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***Hypelasma salevensis* (FAVRE, 1913) from the Upper Kimmeridgian of the French Jura, and the Origin of the Rudist Family Requiieniidae**

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Key words: Requiieniidae, Rudists, Taxonomy, Jura, Kimmeridgian, France.

Abstract

The requieniid rudist species '*Matheronia salevensis* FAVRE, first described from the Tithonian of Mont Salève, eastern France, is transferred to the genus *Hypelasma* PAQUIER, which is distinguished from *Matheronia* by possession of a posterior myophoral ledge in the left (attached) valve. Diminutive specimens from the Upper Kimmeridgian of the southern Jura are described and placed in this species. Hence, *Hypelasma salevensis* (FAVRE) is the stratigraphically oldest known member of the Family Requiieniidae. It may also provide another example of phyletic size increase among rudists. Revised diagnoses are given for the family, genus and species.

The main distinction between the requieniids and the diceratids, from among which they arose, concerns the angle between the coiling axis of the left valve and the commissural plane. In diceratids, this angle is large, such that the often sub-equal umbones tend to twist outwards from the commissural plane, so avoiding mutual interference. In requieniids, by contrast, this angle is small, such that the prominent umbo of the left valve tends to coil across the commissural plane in trochospiral to helicospiral fashion, while that of the right valve is suppressed in compensation, producing an exogyriiform morphology. The requieniid modification of growth geometry, already present in *H. salevensis*, generated an extended basal surface on the flattened anterior wall of the left valve, implying specialized adaptation of these rudists as frictional or attached clingers.

Requiieniid ancestry should be sought among species of the pre-existing diceratid genera *Epidiceras* or *Plesiodiceras*, which also attached by the left valve. Although *Plesiodiceras* is favoured by its already more or less operculiform right valve and relatively small size, the derived condition of its posterior myophoral organisation is problematical. However, its juvenile shell shows some similarity of external form to *H. salevensis*, suggesting the possibility of paedomorphic evolution.

1. INTRODUCTION

The stratigraphically oldest requieniid species on record was originally named *Matheronia salevensis* by Favre, in JOUKOWSKY & FAVRE (1913). Favre's material came from the Tithonian of Mont Salève (Haute-Savoie), SE France (Fig. 1). In recent years, it has also been reported from the Upper Kimmeridgian, in sections some 40 km to the North-West, in the southern Jura (SKELTON, 1999), based on collaborative studies by the present authors on the Upper Jurassic to Lower Cretaceous rudists of the region. Here, we describe the specimens of the species from the French Jura in greater detail, and compare them with the type material. We also address the questions of the generic assignment of the species, and the characterization and evolutionary origins of the Family Requiieniidae.

2. STRATIGRAPHICAL CONTEXT

The geological transect eastwards from the French southern Jura towards the Swiss Alps is a well known example of facies diachroneity, testifying to the Late Jurassic progradation of a carbonate platform into the Bassin Dauphinois (GAILLARD et al., 1984). In Kimmeridgian times, various platform-top facies spread eastwards across the southern Jura, reaching as far as the Cluse-du-Fier, some 20 km west of Annecy. By the Tithonian, massive coral- and rudist-rich limestones (Calcaires coralliens des Etiollets) were accumulating in the area of Mont Salève, south of Geneva, and the entire regional succession was finally capped by Tithonian–Berriasian tidalites (Figs. 1, 2).

The Kimmeridgian reef-associated fauna of the southern Jura was documented from Valfin (just north of the area shown in Fig. 1b) in a classic monograph by DE LORIOU & BOURGEAT (1888), while the succeeding 'Portlandian' (= Tithonian) fauna, from Le Salève (Fig. 1b), was thoroughly described by JOUKOWSKY & FAVRE (1913).

More recent work on Mont Salève (DEVILLE, 1991) locates the rudist-rich beds just below and within the 'Membre des Calcaires à oncoïdes des Etiollets' at the top of the Calcaires coralliens des Etiollets, around the Tithonian/Berriasian boundary (Fig. 2).

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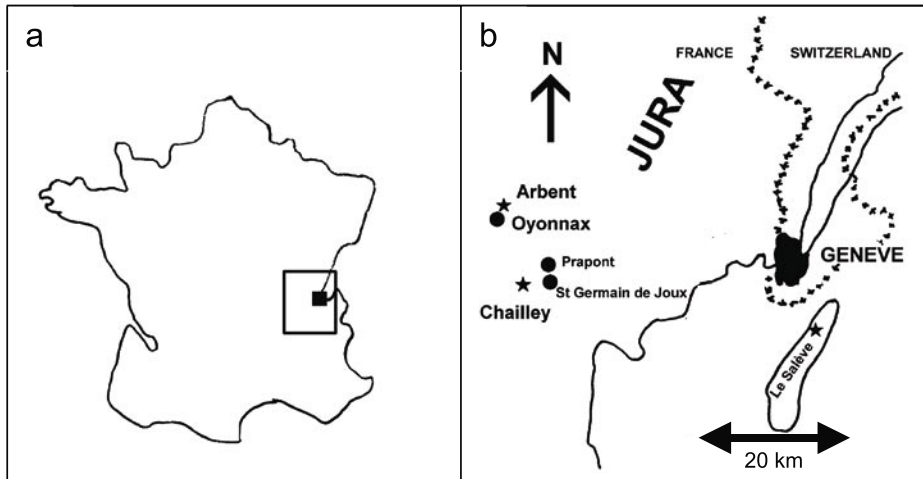


Fig. 1 Localities: (a) situation of study area (boxed) in France; (b) main localities (stars) for specimens of *Hypelasma salevensis* (FAVRE) described in text.

