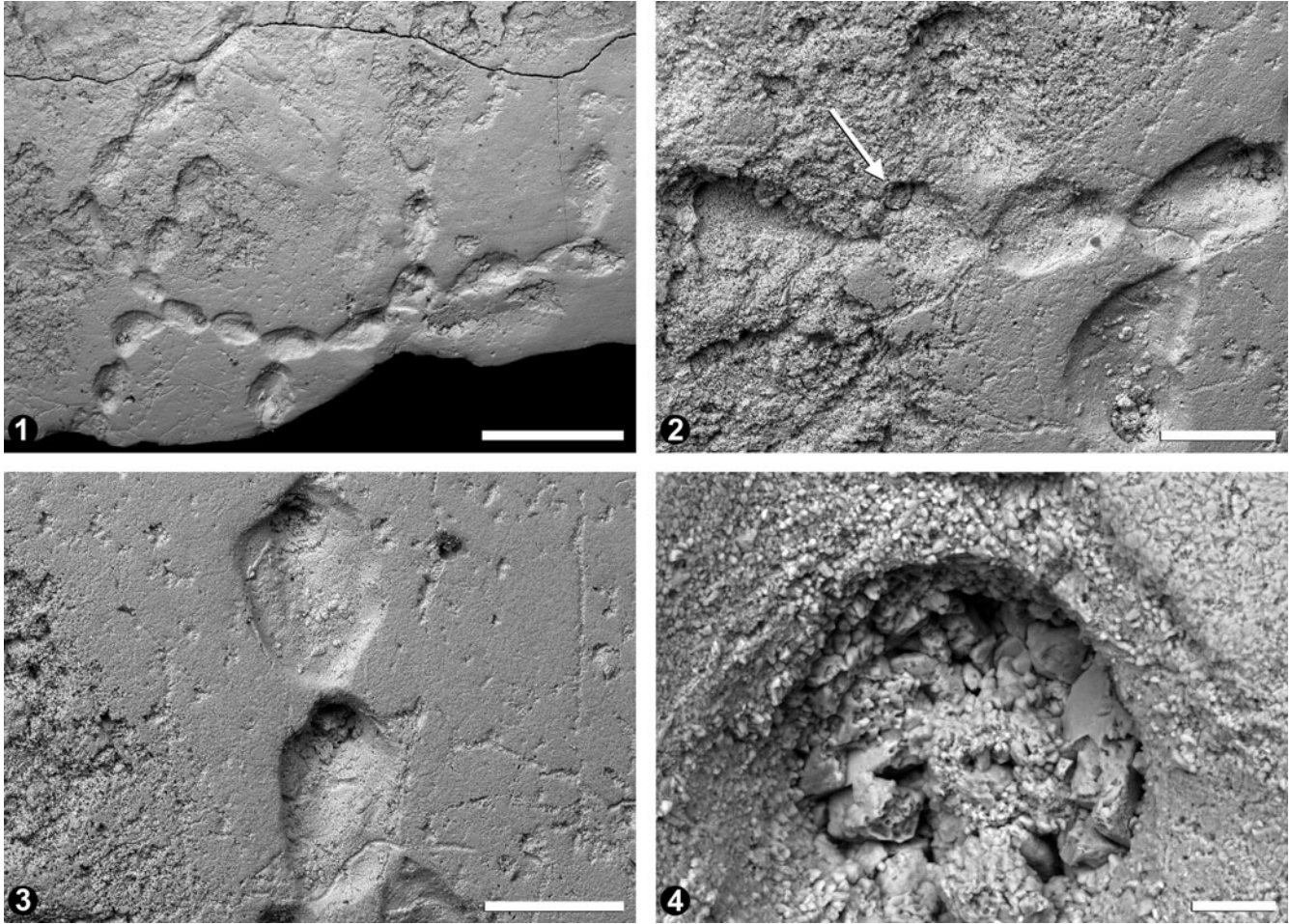
*Description.*—Colony encrusting, uniserial, unilaminar, consisting of slightly curved branches of distally budded autozooids, from which daughter branches arise laterally or proximolaterally and diverge at angles of  $\sim 90^\circ$  to parent branch (Fig. 1.1). Branch ramification frequent, but branch overgrowth not observed. Ancestrula 238  $\mu\text{m}$  long (N = 1) by 181  $\mu\text{m}$  wide (N = 1), budding one proximolateral bud and one distolateral bud (Fig. 1.2). Pore chambers not observed.

Autozooids small, those from early astogeny ovoidal to longitudinally elliptical, 349–502  $\mu\text{m}$  long ( $\bar{X}$  = 416  $\pm$  48  $\mu\text{m}$ ; CV = 12; N = 9) by 198–311  $\mu\text{m}$  wide ( $\bar{X}$  = 259  $\pm$  39  $\mu\text{m}$ ; CV = 15; N = 9) (length/width ratio = 1.61); in later astogeny, elongate-pyriform, 518–675  $\mu\text{m}$  long ( $\bar{X}$  = 600  $\pm$  60  $\mu\text{m}$ ; CV = 10; N = 6) by 252–303  $\mu\text{m}$  wide ( $\bar{X}$  = 273  $\pm$  20  $\mu\text{m}$ ; CV = 7; N = 6) (length/width ratio = 2.20), narrow proximally, rounded distally (Fig. 1.3). Cauda absent or short. Frontal wall gently convex. Orifice terminal, 100–114  $\mu\text{m}$  long ( $\bar{X}$  = 106  $\pm$  6  $\mu\text{m}$ ; CV = 5; N = 5) by 60–84  $\mu\text{m}$  wide ( $\bar{X}$  = 74  $\pm$  9  $\mu\text{m}$ ; CV = 12; N = 5) in elliptical autozooids (length/width ratio = 1.42), and 110–130  $\mu\text{m}$  long ( $\bar{X}$  = 119  $\pm$  8  $\mu\text{m}$ ; CV = 6; N = 5) by 77–99  $\mu\text{m}$  wide ( $\bar{X}$  = 86  $\pm$  9  $\mu\text{m}$ ; CV = 11; N = 5) in pyriform autozooids (length/width ratio = 1.39), D-shaped with a slightly convex proximal edge and more strongly curved distal/lateral edges (Fig. 1.4), wider than long. Spines and kenozooids not observed.

Morphometry measurements were performed on specimen NHMUK BZ8165 (holotype).

*Etymology.*—Named for Jonathan A. Todd (NHMUK), in recognition of his research on bioimmuration, especially of ctenostomes.

*Remarks.*—*Simplicidium jontoddi* n. sp. is a non-boring ctenostome, both of the two known colonies being bioimmured following overgrowth by serpulids. The new species differs from the other two species assigned to *Simplicidium*, *Simplicidium brandesi* Voigt, 1968 and *Simplicidium smithii* (Phillips, 1829), in having: (1) a D-shaped orifice, and (2) new branches arising from irregular positions as lateral or proximolateral buds. In contrast, *Simplicidium smithii* and *Simplicidium brandesi* have circular to subcircular orifices and new branches originating as distal or distolateral buds.



**Figure 1.** *Simplicidium jontoddi* n. sp. from Unit 2 of the Lower Member of the Glen Rose Formation (earliest Albian) of southcentral Texas, USA. Holotype (NHMUK BZ8165). (1) Bioimmured colony; scale bar is 1 mm; (2) ancestrula (white arrow) and early astogeny; scale bar is 250 µm; (3) two autozooids; scale bar is 250 µm; (4) D-shaped orifice; scale bar is 25 µm.

Although bioimmured ctenostome bryozoans are well known from the Late Jurassic (e.g., Taylor, 1990) and the Late Cretaceous (e.g., Voigt, 1966), only one other species has been reported from the Early Cretaceous, *Simplicidium brandesi* Voigt, 1968 from the Berriasian to Barremian of Central and Eastern Europe. Several bioimmured ctenostome species, including arachnidiids, occur in the Grayson Formation (Cenomanian) of the Wishita Group in Texas (Todd, 2000), but have yet to be formally described.

Order Cheilostomata Busk, 1852  
 Suborder Malacostegina Levensen, 1902  
 Superfamily Membraniporoidea Busk, 1854  
 Family Electridae d'Orbigny, 1851  
 Genus *Rhammatopora* Lang, 1915

*Type species.*—*Membranipora gaultina* Vine, 1890 from the late Albian to Cenomanian of several localities in England, United Kingdom; by original designation.

*Rhammatopora glenrosa* new species  
 Figure 2.1–2.6

*Holotype.*—NHMUK BZ8149 (1), early Albian, Glen Rose Formation, Upper Member, Unit 6 (lower *Loriolia* Marker

Bed), cut below water tower at the intersection of FM 620 with Kollmeyer Drive, Lakeway, Travis County, Texas.

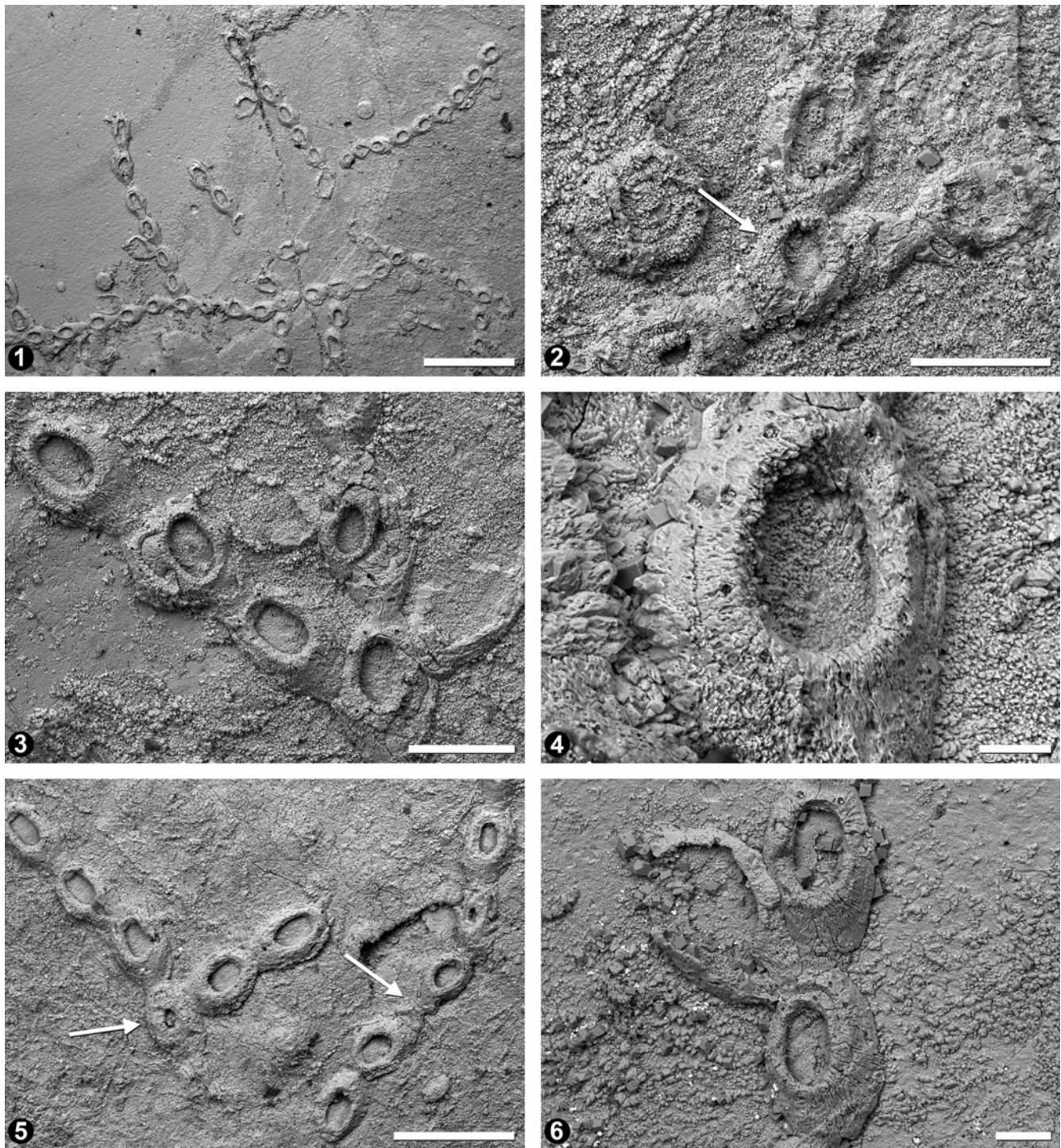
*Paratypes.*—NHMUK BZ8149 (2–6), same locality and stratigraphical information as for the holotype.

