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NEW SPECIES OF THE GENUS *HORIOPLEURA* (BIVALVIA, HIPPURITIDA, POLYCONITIDAE) FROM THE BARREMIAN–LOWER APTIAN DEPOSITS OF THE MEDITERRANEAN REGION: EVOLUTIONARY IMPLICATIONS

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Abstract. Two new species of the genus *Horiopleura* (Family Polyconitidae) are described from the Lower Cretaceous deposits of the Mediterranean Tethys margins. *Horiopleura arabica* comes from the lower Aptian Qishn Formation of southern Oman and *Horiopleura helviorum*, which occurs in the upper Barremian, Urgonian, Rustrel fauna but was primarily recorded in the lower Aptian deposits of Ardèche (SE France). In *Horiopleura arabica* the left valve projects dorsally off the commissural plane and the anterior myophore is a small crest, the right valve posterior myophore is a ledge; radial bands are weak but present. *Horiopleura helviorum*, the smallest species of the genus is characterized by a parietal lamellar anterior myophore on right valve. The two new species, are small and possess a domal left valve. They have a significant biostratigraphic and palaeobiogeographic potential. The new species illustrate a particular mode of arrangement of the anterior myophore on the right valve of *Horiopleura,* leading to a distinctive species grouping during the late Barremian-early Aptian. Our discoveries document a remarkable contemporaneous radiation of the Polyconitidae.

Keywords: Rudist bivalves, new species, Polyconitidae, Hippuritida, Mediterranean Tethys.

INTRODUCTION

Members of the Polyconitidae are common in shallow tropical carbonate platforms from the Barremian to the Cenomanian throughout the Tethys realm. Along the European, northern Tethys margin, their distribution has been documented in both the West European and East European (Carpatho-Cimmerian) regions (Douvillé, 1887, 1889; Paquier, 1905; Rey et al., 1977; Masse, 1996; Masse et al., 1998a; Skelton et al., 2010; Masse and Fenerci-Masse, 2017; Masse et al., 2023). On the southern Arabo-African Tethys margin, polyconitids have long been recognized: in Italy by Di Stefano (1898) and Parona (1909), in Greece by Steuber (1999), in the Levant by Douvillé (1913), in North Africa by Pervinquière (1912) and Chikhi-Aouimeur (1980), in southwestern Africa by Hennig (1916) and Tavani (1948), and in Arabia by Skelton and Masse (2000) and Masse and Fenerci-Masse (2017). In the New World, polyconitids are represented by endemic genera (Palmer, 1928; Pantoja-Alor and Skelton, 1999; Skelton and Smith, 2000; Masse et al., 2007). Finally, they are also present in both the Western Pacific and Tibet regions, where they are characterized by some distinctive endemic taxa (Douvillé, 1926; Yabe and Nagao, 1926; Masse and Shiba, 2010; Sano et al., 2014; Skelton et al., 2013a, b; Sha and Cestari, 2016; Rao et al., 2020).

Since the establishment of polyconitids as a phylogenetically distinct group of rudist bivalves by Mac Gillavry (1937), initially defined to include the two closely related genera *Polyconites* Roulland (1830) and *Horiopleura* Douvillé (1887), this group has been classified as a family Polyconitidae (Masse, 1996; Masse et al., 1998b; Steuber, 1999; Masse and Shiba, 2010). This perspective has gained support from the phylogenetic and cladistic analyses of Skelton and Smith (2000) and Rineau et al. (2020). It was formalized by assigning the Polyconitidae to the Superfamily Radiolitoidea in the rudist classification proposed by Skelton (2013a). Following the taxonomic inventory established by Skelton (2013a) for the members of this family, in addition to *Polyconites* and *Horiopleura*, two genera were retained: *Praecaprotina* Yabe and Nagao (1926) and *Tepeyacia* Palmer (1928). Two other valid genera were later described: *Magallanesia* Sano et al. (2014) and *Shajia* Rao et al. (2020). However, two taxa, *Jerjesia* Alencaster (1986) and *Douvillelia* Alencaster and Pantoja-Alor (1998) were excluded from the Polyconitidae (Masse et al., 2015; Rineau et al., 2020). Furthermore, there are two or three informally described forms, not acknowledged herein (see Steuber et al., 2011; Skelton et al., 2013).

The objectives of this paper are to describe two new species of the genus *Horiopleura* recorded from the Mediterranean Tethys regions, including the Middle-East: in the lower Aptian deposits of Oman and the upper Barremian and lower Aptian of Southeast France.

Our work includes a presentation of the geographical, geological, and stratigraphical settings of the material. The systematic palaeontology section provides a brief review of the characteristics of the genera *Polyconites* and *Horiopleura*, followed by the description of the new species and their comparisons. The historical, evolutionary, and environmental aspects are also

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analyzed. Stratigraphic dating refers to the ammonite zonation of Reboulet et al. (2014). This study contributes to a better understanding of Early Cretaceous rudist faunas from the Middle East and complements the inventory of Urgonian faunas from Southeast France.

GEOGRAPHICAL, GEOLOGICAL AND STRATIGRAPHICAL SETTINGS OF THE FOSSIL LOCALITIES

The Arabian form, *Horiopleura arabica* sp. nov., collected by one of us (J.-P. Platel), was recorded from the Qishn Formation of the Dhofar region (Southern Oman) (Fig. 1a). The regional Qishn Formation has been recognized and described by Roger et al. (1989), Platel et al. (1992) and recently revised by Salad Hersi et al. (2014). At Jabal Samhan (Salalah geological map, sheet 40 -1/250,000) (Fig. 1b), the formation consists of three members: the lowermost Shabon Member, which is essentially terrigenous and p.p. continental, overlies the Paleozoic basement and marks the onset of the Early Cretaceous transgression; the Hinna Member, in the middle, made up of interbedded carbonates and marls, yielding a marine fauna including rudists; and the uppermost Hasheer Member, a massive, rudist-rich carbonate unit somewhat similar to its Central Oman

