



A New Species of Polyconites from the Lower Aptian of Iberia and the Early Evolution of *Polyconitid* Rudists

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Abstract: The main diagnostic character of polyconitid rudists is a distinctive ectomyophoral cavity inserted behind a reflexed posterior myophoral plate in the left valve. The only pre-Aptian Old World polyconitid taxon recognized in the current literature is *Horiopleura dumortieri* (Matheron): this species clearly shows the prominent posterior myophoral shelf in the right valve that is diagnostic of the genus, which continues into the Albian. *Polyconites*, by contrast, has a more depressed (operculiform) left valve and its posterior adductor was inserted on an inward-sloping swelling on the right valve inner wall, with no projecting shelf. Hitherto, the earliest known species of *Polyconites* was *P. verneuli* (Coquand), ranging from the Middle Aptian (Gargasian). However, smaller specimens (of similar size to *H. dumortieri*) from the uppermost Lower Aptian (*Dufrenoyia furcata* zone) of the Maestrat Basin of eastern Spain, together with similar though slightly older specimens from the southern Lusitanian Basin of Portugal show the relatively depressed left valve and myophoral configuration of *Polyconites*, to which genus we refer them as a new species, *P. hadriani*. Its similarity to *P. verneuli* suggests direct chronospecific descent of the latter, with phyletic size increase, as seen in many other rudist lineages. Recognition of the inception of this *Polyconites* lineage from the mid-Lower Aptian resolves the status of certain uppermost Lower Aptian polyconitids previously assigned to *H. baylei* but recognized as problematical. Moreover, we suggest that *H. baylei* (Coquand) and *P. verneuli* may be synonymous.

The progressive depression of the left (free) valve and extension of the right (fixed) valve ventral margin during development in *P. hadriani* allowed upward growth-projection of the compressed ventral valve margins. This new mode of growth, relative to the antecedent *Horiopleura*, permitted imbricate close-packing of individuals, as in living flat oysters and epibyssate pteriaceans such as *Isognomon*, as well as the mid-Cretaceous *Chondrodonta*.

Key Words: rudist, *Polyconites*, new species, evolution, Lower Aptian, Iberia

Iberia'nın Alt Apsiyen'inden Yeni Bir *Polyconites* Türü ve Polyconitid Rudistlerin Erken Evrimi

Özet: Polyconitid rudistlerinin ana diyagnostik özelliği, sol kavkıda bulunan kıvrılmış arka miyofor levhasının arkasındaki belirgin ektomyoforal boşluktur. Günümüz literatüründe tanınan tek Apsiyen öncesi polyconitid taksonu *Horiopleura dumortieri* (Matheron)'dir: bu tür, Albiyende de süreklilik gösteren cinsin diyagnostik özelliği olan sağ kavkıdaki belirgin arka miyofor düzlüğünü açıkça gösterir. *Polyconites* ise daha basık (opercül şekilli) bir sol kavkıya

sahiptir ve arka addüktör kası ise içe doğru eğimli, genişlemiş çıkıntısı olmyan düzlüğe, sağ kavkı iç duvarına yerleşir. Bu güne değin *Polyconites*'in bilinen en yaşlı türü, Orta Apsiyen (Gargasiyen) kadar uzanan *P. verneuili* (Coquand)'dir. Ancak, doğu İspanya'daki Maestrat Havzası'nın enüst Alt Apsiyen'deki (*Dufrenoyia furcata* zonu) daha küçük örnekler (*H. dumortieri* ile benzer boya sahip) bununla birlikte, güney Lusitanian Havzası'ndaki (Portekiz) biraz daha yaşlı örnekler nispeten basık sol kavkı ve *Polyconites*'in miyoforal biçimini gösterir. Bu nedenle, bu örnekleri *Polyconites* cinsinin yeni türü olarak tanımlıyoruz; *P. hadriani*. Türün *P. verneuili*'ye benzerliği, diğer birçok rudist soyunda görüldüğü gibi, filetik boyut artışı ile *P. hadriani*'nin, *P. verneuili*'nin doğrudan kronospesifik atası olduğunu gösterir. Bu *Polyconites* soyunun orta-Alt Apsiyen'de başladığının kabulü, daha önce *H. baylei* olarak tanımlanan fakat problemli olan bazı enüst Alt Apsiyen polyconitidlerinin durumunu açıklığa kavuşturur. Dahası, *H. baylei* (Coquand) ve *P. verneuili*'nin sinonim olabileceğini öneriyoruz.

P. hadriani'nin gelişimi sırasında, sol (serbest) kavkının ilerleyen çöküntüsü ve sağ (sabit) kavkının ventral kenarının uzaması, basık ventral kavkı kenarlarında yukarı yönlü büyüme çıkıntıları oluşmasını sonuçlamıştır. Bu yeni büyüme tarzı, ataları olan *Horiopleura*'ya göre, günümüz düz oysterleri ve *Isognomon*, *Isognomon* gibi epibaysat pteriakenlar ve orta Kretase *Chondrodonta*'ları gibi bireylerin üst üste sık paketlenmesini sağlamıştır.

Anahtar Sözcükler: Rudist, *Polyconites*, yeni tür, evrim, Alt Apsiyen, Iberia

Introduction

The polyconitids were first recognised as a phylogenetically distinct group of rudists by Mac Gillavry (1937, p. 104), who diagnosed them thus: 'In the *Polyconitinae* a cavity develops under the left valve's muscle scar, which becomes a lamina in this way, bearing the muscle on its lower face...'. He thus recognised the close affinity of the genera *Polyconites* and *Horiopleura*, which share this feature, but differ in the orientation of the posterior myophore in the right valve: that in the former genus is depressed to form a mere swelling that slopes down into the body cavity, while in the latter genus it forms a prominent, flat or even backwardly inclined ledge (Figure 1). It was precisely the latter distinction that had caused Douvillé (1889) to separate the two, with *Polyconites* assigned to his 'monopleurid' grouping and *Horiopleura* to his 'gyropleurid' grouping, but, as Mac Gillavry (1937) realised, a simple tilting of this myophoral ledge during growth was all that was necessary to forge an evolutionary link between them.

Although the polyconitid grouping was ignored in the 'Treatise on Invertebrate Paleontology' (Dechaseaux *et al.* 1969), it was subsequently resurrected by Masse (1996) and Masse *et al.* (1998), and received some support in the phylogenetic analysis of Skelton & Smith (2000), who incorporated a number of other taxa in the clade on the basis of shared possession of the distinctive posterior ectomyophoral cavity in the left valve that was originally recognized by Mac Gillavry (1937).

Believing the polyconitids to be derived from a monopleurid root, Mac Gillavry interpreted the 'monopleurid' condition of the posterior myophore in the right valve of *Polyconites* to be the primitive state, arguing that *Horiopleura* was derived from it by uplift and eventual posteriorward tilting of the myophoral ledge. However, this proposed evolutionary sequence is contrary to that of the stratigraphical first appearances of the two genera, since Masse (1996) assigned the Barremian–Bedoulian '*Monopleura dumortieri* Matheron to *Horiopleura* and recognized it as the stratigraphically oldest polyconitid species. The first *Polyconites*, *P. verneuili*, by contrast, was considered not to have appeared until some time later, in the Gargasian (Middle Aptian), alongside a supposedly more derived species of *Horiopleura*, '*H. baylei*'.

