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Abstract

Using recent samplings and specimens from ancient collections, 14 sites and five species of stalked crinoids have been listed in the Miocene of the southern Rhodanian basin (southeastern France). Three species and two genera are new for science: *Papacrinus avignonensis* **n. gen.**, **n sp.** (Balanocrininae), *Paraconocrinus rhodanicus* **n. sp.** (Rhizocrinidae) and *Gastecrinus vinealis* **n. gen., n. sp.** (Incertae sedis). The identification among the Mediterranean Miocene fauna of the genus *Metacrinus*, now

confined to the Indo-Pacific province, was confirmed by the discovery of brachial ossicles attributed to *Metacrinus berthei*. The richest and most diversified site was exposed during temporal excavations at the Place du Palais des Papes in Avignon. Four out of the five stalked crinoid species were found in this fossil assemblage in which *M. berthei* predominates. ?*Endoxocrinus gastaldii* is associated with *M. berthei* in several sites. Using dissociated ossicles, differences in quantitative and qualitative characters between these two species are deeply analyzed with their taphonomical, taxonomical and paleoecological consequences. Paleoreliefs and valleys, which had been incised during the Burdigalian, channeled currents. They favored stalked crinoid settlement on various substrates during the late Burdigalian - Lower Langhian transgression. Comparison with the extant fauna allows us to estimate the depth range of the biotopes with stalked crinoids from 100 to 250 m. These estimates are in agreement with those deduced from other paleontological studies.

Key words Crinoidea, Isocrinida, Rhizocrinidae, *Endoxocrinus*, *Metacrinus*, *Papacrinus*, *Paraconocrinus*, *Gastecrinus*, new taxa, paleoecology, Neogene.

Résumé

A l'aide de récoltes récentes et de spécimens de collections anciennes, 14 gisements et cinq espèces de crinoïdes pédonculés ont été inventoriés dans le Miocène du bassin rhodanien (Sud-Est de la France). Trois espèces et deux genres sont nouveaux : *Papacrinus avignonensis* **n. gen., n sp.** (Balanocrininae), *Paraconocrinus rhodanicus* **n. sp.** (Rhizocrinidae) et *Gastecrinus vinealis* **n. gen., n. sp.** (Incertae sedis). La présence dans le Miocène méditerranéen du genre *Metacrinus*, aujourd'hui confiné à la province indo-pacifique, a pu être confirmée grâce à la découverte de pièces brachiales attribuées à *Metacrinus berthae*. Quatre espèces sur cinq sont présentes dans l'assemblage fossile d'Avignon (Palais des Papes) dominé par *M. berthei*. Dans plusieurs gisements, ?*Endoxocrinus gastaldii* est associé à *M. berthei*. Les différences de caractères quantitatifs et qualitatifs entre ces deux espèces longtemps confondues et leurs variations sont analysées en détail à partir des ossicules dissociés, ainsi que leurs conséquences taphonomiques, taxonomiques et paléoécologiques. Les paléoreliefs et les vallées incisées durant le Burdigalien ont canalisé des courants marins créant des conditions favorables à l'implantation des crinoïdes pédonculés sur des substrats variés au moment de la transgression du Burdigalien supérieur – Langhien inférieur. La comparaison avec la faune actuelle permet d'estimer l'étagement bathymétrique des biotopes à crinoïdes pédonculés entre 100 à 250 m. Ces estimations sont en accord avec celles déduites d'autres études paléontologiques.

Introduction

Most Cenozoic stalked crinoids are known from dissociated ossicles, which often hampers attribution to extant or fossil genera. Only few specimens have been described with their crown preserved (Moore and Vokes 1953; Rasmussen 1972, 1980; Oji 1990; Meyer and Oji 1993; Baumiller and Gazdzicki 1996). The link between the Recent and the Mesozoic fauna thus remains difficult to clarify. Moreover, analyses of molecular phylogeny carried out on the extant fauna have deeply questioned the classical systematics of crinoids, mainly based on the external morphology of the skeleton (Hémery 2011; Hémery *et al.* 2013; Rouse *et al.* 2013). The ecophenotypic convergence (homoplasy) and the frequent evolution through paedomorphy impose the search for more robust discriminant characters and a critical analysis of the

classification (Roux *et al.* 2013). Such traits detected in extant species should be applicable to dissociated fossil ossicles. This method has enabled tracing the lineage of Rhizocrinidae from the Late Cretaceous to the Recent (Roux *et al.* 2019). In Isocrinida, the establishment of a new classification remains controversial (Roux *et al.* 2009; Hess 2011).

In France, during the Eocene, only the Pyrenean and Alpine foreland basins included environments deep enough for stalked crinoids (Roux and Plaziat 1978). In the Miocene, they were described in the southern Rhodanian basin as early as the end of the 19th century (Nicolas 1897, 1898; de Loriol 1897). In northern Italy, the first descriptions were even older (Meneghini 1862, 1876; Michelotti 1847). Nevertheless, no recent detailed revision is available and the taxonomic attributions remain confused due to the lack of sufficiently precise descriptions of the dissociated ossicles. Using field investigations (M.P.) and specimens preserved in museum collections, we propose here a detailed review of the Upper Burdigalian- Lower Langhian fauna of southeastern France with its consequences on the interpretation of depositional environments and their paleobathymetry.

Material and method

The material from the Rhodanian basin is deposited in the following paleontological collections: Musée des Alpilles in Saint-Rémy de Provence (MASRP); Centre "Louis Lortet" de conservation et d'étude des collections, Musée des Confluences, formerly Muséum d'Histoire naturelle de Lyon (MHNL), and Université Claude Bernard Lyon 1 (UCB-FSL); Musée Requien d'Histoire naturelle, Fondation Calvet in Avignon (MRA); Muséum national d'Histoire naturelle in Paris (MNHN) (Tabl. 1).

Observations on articulations and photographs were performed at the MNHN electron microscopy platform using a Jeol-840A scanning electron microscope (SEM) operating at 15 kV. The ossicles were ultrasonically cleaned and coated with a colloidal platinum solution. For general morphological terms see Roux *et al.* (2002) and Hess (2011), for ossicle articulations see the glossary revised by Améziane *et al.* (2021). The parameters measured are shown in Fig. 2.

The crinoid material consists of dissociated ossicles, mainly stalk ossicles, which are likely to be displaced by marine currents. Before distinguishing the various isocrinid taxa and describing them, it is necessary to conduct a preliminary biometric study. This allows us to locate the ossicles within the skeleton and to identify the main morphological modifications during their growth with reference to similar extant species species (see for example David 1998, David et al 2006). The quantitative columnal characters vary markedly along the same stalk and from one individual to another. Biometric data are important to understand these variations and their origin. Moreover, they highlight taphonomic and paleoecological problems. Even when the material seems to be abundant such as the site of Avignon, the totality of collected ossicles represents only a small number of complete individuals (Table 2). The samples are usually insufficient for meaningful statistical analysis and sampling is often biased by the collecting method on outcrop surface and the absence of calibrated sediment washing. Sampling methods and potential biases are unknown for material from historical collections.

TABLE 1. List and locations of specimens of Miocene stalked crinoids from the southern Rhodanian basin. E.: Entrechaux, PdP: Place du Palais des Papes. Ossicles - AC: aboral cup, Br: brachial, Co: columnal, Ci: cirral, Plc: pluricolumnal. (*) Previously published figures, LR: de Loriol 1897, NC: Nicolas 1898.

Taxa	Catalogue Numbers	Sites	Ossicles	Figures (*)
?*Endoxocrinus gastaldii*	MHNL 20.062709	Avignon PdP	2 Plc	7C-D
?*Endoxocrinus gastaldii*	MHNL 20.062710	Avignon PdP	4Co	Not figured
?*Endoxocrinus gastaldii*	MASRP 2020.5012	ND du Château	1Plc	7A, LR18
?*Endoxocrinus gastaldii*	MASRP 2020.5022	ND du Château	1Plc	7B
?*Endoxocrinus gastaldii*	MASRP 2020.5013	ND du Château	1Plc	LR17
?*Endoxocrinus gastaldii*	MHNL 20.062711	Picabrier	1Plc+3Co	7E-J
?*Endoxocrinus gastaldii*	MHNL 20.062712	Picabrier	5Plc+15Co	Not figured
?*Endoxocrinus gastaldii*	UCBL-FSL 200022	Picabrier	8Plc+35Co	Not figured
?*Endoxocrinus gastaldii*	MHNL 20.062713	E. Pt St Michel	1Co	Not figured
?*Endoxocrinus gastaldii*	MHNL 20.062714	E. Ferme Pie	1Plc+1Co	Non figured
Metacrinus berthei	UCBL-FSL 19099-1	Les Angles	2/3 de Plc	8A, NC1A-B
Metacrinus berthei	MRA 3.009.192	Les Angles	1/3 de Plc	8B, NC1A
Metacrinus berthei	UCBL-FSL 19099-2	Les Angles	1Plc	8F, NC1G-F
Metacrinus berthei	MRA 3.009.194.1	Les Angles	1Co	8C, NC1C
Metacrinus berthei	MRA 3.009.194.2	Les Angles	1Co	8D, 9A, NC1D
Metacrinus berthei	UCBL-FSL 19099-3	Les Angles	10Plc+23Co	Not figured
Metacrinus berthei	MRA 3.009.193	Les Angles	1Plc	Not figured
Metacrinus berthei	MASRP 2020.5014	ND du Château	1Plc	9B-C, LR15
Metacrinus berthei	MASRP 2020.5015	ND du Château	1Plc	LR16
Metacrinus berthei	MASRP 2020.5023a	ND du Château	1Co	9D
Metacrinus berthei	MASRP 2020.5023b	ND du Château	20Plc+20Co	Not figured
Metacrinus berthei	MHNL 20.062715	Le Barroux	1PlC	9E
Metacrinus berthei	MHNL 20.062716	Le Barroux	8Plc+1Co	Not figured
Metacrinus berthei	UCBL-FSL 200024	Beaucaire	5Plc+10Co	Not figured
Metacrinus berthei	MHNL 20.062717	Avignon PdP	9Br	10A-L
Metacrinus berthei	MHNL 20.062718	Avignon PdP	Nb Br+Ci	Not figured
Metacrinus berthei	MHNL 20.062719	Avignon PdP	2Plc+10Co	11A-L, 12A-C
Metacrinus berthei	MHNL 20.062720	Avignon PdP	Nb Plc+Co	Not figured
Metacrinus berthei	MHNL 20.062721	Picabrier	2Plc+3Co	9F-K
Metacrinus berthei	MHNL 20.062722	Picabrier	3Plc+47Co	Not figured
Metacrinus berthei	UCBL-FSL 200023	Picabrier	4Plc+56Co	Not figured
Metacrinus berthei	MHNL 20.062723	Vedènes	1Plc+12Co+Br	Not figured
Metacrinus berthei	MNHN.F.A83128	Tarascon	9Plc	Not figured
Metacrinus berthei	MHNL 20.062724	E. Ferme Pie	2Plc+26Co	Not figured
Metacrinus berthei	MHNL 20.062725	E. Pt St Michel	13Co, Ci?	Not figured
Papacrinus avignonensis	MHNL 20.062726	Avignon PdP	1Co	12D-F
Paraconocrinus rhodanicus	MHNL 20.062727	Avignon PdP	4Co	12G-K
Paraconocrinus rhodanicus	MHNL 20.062728	Avignon PdP	26Co	Not figured
Paraconocrinus ?	MHNL 20.062732	Vedène	1AC, 1Co	Not figured
Gastecrinus vinealis	MHNL 20.062729	Vigne-Gaste	1AC	12L
Rhizocrinidae sp.	MHNL 20.062730	E. Ferme Pie	1Co	Not figured
Rhizocrinidae sp.	MHNL 20.062731	Grands Essards	2Co	Not figured

TABLE 2. Sample representability of *Metacrinus berthei* columnals (morphotype B) from the main Miocene sites compared to entire stalk of extant *Metacrinus* species. Values in number of ossicles. For extant species: values the most frequent in one individual (from Améziane-Cominardi 1991). IN: internodal, infraN: infranodal columnal, IN series: maximum number of successive internodals in pluricolumnals, IN/Ndx: estimation of number of internodals per noditaxis from ratio IN/N, (*): same estimation from ratio IN/infraN, (**): value from complete noditaxis.

sites	IN	infraN	IN series	N	IN/Ndx
Tarascon	57	2	10	2 (3)	28-29 (19)
Beaucaire	37	1	13**	1 (2)	37 (18-19)
Avignon	876	62	9	57	14-16
Picabrier	95	4	10	21	4-5
Barroux	64	4		3	16-21
ND Château	138	2	14	7	19-20
Les Angles	100	6	19**	4	16-17* to 25
Extant Ocean	300-400	20-25	--	20-25	7 -17 to 21

Abbreviations used for tables and some descriptions: AC: aboral cup, Br: brachial, Brax : axillary brachial, IBr: primibrachial, IIBr: secondibrachial, IIIBr: tertibrachial, free Br: Br with muscular synarthry on each face, Br1+2: brachials united by synostosis, Ci: cirral, Co: columnal, Cr: crenulae, Cr/PZ: maximum number of crenulae per petaloid zone, D: diameter, H: height (a single ossicle), IN: internodal, IN/N: ratio number of internodals to number of nodals, IN/Ndx: number of internodals per nodotaxis, infraN: infranodal, L: length (several ossicles), N: nodal, Ndx : noditaxis, Plc : pluricolumnal, IPZ: interpetaloid zone, PZ: petaloid zone.

General geological and biogeographical setting

In the southern Rhodanian basin, the Miocene Sea transgressed over a substratum deformed during the Paleogene (Eocene Pyrenean-Provencal folding, Oligocene Western European rifting) and eroded during major fluctuations in sea level, leaving numerous submarine or emerging shoals separated by strongly incised valleys (Demarcq 1970; Besson 2005). The Rhône-Provence Gulf was located at the southwestern end of the peri-alpine molassic channel towards the western Mediterranean Sea, which was opening and deepening. It was framed by two major faults, the Nîmes Fault on its western edge and the Durance Fault on its eastern edge (Fig. 1). The Nîmes Fault delimited a series of shoals aligned on the western border. Near Avignon, some shoals, including that of Les Angles, were parallel. The Middle Durance and Aix faults separated eastern and western Provence. Between these two major faults, other shoals were linked to Pyrenean-Provencal anticlines of an east-west axis: Ventoux-Montagne de Lure, Luberon and Alpilles. The Salon-Cavaillon Fault separates the Luberon from the Alpilles and associated faults limit the western Ventoux massif. The deposits in which the material studied here was collected correspond to a a palaeoclimatological thermal maximum coinciding with the Late Burdigalian-Langhian transition (Demarcq 1984; Chateauneuf *et al.* 2006). After a

phase of intra-Burdigalian sea level fall during which deep incised valleys were carved, the Late Burdigalian-Langhian transgression filled these valleys and submerged most of the shoals (Besson 2005; Besson *et al.* 2005).

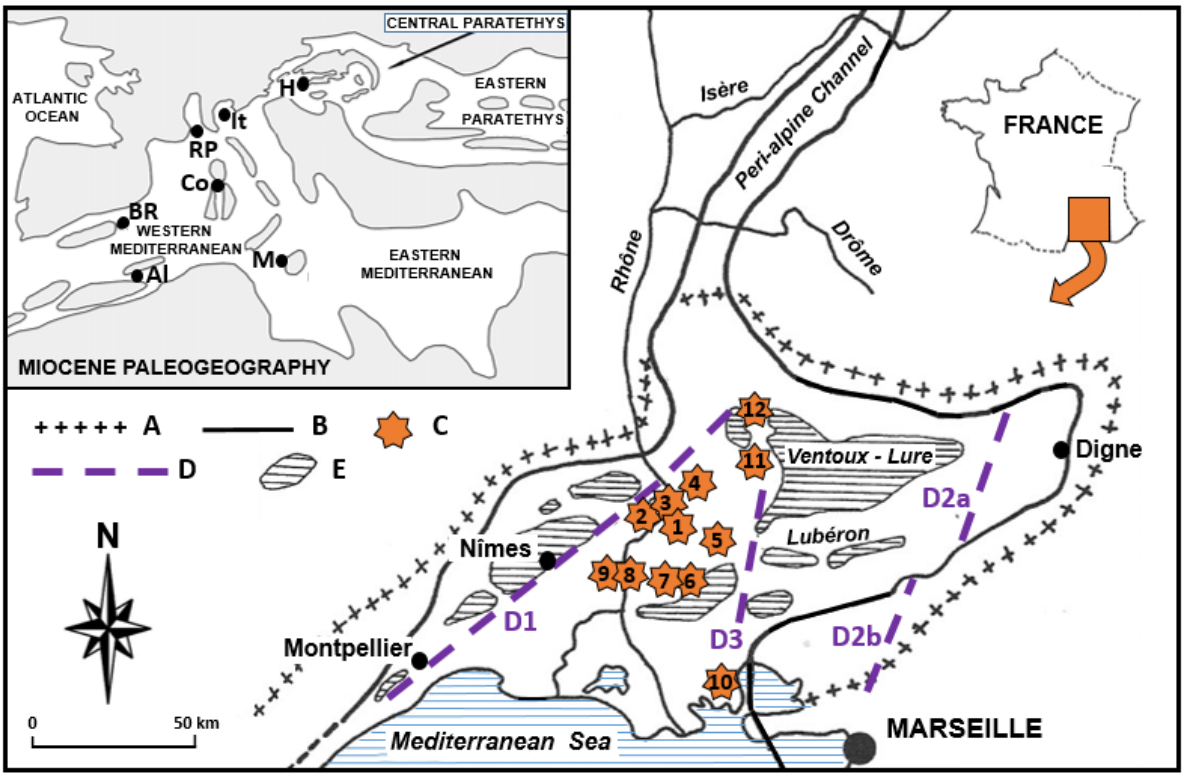

FIGURE 1: Miocene sites with stalked crinoids in western Paratethys area, and detailed locations within the Rhône-Provence Bay. Upper left: paleogeographic map (Al: Algeria, BR: Betic Ranges in Spain, Co: Corsica, It: northern Italy, H: Hungary, M: Malta, RP: Rhône-Provence Bay). Rhône-Provence Basin: schematic map with sites (1: Avignon, Palais des Papes; 2: Les Angles; 3: Pierre Longue; 4: Védène; 5: Picabrier, 6: St Rémy-de-Provence; 7: N.D. du Château; 8: Tarascon, 9: Beaucaire; 10: Vigne Gaste, 11: Le Barroux; 12: Entrechaux; A: presumed limit of the Miocene Rhône-Provence Bay, B: enveloppe of Burdigalian marine sediment outcrops, C: sites with stalked crinoids, D: main faults (D1: Nîmes fault, D2a: middle Durance fault, D2b: Aix fault, D3: Salon-Cavaillon fault), E: island or submarine shoal).