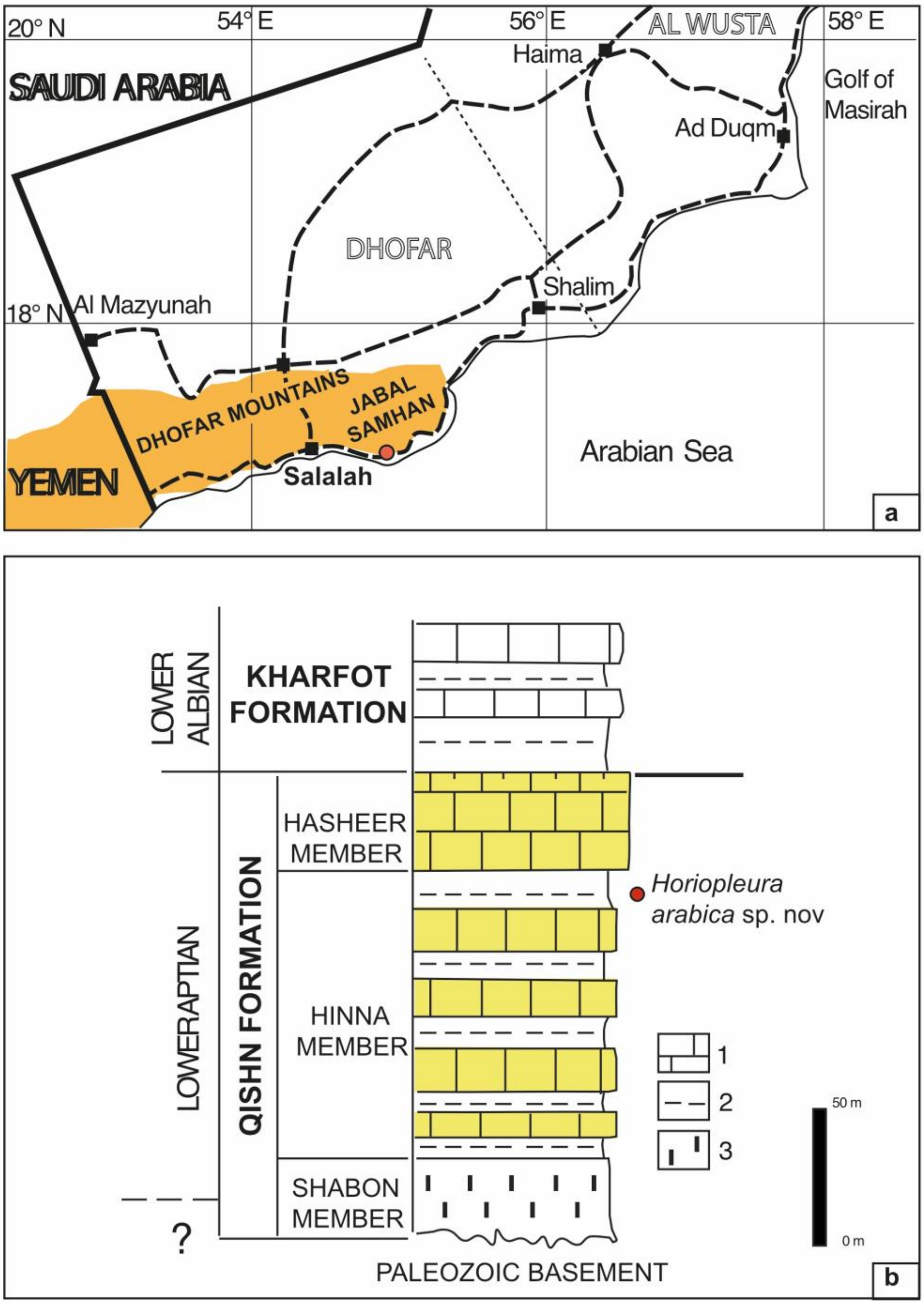

Fig. 1. Geographical and stratigraphical settings of *Horiopleura arabica* sp. nov. in Southern Oman. **a.** Geographical situation of the type area of Jabal Samhan (Dhofar Mountains). **b.** Stratigraphic organisation of the Qishn Formation and position of the type level of *Horiopleura arabica* sp. nov. (modified from Roger et al., 1989). Lithology: (1) limestones, (2) marls, (3) terrigenous.

Kharaib and Shuaiba platform equivalents (see Immenhauser et al., 2004). Our rudist specimens were collected from the marly beds of the Hinna Member, which also yield orbitolinids such as *Palorbitolina lenticularis* (Blumenbach), *Praeorbitolina cormyi* Schröder, and a nautiloid, *Heminautilus saxbii* (Morris) (Platel et al., 1992). According to Beaudoin et al. (2016), *Heminautilus saxbii* is limited to the *Deshayesites forbesi* zone of Reboulet et al. (2014), indicating an early Aptian age. The early Aptian age of the Qishn Formation (except its basal member) is further supported by the aforementioned Orbitolinidae (*Praeorbitolina cormyi*) and dasycladale algae, such as *Salpingoporella dinarica* Radoicic and *Similiclypeina* (formerly *Clypeina*) *somalica* (Conrad et al.) (Roger et al., 1989), the former characteristic of the Tethys Mediterranean Southern margin. This dating tends to conform to the late Barremian p.p. -early Aptian age reported for the carbonate formations from Jebel Akhdar and surroundings areas (e.g., Simmons, 1994; Masse et al., 1998c; Buchem et al., 2010).

