Description of *Priscinachus elongatus* n. gen., n. sp., and Priscinachidae n. fam. for the earliest spider crab (Crustacea, Decapoda, Majoidea), from the French Cretaceous (Cenomanian)

Gérard BRETON
Université de Rennes I, Laboratoire Géosciences, Campus de Beaulieu,
F-35042 Rennes cedex (France)
and 6 rue des réservoirs, F-76600 Le Havre (France)
gerardbreton@free.fr

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KEY WORDS
Crustacea,
Brachyura,
Decapoda,
Priscinachidae n. fam.,
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Paris Basin,
Normandy,
France,
new family,
new genus,
new species.

ABSTRACT

Priscinachus elongatus n. gen., n. sp., is based on four specimens from two lower Cenomanian exposures, separated by 85 km in the western Paris Basin. It is the earliest known spider crab, the Majoidea being previously known only from the lower Eocene. *Priscinachus elongatus* n. gen., n. sp. deserves its own family, the Priscinachidae n. fam., within the Majoidea Samouelle, 1818, due to the original combination of characters which is not found within any other majoid family. In both exposures, the fossils are preserved in a hard-ground, deposited in a shallow but open sea, in a transgressive context. Decapod fossils have been transported and often broken before deposition.

MOTS CLÉS
Crustacea,
Brachyura,
Decapoda,
Priscinachidae n. fam.,
Priscinachus n. gen.,
Crétacé,
Cénomanien,
Bassin de Paris,
Normandie,
France,
famille nouvelle,
genre nouveau,
espèce nouvelle.

RÉSUMÉ

Description de Priscinachus elongatus *n. gen., n. sp., et de Priscinachidae n. fam. pour la plus ancienne araignée de mer connue (Crustacea, Decapoda, Majoidea), du Crétacé (Cénomanien) de France.*

Priscinachus elongatus n. gen., n. sp. est établi d'après quatre spécimens provenant de deux gisements datés du Cénomanien inférieur, distants de 85 km, dans l'ouest du Bassin de Paris. C'est la plus ancienne araignée de mer connue, les plus anciens Majoidea signalés à ce jour datant de l'Éocène inférieur. *Priscinachus elongatus* n. gen., n. sp. est le seul représentant de la famille des Priscinachidae n. fam., au sein des Majoidea Samouelle,1818, du fait de la combinaison originale de caractères qui ne se retrouve dans aucune autre famille des Majoidea. Dans les deux gisements, les fossiles sont préservés dans un hard-ground, déposé en milieu peu profond mais en mer ouverte, en contexte transgressif. Les décapodes ont été transportés avant dépôt et sont souvent cassés.

INTRODUCTION

Two Cenomanian exposures in the western Paris Basin, France, have provided a rich crab fauna, including an undescribed species of spider crab. The first description of this taxon is based on four individuals. The spider crabs (superfamily Majoidea Samouelle, 1818) were known with certainty from the Eocene, all previous records from the upper Cretaceous being dubious. Thus, with the discovery of this new genus and species, the origin of the Majoidea appears to be much older than thought hitherto, at least the Cenomanian (95 million years). Further, *Priscinachus elongatus* n. gen., n. sp. deserves its own family, the Priscinachidae n. fam. based on its unique combination of morphological characters.

ABBREVIATIONS

Biozones and subzones are abbreviated in the species name of the index fossil.

Fm	Formation;
h	height;
L	length;
l	width;
HG	hard-ground;
MNHN	Muséum national d'Histoire naturelle, Paris.

OCCURRENCE AND STRATIGRAPHY

One exposure, located in the small valley of Pétreval, at Annouville-Vilmesnil, 7 km southeast of Fécamp (Seine-Maritime, France) is known erroneously by fossil collectors as "Mentheville" (x = 462.00; y = 223.65). The exposures are ancient quarries of the so-called "Pierre de Fécamp".

The other exposure is a disused quarry on the side of the road to Saint-Pierre-sur-Dives, on the hill of Le Billot, Notre-Dame-de-Fresnay (Calvados, France), known as "Le Billot" or "Montpinçon" (x = 433.80; y = 143.50). The two exposures are *c.* 85 km apart.

The Le Billot section displayed lower Cenomanian beds, from bottom to top (Fig. 1):

– 2 m of fine sands, "Sables de Montormel" beds (Carcitanense);

– 3 m of sandy glauconite (bed 3) overlain by a thick bed of glauconitic calcareous sandstone (bed 4 = HG Montpinçon), top of Carcitanense and ?base of Saxbii;

– 3 m of a grey glauconitic chalk (bed 5) (Saxbii): see Juignet (1974: 309, 310, fig. 77; 1981: 20).

Decapods were collected in beds 3 and 4.

The Pétreval section displays lower and middle Cenomanian beds, from bottom to top (Fig. 2):

– 1.5 m of a whitish calcareous sandstone with few glauconite (bed 1 = "Pierre de Fécamp", formerly exploited in underground quarries);

– 1.5 m of a pinkish – beige coloured nodular sandstone, strongly bioturbated, burrows filled with glauconite (bed 2 = HG "Fécamp");

– 0.2 m of a glauconitic sandy chalk (bed 3);

– 1.3 m of a highly fossiliferous, greenish, nodular, calcareous sandstone, intensely bioturbated, burrows and pockets filled with a dark green glauconite (bed 4 = HG "Rouen 1");

– 0.5 m of glauconitic soft chalk with phosphatic nodules and fossils (bed 5), topped with a bed of calcareous nodules (bed 6 = lateral equivalent of HG "Rouen 2");

– 0.8 m of whitish soft chalk.

Beds 1-4: Craie Glauconieuse Fm (Mantelli and Dixoni), the limit being likely at the top of the bed 2.

Beds 5-7: Craie de Rouen Fm (Rhotomagense).

Decapods are mostly collected in bed 4.

The origin of this bed 4 is explained as follows by Ragot (1989: 33): "This highly fossiliferous bed belongs to an accumulation lenticular level [… in which] is concentrated the fauna of all the upper half of the lower Cenomanian, in an uplifted area, swept across by the currents. Its weak thickness shows that the transport only concerned shells, and thus, there was no reworking *in situ* of the deposit." (translated from French).

The sediments of this bed 4 were deposited on a long-staying shoal; this hard-ground (*sensu* Juignet *et al.* 1980) was a composite one, but the intense bioturbation throughout it erased any internal structures.