*Diagnosis.*—*Rhammatopora* with 6–8 circumopesial spines and with zooids that have a short, broad cauda.

*Occurrence.*—Known from several outcrops west of Austin, Travis County, Texas.

*Description.*—Colony encrusting, uniserial, with runner-like colonies, unilaminar, consisting of straight or slightly curved branches of distally budded autozooids, from which daughter branches arise distolaterally and diverge at angles of ~70–90° to parent branch (Fig. 2.1). Branch bifurcations frequent, but branch overgrowth not observed. Ancestrula 157–216 µm long ( $\bar{X}$  = 179 ± 27; CV = 15; N = 4) by 124–150 µm wide ( $\bar{X}$  = 139 ± 13; CV = 9; N = 4), longitudinally elliptical, spinose, with one distal bud (Fig. 2.2). Pore chambers not observed.

Autozooids small, 233–401 µm long ( $\bar{X}$  = 323 ± 52; CV = 16; N = 28) by 180–255 µm wide ( $\bar{X}$  = 213 ± 21; CV = 10; N = 28); zooids early in astogeny longitudinally elliptical; younger



**Figure 2.** *Rhammatopora glenrosa* n. sp. from Unit 6 of the Upper Member of the Glen Rose Formation (early Albian) of southcentral Texas, USA. Holotype (NHMUK BZ8165). (1) Several uniserial, encrusting colonies; scale bar is 1 mm; (2) ancestrula (arrowed) overgrowing autozooid of another colony and budding one autozooid distally; scale bar is 250 μm; (3) branch trifurcation and several autozooids with three pairs of spine bases; scale bar is 250 μm; (4) autozooid with four pairs of spine bases; scale bar is 50 μm; (5) two uniserial colonies showing an autozooid with closure plate (left arrow) and bipolar zooid pair (right arrow); scale bar is 500 μm; (6) intramural, reparative budding in bottom autozooid; scale bar is 100 μm.

generations of zooids become slightly elongate-pyriform, narrow proximally, rounded distally (Fig. 2.3). Gymnocyst extensive, surrounding opesia, smooth, forming a short, broad cauda in later astogeny. Opesia 155–275 μm long ( $\bar{X}$  = 195 ± 33; CV = 17; N = 24) by 113–168 μm wide ( $\bar{X}$  = 136 ± 16; CV = 11; N = 24), occupying most of frontal surface,

longitudinally elliptical. Spine bases circumopesial, numbering 6–8, one pair distolateral to opesia, second pair at about three-quarters of opesia length, third pair about one-quarter of opesia length, and fourth pair proximolateral to opesia; third pair of spine bases lacking in many autozooids (Fig. 2.3, 2.4). Cryptocyst narrow, sloping steeply into opesia, widest proximally and

narrowing laterally and distally, smooth. Closure plates rare, depressed, with subcircular to longitudinally elliptical opening and a conspicuous crescent-shaped scar from opercular sclerites distally (Fig. 2.5). Bipolar pairs of zooids joined at their proximal ends and growing in opposite directions observed in two colonies (Fig. 2.5). Intramural reparative budding of zooids inside autozooidal opesiae occurs (Fig. 2.6). Kenozooids not observed.

Morphometry measurements were performed on specimen NHMUK BZ8149 (holotype and several paratype colonies).

*Etymology*.—The species is named after the type stratum, the Glen Rose Formation of southcentral Texas.

*Materials*.—For non-type material of this species, see Supplementary Data Set 1.

*Remarks*.—The holotype of *Rhammatopora glenrosa* n. sp. is on a bivalve shell encrusted by several colonies of the new species. It has autozooids with no or very short caudae, and the number of spine pairs varies between three and four, with the spine pair located at about one-quarter of opesial length usually lacking. The arrangement of the spines in *R. glenrosa* n. sp. is comparable to that observed in *Charixa bispinata* n. sp., but in the material examined, all colonies of *R. glenrosa* n. sp. are uniserial and the ancestrula buds only one distal autozooid. The occurrence of bipolar zooid pairs, which are the result of branch lesion followed by regenerative budding from the broken end (see Taylor, 1986a), is another feature of *R. glenrosa* that was not observed in either *Charixa bispinata* n. sp. or in *Charixa bispinata* n. sp.

The new species was previously mentioned in an account of pre-Cenomanian cheilostomes by Ostrovsky et al. (2008) as the oldest representative of the genus *Pyripora* d'Orbigny, 1852. However, the presence of circumopesial spines justifies assignment of the new species to *Rhammatopora* Lang, 1915 instead. The type species of this genus, *Rhammatopora gaultina* (Vine, 1890), has very long, narrow caudae and 15–20 circumopesial spine bases. The only other species assigned to this genus, *Rhammatopora gasteri* Thomas and Larwood, 1956, was described from the early Cenomanian of Sussex, England and has somewhat shorter caudae and only 12 circumopesial spines. The ancestrula has not been observed in either of the two previously described species.

An older, supposedly *Pyripora*-like electrid was described by Mantell (1844) from the Aptian of Kent, United Kingdom as *Crisia johnstoniana* Mantell, 1844. This species was later assigned to the genus *Rhammatopora* by Lang (1915). According to Mantell's drawing, this species has very long caudae, but spine bases are not evident and were not mentioned in the description. Because the type material is lost (Lang, 1915; Taylor, 1986b), *Crisia johnstoniana* is best regarded as a nomen dubium.

#### Genus *Iyarispora* new genus

*Type species*.—*Iyarispora ikaanakiteeh* n. gen. n. sp. from the early Albian of several localities in southcentral Texas, USA.

*Occurrence*.—Early Albian, Glen Rose Formation; Texas, USA. Campanian, Mount Laurel Formation; Delaware, USA. Late Campanian to Maastrichtian, Simsima Formation; Hajar Mountains, Arabian Peninsula. Maastrichtian, Prairie Bluff Chalk; Alabama, USA and Ripley Formation; Tennessee, USA.

*Diagnosis*.—Colony encrusting, multiserial, unilaminar or multilaminar. Autozooids arranged quincunxially. Ancestrula single, budding one distal autozooid and surrounded by six periancestrular zooids. Opesia occupying most of frontal surface, longitudinally elliptical. Closure plates present, perforated by multiple pores, distally indented by sclerites of operculum. Gymnocyst narrow, smooth. Cryptocyst pustulose, narrow, sloping steeply into opesia. Kenozooids small, subtriangular or polygonal, usually at proximolateral corners of each autozooid and sometimes becoming knob- or spine-like. Pore chambers, ovicells, and avicularia absent.

*Etymology*.—From the native American Wichita language *iyari* ('animal') with the ending *-pora* from Greek *πόρος* ('pore').

*Remarks*.—*Iyarispora* n. gen. is erected for electrid malacostegan cheilostomes with encrusting, multiserial colonies and autozooids with closure plates perforated by multiple perforations. The most similar genera are *Wawalia* Dzik, 1975, *Charixa* Lang, 1915, and *Spinicharixa* Taylor, 1986b. However, the closure plates in *Wawalia* and *Spinicharixa* lack distinct perforations, while those of *Charixa* have one large central opening.

Other Cretaceous species that can be included in the new genus were formerly assigned to *Conopeum* Gray, 1848. They include: *C. (Alderina) nelsoni* (Canu and Bassler, 1926); *C. paranelsoni* Taylor and McKinney, 2006; *C. spissamentum* Taylor and McKinney, 2006; and *C. wilsoni* Di Martino and Taylor, 2013. In the type species of *Conopeum* Gray, 1848, the Recent species *Millepora reticulum* Linnaeus, 1767, the ancestrula buds two distolateral autozooids and one proximal autozooid. Closure plates in Recent species of *Conopeum* are rare and, when present, as in *Conopeum seurati* (Canu, 1928), they are incompletely uncalcified and have a single medial opening.

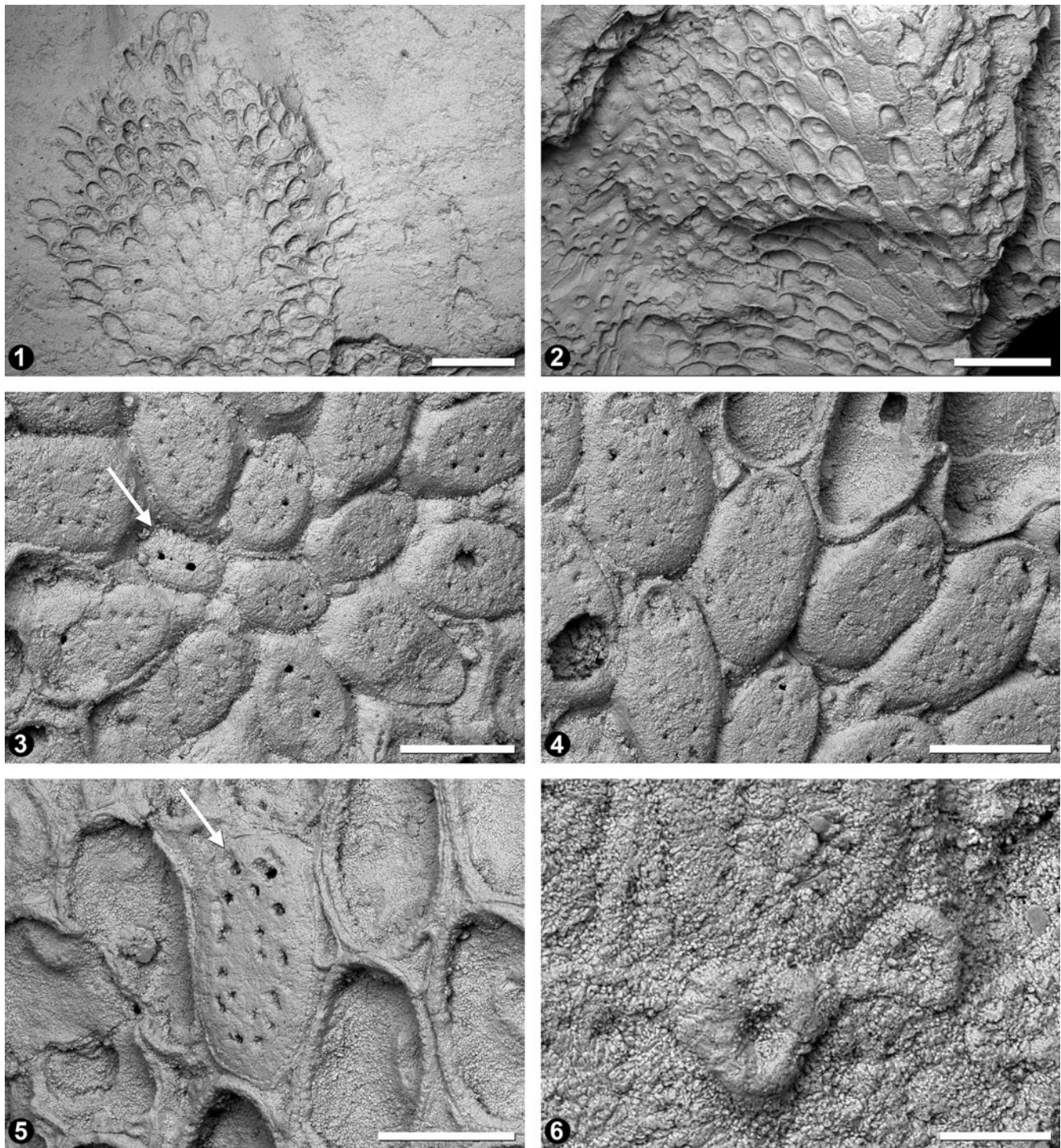
#### *Iyarispora ikaanakiteeh* new species

##### Figure 3.1–3.6

*Holotype*.—NHMUK BZ8111, early Albian, Glen Rose Formation, Upper Member, Unit 2, roadcut along River Ridge Road, Mystic Shores Subdivision, Canyon Lake, Comal County, Texas.