Outside southeastern France, Miocene stalked crinoids (mainly isocrinids) were reported in the Mediterranean area and the Central Parathetys (Fig. 1): in Corsica at Bonifacio (Locard 1877), in Spain in the Betic Cordilleras (Roux and Montenat 1977), in Algeria (Pomel 1887; Dalloni 1917), in Malta (Cooke 1896), in northern Italy (Michelotti 1847; Noelli 1900; Albus 1931), in Austria in the Vienna basin (Kroh 2003) and in Hungary (Sandor 1983). They were dated to the Burdigalian (SE France, Algeria), Langhian (Corsica, northern Italy, Austria, Hungary, Malta) or Late Miocene (Betic Cordilleras).

The extant biogeography of the isocrinids is mainly inherited from the Mesogean Tethys. Since the end of the Cretaceous, the Mesozoic fauna has been split into several provinces by the collisions at the origin of the Alpine belt and by the opening of the Atlantic Ocean (Améziane and Roux 1997). The Diplocrininae present today in the western - central Pacific, northeastern Atlantic and tropical western Atlantic illustrates this ancient Mesogean

distribution. Their ancestors should be present in the Cenozoic fauna of the Paratethys because they have been reported from the Neogene of Japan (Oji 1990) and Caribbean islands (Donovan et al. 2005). The Metacrininae are today restricted to the western Pacific margins and northeastern Indian Ocean (Chippy *et al.* 2018). Their oldest known representatives are found in the Paleocene and Eocene of the Antarctic Peninsula (Rasmussen 1980; Meyer and Oji 1993; Baumiller and Gazdzick 1996). They could be considered as having only an Indo-Pacific heritage (Whittle *et al.* 2018). Nevertheless, Roux and Montenat (1977) had already attributed columnals and a single brachial from the Late Miocene of Spain to the genus *Metacrinus*.

Miocene sites and inventory of stalked crinoids from southern Rhodanian basin

The Miocene sites with stalked crinoids (Tab. 3) are located between the Nîmes Fault and the axis of the Salon-Cavaillon Fault (Franzin 2007) (Fig. 1). Most of them are located near the flanks or at the top of Cretaceous limestone palaeoreliefs described by Demarcq (1970), in areas where Besson (2005) highlighted valleys that were strongly incised during the Burdigalian. They are grouped into three sectors: (1) the northern flank of the Alpilles (Saint-Rémy de Provence, Notre-Dame du Château) and its extension to the West (Tarascon, Beaucaire), (2) the Avignon region (Les Angles, Pierre Longue, Palais des Papes d'Avignon, Picabrier, Vedène), and (3) the sector immediately at west and northwest of the Mont Ventoux (Le Barroux, Entrechaux).

The outcrop, still accessible, of Notre-Dame du Château between Saint-Etienne-du-Grès and Saint-Rémy de Provence is the type-locality of *Pentacrinus miocenicus* de Loriol, 1897. Above a perforated hard ground intersecting the Neocomian substratum, a thin layer of Late Burdigalian marly molasse, rich in bryozoans and containing the crinoids, is preserved under the discordance of the Langhian (Pellat 1897). East of Saint-Rémy de Provence, Joleaud (1907) found *Pentacrinus miocenicus* in a bed with bryozoans and small brachiopods of the Late Burdigalian.

The ancient quarries once opened in the Miocene to the west of the old village of Les Angles, now in an urbanized area, are the type-locality of *Pentacrinus berthei* Nicolas, 1897. Joleaud (1907: 13-14) gives a detailed description of this section in which the echinoderm-rich marly molasse (including several species of feather stars, *Pentacrinus miocenicus* and *Conocrinus*) is located in its upper part above a greenish pebble conglomerate. It is surmounted by a sandstone bed and poorly lithified marlstones attributed to the Late Burdigalian/Langhian transition. To the south of the old village, upstream of the valley used by the expressway toward Avignon, there is a sloping surface perforated by echinids on which Joleaud (1907: 20) collected *P. miocenicus* from a thin bed of white molasse. The sandy-marl (Schlier facies) of the Langhian that outcrop at the bottom of the valley, overlap this surface that intersects the Neocomian limestone. Joleaud also reported *P. miocenicus* at Pierre Longue (Villeneuve-lès-Avignon) at the base of the Langhian Schlier facies overlapping a breccia at the foot of a slope composed of slumping blocks of Neocomian limestone.

The other sites around Avignon are located on the slope of paleoreliefs (Demarcq 1970). Southwest of the village of Vedène, the crinoids come from a conglomerate with white marls. At Picabrier (Caumont-sur-Durance), isocrinids abound in a glauconious layer with greenish

pebbles, which is at base of the "Marnes de Caumont Formation" usually attributed to the Langhien. This layer lies discordantly over a compact Neocomian limestone through several perforated surfaces (Ulysse 1968). Excavation carried out in 1972 on the parking at the Place du Palais des Papes in Avignon temporarily exposed an outcrop of crinoid-rich Burdigalian molasse located at the foot of the Doms' rock constituted of Barremian limestone (Philippe and Granier 1982).

TABLE 3. Miocene sites with stalked crinoids and species identified. (*): collected by M. Philippe, (**): collected by J. Ulysse; other sites: from ancient collections (MASR, MNHN, MRA, UCBL-FSL), (§): record from Joleaud (1907), Ab: abundant, F: frequent, Q: a few, R: rare. See Table 1 for other abbreviations.

Site	Commune	Department	Taxa	Ossicles
Avignon, Place duPalais des Papes Excavation 1972 (*)	Avignon	Vaucluse	?*Endoxocrinus gastaldii* R *Metacrinus berthei* Ab *Papacrinus avignonensis* R *Paraconocrinus rhodanicus* F	Plc, Co Plc, Co, Br, Ci Co Co
Ancient quarries	Les Angles	Gard	*Metacrinus berthei* F *Paraconocrinus*? (§)	Plc, Co, Ci Co
Pierre Longue (Joleaud 1907)	Villeneuve-lès-Avignon	Gard	*Pentacrinus miocenicus* (§) = *Metacrinus berthei*?	Co or Plc?
Picabrier (*) (**)	Caumont-sur-Durance	Vaucluse	?*Endoxocrinus gastaldii* Ab *Metacrinus berthei* Ab	Plc, Co Plc, Co
South west of village, freeway outcrop (*)	Vedène	Vaucluse	*Metacrinus berthei* Q *Paraconocrinus* ? R	Plc, Co, Br? AC, Co, (usé)
Point coté 314.4, South East church (*)	Le Barroux	Vaucluse	*Metacrinus berthei* Q	Plc
Grands Essarts (*)	Entrechaux	Vaucluse	Rhizocrinidae sp. R	Co, (usé)
Ferme Pie (*)	Entrechaux	Vaucluse	?*Endoxocrinus gastaldii* Q *Metacrinus berthei* Q Rhizocrinidae sp. R	Plc, Co Plc Co, (usé)
Pont-Saint-Michel (*)	Entrechaux	Vaucluse	?*Endoxocrinus gastaldii* R *Metacrinus berthei* F	Co Co, Ci ?
Notre-Dame du Château	Saint-Etienne-du-Grès	Bouches du Rhône	?*Endoxocrinus gastaldii* Q *Metacrinus berthei* F	Plc, Co, Ci Plc, Co, Ci
East of the town (Joleaud 1907)	Saint-Rémy de Provence	Bouches du Rhône	«*Pentacrinus miocenicus*»	Co or Plc?
Unknown	Tarascon	Bouches du Rhône	*Metacrinus berthei* Q	Plc
Ancient quarry	Beaucaire	Gard	*Metacrinus berthei* Q	Plc
Vigne-Gaste (*)	Istres	Bouches du Rhône	*Gastecrinus vinealis* R	AC

In the site near Le Barroux northeast of Carpentras, the isocrinids were collected at the contact between Burdigalian limestone and the overlying "Marnes bleues de Faucon Formation". Near Entrechaux, in the vicinity of the flank of a Cretaceous limestone paleorelief, crinoids were found in the "Marnes bleues de Faucon Formation" dated to the Late Burdigalian (Pouyet *et al.* 1984) at the sites known as Ferme Pie and Pont Saint Michel (Philippe 1974).

The locality Vigne-Gaste near Istres is located on the edge of the Lavalduc pond. The single aboral cup of *Gastecrinus vinealis* n. gen., n. sp. was collected just below a bed attributed to the Late Burdigalian (Maurel-Ferrandini 1976: 77-79).

Outline of stalked crinoid morphology

Two groups of stalked crinoids (isocrinids and rhizocrinids) which are well known in modern oceans are found in the Miocene sites studied. Isocrinid columnals are the most common.

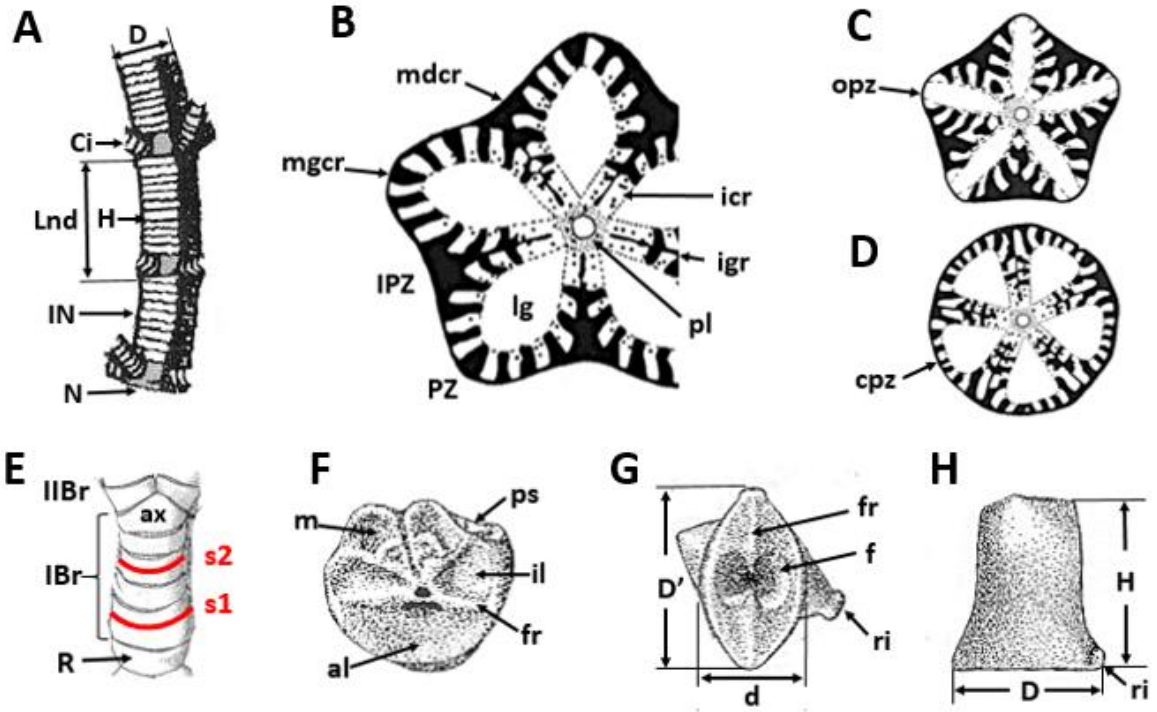

FIGURE 2: Morphology of crinoid ossicles. A-D in isocrinid stalk, A: side view of a stalk segment (Ci: cirrus, IN: internodal, N: nodal, D: diameter, H: columnal height, Lnd: noditaxis length), B: symplexial facet of metacrinine type (IPZ: interpetaloid zone , PZ: petaloid zone, icr: inner crenularium, igr: interpetaloid groove, lg; ligament area, mdcr: middle crenularium, mgcr: marginal crenularium, pl: perilumen), C: symplexial facet of diplocrinine type (opz: open petaloid zone), C: symplexial facet of balanocrinine type (cpz: close petaloid zone); E-F: in isocrinid arm, E: proximal arm pattern in *Metacrinus* (IBr: primibrachials, IIBr: secundibrachials, R: radial, s1: synostosis at IBr1+2, s2: synostosis at IBr4+5); F: facet of muscular synarthry (al: aboral ligament depression, il: inner ligament area, m: muscular area, ps:pinnule socket); G-H: in rhizocrinid columnal, G: distal view, H: side view (fr: fulcral ridge, ri: rhizoid insertion. Measured parameters, D: greatest diameter including insertion of rhizoid, D': greatest articular facet diameter without rhizoid insertion, d: smallest articular facet diameter, H: columnal height, ri: rhizoid insertion).

The heteromorphic isocrinid stalk presents particular columnals, the nodals, bearing a whorl of cirri (Fig. 2A). The cirrus end is a claw-like ossicle that clings to rough substrates. Most of the columnal articulations have pentaradiate facets with a crenularium interlocking

with that of the adjacent columnal facet (symplexy) (Fig. 2B-D). Stalk autotomy at the distal nodal articulation of smooth facets (cryptosymplexy) allows the release of the animal and then its relocation. A noditaxis is a stalk segment between two cryptosymplexies (Fig. 2A). Proximal noditaxes have well open inter-articular pores corresponding to the axis of the interpetaloid zones of the symplexies. These pores close during the increasing of intermodal thickness distally. Some proximal external features of the noditaxes such as the star-shaped section, the irregular size of internodals or the presence of interarticular pores may be maintained more or less distally along the stalk during ontogeny. New columnals appear just below the aboral cup and into the proxistele all along an individual's life. The proximalmost arm division always occurs at the second primibrachial (IBr2ax), except in the subfamily Metacrininae in which it places distally, usually at Br7ax in the genus *Metacrinus* (Fig. 2E). David *et al* (2006) and Tunicliffe *et al.* (2016) provided illustrations of the variety of ecological niches occupied by the isocrinids, their lifestyle and ecophenotypic adaptations. The convergences of external morphology related to the environment are frequent particularly in Metacrininae (Améziane-Cominardi 1991) and Diplocrininae (David *et al.* 2006).

Rhizocrinidae have only been collected from a few Miocene sites of Rhodanian basin, mainly in the Avignon site. Their xenomorphic stalk is devoid of cirri. Rhizoids develop in its distal part (dististele) and ensure fixation by penetrating the soft, mostly muddy sediments. The columnal articulations are bilaterally symmetrical (ligamentary synarthry) with varying orientation giving the stalk a twisted feature (Fig. 2G-H)).

Stalked crinoids are rheophilic suspension feeders. Their crown of arms rises above the sea floor to filter the foodparticles carried by currents. The morpho-functional characters of the stalk favor the crown elevation and its changes in orientation when there is variation in tension related to the pressure exerted by the current on the crown (Roux 1987; Baumiller 2008). Just below the crown, the proxistele formed of numerous thin columnals is the most flexible stalk part. With the columnal growth in thickness distally, the stalk rigidity increases. In isocrinids, the alternation of columnals of variable diameter and height within noditaxis favors either proxistele flexibility or stalk curvature by differential columnal thickening distally. Only the brachial articulations have muscles (muscular synarthry, Fig. 2F). Arm autotomy is possible at the level of ligament articulations (smooth synostosis or syzygy) in variable numbers according to taxa (Fig. 2E).

Biometric analysis of isocrinid columnal morphotypes

- ***General remarks***

The analysis of the main quantitative external characters of columnals is coupled with the qualitative characters of articulations (see Fig. 2A-D). A distinction must be made between (1) the state of development of each columnal, its height and relative thickness (H/D), and (2) the growth stage of the individual to which the stalk belongs. The new columnals permanently appear just below the aboral cup of an individual. Therefore, pre-existant columnals are displaced towards the distal stalk throughout individual ontogeny. The nodals fastly acquire the aboral diameter of the aboral cup and the height that allows the development of cirri. Then the nodal diameter growth is weak or negligible, thus making it a valuable index of individual

growth stage. The diameter growth of internodals that appear between two nodals in the proxistele is slower and sometimes reaches the nodal diameter only more distally. The difference in size between nodals and internodals reduces through noditaxis ontogeny. The same is true for internodal height with more or less allometric growth. In juvenile individuals, columnal growth is faster in height than in diameter and the relative columnal thickness (H/D) increases. In larger (older) individuals, the diameter displays the fastest growth. Therefore, during individual growth after juvenile stage, H/D substantially decreases. These usual general trends are found in the Miocene isocrinids studied in the present paper (Figs. 3-4).

In a first step, four isocrinid columnal morphotypes were empirically distinguished without prejudging precise taxonomic attributions. The strongly star-shaped morphotype A has mature symplexies with narrow ligament areas open outwards (Fig. 2C), bordered by 16 to 20 Cr/ZP, and without a groove separating each petaloid zones. Morphotype B is pentagonal, more or less rounded to slightly star-shaped, with mature symplexies of wider lanceolate ligament areas surrounded by a closed crenularium (Fig. 2B) of 14 to 16 Cr/ZP, and usually a groove separating petaloid zones. Morphotype C differs from the morphotype B in having a more marked pentagonal shape, usually a smaller diameter and a greater H/D. Morphotype D, represented by a single columnal from Avignon, markedly differs from the others in having symplexies of balanocrinine type (Fig. 2D). The latter type is not taken into account in the biometric analysis. Avignon and Picabrier are studied first because they yielded the greatest number of columnals, two sites are firstly studied: Avignon and Picabrier. The results will serve as a framework for the comparison with the data from the other sites.