MATERIAL AND METHODS

Three incomplete and one fragmentary carapaces have been examined. MNHN A27207 and MNHN A27210 come from the lower Cenomanian HG

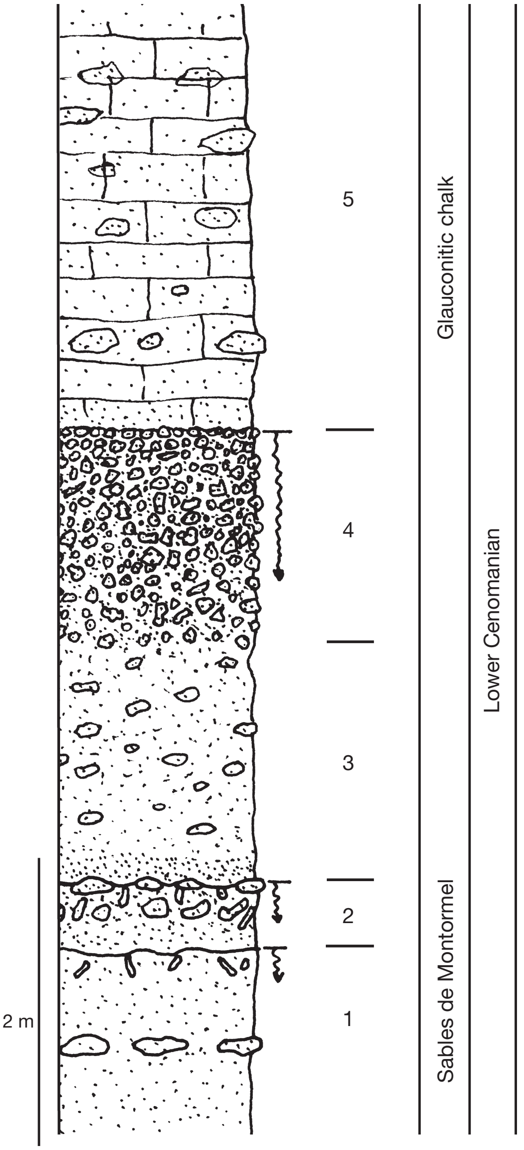

FIG. 1. — Le Billot quarry, Notre-Dame-de-Fresnay, Calvados (France), lithographic section, drawn from Juignet (1974: fig. 77): **1**, **2**, fine grained sands, sables de Montormel beds; **3**, sandy glauconite; **4**, glauconitic calcareous sandstone, HG Montpinçon; **5**, grey glauconitic chalk.

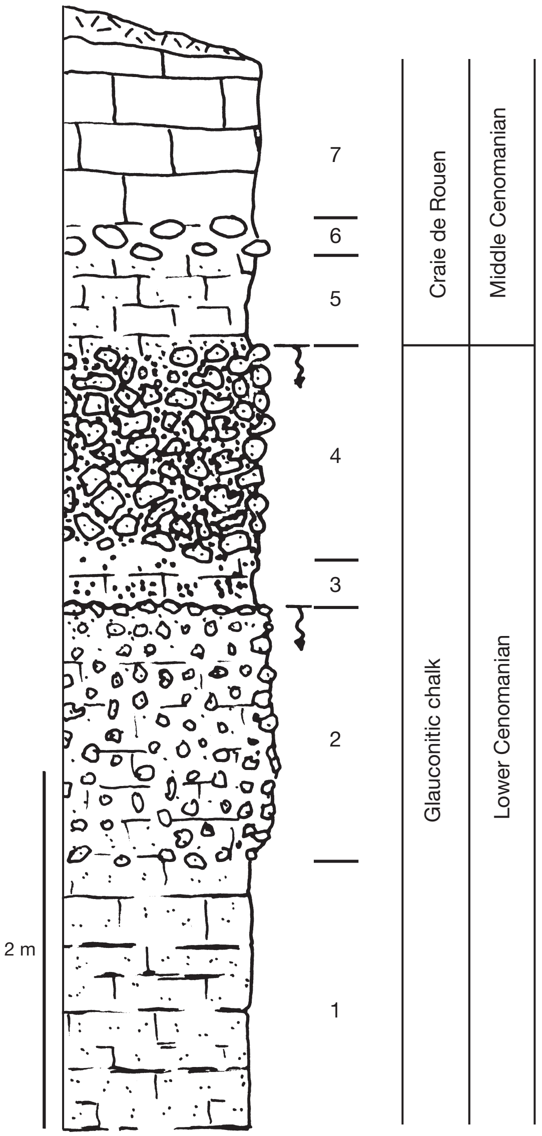

FIG. 2. — Outcrop of Pétreval, Annouville-Vilmesnil, Seine-Maritime (France), lithographic section, drawn from Juignet (1981: 20): **1**, whitish calcareous sandstone with sparse glauconite, "Pierre de Fécamp"; **2**, pinkish-beige coloured nodular sandstone, strongly bioturbated, burrows filled with glauconite, HG "Fécamp"; **3**, glauconitic sandy chalk; **4**, highly fossiliferous, greenish, nodular, calcareous sandstone, intensely bioturbated, burrows and pockets filled with a dark green glauconite, HG "Rouen 1"; **5**, glauconitic chalk with phosphatic nodules and fossils; **6**, chalk with calcareous nodules, lateral equivalent of HG "Rouen 2"; **7**, whitish soft chalk.

Montpinçon at Le Billot; MNHN A27208 and MNHN A27209 come from the lower Cenomanian HG Rouen 1 at Pétreval. All specimens have been prepared in using a hand-held needle under

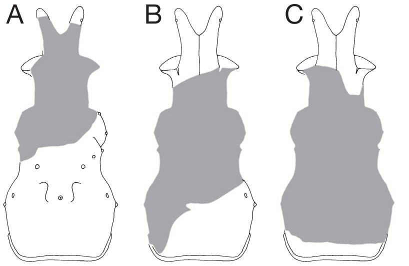

FIG. 3. — Preserved parts (grey) of holotype (**A**), paratype 1 (**B**), and paratype 2 (**C**). Paratype 3 not drawn. Outline based on diagrammatic reconstruction (Fig. 8). Not to scale.

a Leica MZ6 stereomicroscope. The used glue is acetone-soluble so that gluing is reversible. Drawings were made with a camera lucida on the Leica MZ6 stereomicroscope. Photographs were taken with a macro-lens for low magnifications up to × 2, or with the stereomicroscope.