*Paratypes*.—NHMUK BZ8112, BZ8124, same locality and stratigraphical information as for the holotype. NHMUK BZ8109, BZ8110, early Albian, Glen Rose Formation, Upper Member, Unit 1, 13500 Pecan Drive, Lakeway, Travis County, Texas.

*Diagnosis*.—*Iyarispora* n. gen. with clusters of autozooids having closure plates; pores in closure plates arranged in single outer ellipse consisting of ~12 pores, with up to five smaller, inner pores; kenozooids at proximolateral corners of some but not all autozooids, occasionally raised to form knob-like tubercles.



**Figure 3.** *Iyarispora ikaanakiteeh* n. gen. n. sp. from Unit 2 of the Upper Member of the Glen Rose Formation (early Albian) of southcentral Texas, USA (1, 2, 5, 6); from Unit 1 of the Upper Member of the Glen Rose Formation (early Albian) of southcentral Texas, USA (3, 4). (1) Encrusting colony (paratype, NHMUK BZ8124); scale bar is 1 mm; (2) colony encrusting on *Reptomultisparsa mclemoreae* Martha et al., 2019 (holotype, NHMUK BZ8111); scale bar is 1 mm; (3) ancestrula (arrowed) and early astogeny (paratype, NHMUK BZ8109); scale bar is 250 µm; (4) autozooids with multiporous closure plates and kenozooids (paratype, NHMUK BZ8109); scale bar is 250 µm; (5) autozooid with closure plate pierced by outer ellipse of twelve circular pores and incomplete inner ellipse consisting of five pores; the crescent shaped scar from opercular sclerite (arrowed) is also pierced by pores (holotype, NHMUK BZ8111); scale bar is 250 µm; (6) kenozooids, the left showing markedly raised margins (paratype, NHMUK BZ8112); scale bar is 100 µm.

**Occurrence.**—All studied specimens are from units 1 and 2 of the Upper Member of the Glen Rose Formation of Comal, Kendall, and Travis counties in southcentral Texas.

**Description.**—Colony encrusting, multiserial, unilaminar (Fig. 3.1). Autozooids arranged quincunxially, with occasional series divisions. Zooidal boundaries defined by distinct furrows

(Fig. 3.2). Ancestrula single, 197–208  $\mu\text{m}$  long ( $\bar{X} = 203 \pm 8 \mu\text{m}$ ; CV = 4; N = 2) by 118–121  $\mu\text{m}$  wide ( $\bar{X} = 120 \pm 2 \mu\text{m}$ ; CV = 2; N = 2), occluded by closure plate containing one mediiodistal and one medioproximal pore, budding one proximal autozooid, with five other periancestrular zooids budded from later autozooids (Fig. 3.3). Pore chambers not observed.

Autozooids 370–514  $\mu\text{m}$  long ( $\bar{X} = 434 \pm 38 \mu\text{m}$ ; CV = 9; N = 30) by 194–364  $\mu\text{m}$  wide ( $\bar{X} = 253 \pm 31 \mu\text{m}$ ; CV = 12; N = 30), longitudinally elliptical, sometimes almost rectangular with rounded corners (Fig. 3.4). Gymnocyst narrow, surrounding opesia, smooth. Opesia 290–477  $\mu\text{m}$  long ( $\bar{X} = 373 \pm 47 \mu\text{m}$ ; CV = 13; N = 30) by 161–290  $\mu\text{m}$  wide ( $\bar{X} = 209 \pm 27 \mu\text{m}$ ; CV = 13; N = 30), occupying most of frontal surface, longitudinally elliptical. Spine bases not observed. Cryptocyst slightly pustulose, sloping steeply into opesia. Closure plates usually present on all autozooids from early astogeny and in clusters of autozooids later in astogeny, covering entire frontal surface, planar, with conspicuous crescent-shaped scar from opercular sclerites distally, perforated by small, circular countersunk pores, ~12 pores forming an outer ellipse plus up to five inner pores (Fig. 3.5), pores 11–24  $\mu\text{m}$  ( $\bar{X} = 17 \pm 4 \mu\text{m}$ ; CV = 25; N = 24) in diameter. Intramural reparative budding of zooids, ovicells and avicularia not observed.

Kenozooids 90–209  $\mu\text{m}$  long ( $\bar{X} = 138 \pm 24 \mu\text{m}$ ; CV = 18; N = 30) by 66–150  $\mu\text{m}$  wide ( $\bar{X} = 102 \pm 20 \mu\text{m}$ ; CV = 20; N = 30), subtriangular, usually at proximolateral corners of some autozooids, kenozooidal margins sometimes markedly raised to form knob-like tubercles (Fig. 3.3, 3.6). Kenozooidal opesia occupying most of frontal surface and of same shape as kenozooid (Fig. 3.5).

Morphometry measurements were performed on specimen NHMUK BZ8111 (holotype) and specimens NHMUK BZ8112 and NHMUK BZ8112 (paratypes).

*Etymology*.—From Wichita *ika:ʔa* ('rock'), *na* (participle) and *kita* ('on top'), together with the genus name meaning in a Wichita-Greek mixture 'porous animal on top of rock'.

*Materials*.—For non-type material of this species, see Supplementary Data Set 1.

*Remarks*.—*Iyarispora ikaanakiteeh* n. gen. n. sp. is the oldest representative of the new genus, occurring in units 1 and 2 of the Upper Member of the Glen Rose Formation. It differs from *Iyarispora chiass* n. gen. n. sp., with which it does not co-occur, in having smaller and more numerous pores in the closure plates, which include additional pores inside the main ellipse of pores. The number of closure plate pores is usually much greater in younger species from the Campanian and Maastrichtian assigned to the new genus, except for *Iyarispora paranelsoni* (Taylor and McKinney, 2006), in which the number and arrangement of pores is somewhat similar to *I. chiass* n. gen. n. sp.

*Iyarispora chiass* new species  
Figures 4.1–4.6, 5.1–5.6

1969 Unnamed membraniform cheilostome; Boardman and Cheetham, pl. 30, fig. 1.

2008 '*Conopeum*' s.l.; Ostrovsky et al., fig. 1G.

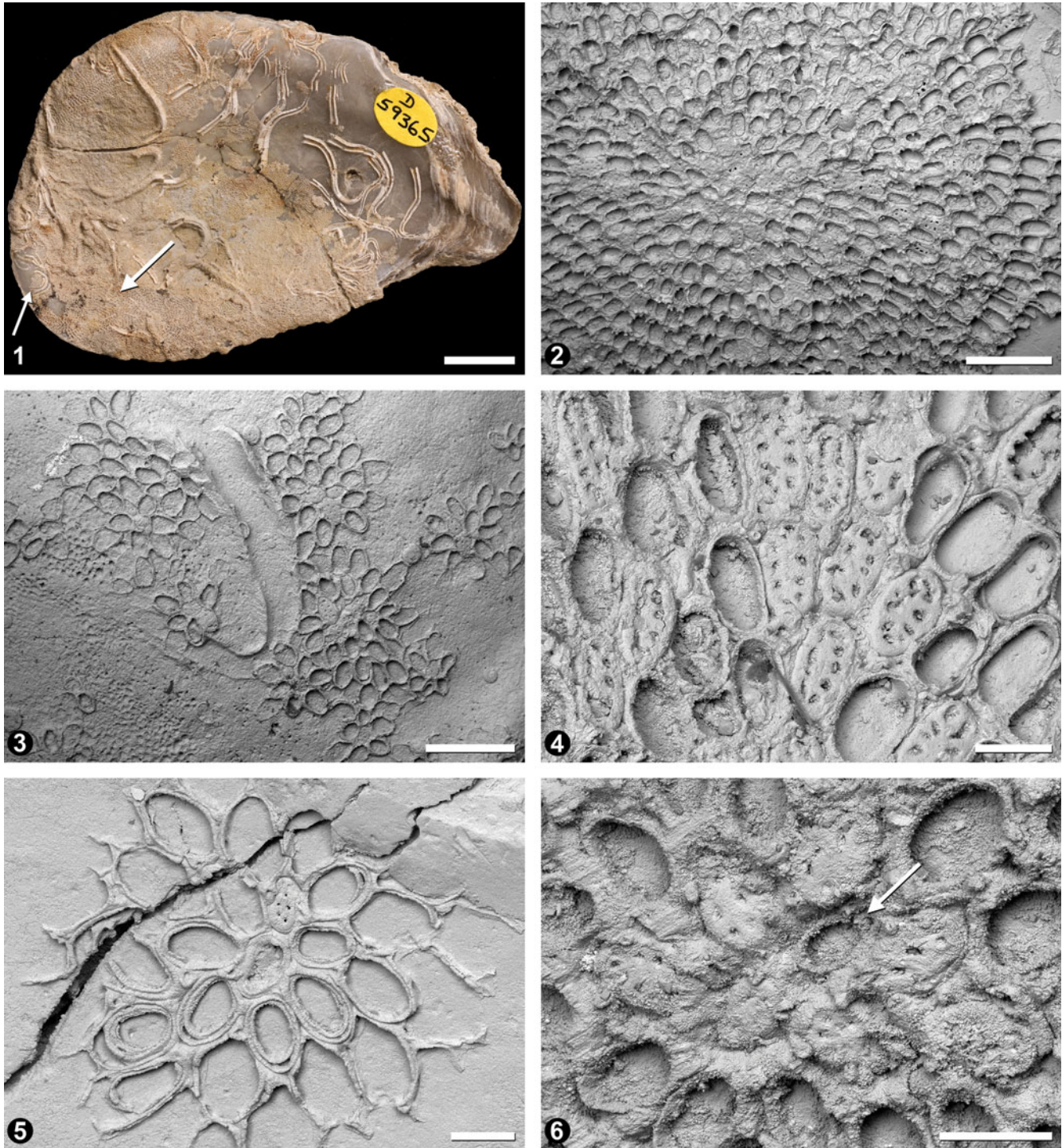
*Holotype*.—NHMUK D59365 (1A), early Albian, Glen Rose Formation, Lower Member, Bed 4, Cedar Brake Camp, Somervell County, Texas.