The type material of *Horiopleura helviorum* sp. nov. comes from Aiguèze, in the Ardèche region (Fig. 2a). The stratigraphic section of the Urgonian limestones of Aiguèze is equivalent to the neighbouring type section of the rudist-bearing Saint-Montan Member, previously described by Lafarge (1978), and presently under revision (Masse et al., in press) The Aptian age of the Saint - Montan member is based on its stratigraphic correlation with the the U3 cherty/ bioclastic member of the Urgonian trilogy (sensu Leenhardt, 1883) of the Monts-de-Vaucluse (Masse, 1976) (Fig. 2b).This member has yield *Peudohaploceras matheroni* (d'Orbigny), *Prochelonicecas* gr. *dechauxi* (Kilian et Reboul) and *Desayesites* sp., an assemblage which typifies the *Deshayesites oglanlensis* Zone (Frau et al., 2018). *Horiopleura helviorum* sp. nov. has also been recorded in the Chaux de la Tour quarry in the U2 Member of the Urgonian trilogy of Leenhardt (1883) and Masse (1976). In this locality our new species belongs to the Rustrel fauna sensu Masse et al. (2020), and its age corresponds approximately to the *Martelites sarasini* zone (topmost Barremian) (Frau et al., 2018). The stratigraphic section including the Chaux de la Tour quarry is a portion of the composite section from the Fontaine-de-Vaucluse, Senanque, and Murs localities in the SW part of the Monts-de-Vaucluse (Masse, 1976; Léonide et al., 2012) (Fig. 2a, b).

SYSTEMATIC PALAEONTOLOGY

Abbreviations used for the taxonomic description and/or figures: L – left, R – right, A – anterior, P – posterior, D – dorsal, V – ventral, which may be combined with other characters. LV – left valve, RV – right valve, AB – anterior band, IB – interband, PB – posterior band, Dap – antero-posterior diameter, Ddv – dorso-ventral diameter, H – shell height, BC – body cavity, pm – posterior myophore, am – anterior myophore, ac – anterior crest, pc – posterior (perimyophoral) cavity, com – commissure. The classification used herein follows Skelton (2013a, b). The study material is stored at the Musée de Paléontologie, Centre Saint-Charles, Aix-Marseille University (Collection J.-P. Masse, JPMA).

In this study, we refer to *Horiopleura* and *Polyconites*. to highlight their generic characteristics, we provide antero-posterior sections of selected Barremian-Aptian species to illustrate their diagnostic LV and RV distinctive generic attributes (Fig. 3). The section of *Horiopleura dumortieri* (Matheron) from the upper Barremian of Orgon (reproduced from Masse and Fenerci-Masse, 2017, fig. 7-3) shows the transversely salient, concave-upward Rpm and sloping Ram, with both LV myophores reflexed (Fig. 3a). *Polyconites hadriani* Skelton et al. (2010), from the latest early Aptian of Maestrazgo (Spain), has RV inward-sloping myophores, with the Lpm reflexed and the Lam buttressed (Fig. 3c) (reproduced from Skelton et al., 2010, fig. 5d). *Polyconites verneuili* (Coquand) has RV inward-sloping myophores, with the Lam as a plate parallel to the opposite valve and the Lpm featuring a well-defined perimyophoral (ectomyophoral) depression (reproduced from Pascual-Cebrian et al., 2012, original figure fig. 4c, a virtual reconstruction of an upper Aptian specimen from the Valencia province, Spain).

To conclude, the key difference between *Horiopleura* and *Polyconites* lies in the organisation of the RV myophores: either located on transverse shell thickenings or on the shell wall, respectively (Fenerci-Masse, 2006; Skelton et al., 2010). In both genera, the LV posterior myophore protrudes downward, is reflexed or arcuate (originating from an internal, dorsal, conical cavity), and is represented by a bent, twisted lamina consisting of a plate subparallel to the commissure, attached to the shell by a pedicle; it is flanked by a posterior perimyophoral cavity. The LV anterior myophore is more variable (Skelton et al., 2010; Rineau et al., 2020; Masse and Fenerci-Masse, 2021) and has a potential to be used for the qualification of species.

Order Hippuritida Newell, 1965
Suborder Hippuritidina Skelton, 2013b
Family Polyconitidae Mac Gillavry, 1937
Genus ***Horiopleura*** Douvillé, 1889
Type species *Horiopleura lamberti* Munier-Chalmas in Douvillé 1889

Horiopleura arabica **sp. nov.**

Figure 4

Derivation of name. From its occurrence in Arabia (Dhofar, Oman)

Fossil Material. The study material consists of twelve free, isolated conjoined LV and RV specimens (eight well-preserved) (JPMA 17861 1 to 12), JPMA 17861-1