TAPHONOMY, PALAEOECOLOGY AND PALAEOETHOLOGY

All the crabs preserved in the HG Montpinçon at Le Billot and in the HG Rouen 1 at Pétreval are disarticulated, that is, isolated carapaces, fragments of chelae and pereiopods. Among the abundant crab remains collected, no ventral side has been found. Moreover, limbs and carapaces are frequently broken (Fig. 3). This is consistent with the transport of remains (the distinction between moults and corpses is not possible) before burial. Carapaces and other parts of the exoskeleton are preserved as a distinct matt, white, soft, calcareous matter, sometimes with a ferruginous stain. Fossils are preserved either as internal casts or with the thickness of the inner shell surface (= decorticated *sensu* Wright & Collins 1972), or totally preserved, more rarely with the outer surface partially preserved. The development of nodulisation and lithification in the matrix is independent of the crab remains. This probably indicates that no organic matter was associated with the exoskeleton at the time of burial.

At both localities, many decapod species have been recognized. In the following provisional list, P and B indicate, respectively, the species known only from Pétreval and from Le Billot and neighbouring site of Mont-Ormel (Orne); otherwise, species occur at both sites. Unidentified galatheid (P); *Wilmingtonia satyrica* Wright & Collins, 1972 (P); *Rathbunopon woodsi* Withers, 1951 (B); *Plagiophtalmus oviformis* Bell, 1863, which is by far the most abundant crab in both sites*; Heeia villersensis* (Hée, 1924); *Glaessnerella kennedyi* Wright & Collins, 1972 (P); *Homolopsis brightoni* Wright & Collins, 1972; *Palaeodromites incertus* (Bell, 1963); *Trachynotocarcinus sulcatus* (Bell, 1863) (B); *Diaulax oweni* (Bell, 1850); *Necrocarcinus labeschii* (J.-A. Deslongchamps, 1835); *Necrocarcinus* n. sp. (new species undescribed [Breton & Collins unpublished data]); *Paranecrocarcinus digitatus* Wright & Collins, 1972; *P. biscissus* Wright & Collins, 1972 (B); *Paranecrocarcinus foersteri* Wright & Collins, 1972 (P); *Paranecrocarcinus* n. sp. (P) (new species undescribed [Breton & Collins unpublished data]); *Cretacoranina ornatus* (Wright & Collins, 1972); *Cenocorystes fournieri* (Collins & Breton, 2009); *Xanthosia buchii* (Reuss, 1845); *Etyxanthosia fossa* (Wright & Collins, 1972) (P); *Xanthosia* sp. (B); *Caloxanthus formosus* A. Milne-Edwards, 1864; *Caloxanthus americanus* Rathbun, 1935; and *Priscinachus elongatus* n. gen., n. sp. For the nomenclature and placement of *Glaessnerella* and *Homolopsis brightoni* I have followed Collins (1997) instead of Glaessner (1980) and Schweitzer *et al.* (2004).

Such a crab fauna is very similar to that of the Cenomanian beds of Wilmington (Devon, Great Britain) (Wright & Collins 1972; section and geological context in Smith *et al.* 1988); a fact which was already underlined by Breton & Decombe (1997). The similarity is easily explained by: 1) the geographical proximity in the Anglo-Paris Basin, in the Boreal Province; 2) the same lower Cenomanian age; and 3) a similar palaeoenvironment, in particular with hard-grounds (*sensu* Juignet & Kennedy 1974; Kennedy & Juignet 1974; Juignet *et al.* 1980). It seems to be impossible to decide if, amongst the rich crab fauna of hard-grounds Montpinçon or Rouen 1, or of Wilmington sandstones, some of the crabs were burrowers and, therefore responsible for the intense bioturbation. At Le Billot and Pétreval, most, if not all, have been transported before fossilization: crabs did not live where they have been

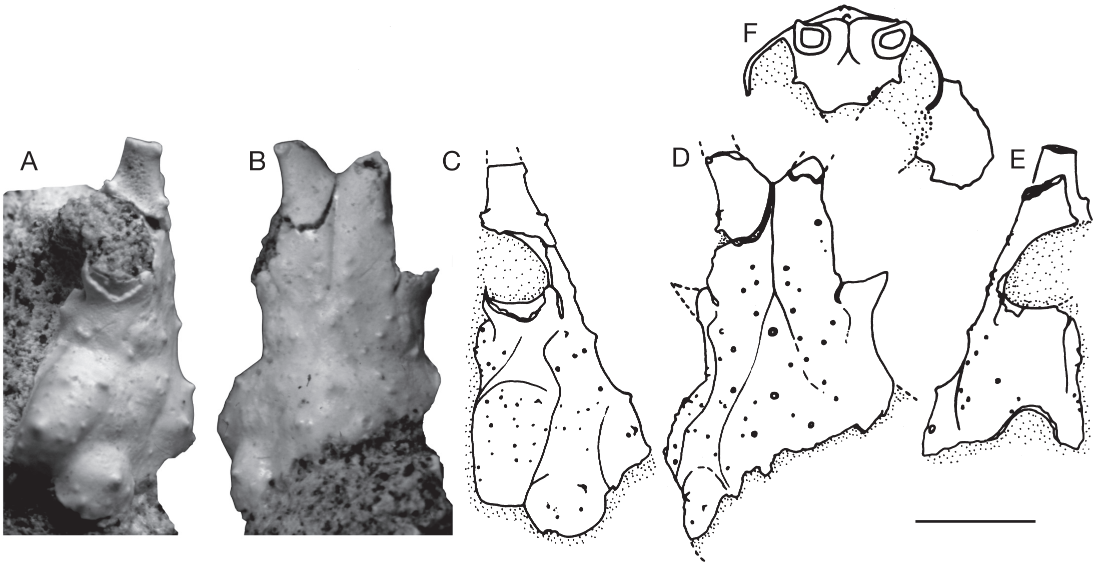

FIG. 4. — *Priscinachus elongatus* n. gen., n. sp., holotype (MNHN A27207), lower Cenomanian (Carcitanense-Mantelli), Fm Craie Glauconieuse, HG Montpinçon, Quarry of Le Billot, Notre-Dame-de-Fresnay, Calvados (France): **A**, **C**, left profile; **B**, **D**, dorsal; **E**, right profile, **F**, anterior. Scale bar: 5 mm.

buried. Most appear more or less allochtonous. Among the crabs listed above, only two species display a functional morphology of burrowers (or more probably the crabs were able to bury themselves). These are the raninids *Cretacoranina ornatus* and *Cenocorystes fournieri*, both being rare.