*Paratypes*.—NHMUK D59364, early Albian, Glen Rose Formation, Middle Member, Bed 10, Barker Branch west of Glen Rose, Somervell County, Texas. NHMUK BZ2338, early Albian, Glen Rose Formation, Upper Member, Bed 14, Cedar Brake Camp, Somervell County, Texas. NHMUK BZ7906, early Albian, Glen Rose Formation, Upper Member, Unit 4, abandoned quarry on north side of SH 290, west of Dripping Springs, Hays County, Texas. NHMUK BZ7949, early Albian, Glen Rose Formation, Upper Member, Unit 6 (lower *Loriolia* Marker Bed), banks along creek beside Target department store off FM 620, Bee Cave, Travis County, Texas. NHMUK BZ8013, early Albian, Glen Rose Formation, Upper Member, Unit 6 (lower *Loriolia* Marker Bed), roadcut on the northwestern side of Quinlan Park Road near University Club Drive, Austin. NHMUK BZ7950, BZ7951, early Albian, Glen Rose Formation, Upper Member, Unit 6 (lower *Loriolia* Marker Bed), construction site at southwest corner of Ming Trail and Destination Way, Lago Vista, Travis County, Texas. NHMUK BZ7984, early Albian, Glen Rose Formation, Upper Member, Unit 6 (lower *Loriolia* Marker Bed), roadcut on the north side of FM 620 northwest of Mansfield Dam, Hudson Bend, Travis County, Texas. NHMUK BZ8017, early Albian, Glen Rose Formation, Upper Member, Unit 6 (lower *Loriolia* Marker Bed), roadcut on the northwestern side of Quinlan Park Road near University Club Drive, Austin. NHMUK BZ7910, early Albian, Glen Rose Formation, Upper Member, Unit 4, abandoned quarry on north side of SH 290, west of Dripping Springs, Hays County, Texas.

*Diagnosis*.—*Iyarispora* n. gen. with closure plates occurring in clusters of autozooids; closure plate pores large, circular, arranged in single ellipse with no inner pores; kenozooids at proximolateral corners of some but not all autozooids, some raised to form knob-like tubercles.

*Occurrence*.—This species has been found at several outcrops of the Lower, Middle, and Upper members of the Glen Rose Formation in Hood and Somervell counties, northcentral Texas, and in units 3–7 of the Upper Member of the Glen Rose Formation in Blanco, Burnet, Comal, Hays, and Travis counties in southcentral Texas. A specimen apparently belonging to this species was figured by Boardman and Cheetham (1969) from the Albian DeQueen Limestone of Highland, Arkansas.

*Description*.—Colony encrusting, multiserial, unilaminar (Fig. 4.1–4.3). Autozooids arranged quincunxially, with occasional series divisions. Zooidal boundaries defined by distinct furrows (Fig. 4.4). Ancestrula single, 147–209  $\mu\text{m}$  long ( $\bar{X} = 183 \pm 32 \mu\text{m}$ ; CV = 18; N = 3) by 83–144  $\mu\text{m}$  wide ( $\bar{X} = 116 \pm 31 \mu\text{m}$ ; CV = 27; N = 3), sometimes occluded by a closure plate pierced by three to five pores, budding one

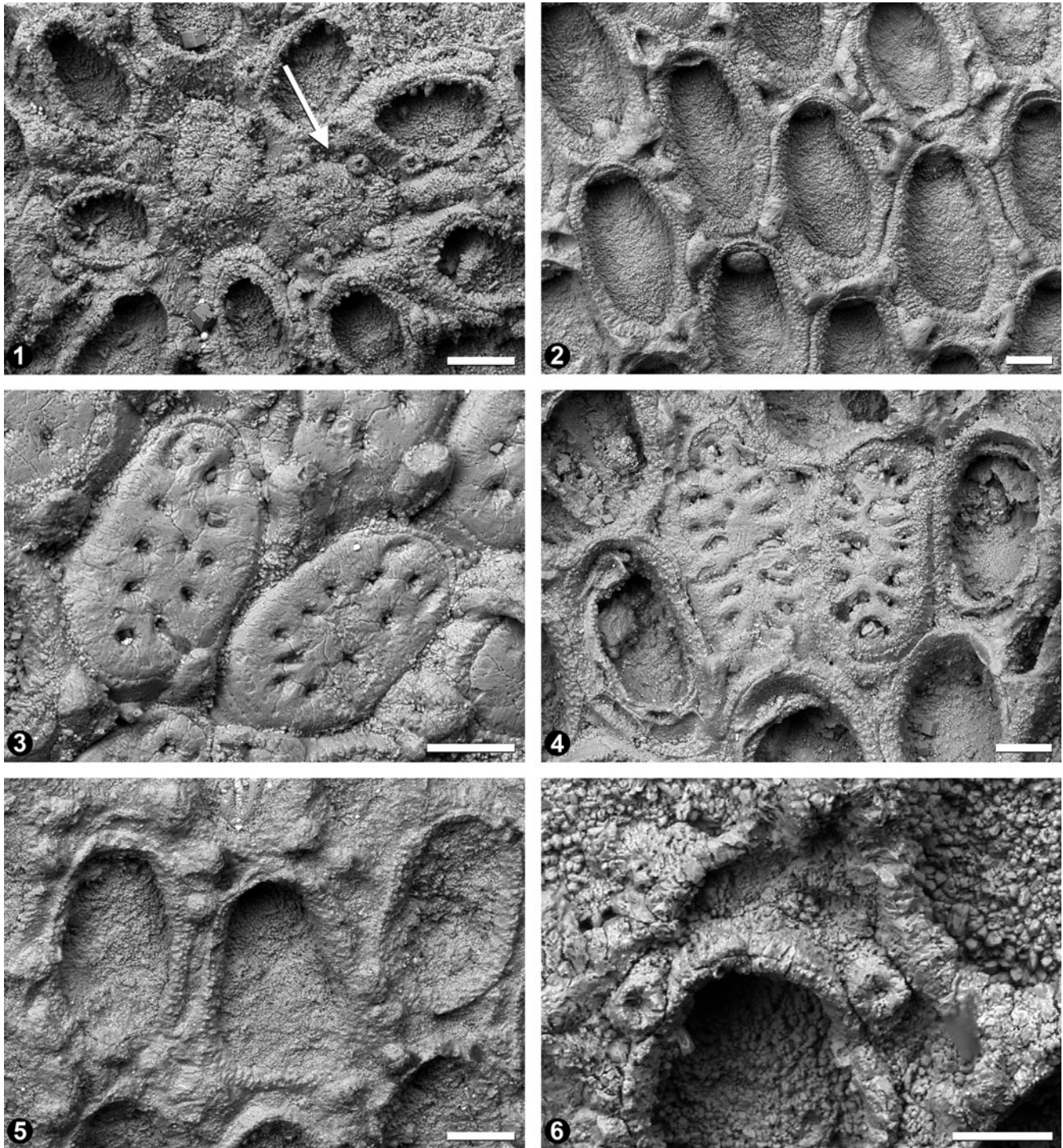


**Figure 4.** *Iyarispora chiass* n. gen. n. sp. from Bed 4 of the Lower Member of the Glen Rose Formation (early Albian) of northcentral Texas, USA (1, 2, 4); from Bed 4 of the Lower Member of the Glen Rose Formation (early Albian) of northcentral Texas, USA (5); from Unit 4 of the Upper Member of the Glen Rose Formation (early Albian) of southcentral Texas, USA (3); from Unit 6 of the Upper Member of the Glen Rose Formation (early Albian) of southcentral Texas, USA (6). (1) Bivalve shell encrusted by multiple colonies of *Iyarispora chiass* n. gen. n. sp. and *Charixa bispinata* n. sp., with the holotype colonies of *Charixa bispinata* n. sp. (left arrow) and *Iyarispora chiass* n. gen. n. sp. (right arrow) indicated (NHMUK D59365); scale bar is 1 cm; (2) encrusting colony, holotype, NHMUK D59365 (1A); scale bar is 1 mm; (3) several small, encrusting colonies, paratype, NHMUK BZ7906; scale bar is 1 mm; (4) autozooids with and without closure plates, holotype, NHMUK D59365 (1A); scale bar is 250  $\mu$ m; (5) ancestrular region of small colony showing several intramural buds, paratype, BZ2338; scale bar is 250  $\mu$ m; (6) ancestrula indicated by white arrow with one distal bud and surrounded by six periancestrular autozooids, paratype, NHMUK BZ8013; scale bar is 250  $\mu$ m.

proximal autozooid only, with other five periancestrular zooids budded from later autozooids (Figs. 4.5, 4.6, 5.1). Pore chambers not observed.

Autozooids 293–393  $\mu$ m long ( $\bar{X}$  = 345  $\pm$  24  $\mu$ m; CV = 7; N = 36) by 155–246  $\mu$ m wide ( $\bar{X}$  = 195  $\pm$  24  $\mu$ m; CV = 12; N = 36), longitudinally elliptical, sometimes almost rectangular





**Figure 5.** *Iyarispora chiass* n. gen. n. sp. from Unit 4 of the Upper Member of the Glen Rose Formation (early Albian) of southcentral Texas, USA (2); from Unit 6 of the Upper Member of the Glen Rose Formation (early Albian) of southcentral Texas, USA (1, 3–6). (1) Early astogeny with ancestrula (arrowed) and small kenozooids, paratype, NHMUK BZ7950; scale bar is 100  $\mu$ m; (2) autozooids surrounded by knob-like kenozooids, paratype, NHMUK BZ7910; scale bar is 100  $\mu$ m; (3) autozooids with closure plates pierced by subcircular pores, paratype, NHMUK BZ7984; scale bar is 100  $\mu$ m; (4) autozooids with closure plates pierced by beveled pores, paratype, NHMUK BZ7951; scale bar is 100  $\mu$ m; (5) knob-like kenozooids, paratype, NHMUK BZ8017; scale bar is 100  $\mu$ m; (6) close-up view of two small kenozooids lateral to aperture, paratype, NHMUK BZ7949; scale bar is 50  $\mu$ m.

with rounded corners (Fig. 4.4). Gymnocyst narrow, surrounding opesia, smooth. Opesia 223–350  $\mu$ m long ( $\bar{X}$  = 275  $\pm$  34  $\mu$ m; CV = 12; N = 36) by 117–185  $\mu$ m wide ( $\bar{X}$  = 151  $\pm$  16  $\mu$ m; CV = 10; N = 36), occupying most of frontal surface, longitudinally elliptical. Unequivocal spine bases not observed.

Cryptocyst pustulose, sloping steeply into opesia (Fig. 5.2). Closure plates sometimes present, occurring in clusters of autozooids or in single autozooids, covering entire frontal surface, planar, with conspicuous crescent-shaped scar of opercular sclerites distally (Fig. 5.3), perforated by ~10–14

large, circular to transverse, countersunk pores arranged in an ellipse, pores 18–41  $\mu\text{m}$  ( $\bar{X} = 27 \pm 6 \mu\text{m}$ ; CV = 23; N = 24) in diameter (Fig. 5.3, 5.4). Intramural reparative budding of zooids occurs (Fig. 5.4, 5.5). Ovicells and avicularia not observed.