However, both these last two Gargasian polyconitid 'species' have been problematical since their inception. '*Caprina Verneuili*' was introduced as a *nomen nudum* by de Verneuil *et al.* (1860), in reference to specimens from Portugaleta (Bilbao), with a mention that they would be described and figured by Bayle. Yet it seems that Bayle, unfortunately, did not go beyond labelling de Verneuil's specimens in the collections of the *École de Mines* as '*Polyconites Verneuili*', even mis-stating their provenance as Santander, according to Douvillé (1889). Thus the first validly published designation of the species (as per ICZN Article 12; Ride *et al.* 1999) appears to be that by Coquand (1865, p. 347), who described it as '*Caprina Verneuili*', in which case the authorship of the species *P. verneuili* should be

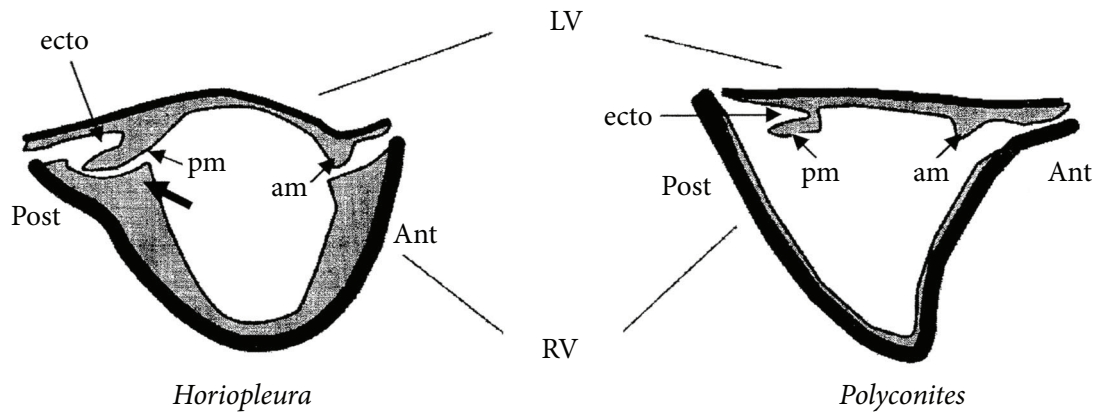


Figure 1. Myophoral organization in *Horiopleura* (left) and *Polyconites* (right), shown in diagrammatic antero-posterior sections across both valves (Modified from Fenerci-Masse 2006, figure 22). Key: am– anterior myophore (of left valve); Ant– anterior; ecto– posterior ectomyophoral cavity (in left valve); LV– left valve; pm– posterior myophore (of left valve); Post– Posterior; RV– right valve; thick arrow shows posterior myophoral ledge in RV of *Horiopleura* (absent in *Polyconites*).

ascribed to Coquand, not to Bayle (as commonly seen in the literature). In the same work, Coquand (1865, p. 346) also described ‘*Caprina Baylei*’, as a new species, though he later (1880) synonymised the two species, as ‘*Monopleura Verneuili*’. While admitting the variability of their external forms, on which Coquand’s original distinction had been based, Douvillé (1889) nevertheless argued to maintain the separation of the two ‘species’. His justifications were a purported difference in degree of development of the supplementary accessory cavity *o*’ in the posterior myophore of the left valve, as indicated by internal moulds (Figure 2), as well as a difference in the relative inclination of the posterior myophore in the right valve.

However, Malchus (1998) noted considerable variability in development of the accessory cavity, with overlap between the two ‘species’, and noted, moreover, that the posterior myophore in the right valve of ‘*H. baylei*’ is ‘more similar to *Polyconites* than to co-generic species’ (Malchus 1998, p. 186).

In addition, Malchus (1998, figure 10, 2) figured an antero-posterior section of ‘*H. baylei*’ from the uppermost Lower Aptian of Mola de Xert, Maestrat, with a clearly inward-sloping posterior myophore in the right valve. Masse *et al.* (1998, p. 200) likewise referred to ‘*Horiopleura* gr. *dumortieri* (Matheron) – *baylei* (Coquand)’ from the uppermost Lower Aptian of Murcia (Sierra de Sopalmu and S. del Carche) that

‘falls within the range of the average dimensions of *Horiopleura dumortieri* and those of the smallest representatives of *Horiopleura baylei*’, but noted the relatively more flattened left valve of ‘*H. baylei*’. They also commented that ‘Actually some representatives of *Horiopleura* do not show the outward deepening posterior myophore nor the adjacent vertical lamina: this configuration typifies the advanced forms as *Horiopleura lamberti* (Munier-Chalmas)’ (Masse *et al.* 1998, p. 203). The distinction between *Horiopleura* and *Polyconites* in the uppermost Lower Aptian thus seems debateable.

Fenerci-Masse (2006, p. 57) noted the relatively minor presence of *H. dumortieri* in the Barremian, but referred to a related form that is important in the Lower Aptian (Bedoulian). The latter was also reported from the Lower Aptian of the southern Lusitanian Basin, Portugal (Skelton & Masse 1998, figure 5), in a level now believed to represent the basal part of the Upper Bedoulian (Burla *et al.* 2008).

Here, we describe polyconitid specimens collected from the uppermost Bedoulian of the Maestrat region, similar to those described from the same stratigraphical level by Malchus (1998) and Masse *et al.* (1998), cited above, as well as some slightly older specimens from the basal Upper Bedoulian of the southern Lusitanian Basin of Portugal, and propose a solution to the various areas of taxonomic uncertainty that are discussed above.

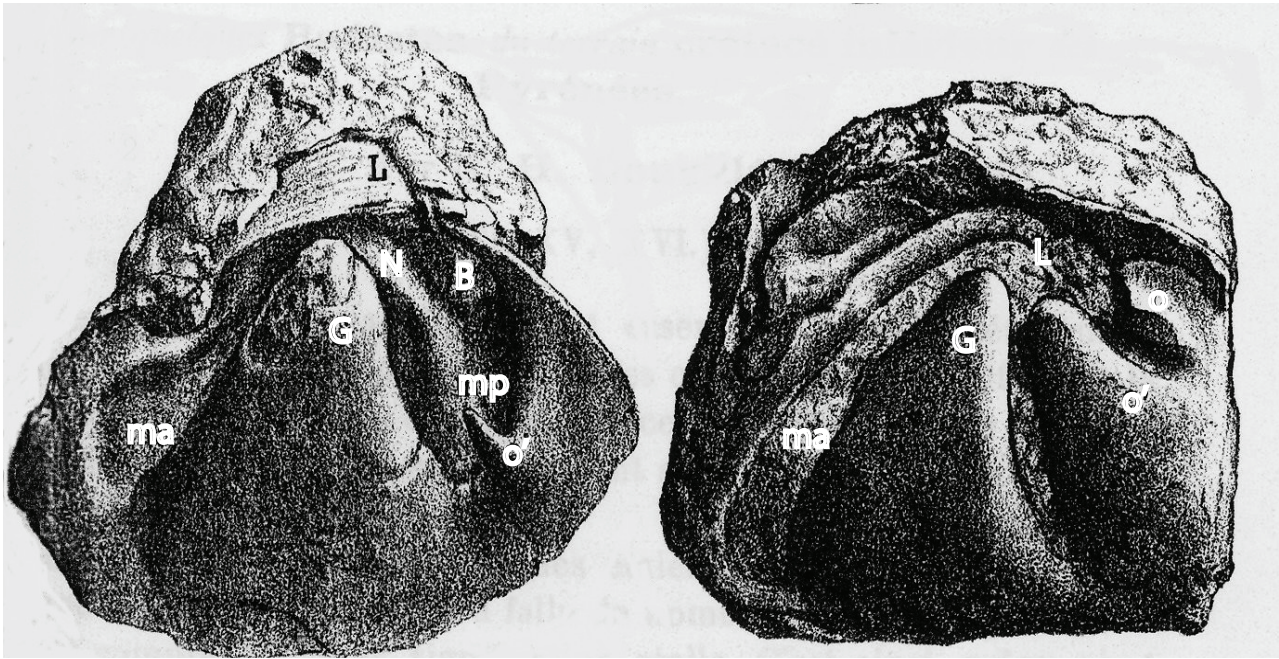


Figure 2. Prepared internal moulds of left valves, with right valves behind, of specimens assigned to (left) *Horiopleura baylei* and (right) *Polyconites verneuli*, by Douvillé (1889; copy of plate 15, figures 2, 6). Note the projections labelled 'O' in each case, representing the internal mould of an annex of the ectomyophoral cavity extending into the base of the posterior myophoral apophysis; Douvillé regarded the contrast in size of this feature as a diagnostic distinction between the two 'species'.

