

An ‘Elvis’ echinoid, *Nucleopygus (Jolyclypus) jolyi*, from the Cenomanian of France: phylogenetic analysis, sexual dimorphism and neotype designation

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Abstract

Newly collected specimens of an uncommon and poorly known irregular echinoid, *Nucleopygus (Jolyclypus) jolyi*, are recorded from Cenomanian strata in Charentes (western France). The first examples of this echinoid to have been described date back to the late nineteenth century; those specimens (i.e., the types) appear to have been lost. What particularly distinguishes this taxon from other Cenomanian echinoids is the singular combination of derived and plesiomorphic morphological characters, the latter being reminiscent of Jurassic irregular echinoids. Derived features concern the appendages, employed in locomotion and feeding, whereas ancestral characters involve the apical system and periproct. This peculiarity has led previous workers to include this echinoid in the stem-group Galeropygidae, which would imply a >40-myr gap in the stratigraphic range of this group or, alternatively, challenge the stratigraphic provenance of the taxon. A detailed examination of newly collected material has now allowed us to resolve the apparent discrepancies, describe a reversal and document sexual dimorphism as well. A phylogenetic analysis was carried out in order to revise the systematic position of the taxon, now transferred to the Cretaceous genus *Nucleopygus*. A neotype is designated.

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1. Introduction

Erwin and Droser (1993) created the concept of ‘Elvis taxa’ to describe the phenomenon of convergent evolution which makes new forms appear similar to pre-existing taxa. They stressed the problem of extensive homoplasy which hinders the recognition of ‘Lazarus taxa’ (Jablonski, 1986) in the context of recovery after mass extinctions. Apart from the context of recovery, homoplasy is a common phenomenon in echinoid evolution. It results from the adaptation of species to similar ecological niches (Kier, 1962, 1974; Smith, 1978, 1981, 1984, 2001; Néraudeau and Moreau, 1989; Kanazawa, 1992;

Suter, 1994; Néraudeau, 1995; Wilkinson et al., 1996; Villier et al., 2004), and tells us about the role played by internal constraints on morphological evolution as well (Jesionek-Szymańska, 1963; Mintz, 1966; Kier, 1974; Saucède et al., 2003). This frequency of homoplastic changes makes them difficult to detect (Suter, 1994), which in turn may lead to taxonomic artefacts and distortion of our apprehension of echinoid evolution. Among homoplastic changes, reversals are rarely documented in echinoid evolution. However, following the example of ‘Elvis taxa’, they make taxa appear similar to pre-existing forms, albeit in the context of common ancestry. Here we show how reversal may lead to taxonomic misconception and to conclusions about stratigraphic incongruence, when such is not detectable by a careful examination of morphological characters.

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Echinoid diversity was severely affected by the Late Palaeozoic and Triassic biotic crises (Kier, 1984), after which it recovered and distinctly increased during the Early Jurassic (Sprinkle, 1983) with the appearance of a new group, the irregular echinoids (Kier, 1974, 1977; Smith, 1984, 1988; Saucède, 2002). This type of echinoid is mostly distinguished from other regular, globose echinoids by bilateral symmetry, which appears secondarily during growth and alters the pentaradial shape of the test. This event corresponds to the migration of the periproct, i.e. the external feature containing the anus, out of the apical system, a circular structure formed by ten elements, the genital and ocular plates. This phenomenon is called ‘exocyclism’, and appears as early as the Early Jurassic. The oldest known irregular echinoids, such as *Plesiechinus hawkinsi* (Sinemurian, Nevada) and *Loriolella ludovicii* (Domerian, Italy), still retain the pattern observed in regular echinoids, namely that the periproct is enclosed by the genital and ocular plates (Jesionek-Szymańska, 1970; Smith and Anzalone, 2000). However, the periproct becomes more eccentric during growth and tends to stretch the posterior plates of the apical system that enclose it. In later irregular echinoids, periproct migration initiates very early during growth, prior to the closure of the apical system, and posterior plates are no longer elongated (Gordon, 1926). This evolutionary trend of the periproct to migrate away from the apical system is realised during the entire Jurassic, so that exocyclism is achieved very progressively in different subgroups of irregular echinoids (Jesionek-Szymańska, 1963; Mintz, 1966). In the Microstomata, an important subset of irregular echinoids to which the present species belongs, the gradual migration of the periproct is accompanied by the development of a deep anal groove. This groove is well developed in species of Middle and Late Jurassic age, but becomes less prominent by the Cretaceous when the periproct moves away from the apical system and finally leaves it, to reach the test margin, or even the oral surface.