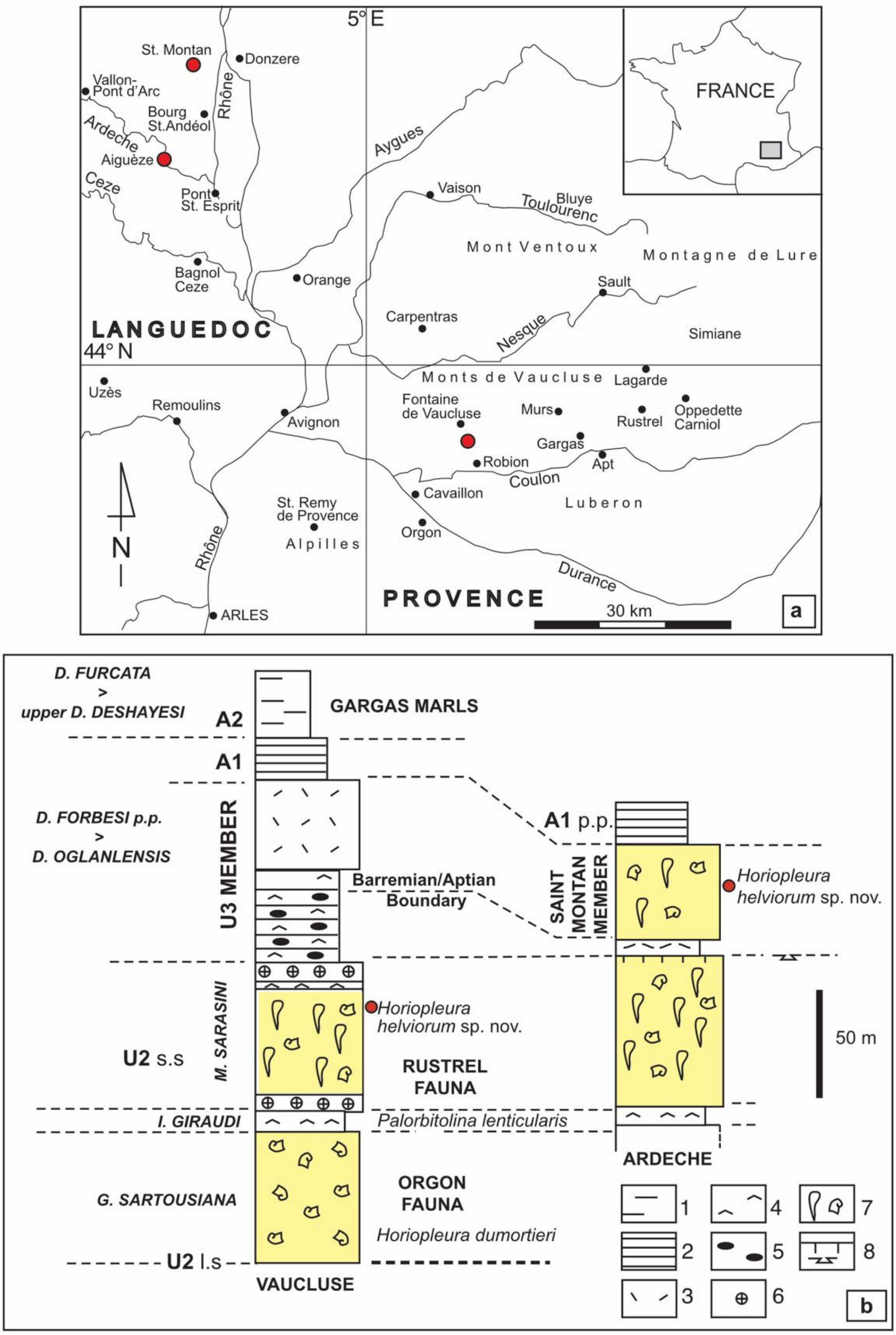

Fig. 2. Geographical and stratigraphical settings of Urgonian rudists from Southeast France. **a.** Geographical situation of Les Chaux de la Tour quarry near Robion and Fontaine-de-Vaucluse (Vaucluse), and Saint-Montan-Aiguèze (Ardèche). **b.** Stratigraphic composite section of Barremian-Lower Aptian Urgonian successions from Fontaine-de-Vaucluse-Senanque-Murs, from the SW part of the Monts- de-Vaucluse (modified from Masse et al. 2020), its correlation with the Saint-Montan-Aiguèze sections from Ardèche, and position of *Horiopleura helviorum* sp. nov. Facies legend: (1) marls, (2) marly limestones, (3) bioclastic limestone, (4) *Palorbitolina* facies, (5) chert, (6) coral facies, (7) rudist facies, (8) sedimentary discontinuity with early exposure.

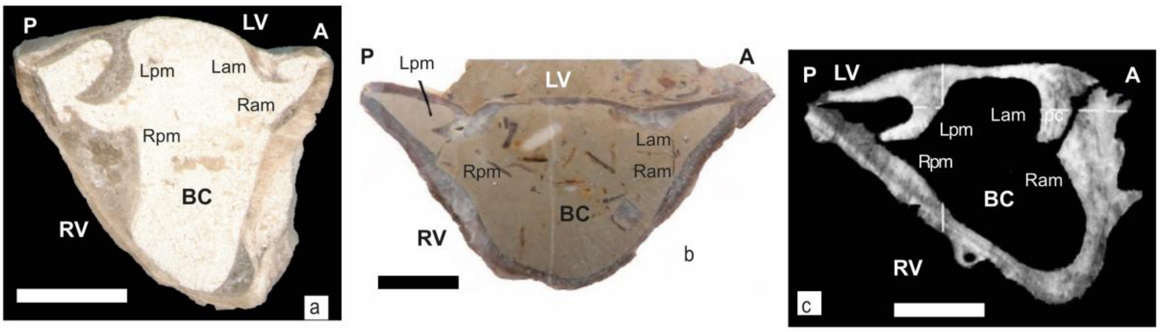

Fig. 3. Reference sections of bivalve specimens of the genera *Horiopleura* and *Polyconites* showing the myophoral organisation, focusing on the morphology of the RV posterior myophores. **a.** *Horiopleura dumortieri* (Matheron), late Barremian, Orgon (from Masse and Fenerci-Masse, 2017). **b.** *Polyconites hadriani* Skelton et al., latest early Aptian, Maestrazgo (from Skelton et al. 2010). **c**. *Polyconites verneuili* (Coquand), late Aptian, Valencia province (from Pascual-Cebrian et al., 2012). Scale bar is 10 mm.

has been selected as holotype, the others being paratypes.

Six specimens have been cut to investigate the internal characters. The study material was originally associated with a fossil assemblage including different Monopleuridae pooled in the sample JP85 of Platel et al. (BRGM internal report).

Holotype. A complete well-preserved articulated shell: JPMA 17861-1.

Paratypes. Eleven conjoined LV and RV specimens (JPMA 17861-2 to 12).

Type level. Hinna Member, early Aptian (based on *Praeorbitolina cormyi* and *Heminautilus saxbii)*

Size of the holotype. Dap: 22 mm; Ddv: 20 mm

Type locality. Jabal Shamal (17° 04’21’’N, 54° 81’ 75’’ E).

Genus placement. The LV posterior myophore is reflexed posteriorly, flanked by a posterior perimyophoral depression, and corresponds to the polyconitid mode described by Mac Gillavry (1937). The RV posterior myophore is a ledge, the anterior is on the shell wall. The transverse inflated posterior myophore on RV conforms to that of *Horiopleura*.