Kenozooids variable in shape and size, larger examples usually subtriangular and at proximolateral corners of some autozooids, 76–158  $\mu\text{m}$  long ( $\bar{X} = 118 \pm 19 \mu\text{m}$ ; CV = 16; N = 36) by 59–136  $\mu\text{m}$  wide ( $\bar{X} = 87 \pm 16 \mu\text{m}$ ; CV = 19; N = 36), their margins occasionally markedly raised (Fig. 5.2); opesia occupying most of frontal surface and of the same shape as the kenozooid. Smaller kenozooids may be knob- (Fig. 5.1, 5.5) or spine-like (Fig. 5.1, 5.3, 5.6), randomly interspersed between autozooids, typically clustered in certain areas of the colony and often present during the early astogeny.

Morphometry measurements were performed on specimen NHMUK D59365 (1A) (holotype) and specimens NHMUK BZ7984 and NHMUK BZ8013 (paratypes).

*Etymology*.—From Wichita *chí?as* ('one' or 'only one'), referring to the species having only one ellipse of pores.

*Materials*.—For non-type material of this species, see Supplementary Data Set 1.

*Remarks*.—*Iyarispora chiass* n. gen. n. sp. is the most common bryozoan species found in the Glen Rose Formation. It is known from >100 colonies from units 3–7 (excluding Unit 5) of the Upper Member of the Glen Rose Formation of southcentral Texas and throughout the Glen Rose Formation of northcentral Texas. However, in the overlying Walnut Formation no colonies of either *Iyarispora chiass* n. gen. n. sp., or of *I. ikaanakiteeh* n. gen. n. sp. were found.

*Iyarispora chiass* n. gen. n. sp. differs from *I. ikaanakiteeh* n. gen. n. sp. in the closure plates containing fewer pores but of larger size and often transversely elongate in shape rather than strictly circular. Closure plate pores of *Iyarispora chiass* n. gen. n. sp. may be beveled. Intermediate stages between circular and transversely elongate pores in *Iyarispora chiass* n. gen. n. sp. occur (Fig. 5.4, 5.5), and both types of pores were occasionally observed in the same colony (e.g., Fig. 4.4). Therefore, we object defining different species based on the shape of the pores inside the closure plates as identification of these would most certainly prove unmanageable with the Glen Rose material.

Another important difference between *Iyarispora chiass* n. gen. n. sp. and *Iyarispora ikaanakiteeh* n. gen. n. sp. is the morphology and abundance of kenozooids. While in *Iyarispora ikaanakiteeh* n. gen. n. sp. they usually occur proximolateral to autozooids and are occasionally knob-like, kenozooids are more interspersed among the autozooids of *Iyarispora chiass* n. gen. n. sp. and are often knob- or spine-like.

The specimen imaged by Boardman and Cheetham (1969, pl. 30, fig. 1) as an unnamed membraniform cheilostome from the Albian DeQueen Limestone of Highland, Alabama shows closure plates with a similar pattern of pores to *I. chiass* n. gen. n. sp. Boardman and Cheetham (1969) interpreted these as marking points of attachment of the parietal muscles to the underside of the frontal membrane. The irregular

distribution of the closure plate pores in the autozooids, as well as the medial position of the pores in the ancestrula, argue against this interpretation.

#### Genus *Charixa* Lang, 1915

*Type species*.—*Charixa vennensis* Lang, 1915 from the Black Ven Cliff near Charmouth, Dorset, England, United Kingdom; by original designation.

*Amended diagnosis*.—Colony encrusting, composite multiserial (= generally multiserial but facultatively uniserial), unilaminar. Ancestrula single, budding one proximal or distal autozooid and occasionally an additional two (proximo-) lateral autozooids. Autozooids vary from caudate to non-caudate, caudate autozooids forming uniserial series, from which non-caudate autozooids bud to fill in spaces between lineal series. Spine bases either absent or present and typically variable in number within the colony, with a pair of oral spine bases being most frequent. Opesia occupying most of frontal surface, longitudinally elliptical. Closure plates present, central opening absent or single and large. Gymnocyst narrow laterally and distally, smooth, surrounding opesia. Cryptocyst slightly pustulose, sloping steeply into opesia. Pore chambers present. Kenozooids may be present. Avicularia and ovicells lacking.

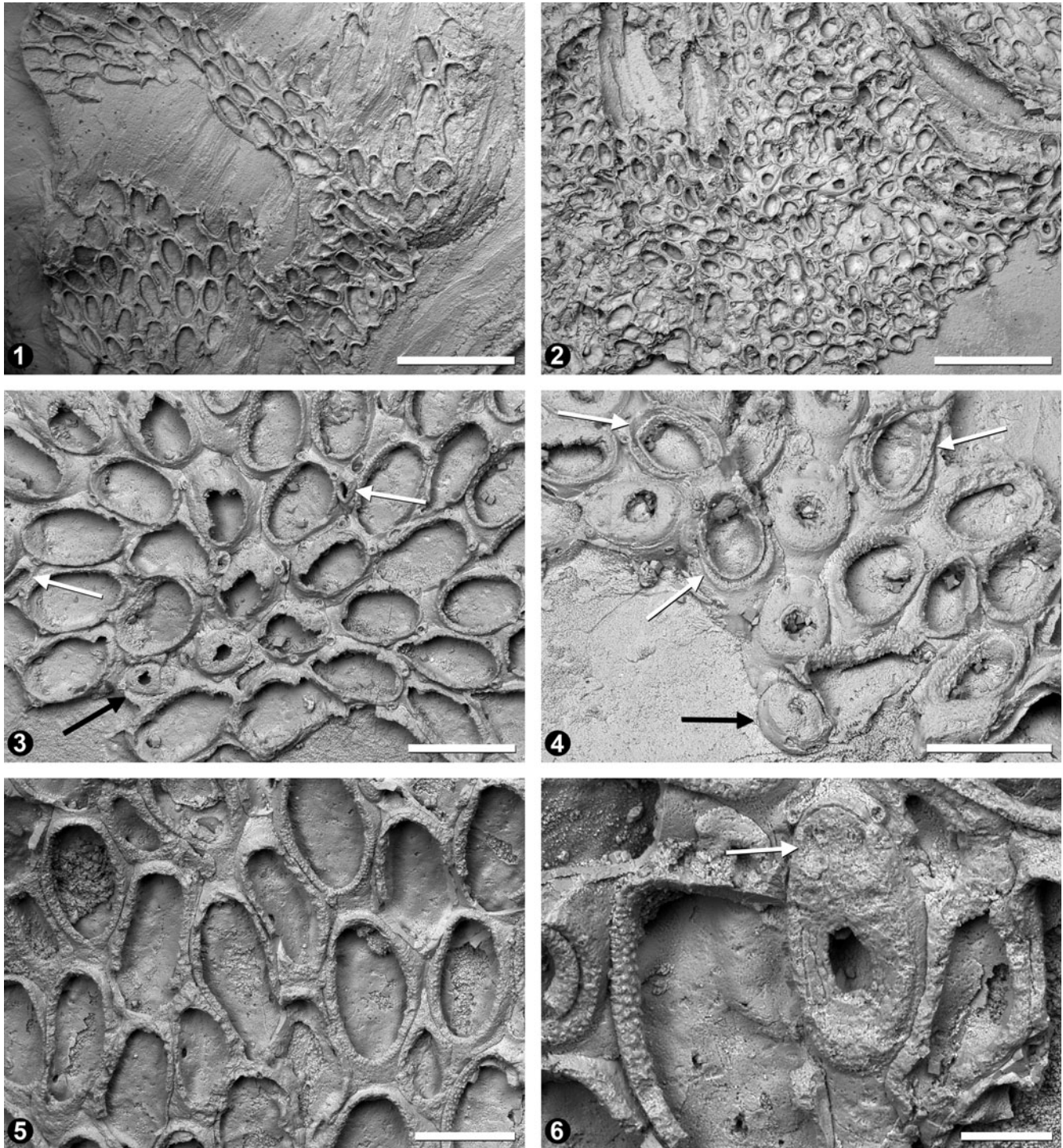
*Remarks*.—The current concept of the two genera *Charixa* and *Spinicharixa* Taylor, 1986b is challenged by the material found in the Glen Rose and Walnut formations. When Taylor (1986b) introduced the new genus *Spinicharixa*, he based it on the presence of circumopesimal spines, in contrast to *Charixa* in which spine bases are absent or oral only. Apart from the type species, *Spinicharixa pittii* Taylor, 1986b, only one other species, *Spinicharixa dimorpha* Taylor, 1986b, has been included in *Spinicharixa*.

*Charixa sexspinata* n. sp. shows a highly variable (0–6) number of spine bases per autozooid. Furthermore, *Charixa bispinata* n. sp. has four circumopesimal spine bases during early astogeny, but two oral spines in later autozooids, while *Charixa emanuelae* n. sp. lacks spine bases entirely. In view of this variability within what seem to be three closely related species, the diagnosis of *Charixa* is amended. As for *Spinicharixa*, this can now be interpreted to include only species in which circumopesimal spine bases are constantly present, even in autozooids from late astogeny, and closure plates lack a large central opening.

#### *Charixa bispinata* new species Figures 4.1, 6.1–6.6

*Holotype*.—NHMUK D59365(2A), early Albian, Glen Rose Formation, Lower Member, Bed 4, Cedar Brake Camp, Somervell County, Texas.

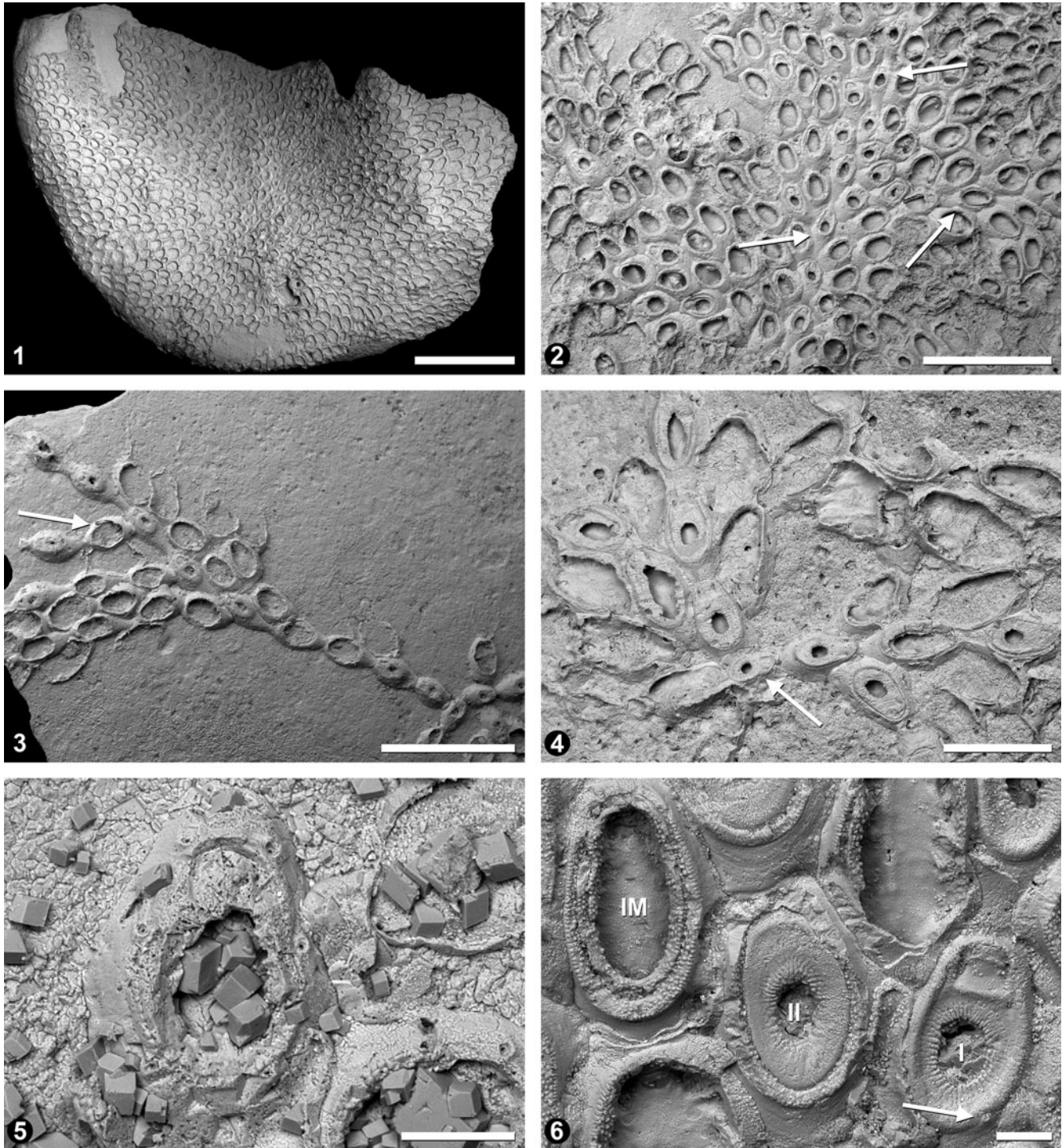
*Paratypes*.—NHMUK D59365(2B, 2C), early Albian, Glen Rose Formation, Lower Member, Bed 4, Cedar Brake Camp, Somervell County, Texas. NHMUK BZ7853, BZ7854, early Albian, Glen Rose Formation, Upper Member, Unit 2, roadcut along River Ridge Road, Mystic Shores Subdivision, Canyon Lake, Comal County, Texas.