In contrast, the functional morphologies of the best represented species, *Plagiophtalmus oviformis* and of the rare spider crab, are not consistent with a burrowing, or even a burying behaviour (for the distinction between the burying and the burrowing activity, see Bellwood 2002). No living spider crab is known to burrow, but some pisids are able to partially bury themselves (personal observation). It is also possible that many of these crabs sheltered in open burrows in the hard-ground, during low-rate sedimentation episodes. Most living majoids are not known to have a cryptic habitat (under stones, in shells, fissures, etc.). Their protection strategy is commonly based on chemical defences, for instance by way of a quasi-permanent association with an urticant sea-anemone or by active allocrypty (*sensu* Minkiewicz 1907) with sponges, hydroids, bryozoans, seaweeds deliberately attached to the hooked setae of their body (hence their name of "decorator crabs": see Wicksten 1993), or by an automimicry ("automimèse" *sensu* Pasteur 1972; Boulard 1997) of the exuvia (Breton *et al.* 2004; Breton 2005). The numerous pits present on the carapace of the specimens of *Priscinachus elongatus* n. gen., n. sp. correspond to the bases of setae and I suppose that they allowed an active camouflage similar to that of the living majoids. However, it is not possible to ascertain such a protection strategy.

SYSTEMATIC PALAEONTOLOGY

Order DECAPODA Latreille, 1802
Infraorder BRACHYURA Latreille, 1802
Section EUBRACHYURA de Saint Laurent, 1980
Subsection HETEROTREMATA Guinot, 1977
Superfamily MAJOIDEA Samouelle,1818

Family PRISCINACHIDAE n. fam.

[For the classification of Majoidea we have followed Martin & Davis (2001) and Ng *et al.* (2008), but not Števčić (2005)].

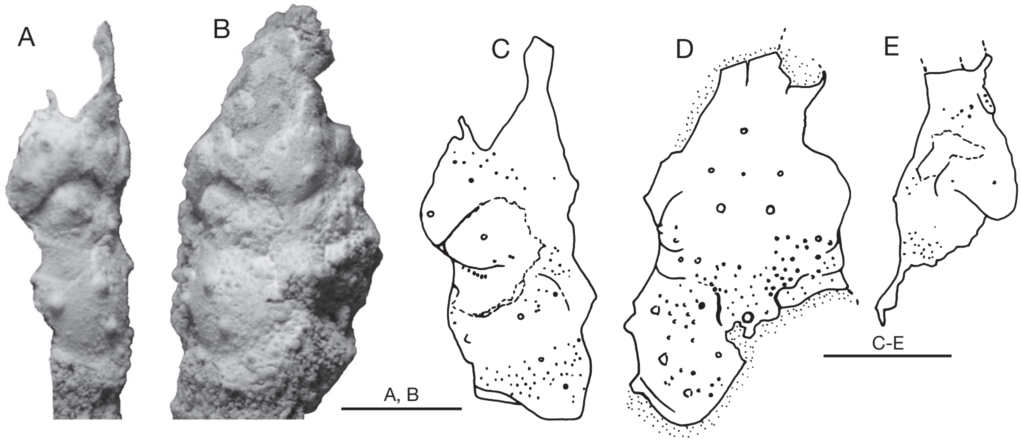

FIG. 5. — *Priscinachus elongatus* n. gen., n. sp., paratype 1 (MNHN A27208), lower Cenomanian (Dixoni), Fm Craie Glauconieuse, HG "Rouen 1", Pétreval, Annouville-Vilmesnil, Seine-Maritime (France): **A**, **C**, left profile; **B**, **D**, dorsal view; **E**, right profile. The differences between the drawing and the photo of A and C, and at a lesser extent, of B and D, come from slight differences of orientation of the fossil under the lens of the camera, and under the camera lucida of the stereomicroscope. Scale bars: 5 mm.

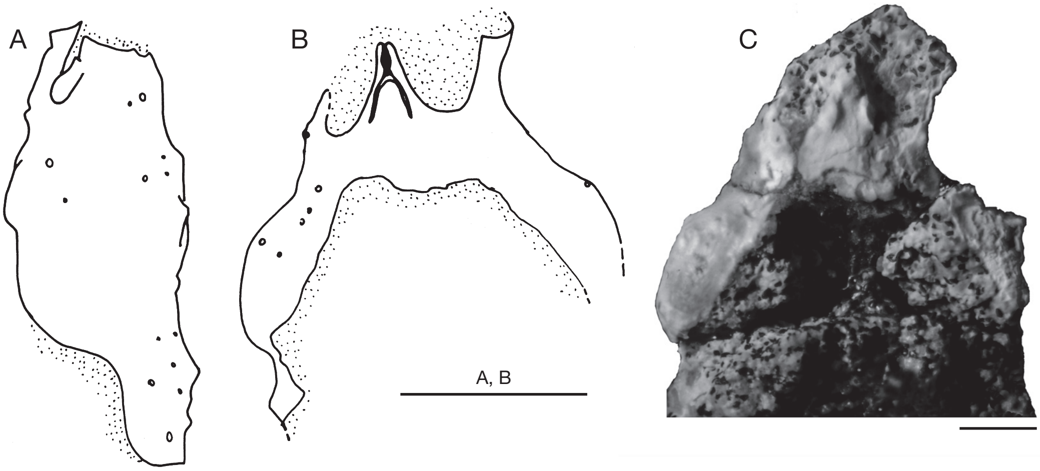

FIG. 6. — *Priscinachus elongatus* n. gen., n. sp., paratype 2 (MNHN A27209), lower Cenomanian (Dixoni), Fm Craie Glauconieuse, HG Rouen 1, Pétreval, Annouville-Vilmesnil, Seine-Maritime (France): **A**, left profile; **B**, **C**, ventral (epistome). Scale bars: A, B, 5 mm; C, 2 mm.

DIAGNOSIS. — Carapace pyriform, elongate. Meso- and metabranchial lobes differentiated. Rostrum bifid, with two stout divergent horn-like tips. Orbits large, directed forward, with a developed eave.

REMARKS

The new taxon described herein displays a unique combination of characters, which substantially distinguishes it from any other majoid (see below). Therefore, a new family, Priscinachidae n. fam. is erected to accommodate this new genus. *Priscinachus* n. gen. is the type genus. The distinctive features of these taxa are examined in the discussion.

Genus *Priscinachus* n. gen.

TYPE SPECIES. — *Priscinachus elongatus* n. sp., designated herein.