Geological and Stratigraphical Setting

The specimens described herein come from the Galve sub-basin of the western Maestrat Basin, which crops out in the eastern Iberian Chain of Spain (Figure 3, inset). The sequence stratigraphical architecture of the area was the subject of study for the doctoral thesis of Bover-Arnal (see Bover-Arnal *et al.* 2009 and 2010).

The type locality for the new polyconitid species – 'Las Mingachas' (Figure 3) – is situated within an extended section through Aptian strata in the eastern limb of the gently folded Camarillas syncline, west of the village of Miravete de la Sierra (Teruel Province), which has been chronostratigraphically dated to a high degree of resolution on the basis of a combination of ammonites, rudists, orbitoline foraminifers and C-isotope stratigraphy (Figure 4; Bover-Arnal *et al.* 2010). The specimens come from rudist- and coral-dominated platform margin limestones in the upper part of the Villarroya de los Pinares Formation (about 155 m on Figure 4). The Villarroya de los Pinares Formation cannot be older than the *furcata* Tethyan ammonite zone because of

the presence of *Dufrenoyia furcata* in the upper slope deposits of its lower part and the marls with thin limestones of the underlying Forcall Formation. Equally, however, the presence within the same platform limestones of rare specimens of the caprinid rudists *Caprina parvula* and *Offneria* sp., limit these beds to the Lower Aptian (Masse 2003). Hence the type material from Las Mingachas may be precisely assigned to the *furcata* zone – i.e. to the uppermost part of the Lower Aptian.

Systematic Palaeontology

(Abbreviations: LV – left valve; RV – right valve)

Superfamily HIPPURITOIDEA Gray 1848

Family POLYCONITIDAE Mac Gillavry 1937

Polyconites Roulland 1830

Type Species. '*Polyconite operculée*' Roulland, p. 166, by monotypy

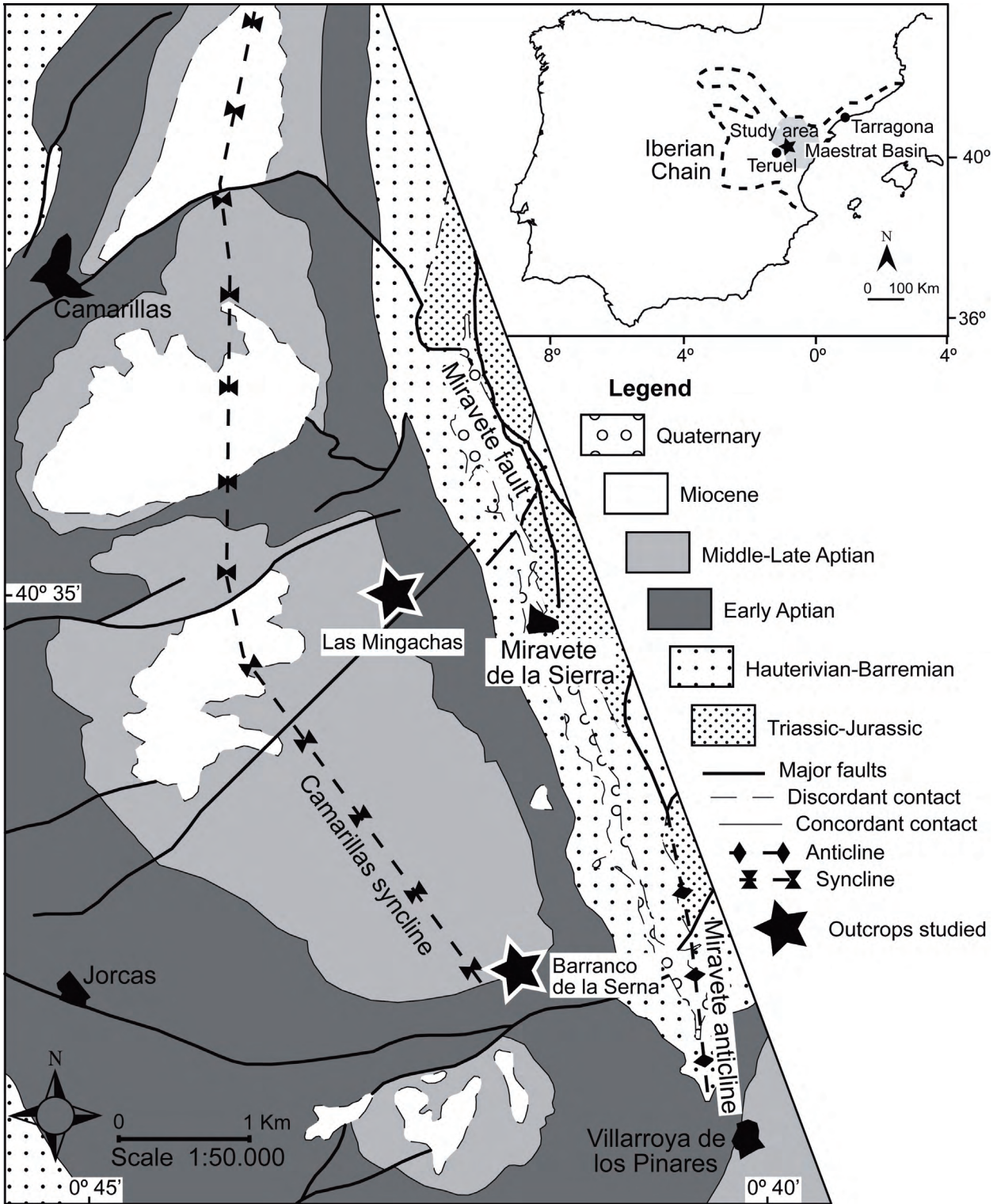


Figure 3. Geological map of part of the Galve sub-basin of the western Maestrat Basin showing the situation of the type locality for *Polygonites hadriani*, new species, 'Las Mingachas' (from Bover-Arnal *et al.* 2009; modified after Gautier 1980). Inset: the situation of the Maestrat Basin in Iberia.

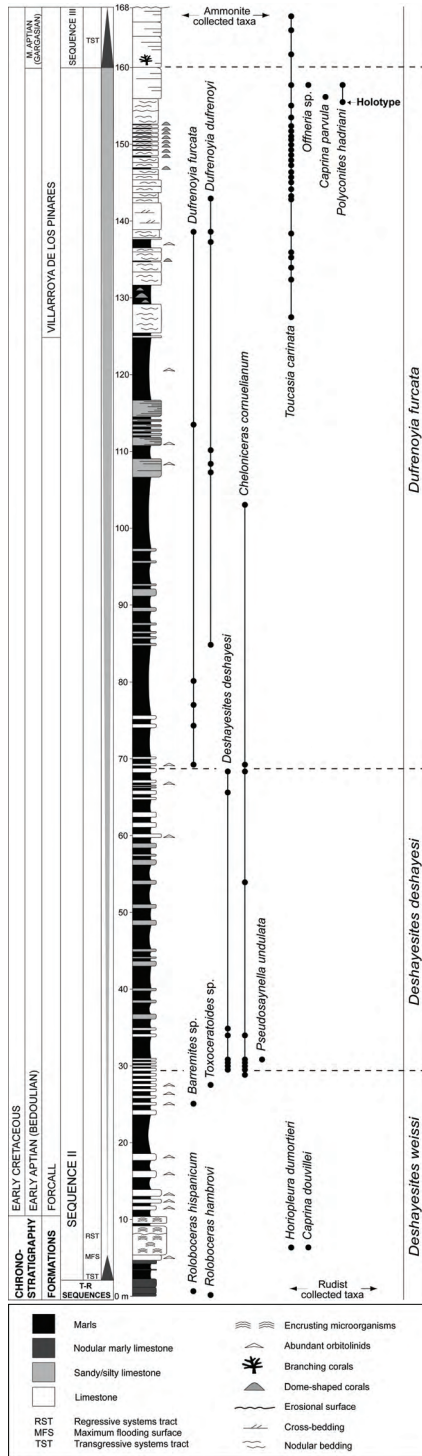


Figure 4. Log of the Lower Aptian succession to the west of Miravete de la Sierra, in the eastern limb of the Camarillas syncline, showing the litho- and biostratigraphical context for the type material of *Polyconites hadriani*, new species (modified from Bover-Arnal *et al.* 2010).