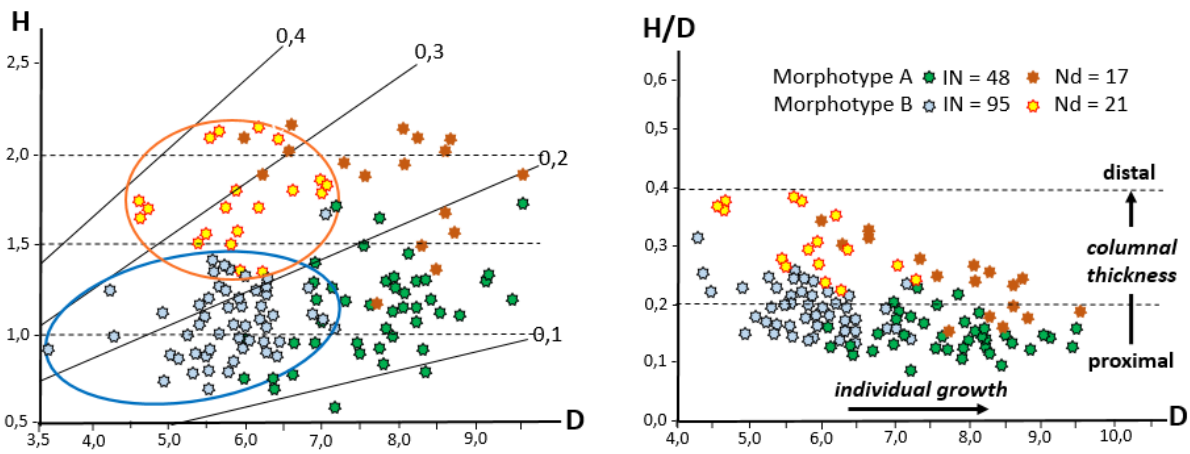

FIGURE 3: Variation in the general shape and size of isocrinid columnals from Picabrier (Caumont-sur-Durance). D: diameter, H: height, IN: internodal, Nd: nodal. Morphotype A is attributed to ?*Endoxocrinus gastaldii* and morphotype B to *Metacrinus berthei* (see text). Values in mm, except ratios and number of columnals (Nd and IN).

- ***Results***

In the Picabrier site (Fig. 3, Tables 4-5), columnals of morphotypes A and B are easily distinguished because intermediate specimens are not observed (Ulysse 1968). The frequencies of columnal diameter values tend towards a bimodal distribution. Internodals of morphotype B

are smaller (D< 7.2 mm) than those of morphotype A (D up to 9.5 mm) with a moderate overlap of values. The range of variation of nodal values in morphotype A widely overlaps those in morphotype B. A substantial difference between H/D of nodals and that of internodals is observed for 4<D<5.7 mm in morphotype B and for 6<D<7.2 mm in morphotype A. It is more restricted in the largest columnals in morphotype A than in morphotype B. All columnals of morphotype A have D>6 mm, which indicates the absence of juvenile individuals. The values of intermodal H/D mostly <0.2 suggest columnals from the proximal stalk. The IN/N ratio is 4 to 5 in both morphotypes although one pluricolumnal of morphotype B displays 10 internodals (Table 2).

TABLE 4. Variation of main quantitative columnal characters in morphotype A from Picabrier. Morphotype A is attributed to ?*Endoxocrinus gastaldii* (see Systematic revision). Values in mm, except for ratios, (*): mode.

	Characters	D	H	H/D	Cr/ZP
IN	Measures	48	48	48	46
	Mean/mode	7.77	1.15	0.15	18*
	Minimum	6.00	0.60	0.08	15
	Maximum	9.45	1.74	0.24	21
N	Measures	17	17	17	17
	Mean/mode	7.83	1.85	0.24	18*
	Minimum	5.98	1.19	0.15	16
	Maximum	9.57	2.15	0.35	20

TABLE 5. Variation of main quantitative columnal characters in morphotype B from Picabrier. Morphotype B is attributed to *Metacrinus berthei* (see Systematic revision). (*): mode. Values in mm, except for ratios.

	Characters	D	H	H/D	Cr/ZP
IN	Measures	72	72	72	69
	Mean	5.77	1.07	0.19	15*
	Minimum	2.71	0.73	0.12	9
	Maximum	7.17	1.67	0.41	19
N	Measures	21	21	21	19
	Mean	5.97	1.71	0.29	15-16*
	Minimum	4.66	1.34	0.22	12
	Maximum	7.00	2.13	0.37	18

In the fauna from the Palais des Papes in Avignon (Figs. 4-5, Table 6), only two pluricolumnals (one of them with 5 internodals) and three isolated internodals of morphotype A were identified corresponding to <1.5% of the total number of columnals. These internodals

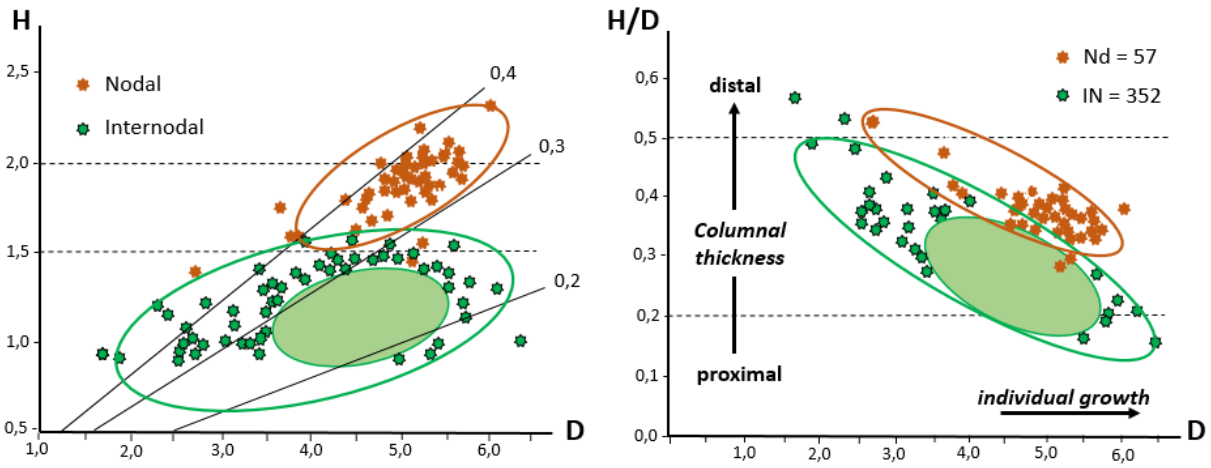

FIGURE 4: Variation in the general shape and size of the isocrinid columnals of morphotype C from the Palais des Papes in Avignon. Morphotype C is attributed to *Metacrinus berthei* (see text). See Fig. 3 for abbreviations. Values in mm, except for ratios and number of columnals (Nd and IN).

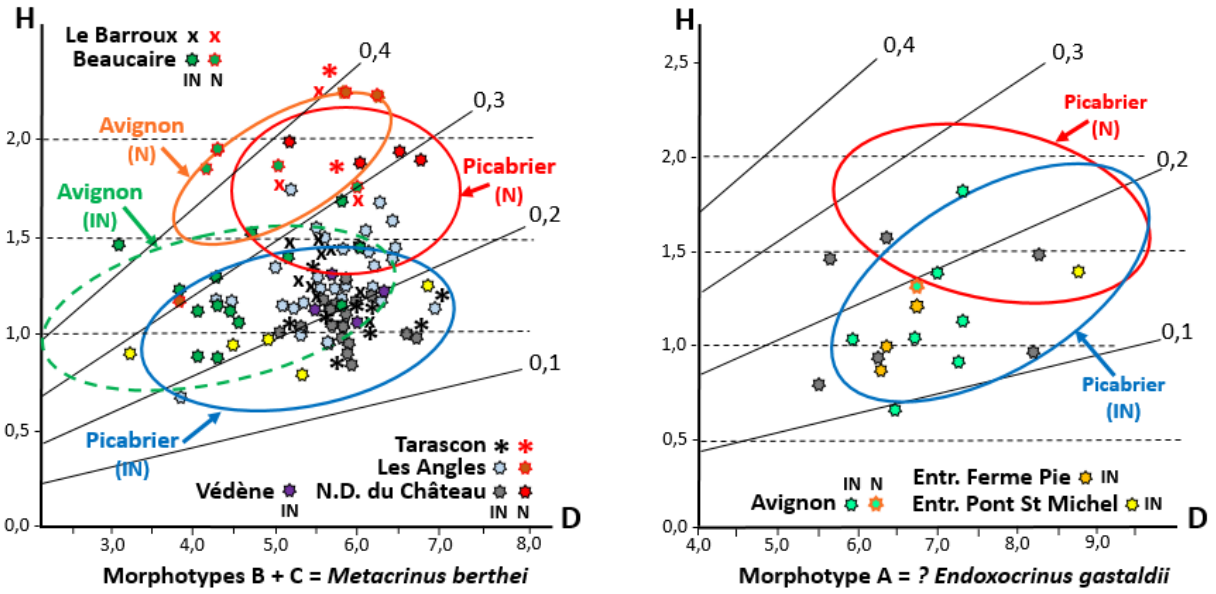

FIGURE 5: Variation in the general shape and size of isocrinid columnals of the two main isocrinid species from the different sites in the Rhône-Provence Bay. Entr.: Entrechaux, IN: internodals, N: nodals. The envelopes of points corresponding to the sites Picabrier and Avignon (Palais des Papes) are only figured (see Figs. 3 and 4), except for *E. gastaldii* from Avignon. Values in mm, except for ratios H/D.

fit into the Picabrier variation field as well as the single proximal nodal (Fig. 5 right). The other columnals and pluricolumnals belong to morphotype C (Fig. 4). A maximum of 9 successive

internodals in a pluricolumnal was observed while the IN/N ratio is nearly 15. The H/D is mostly >0.2, and the difference of H/D values between nodal and internodal remains stable (Fig. 4 right). Numerous juveniles (D<3.0 mm) are present. Intermodal sizes display a mode at 4.5<D<5 mm and a maximum diameter <6.5 mm. The distribution of the internodals of morphotype C from Avignon is very close to that of morphotype B of Picabrier while it is more distinct for the nodals. Qualitative morphological details (such as the convexity of the sides of the pentagonal cross section and the development of ornamentation) vary independently to quantitative characters. Intermediary features with morphotype B are frequent.

TABLE 6. Variation of main columnal quantitative characters in morphotype C from Avignon and Beaucaire. Morphotype C is attributed to *Metacrinus berthei* (See Systematic revision). Av: Avignon, Beau: Beaucaire. Values in mm, except for ratios.

Characters		**Diameter (D)**		**Height (H)**		**H/D**		**Cr/zp**	
Sites		**Av**	**Beau**	**Av**	**Beau**	**Av**	**Beau**	**Av**	**Beau**
IN	Measures	352	14	353	14	353	14	202	5
	Mean/Mode	4.58	4.54	1.18	1.25	0.26	0.29	13	12
	Minimum	1.67	3.03	0.89	0.88	0.16	0.2	5	7
	Maximum	6.04	5.98	1.57	1.71	0.56	0.48	16	14
N	Measures	57	4	57	4	57	4	56	1
	Mean	5.00	4.84	1.90	1.84	0.38	0.39	13	12
	Minimum	2.67	4.11	1.40	1.69	0.28	0.28	9	12
	Maximum	6.02	5.98	2.69	1.95	0.54	0.46	16	12

For the other sites, details on the values and variation of the quantitative characters studied are provided in the Systematic Revision. Specimens of morphotype A from Notre-Dame du Château, and Entrechaux belong to individuals of size mode (8.0<D<8.5 mm) less than or equal to the size mode in Picabrier. They fall within the same fields of variation (Fig. 5 right). Pentagonal columnals from Beaucaire tend to fit into the fields of variation of morphotype C in Avignon. They represent an extreme variation, very regularly pentagonal, with flat, smooth, unornamented lateral faces and nodals of H/D>0.4. Those from the other sites tend to fit into the field of variation of morphotype B from Picabrier (Fig. 5 left). At Notre-Dame du Château, the maximum number of successive internodals in a pluricolumnal is 10 for morphotype A and 14 for morphotype B with a ratio IN/N 19-20. At Les Angles, a distal stalk fragment of morphotype C (syntype 1 of *Metacrinus berthei*) bears a complete noditaxis of 19 internodals with a moderately variable height.

- ***Discussion***

Knowledge of the morphological changes throughout individual growth in extant populations (Roux 1976; Améziane-Cominardi 1991; David *et al.* 2006) allows the interpretation of the graphs (Figs. 3-5) and the different symplexial patterns (Roux 1977, 1981). The external morphology of morphotype A differs from that of morphotypes B and C only in having a markedly star shape and a larger size. These three morphotypes have an external convergent

feature except the star or pentagonal shape: they keep noditaxes with internodals of variable size all along the stalk. This is the main cause of the relatively wide range of variation in the quantitative characters studied.

As for the extant isocrinid stalks, the characters of symplexies distinguish genera or subfamilies and those of cryptosymplexies differentiate species within the same genus. From this point of view, morphotype A with open petaloid zones is attributed to Diplocrininae, while morphotypes B and C with close lanceolate petaloid zones and usually interpetaloid grooves belong to Metacrininae. Are morphotypes B and C two distinct species or intraspecific variations depending on various ecological conditions at different localities? As well-preserved cryptosymplexies are absent in several sites, only the analysis of external morphology can solve this taxonomic problem.

There is substantial overlap between the fields of variation of morphotypes B and C from the different sites (Fig. 5). A substantial part of the differences between the two morphotypes is related to the size of the individuals. The Picabrier sample (morphotype B) could correspond to stable mature populations lacking in juveniles, with a mode at 5.5<D<6 mm and a maximum diameter at ~7 mm. The Avignon sample (morphotype C) includes many juveniles (D<3.0 mm), with a mode at 4.5<D<5 mm and largest individuals not reaching the maximum diameter in Picabrier. In all sites, the maximum number of successive internodals per pluricolumnal is > 10 according to the number of internodals per noditaxis, which is estimated via IN/N ratio >14 except in Picabrier (Table 2). In this former site, IN/N 4-5 indicates a strong deficit in internodals which is also observed in the morphotype A. This suggests a hydrodynamical selection to the detriment of the thinnest internodals rather than a different morphotype. Consequently, we consider that morphotypes B and C belong to the same species having an external morphology highly variable, but without evidence of polymorphism.

We conclude that isocrinid columnals and pluricolumnals from the Rhodanian basin here examined belong to three species (see details below in the Systematic revision). Morphotype A is attributed to ?*Endoxocrinus gastaldii* (Michelotti, 1847) in the subfamily Diplocrininae (Fig. 6), morphotype B+C with variable external morphology to *Metacrinus berthei* (Nicolas, 1897) in the subfamily Metacrininae (Figs. 10-13C), and morphotype D to *Papacrinus avignonensis* **n. gen., n. sp.** in the subfamily Balanocrininae (Fig. 13D-F).

Taphonomy, Paleoecology and Paleobathymetry

- ***Taphonomy***

Burdigalian sites with stalked crinoids are associated with underwater reliefs that can channel water flows. The sloping bottoms and currents facilitate ossicles transport and burial more or less far from the living environment. The presence of different types of ossicles (columnals, brachials and cirrals) indicates the proximity of the biotope and the absence of important selection linked to hydrodynamics. The site in Avignon is the only one with abundant brachials and cirrals associated with isocrinid columnals (Table 3). At Picabrier, the apparent deficit in internodals (see above) suggests an important hydrodynamic selection. The thinnest isolated internodals are more fragile and easily displaced, broken or deformed. The lightness of these ossicles allows them to be transported without conspicuous attrition. During a prolonged stay

on the sea bottom or in the superficial part of the sediment, biocorrosion weakens the external layer of the ossicles, which partially disappears at the slightest displacement or reworking, blunting the joints and angles (Améziane-Cominardi and Roux 1987; Merle and Roux 2018). Around Entrechaux and at Vedene, there is a mixture of well-preserved and worn ossicles. The ossicles of Rhizocrinidae are only well-preserved in Avignon.

Some taphonomic processes are highlighted by the proportion of more or less long pluricolumnals and isolated columnals. A 60 mm long distal stalk fragment including a complete noditaxis bearing proximal cirrus fragments, and noditaxis fragments terminated by their distal nodal or proximal infranodal, have been found only in Les Angles (Fig. 7). Such elements were rapidly buried *in situ*. In the other sites, pluricolumnals of >4 columnals are more often delimited by symplexies (Figs. 6A-C and 8C, E, K, 11A-B) than by cryptosymplexies (Figs. 8J, 11C). In Avignon, there are 86% of isolated columnals, 10% of pluricolumnals with 2 columnals (Franzin 2007) and a single pluricolumnal with >5 columnals (9 IN + 1 N). When autotomy at the level of infranodal cryptosymplexies is the major factor in post-mortem fractionation of isocrinid stalks, complete noditaxes or fragments of noditaxes terminated by their proximal infranodal or by their distal nodal are the most frequent pluricolumnals (Baumiller et al. 1995). This is not the case in most of the Miocene deposits studied here where the relatively rapid ligament decay before burial allows more frequent dissociation at the level of symplexies. No direct evidence of predation was observed on the ossicles. A few rare encrusting bryozoans or worms were noted on distal pluricolumnals. These are likely epibionts rather than evidence of prolonged residence on the sediment surface.