Diagnosis. Modest size *Horiopleura* with a domal LV projecting dorsally off the commissural plane, radial bands weak, represented by colored bands, LV anterior myophore a small crest, RV posterior myophore a ledge.

Description. RV straight, conical, or twisted, with some wavy growth patterns, somewhat flared at the adult stage; LV smooth, domal; beak orthogyrate or prosogyrate, slightly projecting dorsally off the commissural plane (Fig. 4a, b, c, d, e). The dorsal ligamentary groove is well-marked on the RV, short and poorly preserved on the LV. The commissural plane is flat, faintly depressed dorsally. Radial bands are narrow and slightly concave on the LV, with the interband wider and flat. The anterior portion of the shell is larger than the posterior (Fig. 4d). Bands are inconspicuous or weakly marked on the RV, and at the commissure, there is a convex, regular commissural outline. The shell size is modest, with a thin shell thickness. The outer calcitic and internal formerly aragonitic shell layers are in the range of 1-2 mm. Internal characteristics, deduced from longitudinal antero-posterior sections of bivalve specimens and the preparation of two LVs, are as follows:

- LV posterior myophore is reflexed posteriorly, facing a triangular shoulder on the RV. Near its ventral termination, the LV myophore becomes a crest (Fig. 4f, g). In larger specimens, the LV posterior myophore is pediculate, and the facing RV myophore is depressed,
-RV anterior myophore is mostly parietal, located on the shell wall. However, the preparation (milling operation) of the dorsal, anterior side of the LV reveals a short, thin wall (Fig. 4i) with a small triangular ventral termination, which represents the LV anterior myophoral crest.

The cardinal elements are hardly visible. A transverse section of the LV, cut parallel to the commissure, suggests poorly preserved, minute, seemingly subcylindrical teeth located on a narrow cardinal platform, restricted to the dorsal shell side. Meanwhile, a dorso-ventral section of the LV reveals the anterior tooth.

Species characters. The Dap and Ddv values are nearly equal. The average and extreme shell size values (measured on eight well-preserved specimens) are as follows: Dap = 24 mm (range: 15 to 30 mm), Ddv = 24 mm (range: 18 to 33 mm), and H = 27 mm (range: 24 to 34 mm). The height of the LV beak above the commissural plane varies from 8 to 13 mm. The shell is dark or light beige in colour. On dark specimens, the radial bands of the LV are pale beige, a particularly nice and remarkable feature. However, their topographic expression on the shell surface is weak and marked by a discrete depression (Fig. 4b). Variability may include prominent growth banding on both valves and the orientation of the LV beak. In twisted specimens, the ventral side of the RV is more or less convex, and this convexity tends to increase with shell size. The LV posterior myophore has a small perimyophoral cavity and is dorso-ventrally more elongated than the anterior one. As a result, in median transverse antero-posterior sections, the anterior lamina does not appear. The RV posterior myophore is marked by a ledge with a triangular