DIAGNOSIS. — Carapace small, twice as long as wide, with elongate pyriform outline, maximum width at ⁴⁄₅ distance posteriorly (metabranchial lobes), maximum height at mid-length (mesogastric lobe). Mesogastric, cardiac, hepatic, mesobranchial and metabranchial lobes conspicuous, swollen. Grooves rather faint, as shallow depressions. Rostrum large, bifid, with divergent tips. Orbits directed forward. One supraorbital fissure. Ornamentation consisting of dense, very fine setal pits with, among them, numerous spiny tubercles of different sizes.

ETYMOLOGY. — *Priscus*, a, um: antique, ancient, *Priscinachus elongatus* n. gen., n. sp. being thought to be the first known representative of majoids; *-inachus* from the generic name of a living sea-spider. Gender: masculine.

RANGE. — Lower Cenomanian.

Priscinachus elongatus n. gen., n. sp.
(Figs 3-8)

TYPE MATERIAL. — The specimen MNHN A27207 is designated as the holotype (Figs 3A; 4). Paratype 1: specimen MNHN A27208 (Figs 3B; 5). Paratype 2: specimen MNHN A27209 (Figs 3C; 6). Paratype 3: specimen MNHN A27210 (Fig. 7).

ETYMOLOGY. — From the Latin, *elongatus*, a, um: elongated.

STRATIGRAPHIC AND GEOGRAPHIC ORIGIN OF THE TYPES. — Holotype and paratype 3: discussed quarry of Le Billot, Notre-Dame-de-Fresnay (Calvados, France), lower Cenomanian, Craie Glauconieuse Fm (Mantelli). Paratypes 1 and 2: small valley of Pétreval, Annouville-Vilmesnil (Seine-Maritime, France), lower Cenomanian, Craie Galuconieuse Fm (Dixoni).

DIAGNOSIS. — As for the genus.

DESCRIPTION

No complete carapace is known. The holotype is represented by the anterior half of a carapace, from the rostral spines (the tips of which are broken) up to the mesogastric lobe, and a portion of the mesobranchial lobe. The preserved part of paratype 1 extends from the rear of the orbits to the posterior margin. Carapace of paratype 2 is less well preserved – from orbital to cardiac regions – but retains the epistome. Paratype 3 a poor fragment of carapace, mesogastric to cardiac lobes and part of right hepatic to metabranchial lobes.

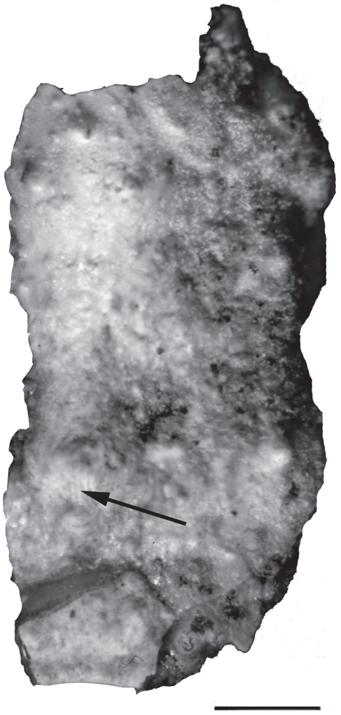

FIG. 7. — *Priscinachus elongatus* n. gen., n. sp, paratype 3 (MNHN A27210), lower Cenomanian (Carcitanense – Mantelli), Fm Craie Glauconieuse, HG Montpinçon, quarry of Le Billot, Notre-Dame-de-Fresnay, Calvados (France), dorsal view. The arrow indicates the tiny, scratch-like grooves, which surround the two cardiac spiniform tubercles. Scale bar: 2 mm.

Carapace small, overall shape cylindro-conical, slender anteriorly, elongate pyriform, widest at position of metabranchial lobes (posterior ⁴⁄₅), highest at mid-length (mesogastric lobe). $l/L = 0.5$; $h/L = 0.3$ to 0.4.

Lobulation of the carapace defined by bulging areas. Grooves weakly marked. Frontal lobe not well delimited, a median sulcus in the continuation of the bifid rostrum. This sulcus divided posteriorly into two branches which form the top of a triangular, elongated mesogastric lobe. Two gastric pits (paratype 3). Urogastric lobe entire. Cardiac lobe raised, delimited by two sigmoid, deep and short grooves. Intestinal lobe not preserved. Hepatic lobe lateral, strong, obliquely elongated and overhanging. Cervical groove faint, horizontal. Mesobranchial lobe smaller, rounded, less tumid, less lateral than hepatic lobe.

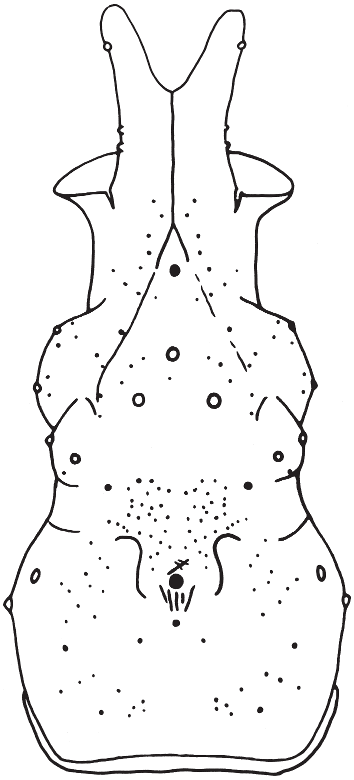

FIG. 8. — *Priscinachus elongatus* n. gen., n. sp., diagrammatic reconstruction, dorsal view. Not to scale.

Metabranchial lobe the largest, regularly rounded and tumid, delimited from the mesobranchial lobe by a wide shallow depression lined by small tubercles, interrupted before its junction with the sigmoid lateral grooves of the cardiac lobe. Lateral margin straight, overhung nearly all its length by branchial lobes. Posterior margin incompletely preserved, lined by a depression. Rostrum (pseudorostrum) large, bifid, with a U-shaped or lyre-shaped pair of stout horn-like rostral spines, fused posteriorly, diverging anteriorly. Base of the basal antennal article slightly behind the orbit, seems to form the ventral rim of the orbit, but does not seem to coalesce with the epistome. Presumed right urinal opening (nephropore) far from base of antenna, near anterior limit of the hepatic lobe (paratype 2). Orbits directed forward, large, supraorbital eave interrupted by a fissure. Epistome showing as an anterior, stout process, triangular in profile with two posterior divergent ridges, behind alignment with antennular fossae.