P. hadriani new species

Figures 5–7

1998 *Horiopleura baylei*; Malchus, figure 10, 2.

1998 *Horiopleura* gr. *dumortieri* (Matheron) – *baylei* (Coquand), Masse *et al.*, p. 200, figure 6(b).

1998 *Horiopleura dumortieri* (Matheron), Skelton & Masse, figure 5a, b.

Derivation of Name. Named for Hadrien Fenerci Masse, both as a nomenclaturally economical way to honour the pioneering work on polyconitid rudists of both his parents, Jean-Pierre Masse and Mükerrerem Fenerci-Masse, and emblematically for the start of a new lineage.

Holotype. Natural History Museum, London, Department of Palaeontology specimen number NHMUK, PI MB 1010 (Figure 5a–e), removed from a small block of pale grey biomicrite containing a number of other specimens, preserved in upright life position (Figure 5f); collected by PWS in May, 2008, at ‘Las Mingachas’ locality (Figure 3) from platform margin facies of Villarroya de los Pinares Formation (Lower Aptian, *furcata* Zone) corresponding to 156 m on the log shown in Figure 4.

Paratypes. Eight specimens illustrated herein (Figure 6a–k, NHMUK nos. PIMB 1011–1018) besides several others collected for measurement, or photographed *in situ* in the field, all from same locality and stratigraphical level as the holotype. In addition, one stratigraphically older paratype specimen from the basal Upper Bedoulian of the southern Lusitanian Basin of Portugal (Figure 6n (NHMUK no. PI MB 1019)), together with another specimen photographed at the outcrop (Figure 6m).

Diagnosis. Small-sized species of *Polyconites* (antero-posterior commissural diameter rarely exceeding ~60 mm, and usually much less) with relatively thin outer shell layer (up to ~2 mm thickness). Ontogeny from juvenile shells with gently convex LV and sub-horizontal RV posterior myophore to adult shells with flat to slightly depressed LV and steeply inward-sloping RV posterior myophore forming low swelling on inner wall of valve.

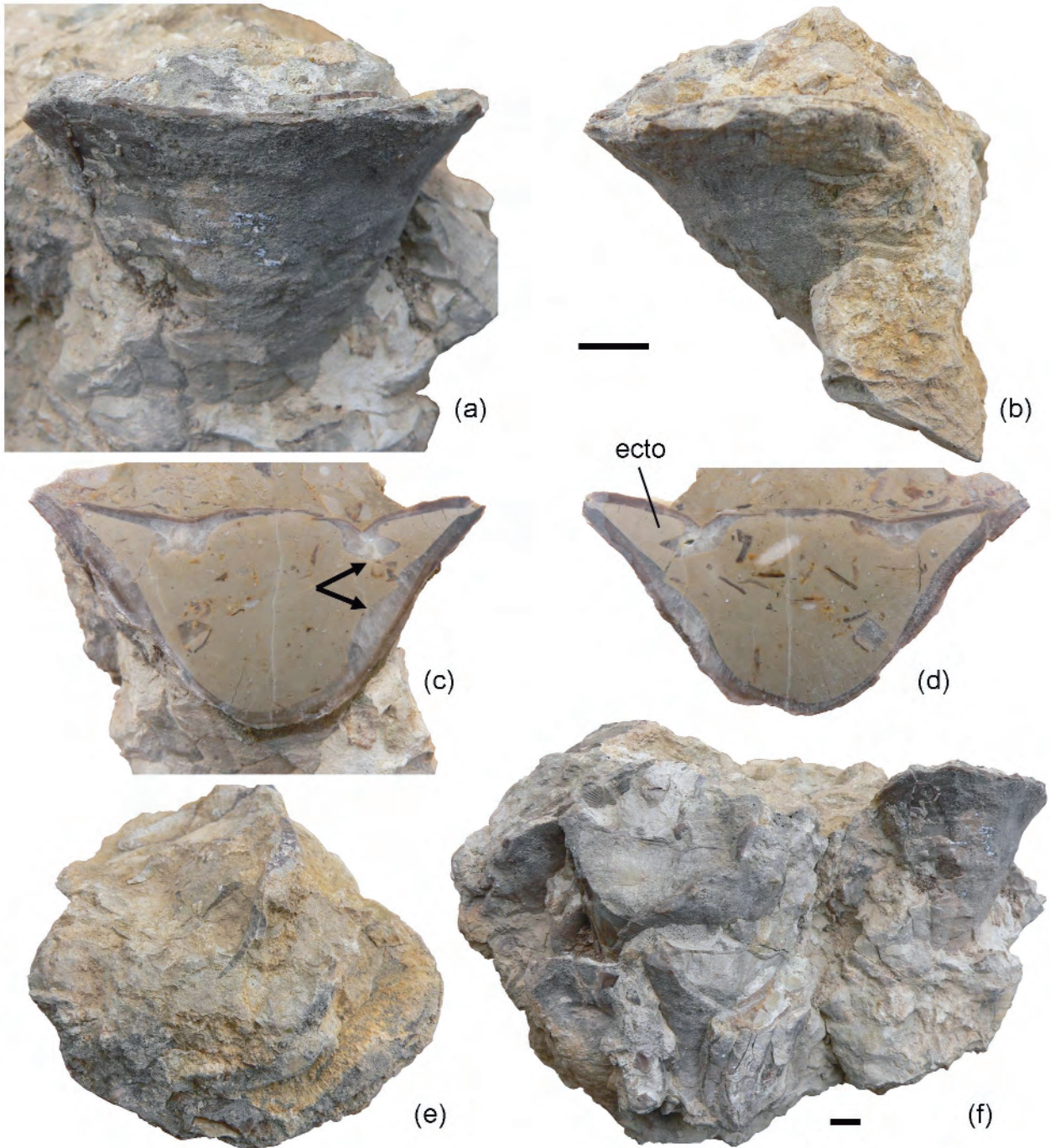


Figure 5. Holotype of *Polyconites hadriani*, new species (Natural History Museum, London; Palaeontological Collections, specimen number NHMUK, PI MB 1010): (a) ventral view; (b) posterior view; (c) antero-posterior section across both valves, viewed towards dorsal side (posterior to right); (d) antero-posterior section across both valves, viewed towards ventral side (posterior to left); (e) view from above left valve (partially covered by matrix); (f) entire block, with other clustered specimens, originally containing holotype (at right). Scale bars = 10 mm: upper bar for (a–e); bar at lower right for (f). Key: ecto– ectomyophoral cavity; thick arrows indicate the posterior myophores in the LV (above) and RV (below).