**Figure 6.** *Charixa bispinata* n. sp. from Unit 2 of the Upper Member of the Glen Rose Formation (early Albian) of southcentral Texas, USA (1); from Bed 4 of the Lower Member of the Glen Rose Formation (early Albian) of northcentral Texas, USA (2, 3). (1) Encrusting colony; paratype, NHMUK BZ7853; scale bar is 1 mm; (2) encrusting colony, paratype, NHMUK D59365 (2B); scale bar is 1 mm; (3) ancestrula (black arrow) with distal bud and autozooids from the early astogeny showing reduction of spine number from four to two; kenozooids are marked with white arrows, holotype, NHMUK D59365 (2A); scale bar is 250  $\mu$ m; (4) ancestrula (black arrow) with one distal bud and autozooids from the early astogeny showing intramural buds (white arrows) and autozooids with two oral spines in both early and later astogeny, paratype, NHMUK D59365 (2C); scale bar is 250  $\mu$ m; (5) autozooids and interzooidal kenozooids, paratype, NHMUK BZ7853; scale bar is 250  $\mu$ m; (6) autozooid showing two oral spine bases and closure plate with straight, parallel scars of opercular sclerite distally (arrowed), paratype, NHMUK BZ7853; scale bar is 100  $\mu$ m.

**Diagnosis.**—*Charixa* with four circumopesial spine bases in autozooids from early astogeny and two oral spine bases in younger autozooids; pronounced autozooidal dimorphism between

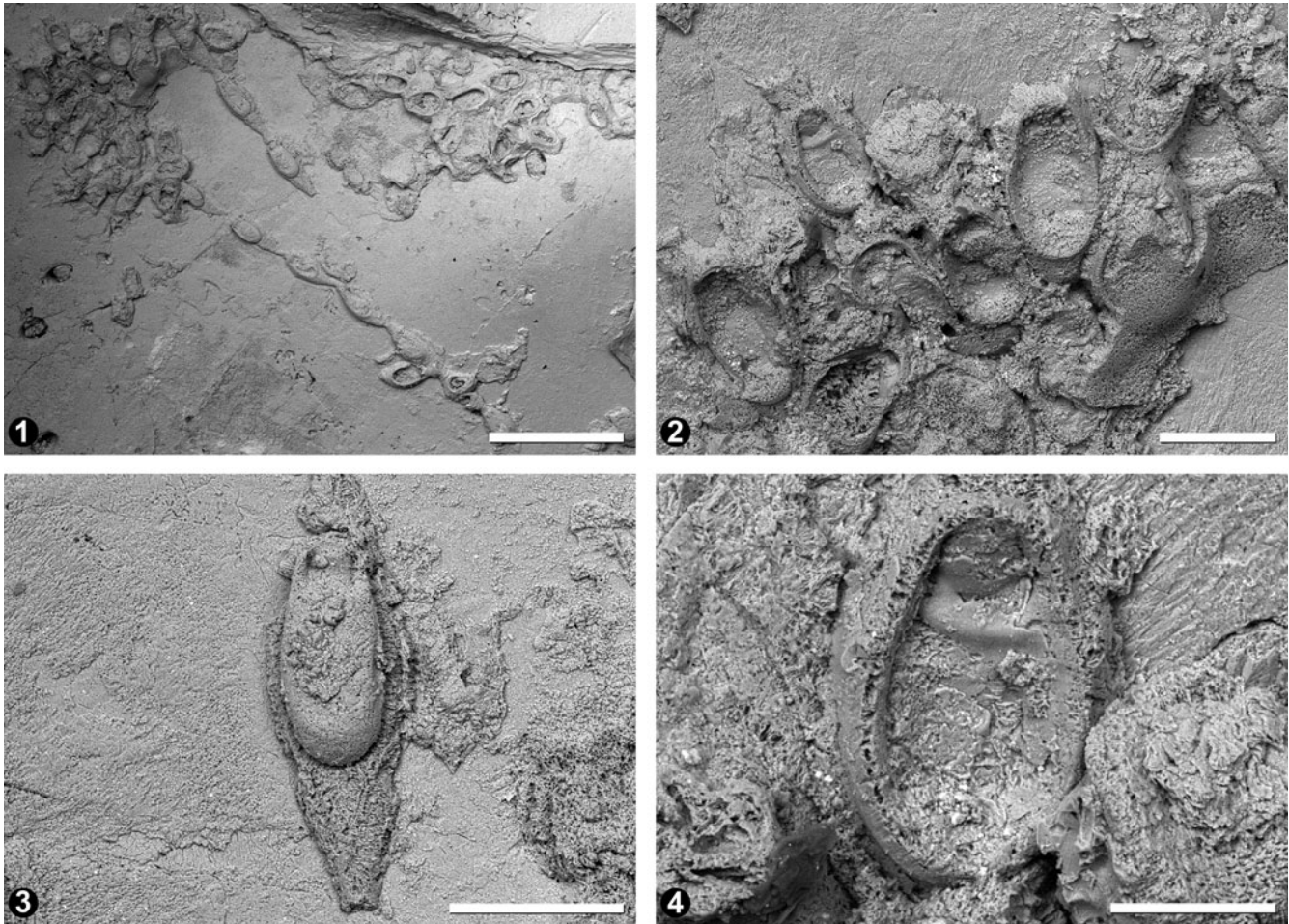
caudate autozooids forming lineal series and non-caudate autozooids filling the spaces between lineal series; closure plates with distocentral circular to longitudinally elliptical opening.



**Figure 7.** *Charixa sexspinata* n. sp. from Unit 3 of the Upper Member of the Glen Rose Formation (early Albian) of southcentral Texas, USA (1); from Unit 4 of the Upper Member of the Glen Rose Formation (early Albian) of southcentral Texas, USA (2); from Unit 7 of the Upper Member of the Glen Rose Formation (early Albian) of southcentral Texas, USA (3, 6); from the Walnut Formation (early Albian) of southcentral Texas, USA (4, 5). (1) Encrusting colony, paratype, NHMUK BZ7864; scale bar is 2.5 mm; (2) caudate autozooids forming uniserial rows (arrows) and non-caudate autozooids, holotype, NHMUK BZ7867; scale bar is 1 mm; (3) uniserial series of caudate autozooids, with new series diverging from the main series beginning with a non-caudate autozooid (arrow) followed by caudate autozooids, paratype, NHMUK BZ7895; scale bar is 1 mm; (4) early astogeny with inferred ancestrula arrowed, NHMUK BZ2056; scale bar is 500  $\mu$ m; (5) autozooid showing six circumopesial spine bases, paratype, NHMUK BZ7896; scale bar is 100  $\mu$ m; (6) three autozooids showing a broken intramural bud (IM), a completely preserved intramural bud with a type II closure plate (II) and a type I closure plate with straight, parallel scars of opercular sclerite distally (I), the latter zooid showing also one proximolateral spine base (arrow), while most other autozooids lack spine bases, paratype, NHMUK BZ2055a; scale bar is 100  $\mu$ m.

**Occurrence.**—The holotype colony and two paratype colonies encrust a bivalve shell from Bed 4 of the Lower Member of the Glen Rose Formation at the Cedar Brake Camp in northcentral

Texas (Fig. 4.1), while additional material comes from Bed 3 of the Lower Member of the Glen Rose Formation of northcentral Texas and from units 2–7 of the Upper Member of the Glen



**Figure 8.** *Charixa emanuelae* n. sp. from Bed 10 of the Middle Member of the Glen Rose Formation (early Albian) of northcentral Texas, USA, holotype, NHMUK BZ2358. (1) Encrusting colony; scale bar is 1 mm; (2) multiserial, non-caudate autozooids; scale bar is 250 µm; (3) eroded caudate autozooid, giving the false impression of a highly convex closure plate; scale bar is 250 µm; (4) non-caudate autozooid with closure plate; scale bar is 100 µm.

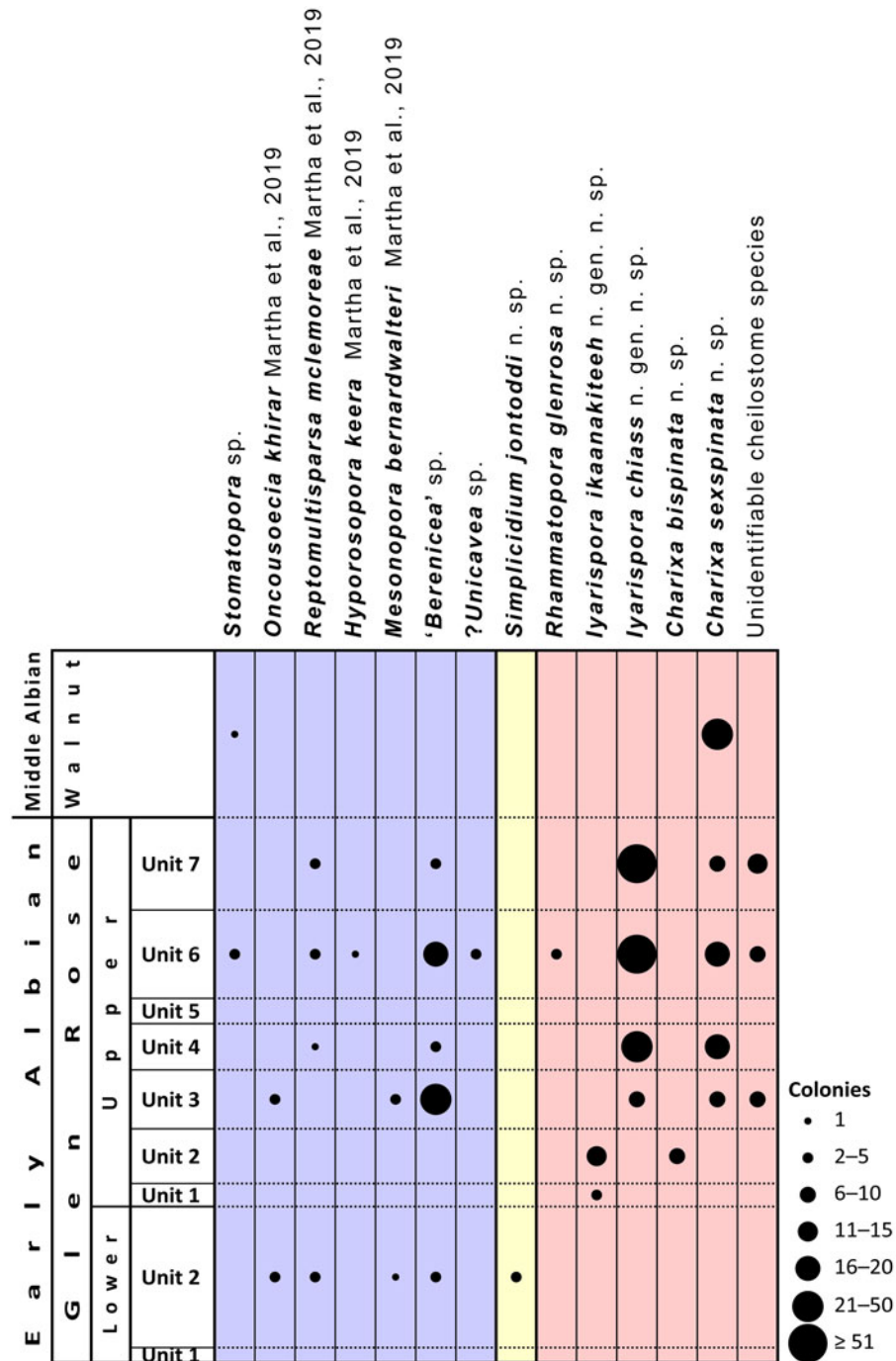
Rose Formation and the Walnut Formation in southcentral Texas (Bell, Burnet, Comal, Hays, and Travis counties).