The stratigraphy and palaeoenvironments of the Upper Kimmeridgian in the southern Jura have been revised in detail by ENAY (1965) and BERNIER (1984). In the area around Saint-Germain-de-Joux (Ain) (Fig. 1b), ENAY (1965) gave the name ‘Couches de Prapont’ to coral- and rudist-rich bioclastic limestones, equivalent to those at Valfin. He noted that this unit was split into lower and upper parts by a distinctive and widespread, oncolite-rich bed (‘le banc à momies intermédiaire’), which BERNIER (1984) named the ‘Calcaires de la Semine’ (Fig. 2). BERNIER (1984, p. 587–589 and 615) inferred that the entire formation of the Couches de Prapont was probably confined to the Upper Kimmeridgian (*Eudoxus* to *Beckeri* Zones), based on scarce ammonite evidence. The ‘Couches du Chailley’ (micritic limestone with burrows), which overlie this formation (Fig. 2), contain the ammonite *Gravesia irius* (D’ORBIGNY) (ENAY, 1966). Though originally referred to the ‘Portlandien inférieur’, this species has more recently been recorded in the uppermost Kimmeridgian *Aulacostephanus* (*A.*) *autissiodorensis* Zone at Kimmeridge Bay itself (MORGANS-BELL et al., 2001, with associated online graphic log). Hence the restriction of the Couches de Prapont to the Upper Kimmeridgian can now be asserted with greater confidence.

Our specimens of ‘*M.* *salevensis*’ were collected by the senior author from Marchon (Commune d’Arbent), on the northern side of Oyonnax (Ain), and to the east of Moulin de Charix (‘Coupe de Chailley’, in BERNIER, 1984, p. 157–167), near Saint-Germain-de-Joux (Fig. 1b). At Oyonnax, they are associated with coral biostromes in the uppermost Kimmeridgian ‘Couches de Prapont supérieures’ (Fig. 2; see also BERNIER, 1984, p. 245–252, though his section was along strike, to the SW of Oyonnax). In the Chailley section, they were found at a lower stratigraphical level, in the ‘Couches de Prapont inférieures’ (BERNIER, 1984, p. 162), associated with abundant specimens of the small diceratid rudists *Epidiceras guirandi* (DE LORIO) and *Plesiodiceras munsteri* (GOLDFUSS).

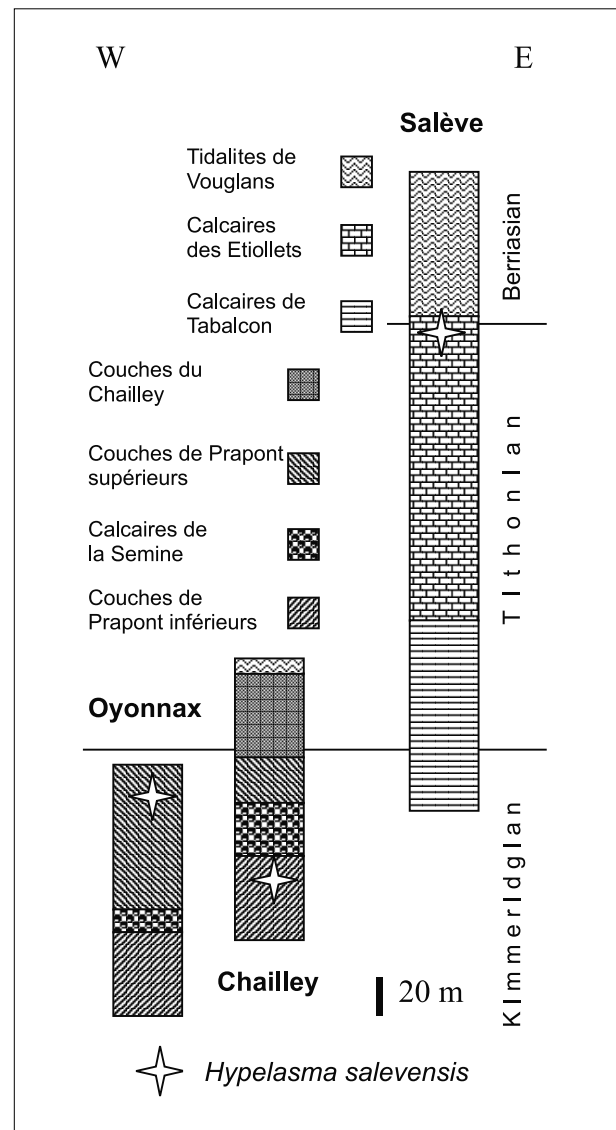


Fig. 2 Summary stratigraphical sections (see Fig. 1 for localities). Approximate thicknesses of units based on BERNIER (1984) for Oyonnax and Chailley, and DEVILLE (1991) for Salève. At Oyonnax, the Couches de Prapont inférieures are represented by the ‘Calcaires oolithiques de Corveissiat’. At Chailley, the ‘Marnes des Abergements’ (= ‘Calcaires à ptérocères’) are included here in the lower half of the unit labelled Couches du Chailley.

3. SYSTEMATIC PALAEOLOGY

Abbreviations: LV – left (in this case, attached) valve; RV – right (in this case, free) valve. Annotations to synonymy list are according to MATTHEWS (1973).

Superfamily Hippuritoidea GRAY, 1848

Family Requiieniidae DOUVILLÉ, 1915

Emended diagnosis: Strongly inequivalve rudists attached by the larger LV. LV coiled trochospirally to helicospirally around an axis that is oriented at a small angle with respect to the commissural plane, so generating a broadly extended basal surface along the anterior valve wall. RV operculiform to more or less inflated posteriorly, with suppressed umbo.

Remarks: DOUVILLÉ's (1915) original definition of the Family Requiieniidae ('Réquiéniidés') was essentially based on taxonomic composition, and lacked an explicit diagnosis of the characters that united its constituents. Thus he envisaged it as defined by the inclusion of the classic Urgonian genera, *Requienia* MATHERON, *Toucasia* MUNIER-CHALMAS and *Matheronia* MUNIER-CHALMAS, which had originally all been contained within MATHERON's (1842) conception of the genus *Requienia*.