Figure 6. (a–k) Paratypes of *Polyconites hadriani*, new species (Natural History Museum, London; Palaeontological Collections, specimen numbers PI MB 1011–1018) from Las Mingachas (see Figure 3): (a) articulated specimen (no. PI MB 1011), view of LV showing two planes of antero-posterior section (1* more dorsal than 2*); (b) the two sections of the specimen indicated in (a), viewed towards dorsal side (posterior to right); (c) section 2* of the specimen in (a), viewed towards ventral side (posterior to left); (d) antero-posterior section across both valves of small articulated specimen (no. PI MB 1012), viewed towards ventral side (posterior to left); (e, f) antero-posterior sections across both valves of partial articulated specimens (no. nos. PI MB 1013, 1014, respectively), viewed towards ventral side (posterior to left); (g) low-conical articulated specimen (no. PI MB 1015), view of left valve; (h) same specimen as in (g), postero-ventral view; (i) elongate-conical articulated specimen (no. PI MB 1016) in postero-ventral view, with RV of smaller specimen attached to its side; (j) large, relatively compressed articulated specimen (no. PI MB 1017) in postero-ventral view, with RV of another specimen attached at right; (k) two small articulated specimens (no. PI MB 1018), conjoined on their dorsal flanks. (l) *Horiopleura cf. dumortieri* (Matheron), in *Lithocodium/Bacinella*-encrusted coral/rudist floatstone of *weissi* Zone age (equivalent to 5 m on log in Figure 4) in the Barranco de la Serna section (see Figure 3), antero-posterior section across both valves (posterior to right); photographed at the outcrop. (m, n) articulated specimens of *P. hadriani*, new species, from basal Upper Bedoulian Praia de Lagoa Member of Cresmina Formation, Cresmina fort headland, Cascais (southern Lusitanian Basin, Portugal): (m) natural antero-posterior section across both valves photographed at the outcrop; (n) broken antero-posterior section across both valves (paratype, NHMUK no. PI MB 1017). Scale for all specimens = 10 mm. Key: ct– central tooth (of right valve); ecto– posterior ectomyophoral cavity (in left valve); pt– posterior tooth (in left valve); thick arrow indicates posterior myophore in right valves.

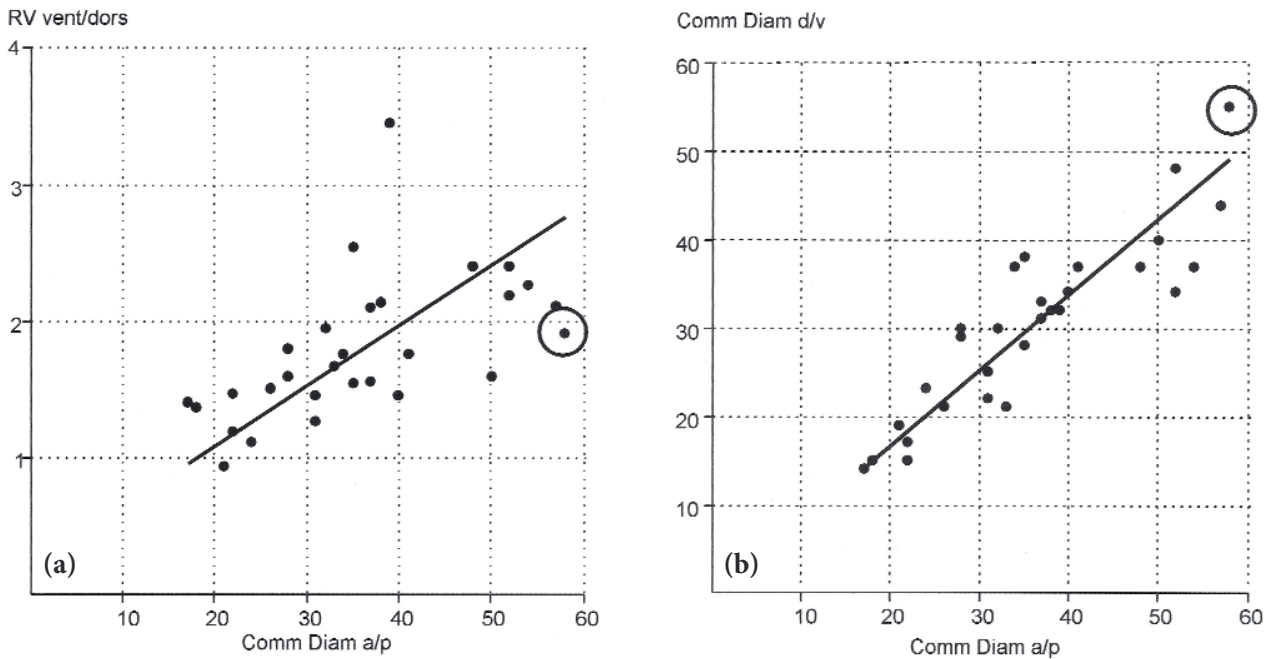


Figure 7. Morphometric data (measured in mm) on 29 specimens of *Polyconites hadriani*, new species, from Las Mingachas type locality (see Figure 3): (a) ratio of distance from umbo to mid-dorsal margin to that from umbo to mid-ventral margin in right valve (RV vent/dors) versus antero-posterior commissural diameter (Comm Diam a/p), with reduced major axis ($r = 0.579$; p for $a = 1$ in log-log plot = 0.105); (b) dorso-ventral commissural diameter (Comm Diam d/v) versus antero-posterior commissural diameter (Comm Diam a/p), with reduced major axis ($r = 0.897$; p for $a = 1$ in log-log plot = 0.605). Holotype is ringed in each case.

Description of Holotype. A relatively large (presumed adult) and intact articulated shell with dorsal area and much of LV partially embedded in matrix (Figure 5a, b), cut and polished along an antero-posterior plane across both valves (Figure 5c, d). RV broadly and asymmetrically conical with flared ventral margin and depressed dorsal rim; LV more or less flat (Figure 5e), with very gently domed central part flanked by slight external depressions corresponding to internal positions of myophores, albeit slightly exaggerated because of compaction of outer shell layer into former cavities left by dissolution of the myophores (Figure 5c, d). Commissure oval in outline. Dimensions: antero-dorsal commissural diameter, 58 mm; postero-ventral commissural diameter, ~55 mm; RV distance between umbonal apex and mid-ventral margin, 57 mm, and between umbonal apex and mid-dorsal margin, ~30 mm. Outer surface smooth except for adpressed foliaceous growth rugae (Figure 5a). Outer

(prismatic calcitic) shell layer brown in section, 1–2 mm thick in RV, slightly thinner in LV. Inner shell (replaced by white to translucent calcite spar) likewise of millimetric thickness except for thickened myophores. Myophores in LV form projecting buttresses, the posterior one reflexed posteriorly around characteristic polyconitid ectomyophoral cavity (Figure 5d). Anterior and posterior myophores in RV both form low swellings on inner valve walls, sloping steeply down into valve interior, the posterior one only slightly thicker than the anterior one (Figure 5c). A small, matching step-like displacement of the inner faces of both posterior myophores is a result of fracturing and slight dislocation of the internal mould following dissolution of the originally aragonitic inner shell (Figure 5d).

Description of the Species. RV varies from having a squat (Figure 6h), to more elongate asymmetrical

conical form (Figure 6k, i) with the ventral flank relatively more extended than the dorsal flank – increasingly so in larger specimens (Figure 7a). LV more or less operculiform with gently domed umbonal region, especially noticeable in smaller specimens (Figure 6a, c, d), though valve exterior may be effectively flat overall or even slightly depressed in larger specimens (Figure 6e, f, j). Commissural outline variable, from rounded (Figure 6a, g) to oval with antero-posterior long axis (Figure 5e). Commissure mainly planar, though larger specimens, especially, may show a pair of gentle undulations on the postero-ventral flank (Figure 6j) corresponding to the radial bands seen in many other rudists. Commissural diameters (antero-posterior and dorso-ventral) may approach 60 mm, though mean values fall between 30 and 40 mm (Figure 7b).

The prismatic calcite outer shell layer commonly reaches up to 2 mm in thickness, especially in the RV (Figure 6e, f), though rarely more than that. The inner shell, originally aragonitic but now replaced by clear sparry calcite, is of similar thickness, except where developed to form the teeth and myophores.