**Description.**—Colony encrusting, consisting of short uniserial runner-like segments and prevalently of multiserial sheet-like segments, unilaminar (Fig. 6.1, 6.2). Autozooidal dimorphism slightly pronounced, caudate autozooids forming uniserial lines and non-caudate autozooids interspersed between lineal series. Caudate autozooids bud one distal caudate autozooid and usually two distolateral non-caudate autozooids, while non-caudate autozooids usually bud up to three distal and distolateral non-caudate autozooids (Fig. 6.3, 6.4). Non-caudate autozooids may bud a distal caudate autozooid giving rise to a new lineal series of caudate autozooids. Ancestrula 133–161 µm long ( $\bar{X} = 147 \pm 20$  µm; CV = 13; N = 2) by 79–115 µm wide ( $\bar{X} = 97 \pm 25$  µm; CV = 26; N = 2), longitudinally elliptical, with closure plate, one proximal spine base ascertained, more spine bases presumed, with one distal bud (Fig. 6.3, 6.4). Pore chambers presumed present.

Caudate autozooids pyriform (Fig. 6.4); non-caudate autozooids elliptical, 217–378 µm long ( $\bar{X} = 282 \pm 49$  µm; CV = 17; N = 36) by 130–255 µm wide ( $\bar{X} = 176 \pm 34$  µm; CV = 19; N = 36) (Fig. 6.5). Gymnocyst completely surrounding opesia,

smooth, forming a long cauda in caudate autozooids, narrowing laterally and distally. Opesia 162–307 µm long ( $\bar{X} = 216 \pm 39$  µm; CV = 18; N = 36) by 96–199 µm wide ( $\bar{X} = 128 \pm 24$  µm; CV = 19; N = 36), occupying most of frontal surface, longitudinally elliptical. Two oral spine bases in many autozooids, in some autozooids from the early astogeny, additional pair at about mid-length of opesia length (Fig. 6.3). Number of spine bases strongly variable, spine bases in many autozooids absent (Fig. 6.5). Cryptocyst narrow, sloping steeply into opesia, widest proximally, and narrowing laterally and distally, ornamented with radial rows of pustules. Closure plates very frequent in caudate autozooids, rare in non-caudate autozooids, covering entire frontal surface, usually slightly convex, with a subcircular to longitudinally elliptical opening distocentrally, 45–80 µm ( $\bar{X} = 67 \pm 9$  µm; CV = 13; N = 12) in diameter, with two conspicuous, straight and parallel scars of opercular sclerite distally (Fig. 6.6). Intramural reparative budding of zooids inside autozooidal opesiae occurs (Fig. 6.4). Kenozooids present, occasionally filling gaps between autozooids and overlapping gymnocyst of adjacent autozooids, variable in shape and size (Fig. 6.3, 6.5).

Morphometry measurements were performed on specimen NHMUK D59365 (2A) (holotype) and specimens NHMUK D59365 (2B) and NHMUK BZ7854 (paratypes).



**Figure 9.** Stratigraphic chart (see Martha et al., 2019, fig. 1.2) with ranges and abundance (number of colonies) of bryozoan species in the Glen Rose and Walnut formations of southcentral Texas. Cyclostome species (see Martha et al., 2019) are in blue, the ctenostome species is in yellow, and cheilostome species are in red. '*Berenicea*' sp. is used as a form-genus name for infertile bereniciform colonies not identified to the species or genus level, while 'Unidentifiable cheilostome species' comprises badly preserved specimens reminiscent of species assigned to *Charixa* and *Rhammatopora*.

**Etymology.**—From Latin '*bis*' ('two') and '*spina*' ('spine') referring to the common number of oral spines observed.

**Materials.**—For non-type material of this species, see Supplementary Data Set 1.

**Remarks.**—*Charixa bispinata* n. sp. is reported from few colonies found encrusting on bivalve shells of the Lower

Member of the Glen Rose Formation in northcentral Texas and of Unit 2 of the Upper Member of the Glen Rose Formation in southcentral Texas. The spine bases are very large. Compared with *Charixa sexspinata* n. sp., *Charixa bispinata* n. sp. shows a less distinct autozooidal dimorphism and the number and distribution of articulated spines is more regular. Radial ridges and grooves around the distocentral opening in closure plates are less pronounced or even absent.

*Charixa sexspinata* new species

Figure 7.1–7.6

**Holotype.**—BZ7867, early Albian, Glen Rose Formation, Upper Member, Unit 4, abandoned quarry on north side of SH 290, west of Dripping Springs, Hays County, Texas.

**Paratypes.**—NHMUK BZ7864, early Albian, Glen Rose Formation, Upper Member, Unit 3, Flanders Road, south of cattle pond, Legends Subdivision, Fischer, Comal County, Texas. NHMUK BZ7866, BZ7882, early Albian, Glen Rose Formation, Upper Member, Unit 4, abandoned quarry on north side of SH 290, west of Dripping Springs, Hays County, Texas. NHMUK BZ7888, early Albian, Glen Rose Formation, Upper Member, Unit 6 (lower *Loriolia* Marker Bed), cut below water tower at the intersection of FM 620 with Kollmeyer Drive, Lakeway, Travis County, Texas. NHMUK BZ7891, early Albian, Glen Rose Formation, Upper Member, Unit 6 (lower *Loriolia* Marker Bed), roadcut on the north side of FM 620 northwest of Mansfield Dam, Hudson Bend, Travis County, Texas. NHMUK BZ7895, BZ7896, early Albian, Glen Rose Formation, Upper Member, Unit 7 (upper *Loriolia* Marker Bed), abandoned quarry on north side of SH 290, west of Dripping Springs, Hays County, Texas. NHMUK BZ2055a, BZ2056, BZ2063, middle Albian, Walnut Formation, Stillhouse Hollow Dam, Spillway, Belton, Bell County, Texas.

**Diagnosis.**—*Charixa* with varying number of circumopesia spine bases (maximum: six); pronounced autozooidal dimorphism between caudate autozooids forming lineal series and non-caudate autozooids filling the spaces between lineal series; closure plates with distocentral circular to longitudinally elliptical opening surrounded by radially aligned ridges and grooves.

**Occurrence.**—The species is reported from several localities in Bell, Burnet, Comal, Hays, and Travis counties in southcentral Texas.

**Description.**—Colony encrusting, consisting of short uniserial runner-like segments and prevalently of multiserial sheet-like segments, unilaminar (Fig. 7.1–7.3). Autozooids dimorphic, caudate autozooids forming uniserial lines and non-caudate autozooids interspersed between lineal series. Caudate autozooids bud one distal caudate autozooid and usually two distolateral non-caudate autozooids, while non-caudate autozooids usually bud up to three distal and distolateral non-caudate autozooids (Fig. 7.2, 7.3). However, the first non-caudate bud from a caudate autozooid may also bud a distal caudate autozooid, thus giving rise to a new lineal series of caudate autozooids (Fig. 7.3). Ancestrula 252  $\mu\text{m}$  long ( $N = 1$ ) by 151  $\mu\text{m}$  wide ( $N = 1$ ), longitudinally elliptical, with closure plate and six spine bases, with one distal and two (proximo-) lateral buds (Fig. 7.4). Pore chambers present.

Caudate autozooids pyriform, 349–654  $\mu\text{m}$  long ( $\bar{X} = 488 \pm 87 \mu\text{m}$ ;  $CV = 18$ ;  $N = 36$ ) by 151–299  $\mu\text{m}$  wide ( $\bar{X} = 223 \pm 37 \mu\text{m}$ ;  $CV = 17$ ;  $N = 36$ ) (length/width ratio = 2.32) (Fig. 7.3). Non-caudate autozooids elliptical, 316–551  $\mu\text{m}$  long ( $\bar{X} = 437 \pm 68 \mu\text{m}$ ;  $CV = 16$ ;  $N = 36$ ) by 167–335  $\mu\text{m}$  wide ( $\bar{X} = 254 \pm 38 \mu\text{m}$ ;  $CV = 15$ ;  $N = 36$ ) (length/width ratio = 1.72) (Fig. 7.4).

Gymnocyst, completely surrounding opesia, smooth, forming a long cauda in caudate autozooids, usually extensive proximally and narrowing laterally and distally. Opesia 175–402  $\mu\text{m}$  long ( $\bar{X} = 296 \pm 65 \mu\text{m}$ ;  $CV = 22$ ;  $N = 36$ ) by 115–223  $\mu\text{m}$  wide ( $\bar{X} = 163 \pm 29 \mu\text{m}$ ;  $CV = 18$ ;  $N = 36$ ) in caudate autozooids (length/width ratio of opesia = 1.87) and 207–433  $\mu\text{m}$  long ( $\bar{X} = 316 \pm 72 \mu\text{m}$ ;  $CV = 23$ ;  $N = 36$ ) by 109–286  $\mu\text{m}$  wide ( $\bar{X} = 183 \pm 43 \mu\text{m}$ ;  $CV = 24$ ;  $N = 36$ ) in non-caudate autozooids (length/width ratio of opesia = 1.67), occupying most of frontal surface, longitudinally elliptical. Up to six spine bases encircling the opesia, one pair distolateral to opesia, second pair at about three-fourths of opesia length, third pair proximolateral to opesia (Fig. 7.5). Number of spine bases strongly variable, often reduced to one distolateral and one proximolateral pair, to one distolateral pair, or occasionally to just one proximolateral spine base (Fig. 7.5, 7.6), or spine bases absent. Cryptocyst narrow, sloping steeply into opesia, widest proximally and narrowing laterally and distally, ornamented with radial rows of pustules. Closure plates very frequent in caudate autozooids, rare in non-caudate autozooids, covering entire frontal surface, of two types. Type I closure plates concave, smooth, with a sub-circular to longitudinally elliptical opening distocentrally that is surrounded by dense, straight, radially oriented ridges and grooves, opening 59–105  $\mu\text{m}$  ( $\bar{X} = 79 \pm 13 \mu\text{m}$ ;  $CV = 16$ ;  $N = 36$ ) in diameter, with two conspicuous, straight and parallel scars of opercular sclerite distally and an elevated ridge perpendicular to the sclerite scars and presumably marking the proximal edge of the orifice (Fig. 7.6). Type II closure plates presumably formed by intramurally budded autozooid, slightly depressed below level of mural rim, slightly concave, smooth, lacking sclerite scars, with a central opening that is surrounded by dense, straight, radially oriented ridges and grooves (Fig. 7.6). Intramural reparative budding of zooids inside autozooidal opesiae present (Fig. 7.6). Kenozooids present, occasionally filling gaps between autozooids and overlapping gymnocyst of adjacent autozooids, variable in shape and size (Fig. 7.6).