In their description of the family, DECHASEAUX et al. (1969) noted the strongly inequivalve condition of the shell and its attachment by the LV. Otherwise, however, their diagnosis was a mixture of primitive character states shared with the diceratids (hence not diagnostic of requieniids *per se*), and derived character states inconsistently distributed among requieniid genera. The plan of the dentition cited by them (one tooth in the LV, two in the RV), even including the incipient posterior tooth in the LV, is shared with the diceratids (see, for example, SKELTON & SMITH, 2000, Fig. 1b), and is thus primitive. The so-called 'siphonal bands' are present only in some requieniid taxa (MASSE, 1994). The alternatives given for the arrangement of the myophores are again either shared with the diceratids, or derived only in certain requieniid taxa (e.g., the suppression of the posterior myophore in the LV of *Matheronia*). Hence, no clear picture emerges from DECHASEAUX et al. (1969) of shared derived character states (synapomorphies) that exclusively unite all the genera currently assigned to the family.

In order to test for requieniid monophyly, and hence establish a reliable diagnosis for the family, it is necessary to take a cladistic perspective. SKELTON & SMITH (2000) substantiated a primary division of the rudists into two major clades (sister groups) according to whether attachment to the substrate was by the LV or by the RV. The clade of rudists attached by the LV comprises just the requieniids together with most of the diceratid genera. Despite the historical lack of an explicit diagnosis for the Requiieniidae, authors

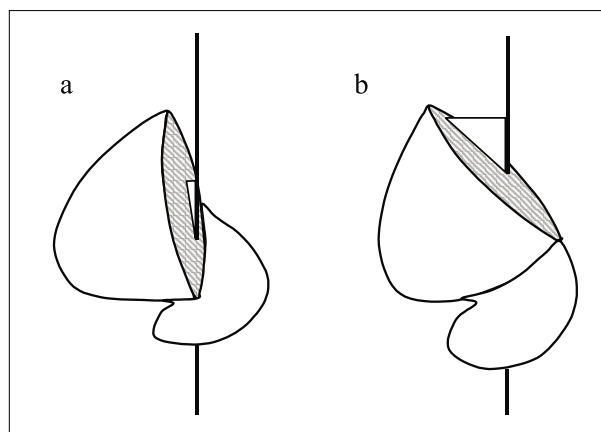


Fig. 3 Diagram showing characteristic growth geometry of left valve (LV) in (a) requieniids, with a small angle between the coiling axis (vertical line) and the commissural plane (hatched), and (b) diceratids, with a relatively large angle. Size varies according to species.

have broadly agreed on its generic composition (e.g., KUTASSY, 1934; DECHASEAUX et al., 1969; MASSE, 1994, and YANIN, 1995, although the last author split it into three families, nevertheless united as a clade in his fig. 12). This agreement suggests the intuitive recognition of some shared derived character or set of characters that distinguishes a requieniid clade from the (paraphyletic) diceratids. The strong relative reduction of the RV noted both by DECHASEAUX et al. (1969) and SKELTON & SMITH (2000) is a promising contender for this role, but is insufficient without further qualification, because *Plesiodiceras* – which has never been regarded as a requieniid – also has a much reduced RV. What does appear to be peculiar to the requieniids is their particular mode of strongly inequivalve growth. The larger LV coils trochospirally to helicospirally around an axis that is oriented at a small angle to the commissural plane (Fig. 3a). Its umbo thus tends to pass across the commissural plane after half a whorl of growth; that of the RV is suppressed in compensation – analogously to the mode of growth in the oyster *Exogyra* (although the latter grew opisthogyrrally, rather than prosogyrrally). The effect of this strongly inequivalve pattern of growth was to provide a broad area of sustained contact with the substratum on the flattened anterior face of the LV (MASSE, 1994, fig. 2). Such a growth geometry is strikingly apparent even in the earliest requieniids, described herein. In the diceratids, by contrast, the axis of coiling of the attached valve is oriented at a much larger angle with respect to the commissural plane, with the effect that the umbo twists outwards, away from the commissural plane (Fig. 3b). This growth geometry avoids mutual interference of the enlarged umbones in sub-equivalve forms, but even in the markedly inequivalve *Plesiodiceras*, the tightly spirogyrate umbo of the adult LV likewise tends to twist away from the commissural plane, thereby distancing the adult growth margin from a discrete apical area of attachment. The distinguishing characteristic of the requieniid clade thus seems to be specialized adaptation

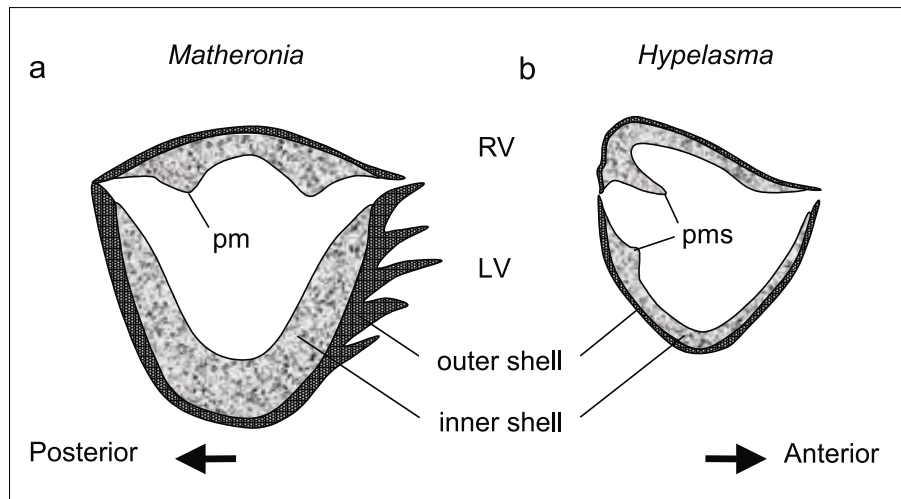


Fig. 4 Diagrammatic posterior to anterior sections across shells (not to scale) of (a) *Matheronia virginiae* (GRAS) and (b) *Hypelasma colloti* PAQUIER, illustrating some of the principal differences between them. The relatively thicker outer shell layer of (a), with coarsely lamellose growth rugae on the (basal) anterior face, is typical of the type species, but not of some of the stratigraphically older species of *Matheronia*. Key: LV, left valve; pm(s) posterior myophore(s); RV, right valve. (a) based on MASSE (1996, pl. 5, fig. 5); (b) on PAQUIER (1897).

as exogyriiform frictional to attached clingers (GILI et al., 1995).