- ***Paleoecology***

The relationships between the stalk morphology of the extant isocrinids and ecological niches have been studied in the western tropical Atlantic (David 1998; David *et al.* 2006). The traits that best differentiate the morphotypes are the number of internodals per noditaxis (IN/Ndx) and stalk length. Most sites on moderately sloping and mixed (rocky and soft sediment) sea bottoms are colonized by two main morphotypes either belonging to the same species (intraspecific polymorphism allowing the distinction of two ecophenotypic subspecies) or corresponding to different taxa: one with a short stalk (IN/Ndx mode 5 to 8, maximum 12) with the filtering crown just above the sea bottom, the other with a long stalk (IN/Ndx mode 12 to 13, maximum 16 or more) raising its crown significantly higher in a more regular laminar water flow of greater velocity. The species of the genus *Cenocrinus* which reaches the largest size lives on various irregular substrates with a predominance of rocks. It often settles at the top of boulders to filter laminar currents. Its IN/Ndx is highly variable, showing a mode at 16-17 with a maximum at 22 (David 1998).

In the Miocene material studied herein, only two cases of complete noditaxes were observed: one of morphotype C at Beaucaire with 13 internodals and 13.3 mm long (D: 4.1 mm), the other of morphotype B at Les Angles with 19 internodals and 30.5 mm long (D: 6.3 mm). The longest pluricolumnal has 10 internodals (morphotype A) or 14 internodals (morphotype B) at Notre-Dame du Château and 10 internodals at Tarascon. The overall IN/N ratio in a site with little or no hydrodynamic selection of the ossicles is nearly equivalent to the average IN/Ndx within a population (Table 2). It is 14 to16, in morphotype C from Avignon, and at Le Barroux (morphotype intermediate between B and C) it could reach 21. *Metacrinus*

berthei seems to be an opportunistic species, which colonized 11 sites out of 14 in various environments (shoals, slopes, hard ground or irregular rocky substrates). It is the dominant species of the fossil assemblage in Avignon. Its variable IN/Ndx, generally >10 and sometimes exceeding 15-16, allowed it to filter the currents at different heights well above the sea bottom. The lowest layer of the sea water column near the sea floor was occupied only by small (young) *M. berthei* or small specimens or other shorter-stalked crinoids such as *Papacrinus avignonensis* n. gen. n. sp., and *Paraconocrinus rhodanicus* n. sp. on marly substrate. The wide range of variation of main quantitative characters in *M. berthei* (Fig. 6), especially at Avignon and Picabrier, is rather related to substrate heterogeneity in shoal environment inducing various ecological niches than to unstable conditions. Morphotype A, attributed to ?*Endoxocrinus gastaldii*, is larger than *M. berthei* and has a less variable stalk morphology. It is less frequent (5 sites out of 14) and an accessory species of the fossil assemblages except in Picabrier. It is always associated with *M. berthei*, but there is no evidence that the two species form a pair of short-stalked/long-stalked ecophenotypes. Data on ?*Endoxocrinus gastaldii* are insufficient to specify its ecological adaptive strategy. Its larger size and the absence of columnals from young individuals suggests that it may be a less opportunistic species than *M. berthei*, and may filter higher in the sea water column.

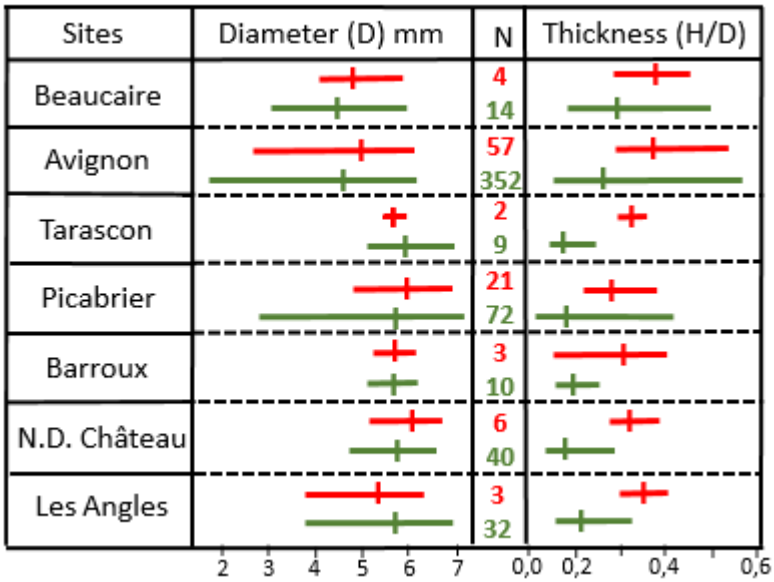

FIGURE 6: Variation in quantitative characters of *Metacrinus berthei* columnals in the main sites studied. N: number of measures, horizontal bar: variation range, vertical bar: mean, in red: nodals, in green: internodals.

In Avignon the fossil assemblage is dominated by the abundant *Metacrinus berthei* which displays the greatest taxonomic diversity of stalked crinoids with four species and genera: three isocrinids, each belonging to a different subfamily, and one rhizocrinid. Such richness indicates an environment particularly favorable to the settlement of a stalked crinoid community.

- ***Paleobathymetry***

Based on the discoveries made during the first major oceanographic cruises such as those described in the Challenger reports (Carpenter 1884), the question of a reappraisal of the paleo-bathymetry in the Miocene Rhodanian basin was raised at the end of the 19th century (Sinard 1892). Would the presence of isocrinids indicate a greater depth of the Miocene sea floor than commonly accepted? Pellat (1897) expressed his disagreement. Nicolas (1897, 1898) was in favor and gave an additional argument: the coocurrence at Pierre Longue of *Pentacrinus miocenicus* and *Pleurotomaria*, a gastropod genus currently living between 120 and 240 m.

More recently, Pouyet (1984) considered that the depth should not exceed 100 to 150 m in the blue marls of Faucon, although Cappetta (in Pouyet *et al.* 1984) had identified many genera of selacians currently living at depths between 200 and 500 m. Making the balance on the paleodepths deduced from Langhian selacian found in the Rhodanian basin, Vialle *et al.* (2011) evaluate water depths between 200 and 300 m and point out that they are located near incised valleys, the excavation of which preceded the Burdigalo-Langhian transgression according to Besson (2005). The same locations were here sampled for stalked crinoids (see above). As the mode of sustentation of stalked crinoids is incompatible with turbulences due to storm waves, their hydrodynamic tolerance threshold is situated around a depth of 100-110 m (Roux 1987; Améziane and Roux 1997). In the Western Pacific, this is the minimum depth where monospecific populations of *Metacrinus* live, sometimes associated with the shallowest extant species belonging to *Democrinus* (Rhizocrinidae), a genus close to *Paraconocrinus*.

Within the genus *Metacrinus*, the shallowest extant species (100-200 m) have the highest values of IN/Ndx and morphological variation range (Bourseau and Roux 1989). In the western tropical Atlantic, *Endoxocrinus* lives at depths >150 m (David *et al.* 2006) and recently *Cenocrinus* has been exceptionally recorded at a depth of 140 m (Etnoyer *et al.* 2019; C.G. Messing 2016). An isocrinid generic diversity such as in Avignon suggests a depth >200 m. A size such as that attained by ?*Endoxocrinus gastaldii* at Picabrier is observed in the western Pacific at depths of 150-250 m. These data lead us to consider that (1) *M. berthei* must have been able to live close to the hydrodynamic tolerance threshold of the stalked crinoids (100-110 m) near the top of the shallowest shoals such as that of Les Angles or deeper, (2) the presence of the large ?*E. gastaldii* indicates a depth equal to or greater than 150 m, and (3) the Avignon and Picabrier sites could be the deepest (200-250 m). These estimated values are those of the biotopes. They could be greater for the depositional environment in the case of gravity transport on a slope.

Conclusion

Although composed of dissociated ossicles, the sites with stalked crinoids of the Miocene Rhodanian basin yield sufficiently abundant and well-preserved material to provide useful taxonomic and paleo-environmental information through comparison with their extant representatives. Similar studies on stalked crinoids from northern Italy and central Europe would significantly improve our knowledge of the Miocene fauna, and its relationship with the extant fauna. The confirmation of the presence of the genus *Metacrinus* in the western Mediterranean area shows that the Metacrininae have not always been confined to the Indo-

Pacific province since their appearance in the Paleocene. It should be possible to find them in the Miocene fauna of the Paratethys. In the current state of knowledge, they do not appear to have reached the Atlantic. However, Astibia et al. (2020) had attributed to the genus *Metacrinus* a few pluricolumnals from the Bartonian of the southwestern Pyrenean basin, which is connected with the northeastern Atlantic area, but this record needs confirmation. The Metacrininae remained in the western Mediterranean until the latest Miocene (Roux and Montenat 1977). The genus *Isselicrinus*, which appeared in the Upper Cretaceous and was distributed worldwide during the Eocene, was still present in the Miocene from Japan to the Caribbean via Crimea and northern Italy (Klikushin 1992; Donovan and Veltkamp 2001; Oji 1990). It is unknown in the extant crinoid fauna. It usually lived on epibathyal muddy sea floors (Roux et al. 2007). The fact that it has not been collected in the Rhodanian basin is probably related to the lack of sufficiently deep environments. Stalked crinoids of Paratethysian origin did not survive the Messinian crisis and the Alpine belt suture. The diplocrinine species *Endoxocrinus wywillethomsoni* Jeffreys, 1870 discovered in the Late Pliocene - Pleistocene of the Strait of Messina came from the bathyal northeastern Atlantic where it lives now (Barrier *et al.* 1989). The same could be true for the two worn diplocrinine-like IN described as *Pentacrinus penezi* Granier, 1966 and associated with the Lower Pliocene (Zanclean) bathyal fauna of the Régalon Gorge in the Petit Luberon (Granier 1966, Fig. 3-2).

In the deepest part of the Miocene Rhodanian basin, biotopes between 100 to 250 m or more were inhabited by a stalked crinoid fauna filtering currents channeled by paleo-reliefs and deeply incised valleys that offered a wide variety of ecological niches on rocky and soft sediment substrates. The fossil assemblage from Avignon is particularly remarkable for its high taxonomic diversity, the abundance of the dominant species *Metacrinus berthei* and the presence of different types of ossicles that indicate burial near the biotopes.

Systematic revision

Order Isocrinida Sieverts-Doreck, 1952

Remarks. The classification of Isocrinida retained by Hess (2011) is based on plesiomorphic characters without phylogenetic significance (Roux *et al.* 2009; Améziane *et al.* 2021). Pending a new classification based on both morphology and molecular data with a redefinition of the different families of Isocrinida (Améziane *et al.* in prep.), we group the subfamilies here cited in the single family Isocrinidae. Roux (1977) has shown that the characters of stalk symplexies differentiated the extant genera. Species belonging to the same genus differ in having peculiar characters of infranodal cryptosymplexies (see also Roux 1981; David *et al.* 2006). Changes during columnal ontogeny such as increase in number of crenulae per petaloid zone, closure of petaloid zones and closure of axial interpetaloid furrow in symplexy should be taken into account.

Family Isocrinidae Gislén, 1924

Subfamily Diplocrininae Roux, 1981

Remarks. *Teliocrinus ojii* (Roux *et al.*, 2009) is the only known undisputed fossil Diplocrininae with its crown preserved found at base of the Middle Miocene in Japan (Oji 1990). The Diplocrininae are mainly distinguished by the substantial reduction in number of brachials per brachitaxis and distal stalk symplexies with petaloid zones that remain open (David *et al.* 2006). This last character being paedomorphic, the attribution to the genus *Endoxocrinus* based only on columnals and pluricolumnals remains in open taxonomy because it is only a parsimonious hypothesis, which remains to be confirmed by the discovery of brachials or proximal arm fragments.

Genus *Endoxocrinus* A.H. Clark, 1908

Type-species. *Encrinus parrae* Gervais, 1835. Recent.

?*Endoxocrinus gastaldii* (Michelotti, 1847)
Figs. 3, 5 (morphotype A), 7, Table 4

Synonymy. *Pentacrinus gastaldii* Michelotti, 1847: 59, pl. 16, fig. 2; *Pentacrinus gastaldi* Locard, 1877: 207-209; *Pentacrinus miocenicus* de Loriol, 1897: 127-129, figs. 17-18; *Pentacrinus gastaldii* Manzoni, 1878: 1-2, fig. 1 ; Noelli, 1900: 24-28, figs. 1-32 pars; Albus, 1931: 283-285, pl. 10 (fig. 7); *Isocrinus gastaldii* Sieverts-Doreck, 1933:165 ; Biese and Sieverts-Doreck, 1939: 37-38; Sandor, 1983: 171-173, figs. 1-3; *Neocrinus* aff. *gastaldii* Roux and Montenat, 1977: 408-409, pl. 16 (figs. 1-2); *Metacrinus gastaldii* Klikushin, 1982: 305; 1992: 128 pars; *Pentacrinus gastaldii* Manni, 2015: 59, fig. 22 pars.

Material examined. Avignon (2 Plc including 1 infraN, 3 isolated IN), Picabrier (14 Plc, 36 isolated IN, 17 isolated N), Entrechaux Ferme Pie (1 Plc + 1 IN), Entrechaux Pont Saint-Michel (1 IN), Notre-Dame du Château (3 Plc).

Emended diagnosis. Large species with a columnal diameter that can exceed 9 mm, columnals usually strongly star-shaped, tending to be more pentagonal in certain distal nodotaxes; maximum number of successive internodals observed 11 ; symplexies with open petaloid zones even in large distal nodotaxes, ligamentary areas fusiform and narrow, always at least four times longer than wide, number of crenulae per petaloid zone usually greater than 16 (mode 18), up to 21, median crenulae longer than the others and may form chevrons with those of adjacent petaloid zones in distal columnals, no furrow separating the petaloid zones except in the most proximal columnals; nodal with cirral insertions substantially wider than high and always intersecting the distal facet border, sometimes also proximal one, cryptosymplexies with more marked symmorphy in the interpetaloid zones, presence of fine interpetaloid grooves and marginal crenulations of variable extension; lateral faces of columnals smooth and convex, without ornamentation. Crown unknown.

Description. Columnals markedly star-shaped, side faces convex; symplexies of open ZP with the areola usually narrow up to 7 times longer than wide, Cr/PZ usually from 17 to 19 and reaching 21 in largest Co, inner crenularium poorly differentiated or flat. Proximal Co highly starred (Fig. 7A, D-E), symplexy with regularly arranged short Cr leaving free most of IPZ (Fig. 7D-E). More distal Co less starry (Fig. 7B) rarely subpentagonal (Fig. 7C) with Cr of

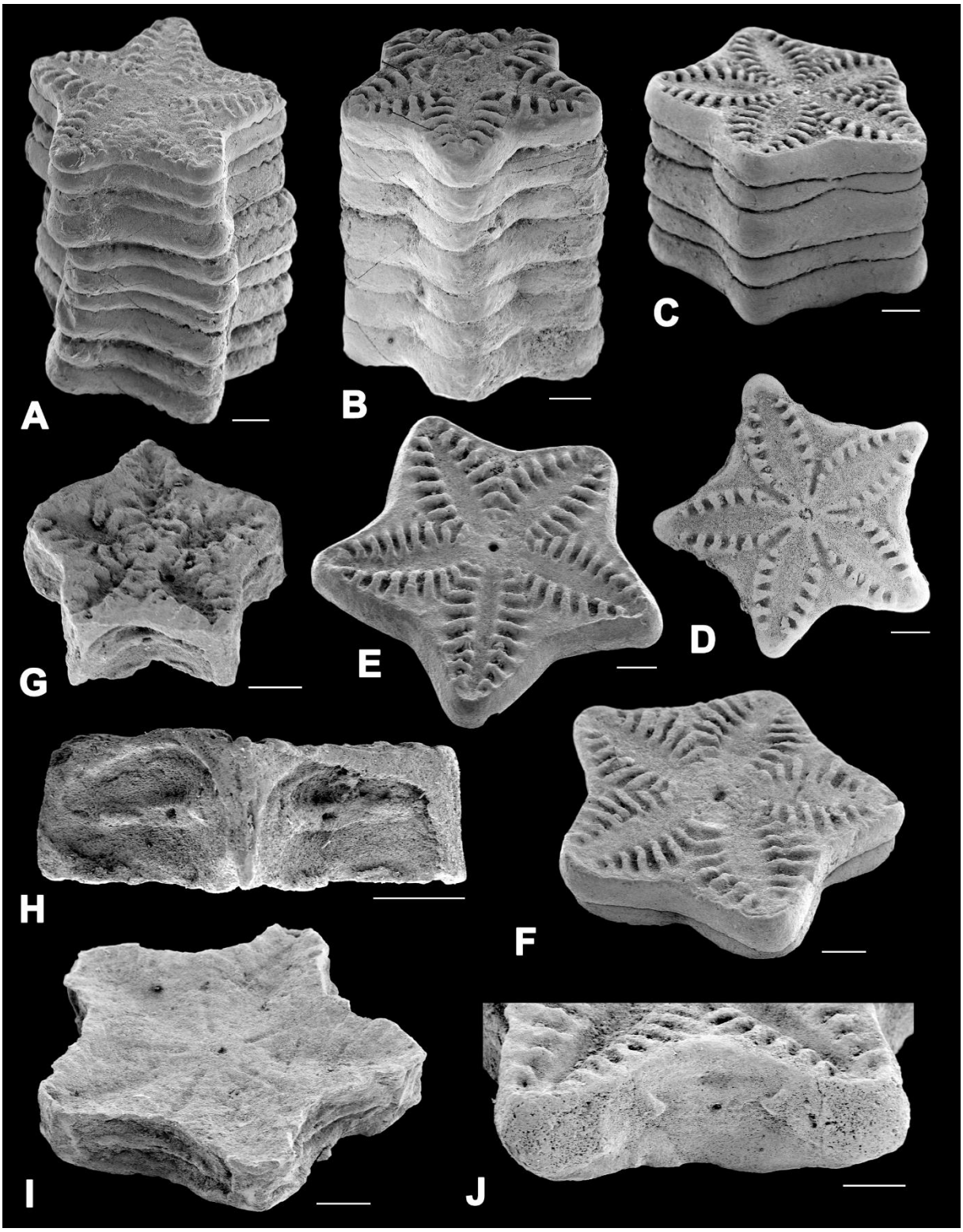

FIGURE 7: Columnals and pluricolumùnals of ?*Endoxocrinus gastaldii*. A-B: from Notre-Dame du Château, A: proximal pluricolumnal (cotype of *Pentacrinus miocenicus* de Loriol, 1897, fig. 18) (MASRP 2020.5012), B: more distal subpentagonal pluricolumnal (MASRP 2020.5022); C-D: from Palais des Papes in Avignon (MHNL 20.062709), C: distal pluricolumnal, D: nodal from proximalmost stalk, proximal symplexial facet; E-J: from Picabrier (MHNL 20.062711), E: internodal from proximal middle stalk, F: internodal from distal middle stalk, G-H: nodal from a young individual, G: oblique proximal view, H: side view showing cirrus sockets, I-J: nodals from large specimens, I: oblique distal view showing the cryptosymplexial facet, J: oblique proximal view showing a cirrus socket. Scale bar equals 1 mm.

median crenularium entirely covering IPZ and forming chevrons (Fig. 7B, F). Ndx with Co of highly variable thickness even distally (Fig. 7C); N markedly thicker than IN, especially in young individuals (Fig. 7G), this difference decreasing with growth (Fig. 5 right), distal facet (cryptosymplexy) more or less regularly concave, about 8 small marginal cr per IPZ (Fig. 7 I); cirrus socket well-developed at least twice as wide as high and usually intersecting distal facet border (Fig. 7H-I), sometimes also on the proximal one (Fig. 7J), low fulcral ridge limited by two triangular culminae often moderately developed. At Picabrier (see Table 4 for quantitative characters): symplexies with 18 to 20 Cr/PZ (60%), 14 or 15 for smallest Co; distal nodal facets and symplexial ligament areas often excessively concave because of pyrite oxidation corrosion; cryptosymplexies rarely well preserved, IPZ usually in relief with a more or less marked axial groove, stalk canal inconspicuous probably obstructed by a dense secondary stereom (Fig. 7I). In other sites, only a small number of specimens, but often with Plc less fragmented (Fig. 7A-C) than in Picabrier. One of them, from Notre-Dame du Château (de Loriol 1897, Fig. 18) is composed of 10 IN without infraN indicating Ndx of at least 11 IN (Fig. 7A).