A dorsally situated antero-posterior section of one specimen (Figure 6b, left) displays a prominent LV posterior tooth seated in its socket in the RV. Although this same section cuts through only the ventralmost edge of the anterior tooth of the LV, the relative development of the posterior tooth suggests that the LV teeth are sub-equal (with the posterior tooth approaching the anterior tooth in size).

Both myophores in the LV form prominent buttresses facing down into the RV, the posterior myophore invariably reflexed posteriorly around an ectomyophoral cavity in that valve (Figure 5c, d; Figure 6b(right)/c and d–f). The corresponding myophores in the RV are merely thickenings of the inner shell, their insertion surfaces sloping down into the shell interior. However, the posterior myophore shows an apparent ontogenetic variation from gentle inward inclination with a distinct inner shoulder, in small specimens (Figure 6d), to increasingly steep inclination with a correspondingly subdued inner margin, in larger specimens (Figure 5c, d, 6c, e, f).

Stratigraphically older specimens are known from the southern Lusitanian Basin of Portugal (Figure 6m, n). These were found in orbitoline-rich marls of the Praia de Lagoa Member of the Cresmina Formation, near Cascais, assigned by Burla *et al.* (2008) to the lowermost part of the Upper Bedoulian (inferred basal *deshayesi* Zone). Although similar isolated LVs from the same horizon, further to the north (Ericeira), were originally assigned to *Horiopleura dumortieri* by Skelton & Masse (1998), the inward inclination of the posterior myophore in the RVs of the two articulated specimens that are illustrated here suggests, instead, that these specimens should also be re-assigned to the new species of *Polyconites*.

Remarks. The diagnostic posterior ectomyophoral cavity in the LV, as well as the sub-equal teeth in that valve and the slight thickening of the outer shell layer (relative to the primitive condition of ~1 mm thickness) leave no doubt about the polyconitid affinity of the specimens described herein (Mac Gillavry 1937; Skelton & Smith 2000). Moreover, the distinct inward inclination of the RV posterior myophore allows us to refer them to the genus *Polyconites*, in contrast to *Horiopleura*, in which the myophore forms a discrete ledge oriented more or less parallel with the commissural plane or is even tilted posteriorly (Figure 1; Masse *et al.* 1998, p. 203).

P. hadriani is the stratigraphically oldest known species of *Polyconites*. Previously, the holder of that record was *P. verneuili*, ranging from the Upper Gargasian to the Albian (Masse *et al.* 1998). Though closely similar in form to *P. hadriani*, the latter species attains larger shell sizes with a somewhat greater thickness of the outer shell layer: for example, specimens observed in the field by the authors in the Upper Aptian Benassal Formation of ‘La Venta’ section, near Benicàssim (Castelló, eastern Spain; Tomás 2007) reach at least 90 mm in commissural diameter, with the outer shell layer of the RV up to 5 mm thick. The new species can thus really only be differentiated from *P. verneuili* on the basis of its appreciably smaller size (maximum commissural diameter of ~60 mm and usually somewhat less than that) and relatively thinner calcitic outer shell layer (rarely exceeding 2 mm in the RV). Given the

morphological similarity and apparent stratigraphical succession of the two species, *P. verneuili* is most simply interpreted as a direct chronospecific descendant of *P. hadriani*, displaying phyletic size increase, as has been observed in several other rudist lineages (Skelton & Masse 1998; Steuber 2003). Although a case might thus be made for combining the two chronospecies, we prefer to highlight the distinction – albeit subtle – between them nomenclaturally on the grounds of its potential biostratigraphical utility.

The most plausible candidate for ancestry of this putative first species of *Polyconites* is the genus *Horiopleura* (Figure 6l), not only by default of any other stratigraphically older polyconitid taxa in the Old World, but also because of the similarities in both external form and size between Bedoulian representatives of the two taxa – which differ only by virtue of the relatively greater flattening of the LV and inward inclination of the RV posterior myophore in *Polyconites*. The Lower Aptian New World endemic, *Douvillelia* (Alencaster & Pantoja-Alor 1998), contrasts both in size and form. This phylogenetic hypothesis is strengthened by the apparent ontogenetic depression of the RV posterior myophore in *P. hadriani* from a condition somewhat similar to that seen in primitive *Horiopleura*, in smaller (presumed juvenile) specimens, to the steeper inward inclination seen in larger (adult) specimens. We postulate that *P. hadriani* was derived from *Horiopleura* by a process of ontogenetic flattening of the LV with the consequent downward projection of the LV posterior myophore causing the progressive inward depression of the opposing myophore in the RV. In view of the questionable distinction between the later ‘species’ *Horiopleura baylei* and *Polyconites verneuili* that was discussed in the Introduction, it is indeed possible that these two forms also merely represent corresponding ontogenetic variants and could thus be synonymous (hence ‘*P. baylei* Coquand’, by page priority, as explained in the Introduction), as already hinted by Malchus (1998) – although further morphometric analysis is required to test this latter taxonomic hypothesis. One effect of the ontogenetic change in *P. hadriani* was to allow more upward growth-projection of the flared ventral valve margins (e.g.,

Figure 6j; see also Figure 7a), hence crowded growth in the manner of flat oysters or chondrodontid bivalves, as discussed in the later section on Palaeoecology.

If the Portuguese specimens were indeed among the first to show the re-configuration of growth geometry described above, it is intriguing to note that it would thus have coincided with the remarkable oceanic and climatic perturbations and associated biotic changes that marked the transition from the early to the late Bedoulian (around the *weissi/deshayesi* zonal boundary) (Masse 2003; Burla *et al.* 2008). Prior to that time, in the early Bedoulian, the only known polyconitids in the Old World – the putative ancestors – were relatively scarce *Horiopleura* sp. (Fenerci-Masse 2006, p. 57). In the Barranco de la Serna section (Figure 3), for example, rare *H. cf. dumortieri* (Matheron) (Figure 6l) are present in the *Lithocodium/Bacinella*-encrusted coral/rudist floatstone of *weissi* Zone age (equivalent to 5 m on the log in Figure 4), though higher up in the marls and thin limestones of the Forcall Formation, *P. hadriani* appears with increasing frequency, to rival *Toucasia* for abundance in the Villarroya de los Pinares Formation.

Notwithstanding the likely derivation of *P. hadriani* from early Bedoulian *Horiopleura* sp., the latter genus also continued through the Aptian and Albian, with representatives known for example from throughout the rest of the Aptian in Arabia (Skelton & Masse 2000) as well as the Aptian/Albian of the northern Tethyan margins (Pudsey *et al.* 1984; Masse *et al.* 1998) and at least the Pelagonian platform within the northern part of the Tethys (Steuber 1999).

Stratigraphical and Geographical Distribution. As discussed above, the currently known stratigraphical range of *P. hadriani* commences from about the Lower/Upper Bedoulian boundary (*weissi/deshayesi* zonal boundary) to at least the top of the Bedoulian (top *furcata* Zone), though because the lineage probably continues thereafter as the enlarged descendent chronospecies *P. verneuili*, the ‘termination’ of the range of *P. hadriani* may be considered arbitrary.

P. hadriani appears to be both widespread and common in carbonate platform facies of late Bedoulian (*deshayesi/furcata* zones) age in Iberia. Besides the localities for the type material, the Synonymy list given above registers its presence elsewhere in the Maestrat Basin (Malchus 1998) and Murcia (SE Spain) (Masse *et al.* 1998). Moreover, our collaborative fieldwork with colleagues from Bilbao (I. Millán, K. Fernández-Mendiola and J. García-Mondéjar) has noted its presence in the Sarastarri Formation (*deshayesi/furcata* transition) of the Aralar Mountains in northern Spain, (García-Mondéjar *et al.* 2009), as well as the Galdames Formation, of corresponding age, in the Pagasarri area, southwest of Bilbao, in both cases in association with relatively infrequent caprinids. Records of indeterminate Bedoulian polyconitids in other regions outside Iberia, especially now-suspect attributions to '*H. baylei*', need further checking.