Genus *Hypelasma* PAQUIER, 1897

Type Species: *Hypelasma colloti* PAQUIER, 1897.

Diagnosis: Small to medium-sized requieniid. LV with low rate of expansion, producing prominent umbo that tends to project markedly across commissural plane, and with acute antero-ventral carina that becomes rounded in last fraction of a whorl, bordering flattish basal (anterior) surface. RV with raised, more or less carinate posterior margin. Small but distinct posterior myophoral ledge in LV, passing under hinge plate, opposed by slightly outwardly tilted projecting shelf attached to hinge plate in RV. Anterior adductor insertions on inner walls of both valves.

Remarks: The generic status of the species '*M.* *salevensis*' FAVRE has, from the start, been problematical. In our view, as discussed below, it should be included in the genus *Hypelasma*, as stated by YANIN (1995, p. 109). In order to address this issue, we illustrate diagrammatically some of the pertinent characters of the Cretaceous type species of *Matheronia*, *M. virginiae* (GRAS) (Fig. 4a), and *Hypelasma* (Fig. 4b), as well as some of the type specimens of '*M.* *salevensis*' (Fig. 5), for comparison.

Favre, in JOUKOWSKY & FAVRE (1913, p. 413), noted the similarity of '*M.* *salevensis*' to *Hypelasma*, in its possession of a rudimentary posterior myophoral ledge in the LV (Fig. 5f, arrowed). Such a feature is seen in the type species of *Hypelasma* (Fig. 4b), but not in that of *Matheronia*, in which the adductor muscle inserted onto the inner face of the posterior valve wall in the LV (Fig. 4a). Yet Favre decided against placing his new species in *Hypelasma*, stating that it lacked the raised posterior side of the RV that is characteristic of the latter genus (Fig. 4b), and had a relatively well developed anterior tooth socket in the LV. He regarded

its general form and hinge characters as most like those of another Tithonian species, *Matheronia* (*Monnieria*) *romani* PAQUIER (for which he regarded the sub-generic distinction as unjustified). Favre concluded that '*M.* *salevensis*' was ancestral to the other species of *Matheronia*, and that this group showed a progressive reduction in relative size of the hinge plates from '*M.* *salevensis*' onwards. However, he proposed that *Hypelasma*, too, had been derived from the new species, involving the enlargement of the posterior myophoral ledge in the LV, which led on, he suggested, to the diagnostic salient myophore of *Toucasia*.

Later general reviews of rudist systematics have mostly treated both *Monnieria* and *Hypelasma* as sub-genera of *Matheronia* (e.g. KUTASSY, 1934; DECHASEAUX, 1952; DECHASEAUX et al., 1969). However, this has had the undesirable effect of rendering *Matheronia* as a broadly defined paraphyletic genus that groups all the various pre-Hauterivian requieniids together with the lineage that includes the younger type species (*M. virginiae*: uppermost Barremian to Lower Aptian; MASSE, 1996). Such a broad generic concept obscures basal phylogenetic relationships within the requieniid clade, and we consider the retention of *Hypelasma* as a separate genus (as in MASSE, 1994, p. 331) to be a useful step towards resolving this problem. If the complete suppression of the posterior myophore in the LV (as in Fig. 4a) can be regarded as a diagnostic derived character state in the genus *Matheronia* (by out-group comparison with the diceratids), then *Hypelasma*, with its residual posterior myophore (Fig. 4b), should remain excluded from that genus. A further distinction concerns the posterior myophore of the RV. In the type species of *Matheronia*, this structure appears as a buttress-like swelling in transverse section (Fig. 4a; cf. MASSE, 1996, pl. 5, fig. 5), but in *Hypelasma*, by contrast, it forms a projecting shelf (Fig. 4b; cf. PAQUIER, 1897, Fig. 2). The difference probably reflects the relatively greater compression of the RV (again, a more derived condition) in *Matheronia*, which left no space