Morphometry measurements were performed on specimen NHMUK BZ7867 (holotype) and specimens NHMUK BZ2055a and NHMUK BZ2056 (paratypes).

**Etymology.**—From Latin ‘*sex*’ (‘six’) and ‘*spina*’ (‘spine’) referring to the maximum number of spines observed.

**Remarks.**—The material here assigned to *Charixa sexspinata* n. sp. most likely represents more than one species. However, the high variability of characters observed in single colonies do not allow the description of several species for the material studied. For instance, the number of spines in *Charixa sexspinata* n. sp. may vary within a single colony. While six circumopesia spines is the highest number of spines observed, spines may be reduced or completely absent. In the holotype colony, autozooids may have six, four, or no spine bases. In some colonies from the Walnut Formation, some autozooids show one proximolateral (always sinistral) spine, while other autozooids completely lack spines and others have four spine bases. A correlation with the position in the colony and the number of spine bases was not observed.

*Charixa sexspinata* n. sp. differs from *Charixa bispinata* n. sp. in the variable number of spine bases and the stronger pronunciation of autozooidal dimorphism. Another clear difference is the budding pattern from the ancestrula with *Charixa bispinata* n. sp. budding one distal bud from the ancestrula, but the ancestrula in *Charixa sexspinata* n. sp. producing also lateral buds. Autozooidal polymorphism and budding pattern in *Charixa sexspinata* n. sp. are comparable to *Spinicharixa dimorpha* Taylor, 1986b from the Albian of England, but *Spinicharixa dimorpha* has up to eight circumopesia spine bases and closure plates with only one small opening.

*Charixa emanuelae* new species

Figure 8.1–8.4

**Holotype.**—NHMUK BZ2358, early Albian, Glen Rose Formation, Middle Member, Bed 10, Barker Branch, west of Glen Rose, Somervell County, Texas.

**Diagnosis.**—*Charixa* lacking spine bases; closure plates lacking a central opening.

**Occurrence.**—The species is known from one specimen from Somervell County in northcentral Texas.

**Description.**—Colony encrusting, composite multiserial, consisting of uniserial rows of caudate autozooids with non-caudate autozooids budded to fill in the spaces between. Ancestrula and early astogeny not observed. Pore chambers not observed.

Caudate autozooids pyriform, 463–562  $\mu\text{m}$  long ( $\bar{X}$  = 505  $\pm$  34  $\mu\text{m}$ ; CV = 7; N = 8) by 135–180  $\mu\text{m}$  wide ( $\bar{X}$  = 164  $\pm$  16  $\mu\text{m}$ ; CV = 10; N = 8) (length/width ratio = 3.09) (Fig. 8.1). Non-caudate autozooids elliptical, 332–421  $\mu\text{m}$  long ( $\bar{X}$  = 378  $\pm$  37  $\mu\text{m}$ ; CV = 10; N = 8) by 200–241  $\mu\text{m}$  wide ( $\bar{X}$  = 222  $\pm$  14  $\mu\text{m}$ ; CV = 6; N = 8) (length/width ratio = 1.70) (Fig. 8.2). Gymnocyst extensive, completely surrounding opesia, smooth, forming a long cauda proximally in caudate autozooids. Opesia 230–320  $\mu\text{m}$  long by 100–190  $\mu\text{m}$  wide in caudate autozooids (length/width ratio of opesia = 2.21) and 234–312  $\mu\text{m}$  long ( $\bar{X}$  = 275  $\pm$  25  $\mu\text{m}$ ; CV = 9; N = 8) by 120–190  $\mu\text{m}$  wide ( $\bar{X}$  = 158  $\pm$  25  $\mu\text{m}$ ; CV = 16; N = 8) in non-caudate autozooids (length/width ratio of opesia = 1.74), occupying most of frontal surface, longitudinally elliptical. Spine bases lacking. Cryptocyst narrow, sloping steeply into opesia, widest proximally and narrowing laterally and distally, ornamented with radial rows of pustules. Closure plates very frequent in both caudate and non-caudate autozooids, covering entire frontal surface, slightly depressed below the level of the mural rim, concave, smooth, sclerite scars not evident but elevated ridge presumably marking the proximal edge of the orifice present (Fig. 8.3, 8.4). Intramura reparative budding of zooids inside autozooidal opesiae occurs. Kenozooids not observed.

Morphometry measurements were performed on specimen NHMUK BZ2358 (holotype).

**Etymology.**—The species is named for Emanuela Di Martino (Siracusa) in recognition of her contributions to bryozoan taxonomy.

**Remarks.**—Unlike in *Charixa bispinata* n. sp. and in *Charixa sexspinata* n. sp., closure plates in *Charixa emanuelae* n. sp. lack a central opening. Furthermore, spine bases were not seen in any of the autozooids in the only known specimen, although the lack of early astogenetic stages in this small colony must be taken into account when evaluating the importance of this observation.

## Discussion

**Cheilostome turnover or facies-related dominance?**—The bryozoan faunas from the early to middle Albian parts of the Glen Rose and Walnut formations has yielded a total of thirteen species, comprising six cyclostomes (Martha et al., 2019), one ctenostome, and six cheilostome species. The cyclostomes are mostly bereniciform sheet-like tubuliporines, while the cheilostomes are all malacostegines. All of the bryozoans studied encrust bivalve shells; no erect colonies were found. Despite a similar cheilostome and cyclostome diversity, the cheilostome colonies are usually much larger and more abundant (Fig. 9). Cyclostomes are dominant only in Unit 2 of the Lower Member, in which no cheilostomes were found, and in Unit 3 of the Upper Member of the Glen Rose Formation. In all other units of the Upper Member of the Glen Rose Formation and in the Walnut Formation, cheilostomes dominate in terms of abundance. The Glen Rose and Walnut formations are therefore the oldest known bryozoan assemblages in which cheilostomes have the largest estimated biomass of any bryozoan order, raising the possibility of a more widespread faunal turnover from cyclostomes to cheilostomes at this time. Cheilostome dominance increases upwards throughout the Glen Rose and Walnut formations. However, cheilostome species richness remains low and, following a peak in Unit 6 of the Upper Member of the Glen Rose Formation, decreases into Unit 7 and the Walnut Formation.

Despite overall cheilostome dominance in terms of numerical abundance and colony size, cyclostomes are the only encrusting bryozoans to have been found on rudist shells. Cyclostomes of Unit 3 of the Upper Member of the Glen Rose Formation are mostly ‘*Berenicea*’ colonies encrusting rudists, while cheilostomes prevail on other bivalve shells in the same unit. The coral-rudist biostromes that developed below normal wave base but above storm wave base are usually found in the Lower Member of the Glen Rose Formation, while the Upper Member of the Glen Rose Formation is dominated by marine limestone and evaporite beds in which rudists are less abundant (Scott et al., 2007). ‘Dominance’ of either cheilostomes or cyclostomes within the Glen Rose and Walnut formations may therefore be facies-related rather than the signal of a precocious cheilostome turnover during the early Albian. Cyclostomes apparently prevailed in more carbonate-rich facies (i.e., rudist-associated facies) that likely represented deposition in clear water, stenohaline environments, while cheilostomes were dominant in nearshore facies deposited above normal wave base that were potentially more turbid and where salinity may also have varied.

**Malacostegine and neocheilostome evolutionary radiations.**—Cheetham (1954, 1976), Thomas and Larwood (1956), and Cheetham et al. (2006) together described a total of nine



cheilostome species from the Kiamchi, Fort Worth, Denton, Weno, Pawpaw, Main Street, and Grayson formations of the late Albian to early Cenomanian Washita Group of northeastern Texas and southeastern Oklahoma. Of these, eight are neocheilostomes assigned to the genus *Wilbertopora* Cheetham, 1954, while malacostegines are represented by only one species, *Pyripora texana* Thomas and Larwood, 1956. The Washita Group overlies the Trinity and Fredericksburg groups and the Washita neocheilostomes are the oldest known cheilostomes with calcified brood chambers (ovicells) and with specialized zooidal polymorphs (avicularia) possessing opesia enlarged to accommodate a mandible. The appearance of *Wilbertopora* during the late Albian of the Washita Group is usually regarded as the onset of the explosive radiation of cheilostomes (e.g., Taylor, 1988), while in contemporary European faunas cheilostomes were still rare and dominated by malacostegines (Martha and Taylor, 2017). The Glen Rose and Walnut cheilostome fauna is therefore of particular interest in the context of cheilostome evolution because it directly underlies the Washita Group and represents a fauna that is only slightly older and comes from the same geographical realm. Yet, the Glen Rose and Walnut bryozoan fauna is very different from that of the Washita Group. In the latter, neocheilostomes are dominant, while malacostegines are low in diversity and abundance (see Cheetham, 1976).

Considering the geographical and stratigraphical proximity of the Glen Rose and Walnut malacostegines with the Washita neocheilostomes, the former might be hypothesized to include the possible ancestors of the Washita neocheilostomes. However, there is no morphological evidence supporting this hypothesis in any of the Glen Rose or Walnut cheilostome species described here. Instead, it is more likely that the Washita neocheilostomes migrated from elsewhere to replace the previously dominant malacostegines, a migration probably related to a change in the paleoenvironment. The mid-Cretaceous carbonate platform of Texas seems to have been particularly suitable for cheilostomes. Furthermore, the two Texan formations show that malacostegines experienced a short-lived, and possibly geographically localized, evolutionary radiation during the Albian before the explosive radiation of neocheilostomes commencing in the late Albian to early Cenomanian.

## Summary and conclusions

Our study allows the following conclusions: (1) the gymnolemate bryozoan fauna of the early to middle Albian Glen Rose and Walnut formations of Texas comprises one ctenostome and six cheilostome species; (2) species diversities of Cheilostomata and Cyclostomata in these formations are similar, but cyclostomes prevail in coral-rudist biostromes deposited below normal wave base, while cheilostomes dominate in terms of abundance and colony size in nearshore facies deposited above normal wave base; (3) the nearshore Glen Rose and Walnut fauna, which is the oldest known bryozoan assemblage dominated by (malacostegine) cheilostomes, slightly antedates the Washita fauna of northeastern Texas and southeastern Oklahoma, which is dominated by neocheilostomes; and (4) malacostegines experienced a short-lived and possibly geographically localized evolutionary radiation during the early to middle

Albian before the onset of neocheilostome radiation in the late Albian to early Cenomanian.

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## Accessibility of supplemental data

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.fq24fr3.4>

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