Remarks. Manni (2015: 59, fig. 22) considered the single specimen (Plc of 3 IN) from the Middle Miocene near Turin used by Michelotti (1847) to describe *Pentacrinus gastaldii* as lost. He proposed that four internodals belonging to the Michelotti's collection (Paleontological Museum of "Sapienza" in University of Rome) constitute the type series. Three of these internodals are star-shaped and correspond well to the original figure. The fourth rounded pentagonal with wide and closed petaloid zone is different. The type-series must be reduced to three columnals which could have the value of neo-syntypes if accompanied by a precise description. The best preserved specimen of ?*E. gastaldii* is a markedly star-shaped stalk, 150 mm long, with the basal circlet at proximal end, that was described by Manzoni (1878). This remarkable specimen comes from Montese molasse (Middle Miocene) near Modena.

Among the four syntypes of *Pentacrinus miocenicus* from Notre-Dame du Château, two belong to ?*E. gastaldii* (Loriol 1897, figs. 17 and 18). Locard (1877) reported one star-shaped pluricolumnal of ?*E. gastaldii*, D 9 mm, from Bonifacio (South Corsica). This specimen, housed in the Péron's collection (MNHN.S.11062), most probably comes from the Lower Langhian (André *et al.* 2011). Cooke (1896) identified ?*E. gastaldii* in the Miocene Globigerine marls of Malta. We have examined several columnals from Malta (MNHN.F.B.33193) belonging to the d'Orbigny's collection (no. 11215): *?E. gastaldii* is associated with *M. berthei*, the two species having morphologies similar to those observed at Picabrier. Since de Loriol (1897) and Noelli (1900), many authors (including Klikushin 1992) have confused the species *berthei*, *gastaldii* and *miocenicus*.

Occurrence in southeastern France. Avignon (Palais des Papes), Caumont-sur-Durance (Picabrier), Entrechaux (Pont Saint-Michel), Entrechaux (Ferme Pie), Saint-Etienne du Grès (Notre-Dame du Château). Late Burdigalian-Early Langhian.

Subfamily Metacrininae Klikushin, 1977

Remarks. Metacrininae differ from all other Isocrinida in having more than 2 IBr with IBr2 bearing the first pinnule, and a muscular synarthry at IIBr1+2. The primibrachitaxis has a synostose at IBr4+5 when the number of IBr is >4. Their stalk symplexies display closed ZP and axial grooves in ZIP (Roux 1977, 1981). Two genera with a synostosis at IBr1+2 are distinguished in extant Metacrininae (Améziane-Cominardi 1991, Bourseau and Roux 1989, Hess 2011, Roux 1981): *Saracrinus* with usually 3-6 IBr (mode 4) and <10 IIBr, and *Metacrinus* having usually >4 IBr (mode 7) and >10 IIBr. The Eocene species *Metacrinus fossilis* Rasmussen, 1980 and *Eometacrinus australis* Baumiller and Gazdzicki, 1996 have a proximal crown with 5 IBr and 9-10 IIBr. Such an arm pattern is intermediate between *Saracrinus* and *Metacrinus*. *Eometacrinus* differs in having an axial ligamentary synarthry at IBr1+2. *Metacrinus seymouriensis* Rasmussen, 1980 is only known from pluricolumnals found in the Maastrichtian.

Genus *Metacrinus* Carpenter, 1882

Type species. *Metacrinus wyvillii* Carpenter, 1884. Recent.

***Metacrinus berthei* (Nicolas, 1897)**
Figs. 4-5 (morphotype B), 6, 8-12A-C; Tables 5-7

Synonymy. *Pentacrinus berthei* Nicolas, 1897: 79-80, fig. 12; *Pentacrinus miocenicus* de Loriol, 1897: 127-129 pars., figs. 15-16; *Pentacrinus berthei* Nicolas, 1898: 396-398, fig. 1; *Pentacrinus berthae* Lambert, 1899: 122; *Pentacrinus berthei* Biese and Sieverts-Doreck, 1939: 45.

Type material. The original description (Nicolas 1897) is based on a type series comprising 1 distal stalk fragment (Fig. 8A-B), 2Plc (Fig. 8E-F) and 2 isolated IN (Fig. 8C-D). There was no indication of the original collector. The Nicolas collection housed at UCBL-FSL comprises 2/3 of the stalk fragment (UCBL-FSL 19.099-1) (Fig. 8B) and 1 Plc (UCBL-FSL 19.099-2) (Fig. 8F). In the Châtelet collection housed at the Requien Museum in Avignon, we found the proximal third of the stalk fragment (MRA 3.009.192) (Fig. 7A) and the two isolated IN (MRA 3.009.194.1-2). The stalk fragment (Fig. 8A+B) is here designated as syntype 1, the Plc (Fig. 8F) as syntype 2, the first isolated IN (Fig. 8C) as syntype 3, and the second (Figs. 8D, 9A) as syntype 4. The syntype 5 (Fig. 8E) can be considered lost.

Etymology. Nicolas dedicated this species to Berthe Sinard who firstly suggested that the Miocene environment at Les Angles was deeper than previously interpreted (Sinard 1892).

Material examined. Les Angles (10 Plc, 21 isolated IN, 2 N); Avignon (111 Plc, 613 isolated IN, 49 isolated N, numerous Br and Ci), Le Barroux (9 Plc, 1 IN); Beaucaire (4 Plc, 10 isolated IN), Entrechaux Ferme Pie (2 Plc, 25 isolated IN, 1 N), Entrechaux Pont Saint-Michel (1 IN), Notre-Dame du Château (22 Plc, 19 isolated IN, 2 isolated N), Picabrier (15Plc, 106 isolated IN, 17 isolated N), Vedènes (1 Plc, 12 isolated IN, Brs), Tarascon (9 Plc).

Type stratum. Late Burdigalian.

Type-locality. Ancient quarries, Les Angles (Gard).

Emended diagnosis. Pentagonal columnals with often rounded edges, most proximal internodals and nodals slightly star-shaped, frequent inter-articular pores; maximum diameter 6. 7 mm, often very variable height within one nodotaxis even distally, maximum number of internodals per nodotaxis 19, average 16-17; symplexies with closed petaloid zones separated by marked grooves, number of crenulae per petaloid zone 15-16 rarely 17, crenulae of about the same size, ligament areas usually twice as long as wide (often less); nodals with oval cirrus sockets not exceeding their height; cryptosymplexy with regular symmorphy often marked and discrete marginal crenularium, facets without interpetaloid furrow; ornamentation absent or discrete, sometimes small knob or ridge at mid-height giving a more rounded to subcircular columnal section. Primibrachiales in number equal or superior to 6 with large pinnular sockets, IBr1+2 synostosis with aboral marginal crenularium, IBr3+4 synostosis smooth with aboral growth lines.

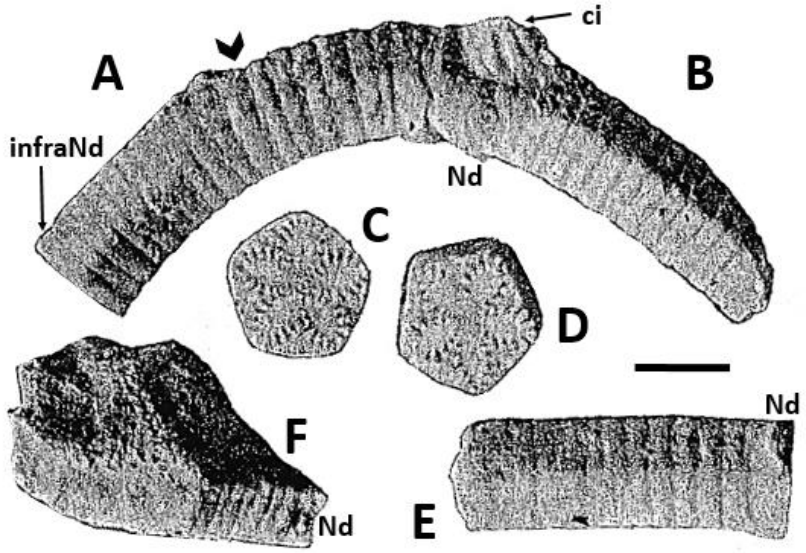

FIGURE 8: Type series of *Metacrinus berthei* from Les Angles (after Nicolas 1898 modified). The arrowhead indicates the break separating in two fragments the syntype 1 (A: fragment MRA 3.009.192; B: fragment UCBL-FSL 19099-1); C-D: isolated internodals, C: syntype 3 (MRA 3.009.194.1), D: syntype 4 (MRA 3.009.194.2); E: syntype 5 considered as lost, F: syntype 2 (UCBL-FSL 19099-2); ci: proximal fragments of cirri (3 to 4 cirrals) connected to the nodal, Nd: nodal. Scale bar equals 5 mm, except in C-D where it equals 4 mm.

Description of syntypes. Distal stalk fragments, IN pentagonal or subpentagonal, N slightly starry. Syntype 1: L 47.4 mm composed of 1 complete Ndx of 19 IN (L 30.5 mm) + 1 incomplete Ndx of 15 IN (Fig. 8A-B), Ndx with marked curvature, no inter-articular pores, proximal end of complete Ndx with smooth, slightly convex infraN facet, N with 4 cirrals connected; internodal D reaching 6.5 mm proximally and decreasing to 6.2 mm at distal end; proximal Ndx with higher IN alternating with slightly lower IN of similar D; nodal H reaching a maximum of 2.2 mm; smaller differences in intermodal H in distal Ndx; smooth and slightly convex columnal side faces. Syntypes 2 and 5: incomplete curved Ndx (8 and 13 IN

respectively) with distal N, similar in morphology to syntype 1, differences in H and D between IN more pronounced in syntype 2 (Fig. 8F). Syntypes 3 and 4 (Fig. 8C-D): IN with the same characters (D 6.1 mm, H/D 0.26, maximum Cr/PZ 17), syntype 4 moderately star-shaped with PZ still slightly open (Fig. 9A).

Other specimens from Les Angles. Plc with at most 7 IN; 60% of symplexies with 16 Cr/PZ, only one case with 17, all PZ closed, internal crenularium poorly differentiated, cryptosymplexy preservation not allowing a detailed description. Quantitative characters including type series in Table 7.

Characters		Diameter (D)		Height (H)		H/D		Cr/PZ	
Sites		LA	NDC	LA	NDC	LA	NDC	LA	NDC
IN	Measures	32	40	31	21	32	21	10	12
	Mean/Mode	5.70	5.84	1.28	1.11	0.23	0.19	16	15
	Minimum	3.80	4.81	0.66	0.84	0.16	0.14	12	12
	Maximum	6.96	6.70	1.74	1.91	0.33	0.29	17	16
N	Measures	3	6	3	5	3	5	-	1
	Mean/Mode	5.30	6.14	1.86	1.92	0.35	0.32	-	16
	Minimum	3.80	5.13	1.15	1.88	0.30	0.28	-	16
	Maximum	6.25	6.71	2.23	1.97	0.38	0.38	-	16

TABLE 7. Variation of main quantitative columnal characters in *Metacrinus* from type localities of *Pentacrinus berthei* Nicolas, 1897 and *P. miocenicus* de Loriol, 1897. LA: Les Angles, NDC: Notre-Dame du Château. Values in mm, except for ratios.

Specimens from Notre-Dame du Château. Quantitative characters including 2 Plc from type series of *Pentacrinus miocenicus* (de Loriol 1897, figs. 15-16) given in Table 7; most Co pentagonal; Plc with maximum of 14 successive IN, ~50% with inter-articular pores more or less marked; most proximal Plc (de Loriol 1897, fig. 16) with columnal H markedly unequal, inter-articular pores widely open, IN star-shaped and a single N without cryptosymplexy despite cirrus sockets being well-developed; another proximal Plc (de Loriol 1897, fig. 15) more distal with IN becoming subpentagonal (Fig. 9B-C); oval cirrus sockets 1.7 times wider than high and tangential to N facet borders (Fig. 9D); all Co with smooth sides. Symplexies most often (62%) with 15-16 Cr/PZ, PZ closed, inner crenularium poorly differentiated. Distal N facet (cryptosymplexy) smooth, slightly concave with 7-8 small marginal Cr/PZ.

Specimens from Avignon. Exceptional variety of Br types preserved (Fig. 10); 9 IBr identified with maximum D 5.17 mm (mean 4.3 mm), muscular synarthries with moderately developed muscle areas and fulcral ridge perpendicular to dorso-ventral axis (Fig. 10C-D), IBr1+2 synostosis with narrow marginal symplexial crenularium (Fig. 10A-B), IBr2 with proximal synostosial facet slightly convex and bearing a large pinnule socket (Fig. 10D-E), IBr4+5 synostosis with aboral growth lines underlined by a thicker stereom (Fig. 10G, J); all Brax with proximal muscular synarthry, fulcral ridges of distal synarthries forming acute angle (Fig. 10H), IBrax with 0.65<H/D<0.87; free IIBr or IIIBr most abundant with oblique fulcral ridge, muscle areas remaining small only in the most proximal IIBr (Fig. 10I) and lengthening

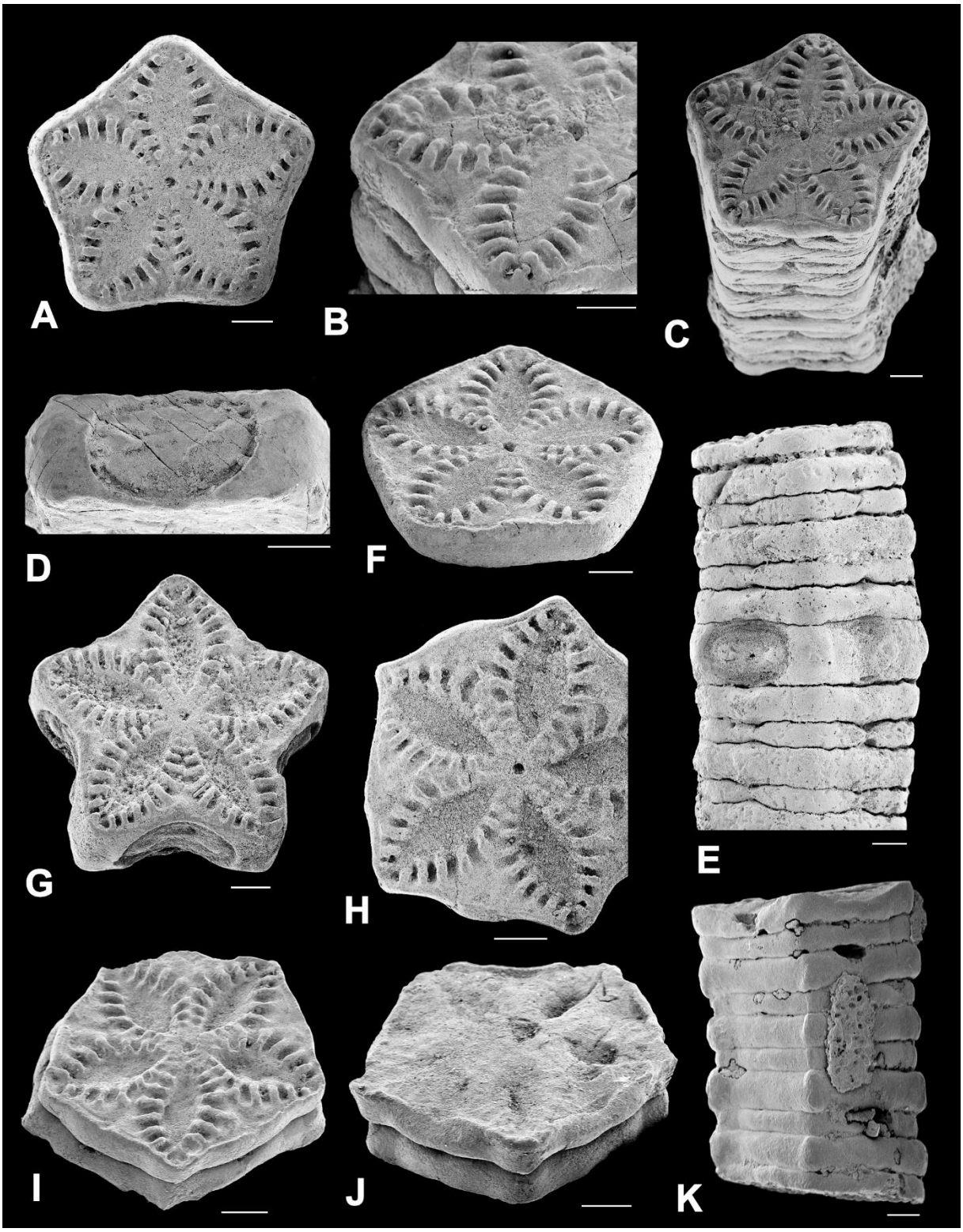

FIGURE 9: Columnals and pluricolumnals of *Metacrinus berthei*. A: from Les Angles, syntype 4, internodal (MRA 3.009.194.2); B-D: from Notre-Dame du Château, B-C: pluricolumnal, cotype of *Pentacrinus miocenicus* de Loriol, 1897, fig. 15 (MASRP 2020.5014); D: nodal, cirrus socket, distal facet below (MASRP 2020.5023a); E: from Le Barroux, pluricolumnal (MHNL 20.062715); F-K: from Picabrier (MHNL 20.062721), F: internodale; G: nodale, H-K: sharp-edged internodals with side faces convex in the center, I-J: proximal end of a noditaxis, I: distal symplexy, J: proximal cryptosymplexy of the infranodal, K: pluricolumnal, side view. Scale bar equals 1 mm.