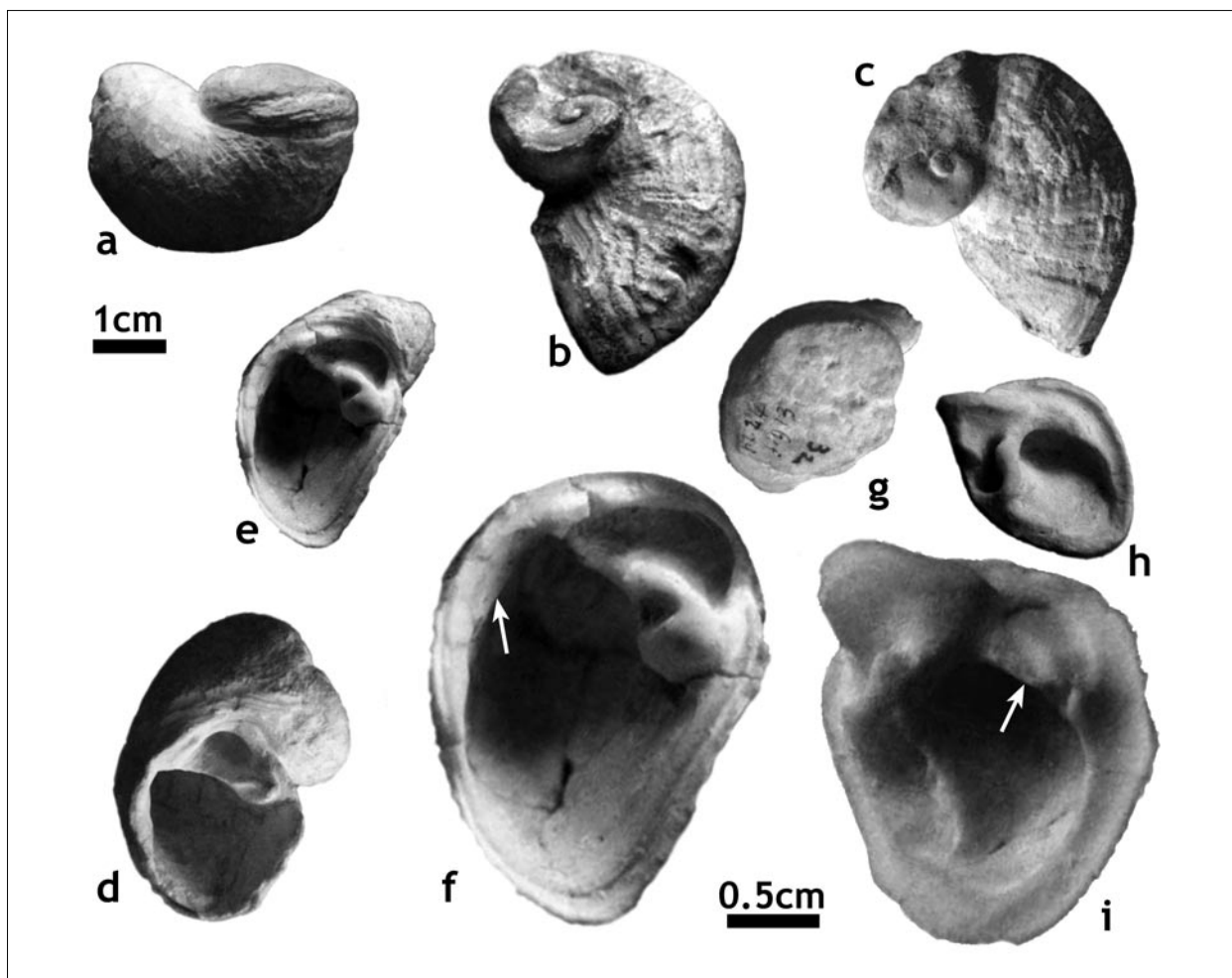


Fig. 5 Selected type specimens of *Hypelasma salevensis* (FAVRE) from around the Tithonian/Berriasian boundary of Mont Salève (Haute-Savoie), France, re-photographed from the Favre collection at the Muséum de la ville de Genève. (a) no. 28911 (JOUKOWSKY & FAVRE, 1913, pl. 24, fig. 5), posterior view of articulated shell; (b) no. 28906 (JOUKOWSKY & FAVRE, 1913, pl. 24, fig. 3), anterior view of left valve; (c) no. 28915 (JOUKOWSKY & FAVRE, 1913, pl. 24, fig. 7), anterior view of left valve; (d) no. 28928 (JOUKOWSKY & FAVRE, 1913, pl. 24, fig. 9), commissural view of prepared left valve; (e) no. 28914 (JOUKOWSKY & FAVRE, 1913, pl. 24, fig. 8), commissural view of prepared left valve, specimen designated as lectotype herein; (f) enlarged view of internal features of (e), white arrow indicates posterior myophore; (g, h) no. 28935 (JOUKOWSKY & FAVRE, 1913, pl. 24, fig. 13), right valve, external and internal views, respectively; (i) no. 28935, another specimen (JOUKOWSKY & FAVRE, 1913, pl. 24, fig. 12), enlarged oblique internal view of RV from ventral side; white arrow indicates posterior myophore. Scale bars: 1 cm for a–e and g, h; 0.5 cm for f, i.

for the extension of the body cavity behind the myophore. Another distinction is the development of a buttress-like anterior myophore in the RV of *Matheronia* (Fig. 4a), matching the posterior one, which contrasts with the relatively depressed anterior adductor insertion site on the inner wall of that valve in *Hypelasma* (Fig. 5i).

The oldest *Toucasia* recorded so far is from the Hauterivian (MASSE et al., 1998) and its evolutionary origins remain unclear. *Toucasia* can be distinguished from *Hypelasma* by its possession of a discrete posterior myophoral ledge in the RV that passes behind the hinge plate, like that in the LV (see MASSE, 1994), instead of joining it, as it does in *Hypelasma* (Fig. 5i). This appears to be a derived condition in *Toucasia*, shared with *Requienia* (MASSE, 1994), and again excluding *Hypelasma*. Hence, we propose that *Hypelasma* should be maintained as a discrete genus.

We can now return to the question of the generic status of '*M.* *salevensis*'. From the argument stated above, this species' possession of a posterior myophoral ledge in the LV, albeit small (Fig. 5f), should, after all, place it in *Hypelasma*, not *Matheronia*. We must therefore re-consider Favre's objections to this assignment (in JOUKOWSKY & FAVRE, 1913). Although the RV of *H. salevensis* is indeed somewhat less convex than that of *H. colloti* (Fig. 4b), it is nevertheless relatively more raised around the posterior than the anterior side, thereby creating a low, obtusely rounded carina there (Fig. 5a, g). Hence, the only, slight, difference between the two species is in the degree of compression of the valve, which is hardly sufficient for distinction at the generic level, especially as such external aspects of morphology may vary with individual age and ecological context. Moreover, Favre's comment regarding the anterior tooth socket of the LV appears to have been