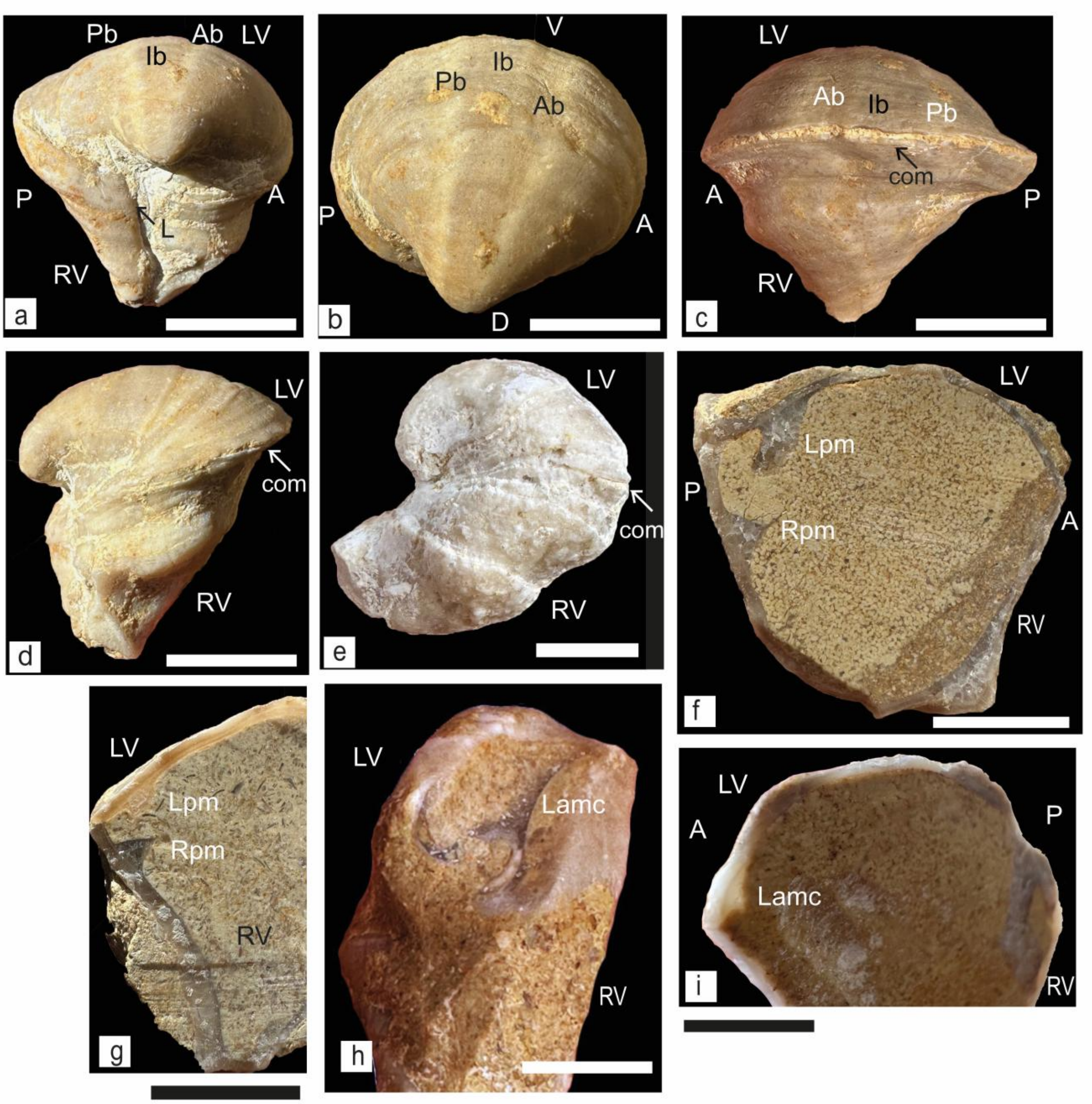

Fig. 4. *Horiopleura arabica* sp. nov., early Aptian, Jabal Samhan. Holotype JPMA17861-1 (**a, b, c, d**). **a.** dorsal view of the two valves showing overall morphology, the ligament groove, and the radial bands on LV with contrasting colours. **b.** LV showing the radial bands and the commissural outline. **c.** ventral view. **d.** anterior view showing the prosogyrate, projecting beak. **e**. anterior view of a twisted specimen, paratype (JPMA 17861-2). Internal characters of paratypes. **f.** antero-posterior longitudinal, median section showing the salient posterior myophores (JPMA 17861-3). **g**. ibidem, ventral section, showing the small buttress like Lpm and Rpm. **h**. internal, anterior view of the Lamc (JPMA 17861-3). **i.** section showing the Lamc (JPMA 17861-4). Scale bar is 10 mm.

cross-sectional shape. This feature, is present in *Polyconites hadriani* (see Fig. 6b, c, d, e of Skelton et al., 2010) in juvenile specimens.

Comparisons. In *Horiopleura arabica* sp. nov., the beak slightly projects dorsally off the commissural plane (Fig. 3a, b, c), a feature that is uncommon in other *Horiopleura* species. The LV posterior myophore is reflexed and arcuate. In other species, e.g. *H. brevis* Masse et al., the LV myophore is more robust and the opposite RV myophore is more transversally inflated. The LV anterior myophore is a short, dorso-ventrally thin crest, an uncommon feature in all other subcontemporaneous species e,g. *H. dumortieri*, *H. brevis* and *H. helviorum* sp. nov. as well. Radial bands are weak but present, represented by contrasted colors and a barely thickened inner shell.

Horiopleura helviorum sp. nov.
Figure 5

Derivation of name. The species was recorded near the village of Aiguèze, alongside the Ardèche River. This area, located in the southern part of the Département de l'Ardèche, corresponds to the ancient territory of the

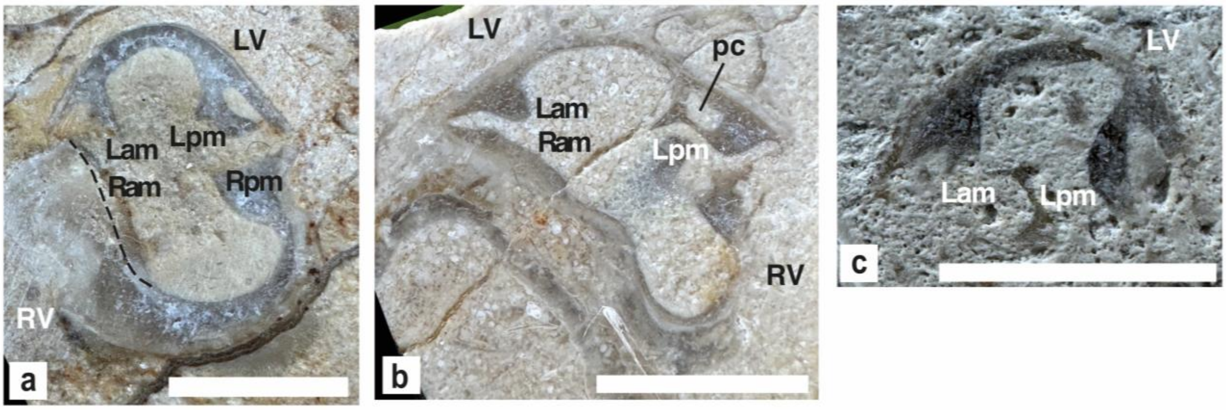

Fig. 5. *Horiopleura helviorum* sp. nov. **a**. antero-posterior, longitudinal section of a bivalve specimen, showing the polycontid organisation of the myophores and the convex left valve (JPMA 18092), early Aptian, Aiguèze. **b**. ibidem, holotype, same age and locality, notice the posterior cavity supporting the left valve myophore (JPMA 18083a). **c**. antero-posterior section of an isolated left valve with the typical polyconitid myophoral organisation (JPMA 18124). Les Chaux de la Tour quarry, late Barremian. Scale bar is 10 mm.

Helvii Gallus tribe.

Fossil material. The type material from Aiguèze is represented into five slabs JPMA 18092, 18062 a-b, and 18083 a-b providing five antero-posterior sections of bivalve specimens, JPMA18083 has been selected as holotype, one section of a LV comes from Chaux de la Tour (Monts-de-Vaucluse) (JPMA18124), (Fig. 2a, b).

Holotype. JPMA18083a.

Paratypes. Four slabs JPMA 18092, 18062 a-b, and 18083b.

Size of the holotype. Dap: 17 mm

Type level. Saint-Montan Member, early Aptian (based on stratigraphic correlations with beds containing *Pseudohaploceras matheroni* and *Deshayesites* sp.)

Type locality. Aiguèze (44° 18’15’’N, 4° 33’ 23’’ E).