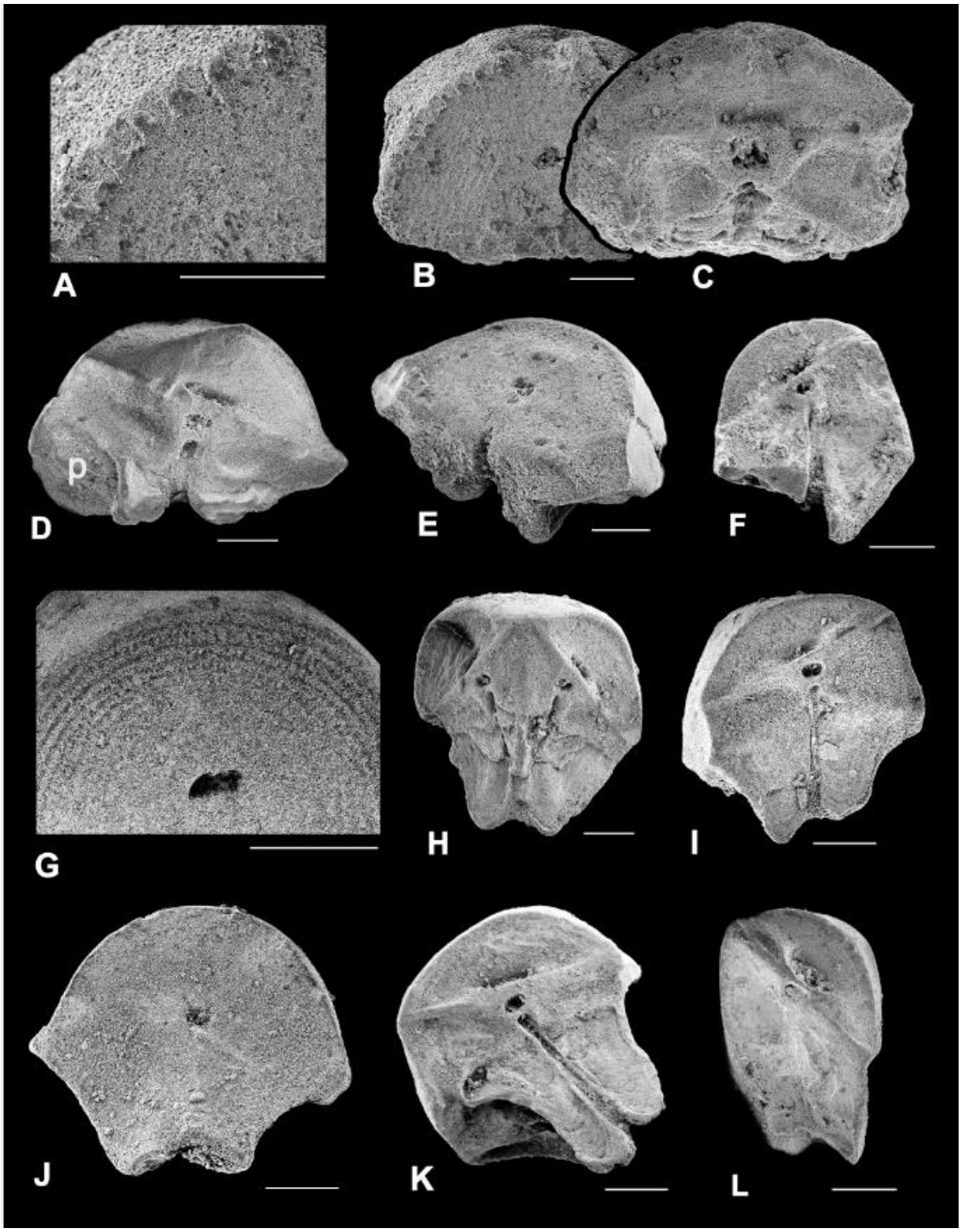

FIGURE 10: Brachials of *Metacrinus berthei* from the Palais des Papes in Avignon (MHNL 20.062717). A-C: IBr1, A-B: distal facet, A: close up of marginal symplexial crenumarium, C: proximal muscular facet; D-E: IBr2, D: oblique distal view showing large pinnule socket (p), E: oblique proximal view showing synostosial facet; F: proximal IIIBr, distal muscular facet; G: IBr4, distal facet with growth lines marked by syzygial stereom; H: IBrax; I: free proximal IIBr, proximal facet; J: IBr5, proximal facet; K: free IBr3, distal facet; L: free IIIBr. Scale bar equals 1 mm.

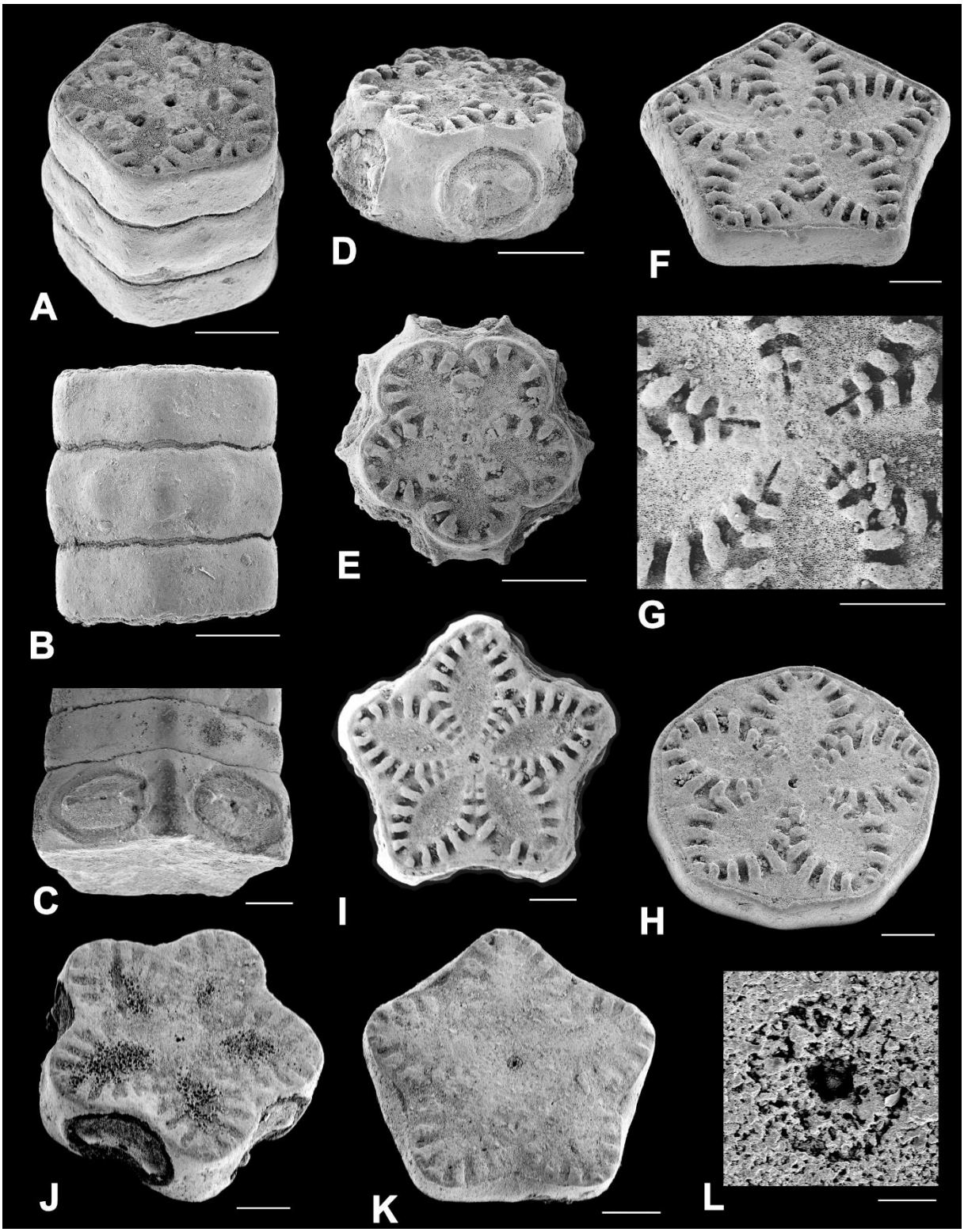

FIGURE 11: Columnals and pluricolumnals of *Metacrinus berthei* from the Palais des Papes in Avignon (MHNL 20.062719). A-B: pluricolumnal from the distal stalk of a young individual, A: oblique view, B: side view; C: distal end of a noditaxis from distal stalk, oblique distal view showing the flat, slightly concave cryptosymplexial facet; D-E: distal nodal from a young individual, D: oblique proximal view, E: proximal symplexial facet; F: pentagonal internodal; G: nodal, proximal symplexial facet, close up of center showing inner crenularium with interpetaloid grooves; H: subcircular internodal; I-J: nodal, I: proximal symplexial facet, J: concave cryptosymplexial facet, oblique distal view; K-L: infranodal, convexe distal cryptosymplexial facet, L: close up of lumen filled in by secondary stereom. Scale bar equals 1 mm, except in L where it equals 0.1 mm.

distally (Fig. 10K-L), pinnule socket on IBr and IIBr remaining large and limiting width of adjacent muscle area on distal Br facet (Fig. 10K), distal IIBr or IIIBr with D<2.5 mm very asymmetrical (Fig. 10L) allowing great flexibility of arm movements. External columnal morphology variable (quantitative characters given in Table 6, Fig. 11); symplexies most often (62%) with 13-14 Cr/PZ; differences in columnal H remaining small in distal Plc from young individuals but increasing during individual growth (Fig. 11A-C); some small Plc with more or less marked bulges on the lateral faces (Fig. 11A-B) becoming less frequent or smooth with growth (Fig. 11F), either widening and making IN subcircular (Fig. 11H) or splitting into granules forming a discrete ornamentation; juvenile Co with H/D>0.5 having subcircular section and symplexies of open PZ (Fig. 12C), N with ligament areas wide (Fig. 11E), cirrus sockets subcircular and occupying only 2/3 of nodal H (Fig. 11D); cirrus sockets becoming more oval with growth (Fig. 11C) and tangential to nodal facet borders (Fig. 13J); 1 N abnormal with only a single cirrus socket; ~50% of symplexial facets having IPZ with narrow and well-marked grooves extended to inner crenularium (Fig. 11G); cryptosymplexies often well preserved, distal N facet (Fig. 11J) moderately concave with a more or less developed marginal crenularium, proximal infraN facet (Fig. 11K) convex with more attenuated marginal crenularium and IPZ without axial groove, axial canal filled by dense secondary stereom with a 5-lobed secondary lumen (Fig. 11L); two Plc having symplexies with four PZ, one of irregular subcircular section (Fig. 12A), the other of quadrangular section (Fig. 12B).

Specimens from other sites. In Beaucaire, Co and Plc belonging to individuals of sizes like in Avignon (see Table 6), one complete Ndx 13.3 mm long with 13 IN; qualitative characters as in Avignon except side faces smooth without ornamentation. In Tarascon, Plc with maximum of 10 successive IN, 5.16<D<7.00 and 0.15<H/D<0.55, ~50% of symplexies with conspicuous furrow at the IPZ axis, external morphology very close to Plc from Les Angles. Among 9 Plc from Le Barroux, 2 with N located at middle length (Fig. 9E), only 1 Plc with 8 successive IN, longest Plc with discrete inter-articular pores and IN of various D and H; symplexies with 13 to 16 Cr/ZP; all pentagonal IN with more or less convex external faces; N with cirrus sockets 1.6 times wider than high with two well-developed culminae (Fig. 9E); 1 N with 4 cirrus sockets. In Picabrier (quantitative characters given in Table 5), symplexies most often (52%) with 15-16 Cr/PZ, two Plc with 10 successive IN; most IN with qualitative characters (Fig. 11F-I) identical to those in Avignon, ~30% of IN with lateral faces more convex in center and more prominent angles (Fig. 11H-J), sometimes forming rougher angles on some Plc (Fig. 11K); cryptosymplexies rarely well-preserved, symmorphy of variable amplitude, patches of denser stereom in place of symplexal crenularium pre-existing articulation ankylosis, ZIP without axial grooves (Fig. 9J). Co from other sites with Co characters entering in main field of variation of those from Picabrier. One IBrax (possibly IBr4ax) with proximal synostosial facet from Vedène.

Remarks. The two species *P. berthei* and *P. miocenicus* were published in the same year of 1897. *Pentacrinus berthei* was based on distal stalk fragments that clearly distinguish it from the species *gastaldii*, one of them with a complete Ndx, while the type-series of *P. miocenicus* contains specimens belonging to two different species. In addition, the two Plcs

belonging to *berthei* figured by de Loriol (1897) are very proximal showing symplexies with specific characters incompletely developed. Therefore, we have given priority to the species whose type-series allows an unambiguous determination. Nicolas (1897, 1898) refers to another species, *Pentacrinus allardi*, found in Avignon molasse and from Beaucaire. Without description or figuration, it remains a nomen nudum. It most probably corresponds to our morphotype C. *Metacrinus mazarronensis* Roux and Montenat, 1977 is very close to *M. berthei*. It differs in having ZIP of cryptosymplexies with axial groove. *Metacrinus berthei* and *M. mazarronensis* share symplexies with characters very close to those of the extant species *M. interruptus* Carpenter, 1884 from the northwestern Pacific (Roux 1981, pl. 6-3 and pl. 7-5).

Occurrence in southeastern France. Avignon (Palais des Papes), Les Angles (ancient quarry), Le Barroux, Beaucaire (ancient quarry), Caumont-sur-Durance (Picabrier), Entrechaux (Pont Saint-Michel), Entrechaux (Ferme Pie, marnes de Faucon), Saint-Etienne du Grès (Notre-Dame du Château), Tarascon, Vedènes, and possibly Villeneuve-lès-Avignon (Pierre Longue) and Saint-Rémy de Provence (= *P. miocenicus* after Joleaud 1907). Late Burdigalian-Early Langhian.

Subfamily Balanocrininae Roux, 1981

***Papacrinus* n. gen.**

Type species. *Papacrinus avignonensis* n. gen., n. sp.

Etymology. From Pape (reference to Palais des Papes in Avignon).

Diagnosis. Stalk symplexies of balanocrine-type, crenularium relif weak with more than 10 crenulae per petaloid zone; thick nodals (H/D 0.3) witout cryptosymplexy at distal articulation; deep, subcircular cirrus sockets much lower than nodal height.

***Papacrinus avignonensis* n. gen., n. sp.**
Fig. 12D-F.

Type material. A single isolated nodal as holotype (MHNL 20.062726).

Etymology. From Avignon (reference to the type locality).

Diagnosis. As in description.

Type stratum. Late Burdigalian.

Type locality. Place du Palais des Papes in Avignon.

Description. Nodal with subcircular to pentalobate facets, H: 1.43 mm, D: 4.65 mm, H/D 0.31, identical symplexy on each facet (Fig. 12D-E) with pyriform to triangular closed petaloid zones, 12 Cr/PZ of variable size including 6 marginal ones, weak crenularium relief, massive protuberance curved proximally prolonging PZ (Fig. 12E); deep, subcircular cirrus sockets much lower than the nodal height, nearly tangent to the distal N facet border, with two strong triangular culminae (Fig. 12F).

Remarks. The symplexial crenularium of *Papacrinus avignonensis* n. gen. n., sp. is of balanocrine-type (see Fig. 2D). Such side protuberances are unknown in extant and fossil Isocrinida. The particular morphology of this nodal justifies the creation of a new genus. Its size and relative thickness suggest that it belongs to the distal stalk of a young individual. The

absence of a cryptosymplexy is usually a paedomorphic character of the proximal nodals without phylogenetic significance. It is retained in the distal stalk of *Proisocrinus*. In this genus, symplexies differ from those of *Papacrinus* n. gen. in having always open PZ; moreover, rudimentary cirri are restricted to proxistele and mid to distal stalk there are only nudinodals (Bourseau *et al.* 1991). Pending new discoveries allowing a more complete description, the symplexial characters lead us to place *Papacrinus* n. gen. provisionally in the subfamily Balanocrininae.