Palaeoecology

At Las Mingachas locality (Figure 3), a clear lithological transition between nearly flat-lying massive platform beds and clinofolds of upper slope facies can be seen within the Villarroya de los Pinares Formation (corresponding to the topmost 20 m or so of the log in Figure 4; Bover-Arnal *et al.* 2010). This transition is illustrated in Figure 8, on which the sampling site for the holotype and paratype specimens of *P. hadriani* from this locality is also indicated with a white star.

At this site, where the massive rudist- and coral-rich platform limestones pass laterally into the slightly more marly and recessive clinofolds, *P. hadriani* is especially abundant, either preserved in life position, in dense clusters (Figure 9a), together with a few platy corals, or as overturned bouquets (Figure 9b), accompanied by other bioclastic debris.

As noted in the previous section, one major effect of the morphological transformation of *Horiopleura* to *Polyconites* was to allow increasingly upward growth-extension of the ventral valve margins, which in turn permitted the kind of imbricate close-packing of individuals seen in Figure 9a. This style of clustered growth is reminiscent of that seen in extant lower littoral- to shallow sub-littoral flat oysters and

epibyssate pteriaceans such as *Isognomon* (e.g., Figure 9c). It is also characteristic of the oyster-like (though unrelated) *Chondrodonta*, which likewise flourished in platform limestones of mid-Cretaceous age, frequently forming similarly dense clusters at the tops of depositional shallowing cycles (Figure 9d). Such a growth strategy perhaps conferred stability in areas where limiting accommodation restricted the net accumulation of potentially supporting sediment, while the surficial water agitation maintained an abundant supply of suspended food particles to sustain such dense populations.

Whether the striking proliferation of polyconitids and chondrodontids – both relatively calcite-rich forms, incidentally – growing in this manner on carbonate platforms at this time was somehow causally linked with the oceanic and climatic perturbations mentioned in the previous section remains an intriguing speculation for future investigation.

Conclusions

1. *Polyconites hadriani*, new species, is described from the uppermost Lower Aptian (*furcata* Zone) Villarroya de los Pinares Formation in the Galve sub-basin of the western Maestrat Basin, eastern Iberian Chain, Spain, with additional specimens from the mid-Lower Aptian (*deshayesi* Zone) Praia de Lagoa Member of the Cresmina Formation, southern Lusitanian Basin, Portugal.
2. This new species is the stratigraphically oldest known species of the genus and is interpreted to have given rise to the Middle Aptian to Albian *P. verneuili* as a descendent chronospecies, with phyletic size increase.
3. The posterior myophore of the right valve forms a gently inwardly inclined ledge (somewhat like that in *Horiopleura*) in small (presumed young) specimens, but becomes more depressed and steeply inwardly inclined, in typical fashion for *Polyconites*, in larger (adult) specimens, in which the left valve also becomes progressively flatter. Accordingly, it is postulated that this species was derived from early Early Aptian *Horiopleura* species of similar size and external form.



Figure 8. ‘Las Mingachas’ locality (see Figure 3 for location), with sampling site for type material of *Polyconites hadriani*, new species, indicated by white star (left of centre). Person for scale indicated by black oval (right of centre). West is to left.

4. It is suggested that the Middle–Late Aptian ‘species’ *H. baylei* and *P. verneuili* may likewise represent corresponding ontogenetic variants and hence be synonymous (thus, ‘*P. baylei* Coquand’ by page priority), though this taxonomic hypothesis requires further testing.
5. *P. hadriani* became especially widespread and abundant on Iberian carbonate platforms in the latest Early Aptian; its occurrence elsewhere requires further investigation.
6. The mode of growth of *P. hadriani* allowed increasingly upward growth-extension of the ventral valve margins, which in turn permitted imbricate close-packing of individuals, as in

living flat oysters and epibyssate pteriaceans such as *Isognomon*, as well as the mid-Cretaceous *Chondrodonta*. It is suggested that this growth strategy may have conferred stability in areas where limiting accommodation restricted the net accumulation of potentially supporting sediment, while the surficial water agitation maintained an abundant supply of suspended food particles to sustain such dense populations.

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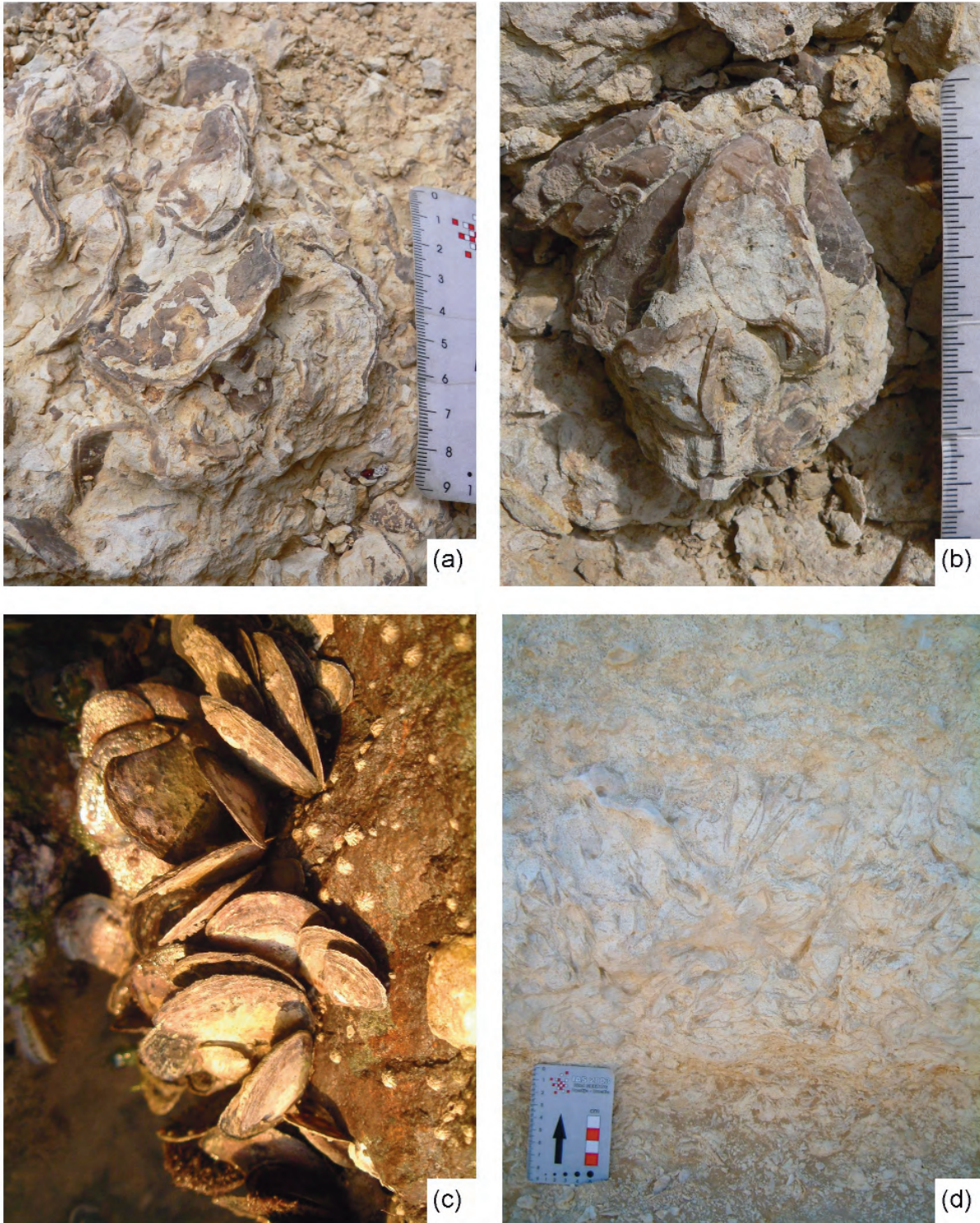


Figure 9. (a, b) *Polyconites hadriani*, new species, at the outcrop at Las Mingachas (see Figures 3, 8): (a) cluster of specimens preserved in life position, viewed from above; (b) overturned bouquet of specimens *in situ*. (c) cluster of live *Isognomon* sp., in life position on rocky shore, SW Puerto Rico (specimens of similar size to *P. hadriani* specimens in (a)). (d) clustered *Chondrodonta* sp., preserved in life position in wackestone matrix in natural vertical section through top of minor depositional cycle in Lower Aptian Qishn Formation of SW Huqf area, Oman.