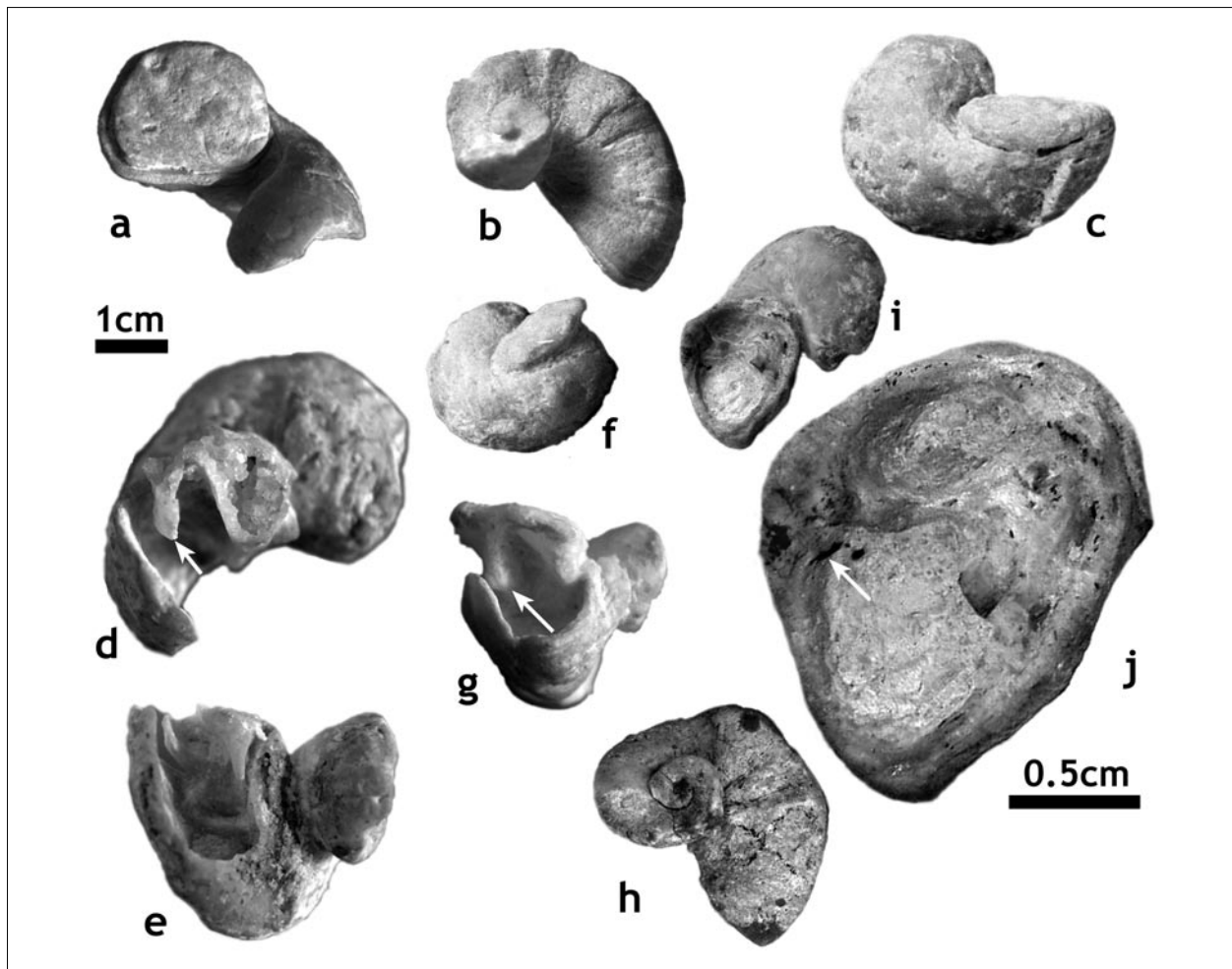


Fig. 6 Specimens of *Hypelasma salevensis* (FAVRE) from the Upper Kimmeridgian of Oyonnax and Chailley (Ain), French Jura (Gourrat collection, Société des Naturalistes d'Oyonnax) (a-g), and Valfin (Guirand collection, Université Claude-Bernard, Lyon) (h-j). (a, b) no. J7 (Chailley), articulated shell, viewed from right side and in anterior view, respectively; (c) no. J1 (Chailley), articulated shell, posterior view; (d, e) no. J2 (Oyonnax), partial articulated shell, (d) showing transverse section of myocardinal apparatus of right valve (posterior myophore arrowed; hinge plate to right), and (e) in ventral aspect, with ventral wall of left valve broken away to reveal projecting right valve posterior myophore (at left) and tooth (at right); (f, g) no. J4 (Oyonnax), partial articulated shell, in (f) posterior view, and (g) ventral aspect, with ventral wall of left valve broken away to reveal projecting right valve posterior myophore (arrowed) and tooth (at right); (h, i, j) no. ML14236, left valve, originally described by De Loriol as '*Diceras bourgeati*' (in DE LORIOL & BOURGEAT, 1888, pl. 29, fig. 2), (h) in anterior view, (i) in commissural view, with (j) enlargement of the internal features (posterior myophore arrowed). Scale bars: 1 cm for a-h; 0.5 cm for j.

based on a single specimen (Fig. 5e). Only one other LV in the type series shows its dentition (Fig. 5d), and it is clear even from this example that the relative size of the anterior tooth socket is quite variable. Indeed, the dentition in this latter specimen appears remarkably similar to that of *H. colloti*, as illustrated by PAQUIER (1897). It is worth recording in this context that DOUVILLÉ (1915, p. 384) likewise noted the rather variable development of the anterior tooth socket among requieniids and advised against exaggerating its importance for taxonomy. So there is no compelling justification, after all, for excluding Favre's species from *Hypelasma*. In addition, we note the projecting, ledge-like form of the posterior myophore in the RV (Fig. 5h, i), which, as mentioned above, is typical of *Hypelasma* (Fig. 4b). Consequently, we hereby formally re-classify Favre's species as *Hypelasma salevensis* (FAVRE).