ORNAMENTATION

Numerous spiniform tubercles of various sizes, the most conspicuous being three mesogastric, forming a triangle, and two median cardiac, the anterior one larger (Figs 4; 8). A dense pattern of fine pits, presumably for insertion of setae. Spiniform tubercles and pits seemingly more dense on the posterior half of the carapace. On cardiac lobe of paratype 3, about 20 scratch-like, minute grooves, longitudinal medially, oblique laterally, crossed anteriorly, surrounding the two cardiac tubercles.

MEASUREMENTS

See Table 1.

OCCURRENCES

The only known specimens are those of the type series: lower Cenomanian, western Paris Basin, France.

DISCUSSION

COMPARISON OF THE PRISCINACHIDAE N. FAM. WITH OTHER MAJOID REPRESENTATIVES

Ng *et al.* (2008) recognized, within the superfamily Majoidea Samouelle, 1819, the following extant families:

1. the Majidae Samouelle, 1819, includes four extant subfamilies among which are the Majinae Samouelle, 1819, and the Mithracinae MacLeay, 1838. The Micromaiinae Beurlen, 1930 (erected provisionally by Beurlen in 1930) is only known as fossils. Majines and mithracines are also known from the Cenozoic;
2. the Inachidae MacLeay, 1838. One inachid genus is known from the Eocene of Pakistan;
3. the Inachoididae Dana, 1851. One Eocene representative is known from Venezuela;
4. the Oregoniidae Garth, 1958;
5. the Epialtidae MacLeay, 1838, includes the Epialtinae MacLeay, 1838; the Pisinae Dana, 1851 (known as fossils since the Miocene); the Pliosomatinae Števčič, 1994, and the Tychiinae Dana, 1851;

TABLE 1. — Measurements (in mm) of the holotype and paratypes of *Priscinachus elongatus* n. gen., n. sp. Abbreviations: **L**, length; rostral spines excluded; **h**, height; **l**, width.

	Holotype	**Paratype 1**	**Paratype 2**	**Paratype 3**
L preserved	15.7	15.4	17.8	14.0
L estimated	26.0	17.5	22.6	18.4
l preserved	10.0	7.0	11.5	
l max estimated	12.5	8.0	11.5	
h preserved	6.9	7.3	6.5	
h max estimated	7.0	7.3	8.0?	

(6). Ng *et al.* (2008) added, provisionally, the Hymenosomatidae MacLeay, 1838.

Ng et al. (2008) stated that:

1. the majoids (together with the Hymenosomatidae) are monophyletic;
2. the characters traditionally, used for example by Griffin & Tranter (1986), dealing with the rich Indo-West Pacific fauna, to separate the families are often too vague and subjective. Most workers then prefer work directly with genera instead of considering families. Indeed, many of these families and subfamilies are poorly defined;
3. members of Oregoniidae are thought to be rather primitive majoids; the Majinae and Mithracinae form a second group, characterized by the possession of complete or almost complete orbits, presence of specialized hook setae for carrying objects, and with relatively broad basal antennal article. Both the Inachidae and Inachoididae are different from the other majoids in the form of their carapace (whether they are closely related together or inachoids could be a subfamily of the Inachidae is discussed by Ng *et al.* 2008). Epialtidae (i.e. Pisinae, Tychiinae and Epialtinae) is the most heterogeneous family and the subfamilies as well as the genera are often difficult to separate, all having orbits that are poorly developed or absent.

I add to the extant majoid families a seventh, albeit extinct family, the Priscinachidae n. fam., defined herein (see above). The comparison of this new family with other majoids, especially with their extant representatives, is difficult because the extant taxa are defined at familial, subfamilial or generic level (sometimes poorly; see Ng *et al.* 2008: 98, 99) by characters of the ventral side, of the appendages or by larval characters (see, for example, Marques & Pohle 1998) that are not available for this new fossil family, of which only the carapace morphology is known. For instance, Garth (1958), when providing a diagnosis of his new subfamily Oregoniinae, considered only the male abdomen and the male first pleopod.

Moreover, the following characters of the carapace are often variable within one family, one subfamily or even one genus of the extant majoids: overall shape; ratio L/l of the carapace; ornamentation; size and orientation of the orbits; presence and size of the supraorbital eave and postorbital spine; basal article of antenna; structure, size and shape of the rostrum.

Priscinachidae n. fam. vs. Hymenosomatidae

With their carapace which is thin and flat, triangular to subcircular, devoid of orbits, and with a short rostrum, the Hymenosomatidae share nearly no diagnostic character with the Priscinachidae n. fam.

Priscinachidae n. fam. vs. Oregoniidae

In the family Oregoniidae, defined by Garth (1958) on the basis of the male abdomen and the first pleopod only, the characters of the carapace are very variable: outline triangular, pyriform, lyrate, shield-shaped, never long; surface varying from unornamented to tuberculate or spinose. Rostrum varying from two flat triangular short horns, that are divergent (*Oregonia* Dana, 1851 *pars*; *Chionoecetes* Krøyer, 1838, illustrated herein, Fig. 9) or not divergent (*Hyas* Leach, 1814), to two long slender parallel horns (*Oregonia pars*). Postocular tooth or spine. Supraocular eave present, fissured (*Hyas*; *Chionoecetes* spp.) or

TABLE 2. — Some instances of Eocene spider crab (Majoidea). Taxonomic list of genera and references not exhaustive.

Genus	Family Subfamily	Distribution Country	References
Periacanthus Bittner, 1875	Majidae	Great Britain Hungary Spain Italy	Lörenthey & Beurlen 1929 Via Boada 1969 Quayle & Collins 1981 De Angeli & Beschin 2001 Beschin *et al.* 2005
Micromaia Bittner, 1875	Majidae Micromaiinae	Great Britain Hungary Spain Italy Egypt Senegal	Lörenthey & Beurlen 1929 Gorodiski & Remy 1959 Via Boada 1969 Quayle & Collins 1981 De Angeli & Beschin 2001 Beschin *et al.* 2002
Pisomaja Lörenthey, 1929	Majidae Micromaiinae	Hungary	Lörenthey & Beurlen 1929
Mithracia Bell, 1858	Mithracidae	Germany Italy	Förster & Mundlos 1982 Larghi 2002
Eoinachoides Van Straelen, 1933	Inachoididae	Venezuela	Van Straelen 1933
Pyromaja Stimpson, 1871	Inachidae	Pakistan	Collins & Morris 1978

absent (*Oregonia*). Basal antennal article varying from large (*Hyas)* to narrow (*Oregonia*). Most of the characters of the carapace of Priscinachidae n. fam. could then be found in oregoniids, but scattered between different genera, or even species, and not combined together in a single taxon. The overall shape of the carapace, its elongation, the development of the orbits and orbital eave, the two stout divergent rostral horns distinguish the Priscinachidae n. fam. from all the known oregoniids.