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References

- ALENCASTER, G. & PANTOJA-ALOR, J. 1998. Two new Lower Cretaceous rudists (Bivalvia-Hippuritacea) from the Huetamo region; southwestern Mexico. *Geobios, Mémoire Spécial* **22**, 15–28.
- BOVER-ARNAL, T., MORENO-BEDMAR, J.A. SALAS, R., SKELTON, P.W., & BITZER, K. & GILI, E. 2010. Sedimentary evolution of an Aptian syn-rift carbonate system (Maestrat basin, E Spain): effects of accommodation and environmental change. *Geologica Acta* **8**, 249–280.
- BOVER-ARNAL, T., SALAS, R., MORENO-BEDMAR, J.A. & BITZER, K. 2009. Sequence stratigraphy and architecture of a late Early–Middle Aptian carbonate platform succession from the western Maestrat basin (Iberian Chain, Spain). *Sedimentary Geology* **219**, 280–301.
- BURLA, S., HEIMHOFER, U., HOCHULI, P.A., WEISSERT, H. & SKELTON, P. W. 2008. Changes in sedimentary patterns of coastal and deep-sea successions from the North Atlantic (Portugal) linked to Early Cretaceous environmental change. *Palaeogeography, Palaeoclimatology, Palaeoecology* **257**, 38–57.
- COQUAND, H. 1865. Monographie de l'étage Aptien de l'Espagne. *Mémoires de la Société d'Emulation de la Provence* **5**, 191–413, Marseille.
- COQUAND, H. 1880. Etudes supplémentaires sur la paléontologie algérienne faisant suite à la description géologique et paléontologique de la région sud de la province de Constantine. *Bulletin de l'Académie d'Hippone* **15**, 1–449, Bône.
- DECHASEAUX, C., COX, L.R., COOGAN, A.H. & PERKINS, B.F. 1969. Superfamily Hippuritacea Gray, 1848. In: MOORE, R.C. (ed), *Treatise on Invertebrate Paleontology, Part N, Mollusca* **6**, Bivalvia, 2. University of Kansas, Lawrence, Kansas & Geological Society of America, N749–817.
- DOUVILLÉ, H. 1889. Sur quelques rudistes du terrain crétacé inférieur des Pyrénées. *Bulletin de la Société géologique de France* **17**, 627–635.
- FENERCI-MASSE, M. 2006. *Les communautés à Rudistes du Crétacé inférieur de la marge ouest européenne de la Téthys*. PhD Thesis, Université de Provence, Aix-Marseille I [unpublished].
- GARCÍA-MONDEJAR, J., OWEN, H.G., RAISOSSADAT, N., MILLÁN, M.I. & FERNÁNDEZ-MENDIOLA, P.A. 2009. The Early Aptian of Aralar (northern Spain): stratigraphy, sedimentology, ammonite biozonation, and OAE1. *Cretaceous Research* **30**, 434–464.
- GAUTIER, F. 1980. Villarluengo, hoja nº 543. *Mapa Geológico de España 1:50.000. 2ª Serie. 1ª Edición*, Servicio de Publicaciones, Ministerio de Industria y Energía, Madrid.
- GRAY, J.E. 1848. On the arrangement of the Brachiopoda. *Annals and Magazine of Natural History* **2**, 435–440.
- MAC GILLAVRY, H.J. 1937. Geology of the province of Camagüey, Cuba, with revisional studies in rudist paleontology. *Geographische en Geologische Mededeelingen, Physiographisch-Geologische reeks* **14**.
- MALCHUS, N. 1998. Aptian (Lower Cretaceous) rudist bivalves from NE Spain: taxonomic problems and preliminary results. *Geobios, Mémoire Spécial* **22**, 181–191.
- MASSE, J.-P. 1996. Lower Cretaceous rudist biostratigraphy of southern France – a reference for Mesogean correlations. *Revista Mexicana de Ciencias Geológicas* **12** (for 1995), 236–256.
- MASSE, J.-P. 2003. Integrated stratigraphy of the Lower Aptian and applications to carbonate platforms: a state of the art. In: GILI, E., NEGRA, H. & SKELTON, P.W. (eds), *North African Cretaceous Carbonate Platform Systems*. NATO Science Series, IV, Earth and Environmental Studies **28**, 203–214, Kluwer Academic Publishers BV.
- MASSE, J.-P., ARIAS, C. & VILAS, L. 1998. Lower Cretaceous rudist faunas of southeast Spain: an overview. *Geobios, Mémoire Spécial* **22**, 193–210.
- PUDSEY, C., SCHROEDER, R. & SKELTON, P.W. 1985. Cretaceous (Aptian/Albian) age for island-arc volcanics, Kohistan, N. Pakistan. *Contributions to Himalayan Geology* **3**, 150–168.
- RIDE, W.D.L., COGGER, H.G., DUPUIS, C., KRAUS, O., MINELLI, A., THOMPSON, F.C. & TUBBS, P.K. (eds) 1999. *International Code of Zoological Nomenclature*. Fourth Edition. International Trust for Zoological Nomenclature, c/o The Natural History Museum, London, UK.
- ROULLAND, L. 1830. Nouvelles observations sur les *Ichthyosarcolites*. *Actes de la Société Linnéenne de Bordeaux* **4**, 164–166.
- SKELTON, P.W. & MASSE, J.-P. 1998. Revision of the Lower Cretaceous rudist genera *Pachytraga* Paquier and *Retha* Cox (Bivalvia: Hippuritacea), and the origins of the Caprinidae. *Geobios, Mémoire Spécial* **22**, 331–370.
- SKELTON, P.W. & MASSE, J.-P. 2000. Synoptic guide to the Lower Cretaceous rudist bivalves of Arabia, *Society of Economic Paleontologists and Mineralogists, Special Publication* **69**, 85–95.

- SKELTON, P.W. & SMITH, A.B. 2000. A preliminary phylogeny for rudist bivalves: sifting clades from grades. *In*: HARPER, E.M., TAYLOR, J.D. & CRAME, J.A. (eds), *The Evolutionary Biology of the Bivalvia*. Geological Society, London, Special Publications **177**, 97–127.
- STEUBER, T. 1999. *Cretaceous Rudists of Boeotia, central Greece*. Special Papers in Palaeontology **61**.
- STEUBER, T. 2003. Strontium isotope stratigraphy of Cretaceous hippuritid rudist bivalves: rates of morphological change and heterochronic evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology* **200**, 221–243.
- TOMÁS, S. 2007. *Sistemas arrecifales del Cretácico inferior de la Cuenca del Maestrat. Modelos deposicionales, paleontológicos y diagenéticos*. PhD Thesis Universitat de Barcelona.
- VERNEUIL, E. DE, COLLOMB, E. & TRIGER, A. 1860. Note sur une partie du pays basque espagnol, accompagnée d'une carte. *Bulletin de la Société géologique de France* **17**, 333–372.