With the re-instatement of *Hypelasma* as a distinct genus, it is perhaps also appropriate to re-confirm its inclusion in the Family Requieniidae, as diagnosed above, on the basis of its trochospirally to helicospirally coiled LV with a broad anterior face of original attachment (Fig. 5b, c).

Hypelasma salevensis (FAVRE, in JOUKOWSKY & FAVRE, 1913)

Fig. 5a-i; Fig. 6a-j

v. 1888 *Diceras bourgeati* P. DE LORIOL; DE LORIOL, pl. 29, fig. 2 (*non* fig. 1).

v*1913 *Matheronia salevensis* n.sp.; FAVRE, p. 410-413, pl. 24, figs. 1-14.

1931 *Matheronia salevensis* FAVRE; YIN, pl. 13, figs. 5-6, pl. 14, fig. 1.

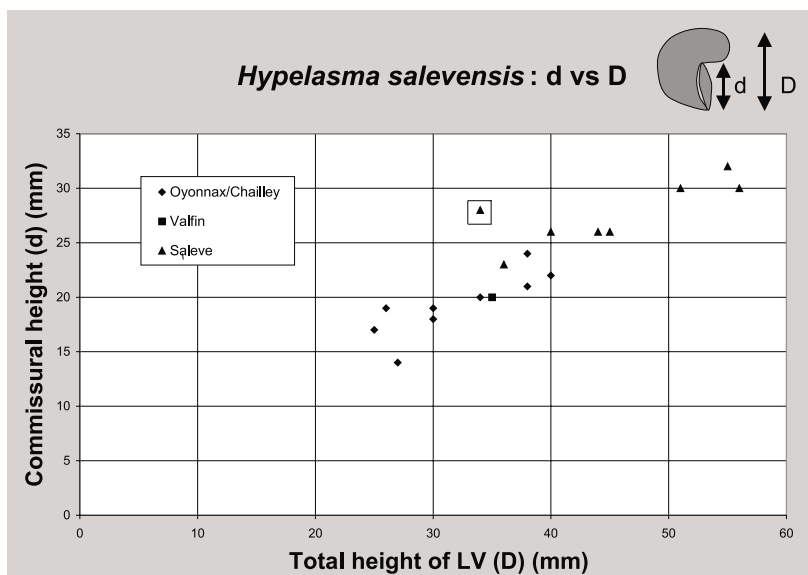


Fig. 7 Bivariate scatter of dorso-ventral commissural height (= height of right valve), (d), versus full height of left valve, from ventral margin to top of umbo, (D), for specimens of *Hypelasma salevensis* FAVRE from the Upper Kimmeridgian of Oyonnax and Chailley (Ain), and Valfin (Jura), and around the Tithonian/Berriasian boundary at Mont Salève (Haute-Savoie), eastern France. The data point for the lectotype, selected herein, is boxed.

v 1999 *Matheronia salevensis* JOUKOWSKY & FAVRE; SKELTON, p. 86, pl. 3, figs. 7, 8.

Type material: The Favre collection is housed in the Muséum de la ville de Genève (Département GEPI). In his description, Favre did not designate a holotype from the 100 specimens from Le Salève (Les Etiollets, Chavardon) that he reported having studied (only a few of which he illustrated). Nor, to our knowledge, has any later author selected a lectotype from among his syntypes, some of which are re-illustrated in Fig. 5 herein. Of the specimens illustrated in JOUKOWSKY & FAVRE (1913, pl. 24, figs. 1–14), the prepared LV shown there as fig. 8 (specimen no. 28914) most clearly exhibits the distinctive incipient posterior myophore as well as the dental plan of the species (Fig. 5e, f), despite showing an atypically large ratio of commissural height to total valve height in the LV (d/D in fig. 7). Accordingly, we designate this specimen as the name-bearing lectotype of the species (re-illustrated herein as Fig. 5e and f), as provided for in Article 74 of the *International Code of Zoological Nomenclature* (RIDE et al., 1999), and the remaining specimens thereby become paralectotypes.

Diagnosis: Relatively small species of *Hypelasma* (dorso-ventral commissural diameter up to 3.5 cm). LV sometimes exceeding 3 whorls in adult; RV sub-operculiform, though with slightly raised posterior margin, producing weak carina. Hinge plates relatively large, occupying up to a third of the commissural area. Posterior myophoral ledge in LV weakly developed.

Material studied: Besides some of the type specimens (Fig. 5), we have studied nine specimens from the Upper Kimmeridgian of the southern Jura, from the rudist collections of the senior author housed at the Société des Naturalistes d'Oyonnax, and comprising three articulated specimens, three LVs and three more LVs with partial RVs. Some of these specimens

are illustrated in Fig. 6a–g. Also shown is a single LV from Valfin (Fig. 6h–j), from the Guirand collection at the Université Claude-Bernard, Lyon (specimen no. ML14236), which was originally described by De Loriol as '*Diceras bourgeati*' (in DE LORIOL & BOURGEAT, 1888, pl. 29, fig. 2).

Description: The specimens from the Jura are generally smaller (LV height, from ventral margin to top of umbo, 26 to 40 mm) than those from Le Salève (LV height, 36 to 56 mm), though with some overlap in size (Fig. 7). Otherwise, they conform well to Favre's description, with only minor differences in the internal features of the few specimens in which they can be seen.

The LVs of the Jura specimens show the low expansion rate typical of the species, yielding a trochospiral (Fig. 6c, f) to helicospiral (Fig. 6a, e) external form, with 2–3 whorls in adult shells. The broad basal area on the anterior wall of the LV (Fig. 6b) is bounded by the characteristically sharp, but later rounded, antero-ventral carina, and shows coarse growth rugae, accompanied, in one example (not illustrated), by some weak longitudinal ribbing. The Valfin specimen (Fig. 6h, i) agrees in all these particulars and plots comfortably within the morphometric field of our specimens (Fig. 7). The RV (Fig. 6a, c, f) is almost operculiform, though slightly raised posteriorly, with a weakly expressed posterior carina.