Genus placement. The LV posterior myophore is reflexed posteriorly, flanked by a posterior perimyophoral depression, and matches the polyconitid mode described by Mac Gillavry (1937). The RV anterior myophore is on the shell wall, while the posterior forms a transverse shell thickening. This myophoral organisation conforms to that of *Horiopleura.* The transverse posterior commissural thickening of the RV, facing the LV pedunculate myophore, is restricted to the commissural area. In the RV anterior shell (though partly recrystallized), the anterior myophoral plate of the LV is tangential, i.e., facing the inner shell side, as for instance in *Polyconites verneuili* (Fig. 3b).

Diagnosis. Small *Horiopleura* with domal LV, transverse posterior myophoral thickening of the RV, nearly commissural, and LV sublamellar myophore facing the inner shell wall of RV.

Description. LV low convex, nearly symmetrical, with the inner face exhibiting projecting myophores. The posterior is reflexed posteriorly and flanked by a posterior perimyophoral depression, while the anterior forms a thick, lamellar crest, protruding below the commissure. RV subconical, with a posterior commissural myophoral shoulder-like shell thickening, and the RV anterior myophore located on the inner shell (Fig. 5a, b, c). The section JPMA18083 (holotype) shows the occurrence of the posterior canal (Fig. 5b), a feature typically recorded in dorsal sections of advanced upper Aptian-Albian polyconitids, such as *Horiopleura almerae* Paquier (Masse and Fenerci-Masse, 2017).

Species characters. The small size (Dap = 15 mm, range 14-17 mm; H = 19 mm, range 15-20 mm, n = 5), domal LV, the RV posterior, commissural transverse thickening and the lamellar LV myophore of *H. helviorum* sp. nov. are assumed as distinctive attributes of the species.

Comparisons. *H. helviorum* sp. nov. is the smallest species recorded so far.

RELATIONSHIPS WITH OTHER SPECIES, EVOLUTIONARY ASPECTS AND PALAEOENVIRONMENT

The characters of the new species and the other subcontemporaneous species, described earlier, are illustrated on figure 6.

The two new species belong to the group of small species (Dap< 50 mm) which includes *H. dumortieri* and the Barremian individuals of *H. brevis*, and we didn’t record any shell dimorphism, so far documented for larger species (Masse and Fenerci-Masse, 2017). The dimensions (Dap) are in the range of 14-17 mm for *H. helviorum* and 15-30 mm for *H. arabica*, i.e. much smaller than those of *H. dumortieri* (33-35 mm) and *H. brevis* (35-50 mm). From the foregoing stratigraphic data, it appears that our small new species are essentially early Aptian in age, the two others, larger, late Barremian. This apparent anomaly in size which disagrees with the Cope Rule, most frequent in rudist bivalves (e.g. Masse and Fenerci-Masse, 2017, 2020), may reflect some environmental controls. But we notice that the phyletic