Occurrence. Only known from Avignon (Palais des Papes), Late Burdigalian.

Order Comatulida A.H. Clark, 1908

Family Rhizocrinidae Jaeckel, 1918

Genus *Paraconocrinus* Roux, Eléaume and Améziane, 2019

Type species. *Eugeniacrinus pyriformis* Münster in Goldfuss, 1826.

***Paraconocrinus rhodanicus* n. sp.**
Fig. 12G-K, 13, Table 8

Type material. 26 Co not figured (MHNL 20062728) + 4 Co figured (MHNL 20062727).

Etymology. Reference to the Rhodanian basin.

Additional material. 1 AC, 1 Co from Vedène.

Diagnosis. As in description.

Type stratum. Late Burdigalian.

Type locality. Place du Palais des Papes in Avignon.

Description. 30 Co (quantitative characters given in Table 8) corresponding to a stalk length of 62.5 mm. Co from distal stalk with proximal facet having one or more projections ended by rhizoid insertion at one (Fig. 12G) or both sides (Fig. 12J-K) of fulcral ridge. Co from mesistele without rhizoid, more elongated (1<H/D<1.5) with oval (D/d <0.85) synarthries (Fig. 14I). Distally, Co with weaker H/D (tending to 0.7), narrower (D/d tending to 2.5) spindle-shaped synarthries (Figs.12G, J) with more robust rhizoid socket (Fig. 12J). Synarthrial facets of classical *Conocrinus* type (see Roux *et al.* 2019) with a deep 8-shaped ligament fossa; fulcral ridge of two segments with axis hollowed, regular crenularium reaching ~20 small Cr on each side and bordered by slightly depressed ligament areas (Fig. 12H).

TABLE 8. Variation of main quantitative columnal characters in the type series of *Paraconocrinus rhodanicus* n. sp. from Avignon. For abbreviations see Fig. 4. Values in mm, except for ratios.

Characters	H	D	D’	H/D’1	H/D2	D/d
Measures	28	28	27	28	27	19
Mean	2.08	2.12	1.80	1.01	1.17	1.89
Minimum	1.56	1.25	1.24	0.75	0.93	1.56
Maximum	2.64	2.96	2.40	1.34	1.46	2.43

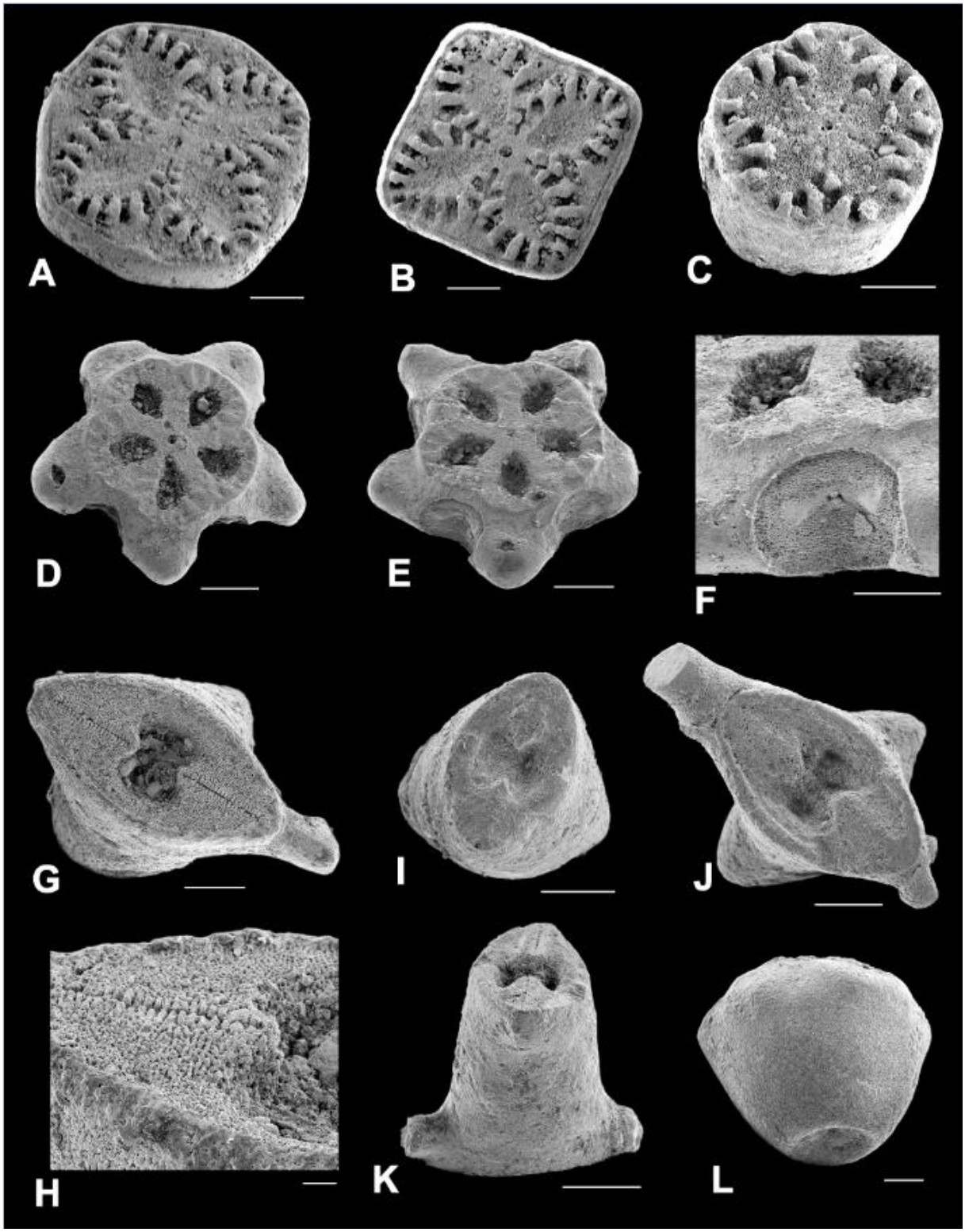

FIGURE 12: Isocrinid and rhizocrinid columnals. A-K: from Palais des Papes in Avignon; A-C: *Metacrinus berthei* (MHNL 20.062719), A-B: symplexies with anomalous 4-symmetry, C: distal internodal from a young individual; D-F: *Papacrinus avignonensis* **n. gen., n. sp.** (MHNL 20.062726) , D: oblique distal view, E-F: oblique proximal view, F: close up of cirrus socket; G-K: *Paraconocrinus rhodanicus* **n. sp.** (MHNL 20.062727), G-H: columnal from dististele, G:proximal view, H: close up of fulcral ridge, oblique view, I: columnal from middle mesistele, J: columnal from proximal dististele, proximal view, K: columnal from proximal dististele, side distal view; L: *Gastecrinus viticolis* **n. gen., n. sp.** from Vigne Gaste (Istres), aboral cup (MHNL 20.062729). Scale bar equals 1 mm in A-F and L, 0.5 mm in G and I-K, 0.1 mm in H.

Worn material from Vedène presumedly belonging to *P. rhodanicus* n. sp. Oblong aboral cup, preserved H 6.9 mm, D maximum 4.0 mm, stalk insertion 1.98 mm. Co with H 2.70 mm, D 2.95 mm and d 2.10 mm.

Remarks. *Paraconocrinus rhodanicus* n. sp. is a small species with distal Co articulated by narrow synarthries of fulcral ridge bordered by slightly depressed areas as in most species of the genus *Paraconocrinus* (Merle and Roux 2018; Roux *et al.* 2019). The Co figured from the Middle Miocene near Turin (see especially Albus 1931 and Manni 2005) differ in having a larger size and more massive shape. As previously usual, isolated Miocene rhizocrinid Co had been attributed to the most classically cited Eocene species: "*Conocrinus*" *thorenti* (d'Archiac 1846) or "*Conocrinus*" *pyriformis* (Münster *in* Goldfuss, 1826). "*Conocrinus*" *seguenzai* Meneghini, 1875, known only from aboral cups from the Miocene of Piedmont (Noelli 1900; Manni 2005), is the only rhizocrinid species clearly identified, but the published figures are too imprecise to attribute it to one of the genera distinguished by Roux *et al.* (2019). Although very worn, the aboral cup from Vedènes, which may belong to *P. rhodanicus* n. sp., differs markedly from "*Conocrinus*" *seguenzai*.

Occurrence in southeastern France. Avignon (Place du Palais des Papes), Les Angles ?, Vedène ?, Late Burdigalian, Early Langhian?

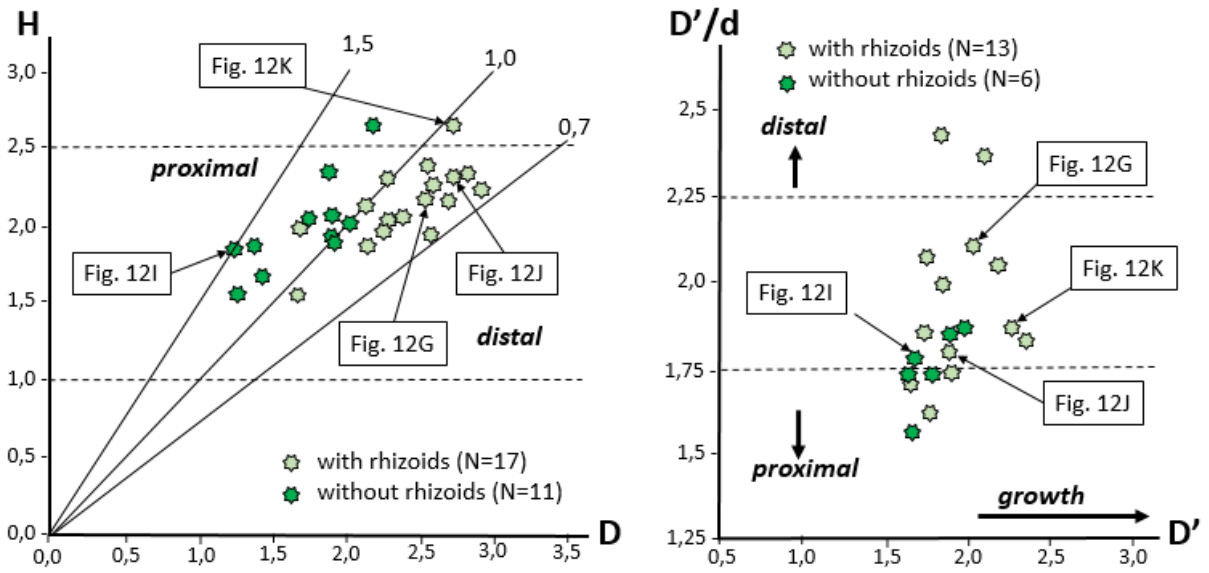

FIGURE 13: Variations in columnal general shape of *Paraconocrinus rhodanicus* **n. sp.** from the Palais des Papes in Avignon. See Fig. 2G-H for abbreviations. Values in mm, except for ratios.

Rhizocrinid columnals of *Conocrinus*-type

A single mesistele Co (H 1.59 mm, D 1.50, D/d 1.11) of the *Conocrinus*-type was collected in the blue marls of Faucon near Entrechaux (Ferme Pie). It differs from *P. rhodanicus* n. sp. in

having a larger size and articular facets which are only slightly oval. Two small worn columnals coming from the Grands Essarts (Entrechaux) are indeterminable. Joleaud (1907) also reported the presence of "*Conocrinus*" (most probably columnals) in the echinoderm-rich bed of Les Angles (ancient quarries).

Family uncertain

***Gastecrinus* n. gen.**

Type-species. *Gastecrinus vinealis* n. gen., n. sp.

Etymology. From Gaste, reference to the type locality Vigne Gaste.

Diagnosis. Dorsal cup of inverted truncated cone-shape, wider than hight, external surface smooth without distinct sutures, large radials suggesting robust arms, conspicuous stalk socket forming a conical depression; stalk and arms unknown.

***Gastecrinus vinealis* n. gen., n. sp.**
Fig. 12L

Type material. A single aboral cup (MHNL 20062729).

Etymology. From Vigne, reference to the type-locality Vigne Gaste.

Diagnosis. As in description.

Type stratum. Just above the calcareous limestone dated Late Burdigalian.

Type locality. Vigne Gaste (Istres).

Description. Dorsal cup of inverted truncated cone-shape, wider than high, external surface convex and smooth, conspicuous stalk socket forming a conical depression, sutures between cup plates indistinct, adoral D 6.11 mm, stalk socket D 2.45 mm, estimated H 4.3 mm. Adoral part recrystallized and worn, location of radials suggested by a discrete relief allowing to estimate a maximum width of about 2.6 mm.

Remark. This aboral cup differs from that of the Rhizocrinidae in having large radials suggesting robust arms and a very large stalk socket. The poor preservation of its adoral side does not allow to attribute it to a known post-Paleozoic taxon.

Occurrence. Only known from Vigne-Gaste (Istres), Late Burdigalian.

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References

Albus, L. (1931) Nuove ricerche sui crinoidi miocenici della collina di Torino. *Bollettino della Societa geologica italiana*, 49, 279-296.

Améziane, N., Eléaume, M. & Roux, M. (2021) Ontogeny of non-muscular brachial articulations in Balanocrininae (Echinodermata, Crinoidea): iterative trajectories or phylogenetic significance? *Zoomorphology*, 140**,** 47–67. https://doi.org/10.1007/s00435-020-00508-y.

Améziane, N. & Roux, M. (1997) Biodiversity and historical biogeography of stalked crinoids (Echinodermata). *Biodiversity and Conservation*, 6, 1557-1570. https://doi.org/10.1023/A:1018370620870

Améziane-Cominardi, N. (1991) Distribution bathymétrique des pentacrines du Pacifique occidental. Essai de modélisation et d'application aux faunes du Lias (problèmes de tectono-eustatisme au cours du rifting téthysien). *Documents du Laboratoire de Géologie, Lyon*, 116, 1-253.

Améziane-Cominardi, N. & Roux, M. (1987) Biocorrosion et micritisation des ossicules d'échinodermes en milieu bathyal au large de la Nouvelle-Calédonie. *Comptes Rendus de l'Académie des Sciences, Paris*, 305, 701-705.

André, J.P., Barthet, Y., Ferrandini, M., Ferrandini, J., Reynaud, J.Y. & Tessier, B. (2011) The Bonifacio formation (Miocene of Corsica): transition from a wave- to tide-dominated coastal system in mixed carbonate-siliciclastic setting. *Bulletin de la Société géologique de France*, 182, 3, 221-230.

Archiac, A. d' (1846) Description des fossiles recueillis par M. Thorent dans les couches à Nummulites des environs de Bayonne. Mémoires de la Société géologique de France, 4 (2) 2, 189–217.

Astibia, H., Corral J.C., Álvarez-Pérez, G., López Horgue, M.A. & Payros, A. (2020) Nuevos datos sobre las faunas marinas del Eoceno medio–superior de Navarra (área surpirenaica occidental). Revisión de los fósiles de la colección Ruiz de Gaona. *Estudios Geológicos* 76, 2, e130, 1-43. https://doi.org/10.3989/egeol.43621.545.

Barrier, P., Di Geronimo, I., Montenat, C., Roux, M. & Zibrowius, H. (1989) Présence de faunes bathyales atlantiques dans le Pliocène et le Pléistocène de Méditerranée. *Bulletin de la Société géologique de France*, 8, 5, 787-796.

Baumiller, T.K. (2008) Crinoid ecological morphology. *Annual Review in Earth and Planetary Science*, 36, 221–249.

Baumiller, T.K. & Gazdzicki, A. (1996) New crinoids from the Eocene La Meseta formation of Seymour Island, Antarctic Peninsula. *Palaeontologia Polonica*, 55**,** 101–116.

Baumiller, T.K., Llewellyn, C.G., Messing, C.G. & Ausich, W.I. (1995) Taphonomy of isocrinid stalk: influence of decay and autotomy. *Palaïos*, 10, 87-95.

Besson, D. (2005) *Architecture du bassin rhodano-provençal miocène (Alpes, SE France). Relations entre déformation, physiographie et sédimentation dans un bassin molassique d'avant-pays*. Unpubl. PhD thesis, École des Mines, Paris, 438 pp.

Besson, D., Parize, O., Rubino, J.L., Aguilar, J.P., Aubry, M.P., Beaudoin, B., Berggren, W.A., Clauzon, G., Crumeyrolle, P., Dexcoté, Y., Fiet, N., Iaccarino, S., Jiménez-Moreno, G., Laporte-Galaa, C., Michaux, J., von Salis, K., Suc, J.P., Reynaud, J.Y. & Wernli, R. (2005) Un réseau fluviatile d'âge Burdigalien terminal dans le Sud-Est de la France : remplissage, extension, âge, implications. *Comptes rendus Géoscience*, 337, 1045-1054.

Biese, W. & Sieverts-Doreck, H. (1939) Crinoidea caenozoica. *In* Quenstedt, W. (Ed.), *Fossilium Catalogus, I: Animalia*, 80. W. Junk's Gravenhage, pp. 1–155.

Bourseau, J.P. & Roux, M. (1989) Echinodermes : Crinoïdes Pentacrinidae (MUSORSTOM 2 & CORINDON 2). *Mémoires du Museum National d'Histoire Naturelle, Paris*, A, 143, 113-201.

Carpenter P.H. (1882) The stalked crinoids of the Caribbean Sea. *In*: Reports on the results of dredging under the supervision of Alexander Agassiz, in the gulf of Mexico (1877–78), and inthe Carribbean Sea (1878–79), by the U.S. Coast Survey Steamer "Blake", *Bulletin of the Museum of Comparative Zoology*, Cambridge, USA, 10, 4, 165–181.