The internal features can be discerned only in two of the incomplete, partially articulated specimens (Fig. 6d–e and g), though they are also visible in the LV from Valfin (Fig. 6i–j). Most importantly, although some of the ventral valve margin is missing from the latter specimen, it does show a small part of the weak posterior myophore passing beneath the hinge plate (Fig. 6j, arrowed). The posterior myophore of the RV is a strongly projecting shelf extending ventrally from the hinge plate (Fig. 6d–e and g, arrowed). Though perhaps a little more erect than in the specimens from le Salève

(e.g. Fig. 5h, i), its form and position are similar, and match the diagnosis for the genus (cf. Fig. 4b).

Remarks: From the above description, it is evident that the Valfin specimen shows no significant differences, either in size or form, from our specimens of the same age from a little farther south, and may accordingly be classified with them. Its inclusion in *Diceras bourgeati* DE LORIOI by De Lorient (in DE LORIOI & BOURGEAT, 1888) was obviously erroneous. In erecting the latter species, De Lorient stated that it attached by the right valve, and his description clearly relates to the large, articulated sub-equivalve specimen that he illustrated in his pl. 29, fig. 1, in which an attachment scar is indeed visible on the RV. That species can unquestionably be assigned to the genus *Diceras* LAMARCK, but, from DE LORIOI & BOURGEAT (1888), only the single specimen shown in fig. 1 of pl. 29 can be assigned to it (for which it becomes the holotype, by monotypy). By contrast, the specimen shown in their pl. 29, fig. 2 (= Fig. 6h–j herein) is hereby transferred to *H. salevensis*.

It is also apparent from the above description that the Jura specimens are closely comparable in external form to those from Mont Salève, differing from them only in mean size (Fig. 7). Their myocardial arrangements likewise appear similar. With so few specimens available in which internal features can be observed, no significance can yet be attached to the minor differences between them. Moreover, the bivariate scatter in Fig. 7, relating dorso-ventral commissural diameter (d , also equivalent to RV height) to the full height of the LV (D), shows a remarkable consistency of trend from the Jura specimens to those from Mont Salève. The simplest interpretation is that the two sets of specimens come from a single species (*H. salevensis*) that shows phyletic size increase – an evolutionary pattern that has been documented in a number of other rudist lineages (STEUBER, 2003). Similar small requieniids are not uncommon in Tithonian platform carbonates elsewhere, and YIN (1931), for example, reported the species from the Tithonian of Gard and l'Hérault. Re-study of such material would allow the hypothesis of phyletic size increase to be tested.

Based on the description of PAQUIER (1897), *H. colloti* appears to be somewhat larger than *H. salevensis*, the posterior part of its RV is more raised, and the posterior myophoral ledge in the LV has slightly more marked development. As long as Favre's material was believed to be of early Tithonian age (as proposed in JOUKOWSKY & FAVRE, 1913), *H. colloti* could have been considered as a possible descendent chronospecies, continuing the trend for phyletic size increase. However, according to DEVILLE (1991), the Salève specimens come from around the Tithonian/Berriasian boundary, so may be even younger than Paquier's material. Further comparative study of the two species is thus needed to establish the relationship between them more clearly.

4. THE EVOLUTIONARY ORIGIN OF *Hypelasma salevensis*

H. salevensis makes an abrupt appearance in the Upper Kimmeridgian of the southern Jura alongside several diceratid species (SKELTON, 1999), all of larger shell size. *H. salevensis* is likely to have been derived from one of the species of the two pre-existing diceratid genera in which attachment was by the LV, namely *Epidiceras* and *Plesiodiceras* (*Diceras* can be rejected because it attached by the RV).

Despite some variation in the degree of relative reduction of the RV, none of the species of *Epidiceras* approaches the characteristic requieniid growth geometry of *Hypelasma*, and only one (*E. guirandi* (DE LORIOI)) comes close to its smaller shell size. Favre (in JOUKOWSKY & FAVRE, 1913) suggested that *H. salevensis* was derived from *Plesiodiceras munsteri* GOLDFUSS, on the basis of the similarity of their more or less operculiform RVs. Even in the Kimmeridgian specimens of *H. salevensis*, however, the posterior adductor muscle inserted onto a low myophoral ledge in the LV, which passes beneath the hinge plate, instead of a myophoral shelf adjoining the hinge plate, as seen in *P. munsteri*. Moreover, the posterior muscle insertions in *Plesiodiceras* extend dorsally onto the posterior parts of the hinge plates, whereas in *H. salevensis* they are wholly ventral to the hinge plates, as in *Epidiceras*. These differences leave the proposed link between *Plesiodiceras* and *Hypelasma* open to question, because the myophoral condition of *Plesiodiceras* appears relatively more derived. In addition, the adult LV of *P. munsteri* has a tightly ascending spiral form, lacking a pronounced antero-ventral carina, associated with its upright growth habit, in contrast to the broadly trocho- to helicospiral, strongly carinate shape of the same valve in *H. salevensis*.

Nevertheless, the juvenile LV of *P. munsteri* (up to 1–2 cm dorso-ventral commissural diameter), which represents the stage of attachment to the substrate, is broadly spiral and carinate, with a large basal area on its anterior face, as in *Hypelasma*. This similarity suggests the possibility of heterochrony: *H. salevensis* could have evolved from *P. munsteri* (or another species), as a paedomorphic derivative. The relatively small size of the oldest specimens of *H. salevensis* would also be consistent with this interpretation. However, testing the hypothesis will require knowledge of the condition of the posterior adductor insertions in the juvenile shell of *P. munsteri*, which is presently lacking.

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