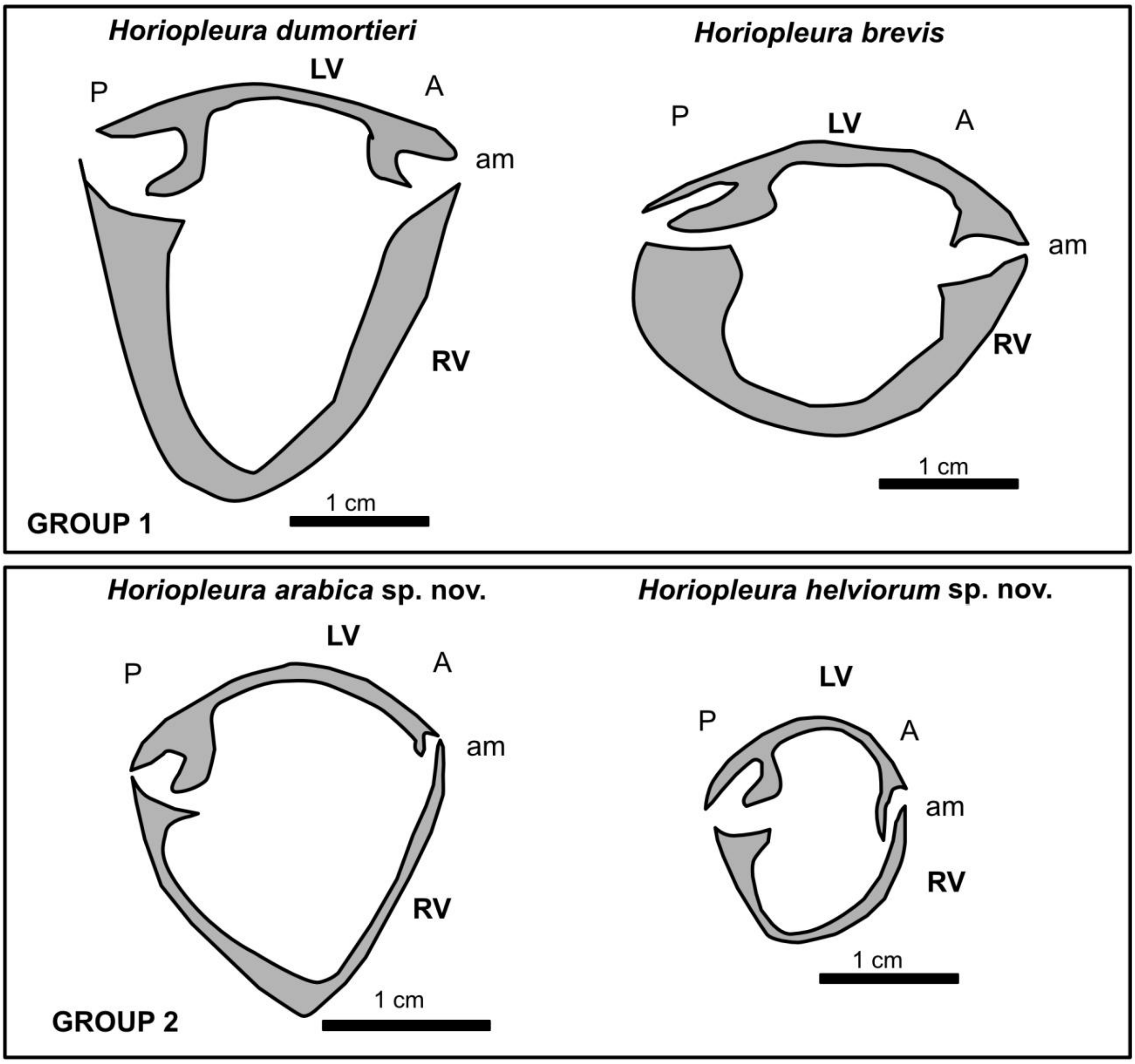

Fig. 6. Comparative illustrations of Barremian-early Aptian *Horiopleura* species, based on longitudinal cross-sections. Species groups 1 and 2 refer to the organisation of the anterior myophore.

derivation of *H. brevis* from *H. dumortieri* in the late Barremian (Masse and Fenerci-Masse, 2017) is coupled with size increase, and this trend, matching the Cope rule, is enhanced in early Aptian representatives of *H. brevis.*

The domal shape of LV decreases with shell size. The shape of the LV posterior myophore is somewhat variable, mostly the development of the pedicle either thin, in *H. dumortieri*, or massive in *H. brevis,* and its length as well. The RV posterior myophore is subparallel to the commissure in *H. dumortieri*, *H. brevis* and *H. helviorum* sp. nov., and we notice that in our two new species the inflated portion of the myophore is restricted to the commissural zone, and in the case of *H. arabica* sp. nov. it is reduced to a cross-sectional triangular shoulder, as in *Polyconites hadriani*.

We contend that the distinctive habit of the LV and RV anterior myophores has a prominent taxonomic value. The LV anterior myophore is reflexed symmetrically to its posterior counterpart in *H. dumortieri* where it turns to a crest ventrally. In *H. brevis* the anterior myophore is obliquely, transversally inflated. By contrast in *H. arabica* sp. nov. the anterior myophore is a small crest, whereas in *H. helviorum* sp. nov. it is a thin lamaella protruding into the opposite valve. On the RV of *Horiopleura dumortieri* and *H. brevis* the transversally inflated anterior myophore complies with the organization of *Homopleura* Masse and Fenerci-Masse (2019) or of late Aptian- Albian members of *Horiopleura* (Masse and Fenerci-Masse, 2017). In contrast the flattened RV anterior myophore of *Horiopleura arabica* sp. nov. and *H. helviorum* sp. nov. departs from this model and complies with the organization of *Monopleura* or *Debrunia*, and are therefore much similar to that of advanced *Polyconites*, e.g. *P. verneuili* (Pascual-Cebrian et al., 2012; Jaillard et al., 2022). This dual pattern of species grouping (see figure 6) may suggest contrasting evolutionary modes: the group 1 correspond to the "inflated mode" directly inherited from *Homopleura,* in accord with the evolutionary origin of the Polyconitidae proposed by Masse and Fenerci-Masse (2019), whereas the group 2 with "flattened mode" may be either inherited from *Monopleura* or derived from the detumescence of the inflated anterior myophore of *Homopleura.*

Until now, the genus *Horiopleura* was, and still is, considered the oldest member of the Polyconitidae, with its First Appearance Datum (FAD) in the late Barremian, specifically in the *Hemihoplites feraudianus* Subzone of the *Gerardhtia sartousiana* zone (Masse, 1996; Masse and Fenerci-Masse, 2017). The description of our new species bears out that the late Barremian-early Aptian is coincident with a major radiation of the Polyconitidae and this event is coeval with the sharp rise in the proportion of uncoiled relatively to the spirogyrate rudists (Skelton, 1985). The major radiation of the Polyconitidae, with four species of the genus *Horiopleura*, postdates the "*Agriopleura* extinction event", a major crisis in rudist evolution, and is associated with the subsequent post-event recovery phase (Masse and Fenerci-Masse, 2013, 2022).

Horiopleura arabica sp. nov., associated with marly sediments, may be considered a clinger sensu Skelton and Gili (2002), whereas both this species and *H. helviorum* sp. nov. are frequently attached to other rudist shells, a behavior typically observed in juvenile or smaller specimens. *H. arabica* sp. nov. was thriving in shallow coastal (i.e., terrigenous) environments. *H. helviorum* sp. nov., relatively uncommon, is a member of polytaxic rudist assemblages (dominated by Requieniidae and Caprinidae) found in the regional Urgonian carbonate platform with *H. brevis*.

CONCLUSIONS

Two species of the genus *Horiopleura* (Family Polyconitidae) are described from the Barremian to lower Aptian platform carbonates of Dhofar (Oman) and Provence-Languedoc (Southeast France). *Horiopleura arabica* sp. nov. occurs in the Southern Oman Qishn Formation of early Aptian age, while *Horiopleura helviorum* sp. nov. is associated with the upper Barremian Rustrel fauna from the U2 Urgonian Formation of the Monts-de-Vaucluse, though it is primarily recorded in the lower Aptian Saint-Montan fauna from Ardèche. We assume that the new species possess a significant biostratigraphic potential. Their occurrence in distant regions of the Tethys Mediterranean realm (SE France and Oman) corroborates the wide geographic distribution of the genus *Horiopleura* formely mostly documented for late Aptian-Albian species from Europe, Africa and SE Asia. The two late Barremian *Horiopleura* species, described earlier, plus the two new early Aptian species described herein, illustrate a dual stratigraphic and evolutionary species grouping. It also bears out the existence of an important contemporaneous radiation of the Polyconitidae. This radiation mostly coincided with the recovery phase following a major rudist crisis, the "*Agriopleura* extinction event ".

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