Carpenter, P.H. (1884) Report upon the Crinoidea collected during the voyage of H.M.S. "Challenger" during the years 1873–1876. Part I, General morphology, with description of the stalked crinoids. *Report on the scientific results of the exploringvoyage H.M.S. Challenger*, Zoology, (11) 32, 1–440.

Chateauneuf, J.J., Bauer, H. & Cojan, I. (2006) Présence d'une mangrove à *Avicennia* au Miocène moyen dans la région de Digne (Alpes-de-Haute-Provence, France) : implications stratigraphiques et paléoclimatiques. *Comptes Rendus Geosciences*, 338, 197-205.

Chippy, K., Saravanane, N., Kishore Kumar, B. & Sanjeevan, V.N. (2018) New record of the stalked crinoid *Saracrinus angulatus* (Echinodermata: Crinoidea: Isocrinida) from Andaman Sea, Northern Indian Ocean. *Marine Biodiversity*, 48, 1429-1437. https://doi.org/10.1007/s12526-016-0626-7

Clark A.H. (1908) Two new crinoid genera. *Proceedings of the Biological Society of Washington*, 21, 149–152.

Clark A.H. (1908) New genera of unstalked crinoids. *Proceedings of the Biological Society of Washington*, 21, 125–136.

Cooke, J.H. (1896) Notes on the *Globigerina* limestones of the Maltese Islands. *Geological Magazine*, 4, 3, 502-511.

Dalloni, M. (1917) Sur le facies du Miocène inférieur au sud du Tell et la faune du Carténien d'Uzès-le-Duc (Algérie). *Comptes rendus des séances de l'Académie des Sciences, Paris*, 165, 4, 163-165.

David, J. (1998) *Adaptation morphologique, croissance et production bioclastique chez les crinoïdes pédonculés actuels et fossiles (Pentacrines et Millericrinina). Application paléoécologique aux gisements du Jurassique supérieur des Charentes et du Nord-Est du Bassin de Paris*. Unpubl. PhD thesis, Université de Reims, Sciences de la Terre, 2 vol., 551 pp.

David, J., Roux, M., Messing, C.G., Améziane, N. (2006) Revision of the pentacrinid stalked crinoids of the genus *Endoxocrinus* (Echinodermata, Crinoidea), with a study of environmental control of characters and its consequences for taxonomy. *Zootaxa*, 1156, 1-50.
https://doi.org/10.11646 /zootaxa.1156.1.1

Demarcq, G. (1970) Étude stratigraphique du Miocène rhodanien. *Mémoires du Bureau de Recherches géologiques et minières*, 61, 1-257.

Demarcq, G. (1984) Importance des mégafaunes marines benthiques dans l'évolution paléothermique de la Méditerranée au Néogène. *Annales de Géologie des Pays helléniques*, 32, 87-95.

Donovan, S.K., Portell, R.W. & Veltkamp, C.J. (2005) Lower Miocene echinoderms of Jamaica, West Indies. *Scripta Geologica*, 129, 91-130.

Donovan, S.K. & Veltkamp, C.J. (2001) The Antillean Tertiary crinoid fauna. Journal of Paleontology, 75, 721–731.

Etnoyer, P. J., Messing, C.G., Stanley, K.A., Baumiller, T.K. & Shirley, T. C. (2019) Ecology, distribution and time-series analyses of mesophotic and deep-water coral assemblages on a tropical island slope, Isla Roatán, Honduras. 7th International Symposium on Deep-Sea Corals, 29 July – 2 August 2019, Cartagena, Colombia, Abstract.

Franzin, B. (2007) *Les Crinoïdes pédonculés du Miocène rhodanien*. Unpubl. Rapport de stage de Master Sciences de la Terre, Université Claude Bernard Lyon 1, 22 pp.

Gervais F.L.P. (1835) Encrines. *In*: Guérin, Dictionnaire pittoresque d'histoire naturelle et des phénomènes de la nature, Lenormand (Ed.), Paris, 3, 48–49.

Gislèn T. (1924) Echinoderm studies. *Zoologiska bidrag fran Uppsala*, 9, 1–316.

Goldfuss, G.A. (1826) Petrefacta Germaniae, divisio secunda. Radiarorum reliquiae. Vol. 1. Arnz & Co, Düsseldorf, pp. 115– 221.

Granier, J. (1966) Stratigraphie et faune des dépôts Astiens des gorges de Régalon, à Cheval Blanc (Vaucluse). *Bulletin de la Société d'Etude des Sciences naturelles du Vaucluse*, 1966, 35-45.

Hemery, L.G. (2011) *Diversité moléculaire, phylogénie et phylogéographie des Crinoïdes (Echinodermes) dans un environnement extrême: l'océan Austral*. Unpubl. PhD thesis, Muséum national d'Histoire naturelle, Paris, 381 pp.

Hemery, L.G., Roux, M., Améziane, N. & Eléaume, M. (2013) High-resolution crinoid phyletic inter-relationships derived from molecular data. *Cahiers de Biologie Marine*, 54, 511–523.

Hess, H. (2011) Isocrinida. *In* H. Hess, C.G. Messing & W.I. Ausich (Eds.), Treatise on Invertebrate Paleontology, Part T, Echinodermata 2 Revised, Crinoidea, 3 (pp. 42-69). Lawrence: University of Kansas Press. https://doi.org/10.17161/dt.v0i0.5392

Jaekel, O. (1918) Phylogenie und System der Pelmatozoen. *Paläontologische Zeitschrift*, 3 (1), 1–128. https://doi.org/10.1007/BF03190413

Jeffreys G.J. (1870) Preliminary report of the scientific exploration of the deep-sea in H.M.S. "Porcupine" during the summer of 1869. *Proceedings of the Royal Society of London*, 19, 157.

Joleaud, L. (1907) *Géologie et paléontologie de la plaine du Comtat et de ses abords. Description des terrains néogènes. Fascicule I.* Seguin, Avignon, 102 pp.

Klikushin, V.G. (1977) Sea lilies of the genus Isselicrinus. *Paleontologicheskiy Zhurnal*, 1: 87-95. In Russian.

Klikushin, V.G. (1982) Taxonomic survey of fossil isocrinids with a list of the species found in the USSR. *Geobios*, 15, 3, 299-325.

Klikushin, V.G. (1992) *Fossil pentacrinid crinoids and their occurrence in the USSR*. Leningrad Paleontological Laboratory, Leningrad, 358 pp., in Russian.

Kroh, A. (2003) The Echinodermata of the Langhian (Lower Badenian) of the molasse zone and the northern Vienna basin (Austria). *Annalen des Naturhistorischen Museums, Wien*, 104A, 155-183.

Lambert, J. (1899) Etude sur les terrains tertiaires des environs d'Avignon par H. Nicolas. *Revue critique de Paléozoologie, Paris*, 1, 121-122.

Locard, A. (1877) *Description de la faune des terrains tertiaires moyens de la Corse*. Savy, Paris, 360 pp.

Loriol, P. de (1897) Description de quelques Echinodermes. Appendice à la note de M.E. Pellat sur le Burdigalien supérieur. *Bulletin de la Société géologique de France*, 3, 25, 115–129.

Manni, R. (2005) The non-isocrinid crinoids of the Michelotti Collection. *Bolletino della Societa paleontologica italiana*, 44, 3, 211-218.

Manni, R. (2015) Catalogue of the fossils stored in the Paleontological Museum of "Sapienza" University of Rome: 3. *Journal of Mediterranean Earth Science*, 7, 51-62.

Manzoni, A. (1878) Considerazioni geologishe a proposito del *Pentacrinus gastaldi* della molassa di Montese. *Annuario della Societa dei naturalisti in Modena*, 12, 1-6.

Maurel-Ferrandini, M. (1976) Reconstitution paléographique du Burdigalien du littoral de la chaîne de la Nerthe et de la région des Etangs (B.d.Rh., France). *Travaux du Laboratoire de Géologie historique et de Paléontologie, Université de Provence, Centre Saint Charles, Marseille*, 7, 1-135.

Meneghini, G. (1862) Slugi Echinodermi fossili neogenici di Toscana. *Atti della riunione degli Scienzati italiani tenuta, Siena*, 1-31.

Meneghini, G. (1876) I crinoidi tertiarii. *Atti della Societa Toscana di Scienze naturali, Pisa*, 2, 1, 36-59.

Merle, D. & Roux, M. (2018) Stalked crinoids from Gan (Late Ypresian, southwestern France): exceptional stereom preservation, paleoecology and taxonomic affinities. *Swiss Journal of Paleontology*, 137, 2, 225–244. https://doi.org/10.1007/s13358-018-0162-0

Messing, C.G. (2016) Time-series observations of crinoid assemblages on a deep tropical island slope, Isla Roatán, Honduras. HCNSO Ocean Science Jamboree, May 16-20 2016, NSU, Florida: abstract.

Meyer, D.L. & Oji, T. (1993) Eocene crinoids from Seymour Island, Antarctic Peninsula: paleobiogeographic and paleoecologic implications. *Journal of Paleontology*, 67, 250-257.

Michelotti, J. (1847) Précis de la faune miocène de la Haute Italie. *Natuurkundige Verhanddelingen van de Hollandshe Maatschappij der Wetenschapen te Haarlem*, 3, 1-408.

Moore, R.C. & Vokes, H.E. (1953) Lower Tertiary crinoids from Northwestern Oregon. *United State Geological Survey Professional Paper* 233-E, 111-147.

Nicolas, H. (1897) Etude sur les terrains tertiaires des environs d'Avignon. Le Miocène. *Mémoires de l'Académie du Vaucluse, Avignon*, 16, 60-152.

Nicolas, H. (1898) Etude des terrains tertiaires des environs d'Avignon. Miocène. Note complémentaire sur la faune de la « Femme de Loth » et révision des Antedons de ce même horizon. Association française pour l'Avancement des Sciences. Compte rendu de la 26ème session, Congrès de Saint-Etienne, 1897, Notes et Mémoires (pp. 383-413). Masson, Paris.

Noelli, A. (1900) Contribuzione allo studio dei Crinoidi terziari del Piemonte. *Atti della Societa italiana di Scienze naturali e del Museo Civico di Storia naturale, Milano*, 39, 1:19-50.

Oji, T. (1990) Miocene Isocrinidae (stalked crinoids) from Japan and their biogeographic implication. *Transactions and Proceedings of the Palaeontological Society of Japan*, 1, 57, 412-429.

Pellat, E. (1897) Sur l'assise terminale de l'étage Burdigalien près des Angles (Gard) et près de Saint-Etienne-du-Grès (Bouches-du-Rhône). *Bulletin de la Société géologique de France*, 3, 25, 111–114.

Philippe, M. (1974) Découverte de gisements à faune burdigalienne dans les «marnes bleues de Faucon» à Entrechaux (Vaucluse) et à Mollans (Drôme*). Bulletin mensuel de la Société linnéenne de Lyon*, 43, 1, 5-8. https://doi.org/10.3406/linly.1974.10096

Philippe, M. & Granier, J. (1982) Premières découvertes de Rhyncholites (Cephalopoda) dans le Miocène du Bassin du Rhône (sud-est de la France) et interprétations. *Bulletin de la Société d'Etude des Sciences naturelles du Vaucluse*, 1979-1981, 71-83.

Pomel, N.A. (1887) *Paléontologie ou description des animaux fossiles de l'Algérie*. Zoophytes, 2, 2, Fontana, Alger, 344 pp.

Pouyet, S. (1984) La faune du faciès « Marnes bleues », Burdigalien du bassin de Faucon-Mollans-Malaucène (Sud-Est de la France). *Nouvelles archives du Muséum d'Histoire naturelle de Lyon*, 22, 51-123.

Pouyet, S., David, L., Demarcq, G., Latreille, G., Carbonnel, G., Prieur, A., Philippe, M., Laurain, M., Pajaud, D., Capetta, H., Barbillat, R., Chevalier, J.P. (1984) La faune du faciès « Marnes bleues » du Burdigalien du bassin de Faucon-Mollans-Malaucène (Sud-Est de la France) : essai de synthèse paléoécologique et paléogéographique. *Géologie de la France*, 1-2, 123-130.

Rasmussen, H.W. (1972) Lower Tertiary Crinoidea, Asteroidea and Ophiuridea from northern Europe and Greenland. *Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter*, 19, 7, 1-83.

Rasmussen, H.W. (1980) Crinodeos del Cretacico superior y del Terciario inferior de la isla Vicecomodoro Marambio (Seymour Island), Antarctica. *Contribucion del Instituto Antarctico Argentino*, 261, 4, 79-97.

Rouse, G.W., Jermiin, L.S., Wilson, N.G., Eeckhaut, I., Lanterbecq, D., Oji, T., Young, C.M., Browning, T., Cisternas, P., Helgen, L.E., Stuckey, M., Messing, C.G. (2013) Fixed, free and fixed: The fickle phylogeny of extant Crinoidea (Echinodermata) and their Permian-Triassic origin. *Molecular Phylogenetics and Evolution*, 66, 1, 161-181. https://doi.org/10.1016/j.ympev.2012.09.018

Roux, M. (1976) Aspects de la variabilité et de la croissance au sein d'une population de la pentacrine actuelle: *Annacrinus wyvillethomsoni* Jeffreys (Crinoidea). *Thallassia Jugoslavica*, 12, 1, 307-320.

Roux, M. (1977) The stalk-joints of recent Isocrinidae (Crinoidea*). Bulletin of the British Museum (Natural History), Zoology*, 3, 3, 45-64.

Roux, M. (1981) Echinodermes: Crinoïdes Isocrinidae. *Mémoires O.R.S.T.O.M., Paris*, 91, 477-543.

Roux, M. (1987) Evolutionary ecology and biogeography of recent stalked crinoids as a model for the fossil record. *In*: M. Jangoux & J.M. Lawrence (Eds.), Echinoderm Studies, 2 (pp.1-53). A.A. Balkema, Rotterdam.

Roux, M., Ameziane, N. & Eléaume, M. (2009) The genus *Teliocrinus* (Crinoidea, Echinodermata): a key taxon among pentacrinid stalked crinoids. *Zoological Journal of the Linnean Society*, 155, 22–39. https://doi.org/10.1007/s12526-015-0369-x

Roux, M., Eléaume, M., Améziane, N. (2019) A revision of the genus *Conocrinus* d'Orbigny (Echinodermata, Crinoidea, Rhizocrinidae) and its place among extant and fossil crinoids with a xenomorphic stalk. *Zootaxa*, 4560, 51-84. https://doi.org/10.11646/zootaxa.4560.1.3

Roux, M., Eléaume, M., Hemery, L.G. & Améziane, N. (2013) When morphology meets molecular data in crinoid phylogeny: a challenge. *Cahiers de Biologie Marine*, 54, 541–548.

Roux, M., Messing, C.G. & Améziane, N. (2002) Artificial keys to the genera of living stalked crinoids (Echinodermata*). Bulletin of Marine Science*, 70, 3, 799-830.

Roux, M. & Montenat, C. (1977) Sites à Crinoïdes pédonculés et bathymétrie des bassins messiniens dans les Cordillières bétiques orientales (Espagne méridionale). *Bulletin de la Société géologique de France*, 7, 19, 405-416.

Roux, M., Plaziat, J.C. (1978) Inventaire des Crinoïdes et interprétation paléobathymétrique des gisements du Paléogène pyrénéen franco-espagnol. *Bulletin de la Société géologique de France*, 7, 10, 299–308. https://doi.org/10.2113/gssgfbull.S7-XX.3.299

Sandor, M. (1983) Lower Badenian Crinoidea-find from the Börzsöny Mountains, northern Hungary. *Bulletin of the Hungarian Geological Society*, 113, 171-174. In Hungarian.

Sieverts-Doreck, H. (1933) Jungtertiäre Crinoiden von Seran and Borneo. *Neues Jahrbuch für Mineralogie, Geologie, Paläontologie*, 69B, 145-168.

Sieverts-Doreck, H. (1952). Articulata. *In* R.C. Moore, C.G. Lalicker & A.G. Fischer (Eds.), Invertebrate fossils. New York, Toronto, London: McGraw-Hill, 614.

Hess, H. (2011) Isocrinida. *In* H. Hess, C.G. Messing & W.I. Ausich (Eds.), Treatise on Invertebrate Paleontology, Part T, Echinodermata 2 Revised, Crinoidea, 3 (pp. 42-69). Lawrence: University of Kansas Press.

Sinard, B. (1892) Sur la présence de *Pentacrinus* dans le Miocène des Angles (Gard). *Association française pour l'Avancement des Sciences, Congrès de Marseille, 1891*, 402-404.

Tunnicliffe, V., Roux, M., Eléaume, M. & Schornagel, D. (2016) The stalked crinoid fauna (Echinodermata) of the Molucca and Celebes seas, Indonesia: taxonomic diversity and observations from remotely operated vehicle imagery. *Marine Biodiversity*, 46, 365–388. https://doi.org/10.1007/s12526-015-0369-x

Ulysse, J. (1968) *Contribution à l'étude des gisements miocènes de Caumont et de Bompas (Vaucluse)*. Unpubl. Mémoire de Diplôme d'Etudes Supérieures de Géologie. Université Claude Bernard Lyon 1, 205 pp.

Vialle, N., Adnet, S. & Cappetta, H. (2011) A new shark and ray fauna from the Middle Miocene of Mazan, Vaucluse (southern France) and its importance in interpreting the paleoenvironment of marine deposits in the southern Rhodanian Basin. *Swiss Journal of Palaeontology*, 130, 241–258.

Whittle, J.R., Hunter, A.W., Cantrill, D.J., McNamara, K.J. (2018) Globally discordant Isocrinida (Crinoidea) migration confirms asynchronous Marine Mesozoic Revolution. *Communications Biology*, 1, 46, 1-10.