Priscinachidae n. fam. vs. Epialtidae

The characters of the carapace of the Epialtidae are also very variable. The carapace is generally short, but it can be also longer than wide. Its shape is variable: subdeltoid (Pisinae), with subparallel sides (*Acanthonyx* Latreille, 1828; *Pugettia* Dana, 1851) or rounded (*Taliepus* A. Milne-Edwards, 1878). Carapace is commonly spinose. The rostrum is either simple or bifid, the rostral spines are parallel or divergent, slender or stout, varying from short (*Pitho* Bell, 1835) to long or very long (*Sphenocarcinus* Milne-Edwards, 1878). The orbits are directed laterally (Epialtinae, Tychiinae and Pisinae *pars*), oblique or directed forward (Pisinae *pars*). The orbits are reduced. The supraocular eave is often produced forward as a spine in the Pisinae, can occur in the Epialtinae (for instance in *Menaethiops* Alcock, 1895, see Rathbun 1925: 189) and is developed in *Tyche* Bell, 1835. Basal antennal article triangular to trapezoidal. The same observation can be made as for Oregoniidae: I can quote several characters of the carapace of Priscinachidae n. fam. in Epialtidae, but never combined together in one genus or one subfamily. The large orbits directed forward, the shape of the rostrum and the overall shape of the carapace differentiate Priscinachidae n. fam. from any Epialtidae.

Priscinachidae n. fam. vs. Inachoididae

The carapace of inachoidids is subpyriform to triangular, never elongate, spiny to tuberculate or granulate (or both: *Pyromaia* Stimpson, 1871), the regions are well defined. Rostrum very short or short, entire or bifid, often triangular. No orbit, no suparorbital eave, but a supraorbital arch can be present (*Collodes* Stimpson, 1860, *Euprognatha* Stimpson, 1871) separated by a fissure from the postorbital spine. Postorbital lobe distinct, projecting laterally, forming a spine which can be prominent (*Anasimus* A. Milne-Edwards, 1880, *Arachnopsis* Stimpson, 1871). Basal antennal article varying from flat, fused to the carapace to long and narrow, tapering anteriorly (*Pyromaia*). Inachoididae seem morphologically closer to Priscinachidae n. fam. than Epialtidae or Oregoniidae: the main differences are the absence of orbit or of a developed eave, and a shorter carapace.

Priscinachidae n. fam. vs. Inachidae
Garth (1958: 37) quoted the following characters of the carapace in the diagnosis of the Inachidae: "Eyes without orbits, eyestalks generally long, either non-retractile or retractile against sides of carapace or against an acute postocular spine affording no concealment. Basal article of antennae extremely slender throughout its extent, and usually long [and free from its base or partly fused.]" Griffin & Tranter (1986: 3) added that "[inachids are] generally regarded as a discrete group of small majids [= majoids] with long eyestalks unprotected above by orbits, […] some with a double rostrum and others with a single rostrum". The carapace is often pyriform or triangular, but, less commonly, may be elongate and subcylindrical (*Anomalothir* Miers, 1879). The regions can be tumid (*Inachus* Weber, 1795, *Macropodia* Leach, 1814). Meso- and metabranchial lobes rarely differentiated, the *Macropodia* species rarely showing such a differentiation (Forest & Zariquiey Alvarez 1964; Forest 1978). Carapace spinous or tuberculate to smooth (*Stenorhynchus* Lamarck, 1818). The rostrum can be simple and slender (*Erileptus* Rathbun, 1894), absent (*Chalaroacheus* De Man, 1902), bifid, with spines either contiguous or separate (*Eucinetops*), directed laterally or forward. There is no preorbital spine. A small to conspicuous postorbital spine is present and, uncommonly, a rudimentary orbital eave (*Cyrtomaia* Miers, 1886), with a fissure (*Chalaroacheus*, *Chorinachus* Griffin & Tranter, 1986, *Sunipea* Griffin & Tranter, 1986). *Priscinachus* n. gen. shares with Inachidae a pyriform shape of the carapace, tumid regions, a spinous carapace, and a two-horned rostrum. The well-developed, forward directed orbit, with a large fissured eave, but devoid of spines, does not allow the placement of *Priscinachus* n. gen within the family Inachidae. Nevertheless, I assume that the prischinachids and the inachids are closely related.

Priscinachidae n. fam. vs. Majidae s.s.
The carapace of the Majidae is rarely much longer than wide. The carapace shape varies from subpyriform to subcircular (Majinae, Micromaiinae), from irregularly subrectangular (Planoterginae) to wider than long, from depressed to vaulted (Eurynolambrinae); it may be also subpyriform ovate to oblong ovate. The carapace can be widened anteriorly by orbits (*Mithrax spinosissimus* (Lamarck, 1818), *Macrocoeloma* Miers, 1879). The dorsal surface is unarmed, spiny or tuberculated. The rostrum varies from small (Planoterginae; Micromaiinae; some Mithacinae: *Thoe* Bell, 1835, *Mithrax* spp. Desmarest, 1823) to developed, generally with more or less long straight spines (Majinae; some Mithracinae) diverging from their base. The eyes are either unprotected (Planoterginae) or protected by a nearly complete orbit, often large (Mithracinae, Majinae). The orbit is formed by a supraorbital eave and postorbital spine; it may be tubular (Mithracinae). The Micromaiinae have incomplete small orbits, directed forward, with a postorbital spine. When large, the carapace widens at the level of the orbits. The basal antennal article may be very broad, and sometimes forms the floor of the orbit (Majinae, Mithracinae). The Priscinachidae n. fam. share with the Majidae developed orbits, with a supraorbital eave, protecting the eye, but the Priscinachidae n. fam. lack a developed postorbital spine. Overall shape of the carapace, ornamentation, and rostrum of priscinachids are closer to inachids than majids.

OCCURRENCE OF FOSSIL SPIDER-CRABS

Especially during the middle-upper Eocene, spider crabs are found nearly all over the world. They are relatively common and diversified, distributed within at least three families, and some genera such as *Micromaia*, include several species (Table 2).

Contrasting with this flourishing representation, the Cretaceous record of spider crabs is very poor, as already noted by Glaessner (1969), Collins & Morris (1978) and Vega *et al.* (1995). *Stenociops primus*

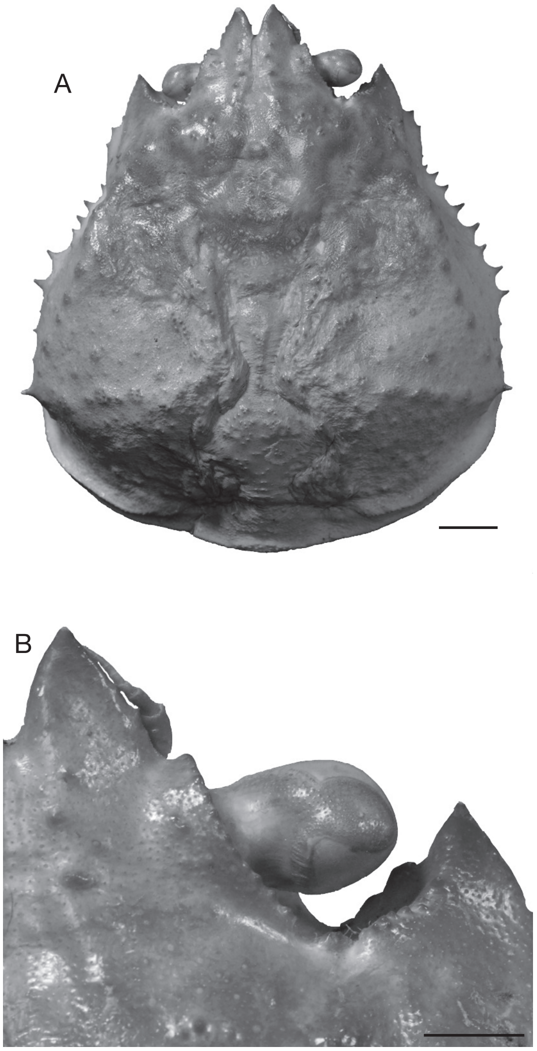

FIG. 9. — *Chionoecetes* sp., carapace of a stuffed crab from a Chinese grocery: **A**, overall view; **B**, detail of the orbital region with an unprotected eye. Scale bars: A, 10 mm; B, 5 mm.

Rathbun, 1935, from the early Campanian of the USA, is based upon a unique “proximal portion of a right manus” and was assigned to the Majidae only with respect to its strong resemblance to that of a living *Stenociops* (Rathbun 1935). Bishop (1986: 137) quoted this species as “poor” i.e. “material and description inadequate”. Vega *et al.* (1995) assigned to the Majidae, with reservation, the carapace (frontal and anterolateral regions missing) of an unnamed, moderately small crab, pyriform in outline and coarsely pustulose. This occurrence provides a possible Maastrichtian spider crab (Majidae, Micromaiinae), but such a placement is equivocal in the absence of the front and anterolateral regions. The oldest known unequivocal majoid species is *Pyromaia inflata* Collins & Morris, 1978, from the lower Eocene of Pakistan. Discussing the ancestry of *Pyromaia* Stimpson, 1871 (a genus ranging from Eocene to Recent), and of the Majoidea, Collins & Morris (1978: 965) remarked about this hypothesis: “An ancestry through the Oxystomata and *Latreillia* […], now assigned to the family Latreillidae within the Dromiacea […] has been suggested. In further support of a dromiacean origin, the marked resemblance of [*Pyromaia inflata*] to *Rathbunopon* (particularly *R. woodsi* (Withers) […] cannot be overlooked.”

PROTECTION OF THE EYE AND MASKING BEHAVIOUR OF MAJOIDS

I am not sure that *Priscinachus* n. gen. was covered with hooked setae. The basal pits of setae are preserved, but these setae, if they were not hooked or hamate, did not permit attachment of foreign material on the exoskeleton, known as “masking” and “generally assumed to be primarily a means of concealment from predators” (Szebeni & Hartnoll 2005: 3795; see also Breton *et al.* 2004). It could be supposed that such a camouflage behaviour makes unnecessary any further protection, for instance, of the eyes as illustrated by living inachids. This hypothesis is unsatisfactory because some majids have both protected eyes and masking behaviour (personal observations), and the role of the upper part of the orbit or of an eave is ambiguous. If we consider, for example, an oregoniid such as *Chionoecetes* sp., the unprotected eye is well visible in dorsal view (Fig. 9), but the absence of any eave extends the visual field upwards (except for the median part of the cornea devoid of ommatidia) and the crab is better detecting the approach from above of a predator. It is then plausible that the presence or absence of an orbit or an eave and a protection strategy as masking behaviour are characters which evolve independently.

PHYLETIC RELATIONSHIPS OF THE PRISCINACHIDAE N. FAM.

Though the morphological resemblance cannot be retained as a conclusive argument for a phyletic origin, it must be pointed out that *Priscinachus elongatus* n. gen., n. sp. superficially resembles *Heeia villersensis* (Hée, 1924), present in the Cenomanian beds at Pétreval. Worn specimens lacking frontal region and ornamentation are particularly misleading (cf. the illustration of Hée 1924: pl. 5, fig. 1a, b). *Priscinachus elongatus* n. gen., n. sp. can be distinguished from elongate prosopids by its very spinose ornamentation, rostrum and orbits.

Priscinachus elongatus n. gen., n. sp. cannot be satisfactorily placed within any subfamily or be considered as a member of a new subfamily within a known family of the Majoidea. I thus erect a new family, the Priscinachidae n. fam. A priscinachid is at best defined as an inachid-like spider-crab having the orbits and orbital eaves of a majid. The phyletic relations of priscinachids are thus not clear.

Assuming hypothetically, on the sole account of its cylindrical elongate carapace with inflated regions, that *Priscinachus* n. gen. evolved from a Jurassic or an early Cretaceous prosopid, its orbits and orbital eaves show as derived character since its supposed ancestor had no device for the protection of the eye. Then, the possible direct descendants of *Priscinachus* n. gen. are more probably the majids, some members of which have well developed orbits, rather than the inachids, for which we should postulate a reversion of the development of the orbit. But all this remains very hypothetical, owing the long lack of fossil majoids, at least during 40 million years. New finds of Cretaceous spider-crabs are necessary to better understand the phyletic relationships of *Priscinachus* n. gen.

CONCLUSION

Contrasting with a wealthy Cenozoic record, the Cretaceous record of spider crabs is poor and mainly dubious. *Priscinachus elongatus* n. gen., n. sp., of which four specimens are now known from the Cenomanian of the western Paris Basin, is an early representative of these heterotreme crabs. It displays original morphological characters of the carapace which allow its placement in a new family within the Majoidea. As a consequence, the ancestry of the Majoidea is established as Cenomanian or older in age.

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