Periproct migration is not the only event to characterise the evolution of irregular echinoids. Other morphological innovations occurred as well, all linked to colonisation of and adaptation to new behavioural patterns and habitats, mostly controlled by the nature of the sea floor in and upon which irregular sea urchins fed. Among the principal innovations are the anterior displacement of the mouth, the evolution of tubercle morphology and arrangement which demonstrates locomotory specialisation, and modification of ambulacral podial pores which reflects the development of a more efficient food particle picking mechanism (Telford and Mooi, 1996).

Hitherto, the only material of *Nucleopygus (Jolyclypus) jolyi* known was the original collection described by Gauthier (1898). Now, we have newly collected specimens that allow us to revise this taxon. It is distinct from other Cenomanian echinoids by showing a peculiar combination of derived and ancestral morphological characters, the latter being reminiscent of Jurassic irregular echinoids. Previously, mostly ancestral characters (Gauthier, 1898; Lambert, 1918, 1920; Mintz, 1966) received attention, and this taxon was assigned to the Jurassic family Galeropygidae. Such an assignment would imply a >40-myrr gap in the stratigraphic range of that family.

Alternatively, when derived characters are considered more important and the taxon is compared to any one of its contemporaries, ‘ancestral-like’ features must be explained by reversal. In the present paper, the phylogenetic position of *Nucleopygus (Jolyclypus) jolyi* is reappraised, considering apomorphies shared with the genus *Nucleopygus* and reversal of some characters to the ancestral states.

2. Geological setting and stratigraphy

The echinoids described here have been collected mainly from Cenomanian strata that crop out on the Ile Madame off the west coast of France (Charente-Maritime; Fig. 1). We have nine specimens from there, three of which come from a bioclastic marly lens in the uppermost lower Cenomanian, at the boundary between lithological subunits B3 and C1 (Fig. 2), as defined by Néraudeau and Moreau (1989). The other six are from a silty, bioclastic limestone level in the lowest upper Cenomanian unit (Fig. 2), lithological unit F (sensu Néraudeau and Moreau, 1989). Another specimen stems from unit F (Cenomanian) at La Couronne, near Angoulême (Charente, SW France; Fig. 1).

In view of the rarity of this echinoid, the recent discovery of ten new specimens is of importance, since, like Kier (1962) and Mintz (1966), we have been unable to trace any of the specimens described by Gauthier (1898), which we presume to have been lost. In the absence of the original specimens, and in view of their peculiar morphology, Kier (1962, 1966) expressed doubts over the stratigraphic provenance of the material as indicated by Gauthier (1898) and Lambert (1918).

The uppermost lower Cenomanian (B3/C1 boundary) of Ile Madame comprises a marly and bioclastic lens, with an abundant benthic fauna of brachiopods (*Terebratulina biplicata*), crinoids (*Pentacrinus cenomanensis*), asteroids (astropectinids, *Caletaster romani*) and oysters (*Rastellum carinatum*, *Rhynchostreon suborbiculatum*). Such an assemblage is typical of an infralittoral setting (sensu Néraudeau and Floquet, 1991; Néraudeau et al., 2001). Echinoids are common as well, predominantly the saleniid *Hyposalenia acanthoides* and a few irregular species such as *Archiacia sandalina*, *Catopygus carinatus*, *Echinogalerus faba* and *Nucleopygus similis*.

In addition to echinoids, unit F (upper Cenomanian) yields mainly brachiopods (*Gemmarcula menardi*, *T. biplicata*), rudistid bivalves (*Ichthyosarcolithes triangularis*, *Radiolites fleuriau*), oysters (*Rastellum diluvianum*, *R. carinatum*, *Rh. suborbiculatum*) and asteroids (astropectinids, *C. romani*), which are regarded as typical of nearshore, infralittoral environments (Videt, 2004). Echinoids are more abundant and show a higher diversity than in the uppermost lower Cenomanian. The commonest taxa are the regular species *Polydiadema aff. tenue*, *Temnocidaris cenomanensis* and *Tetragramma variolare*, and the irregulars *Archiacia santonensis*, *C. carinatus*, *Coenholectypus excisus*, *E. faba*, *Mecaster cf. grossouvrei* and *Nucleopygus aff. parallelus*.

Among irregular echinoids, cassiduloids and holoctypoids are well represented at both levels, in particular by small cassiduloids (*Catopygus*, *Nucleopygus*), which generally are

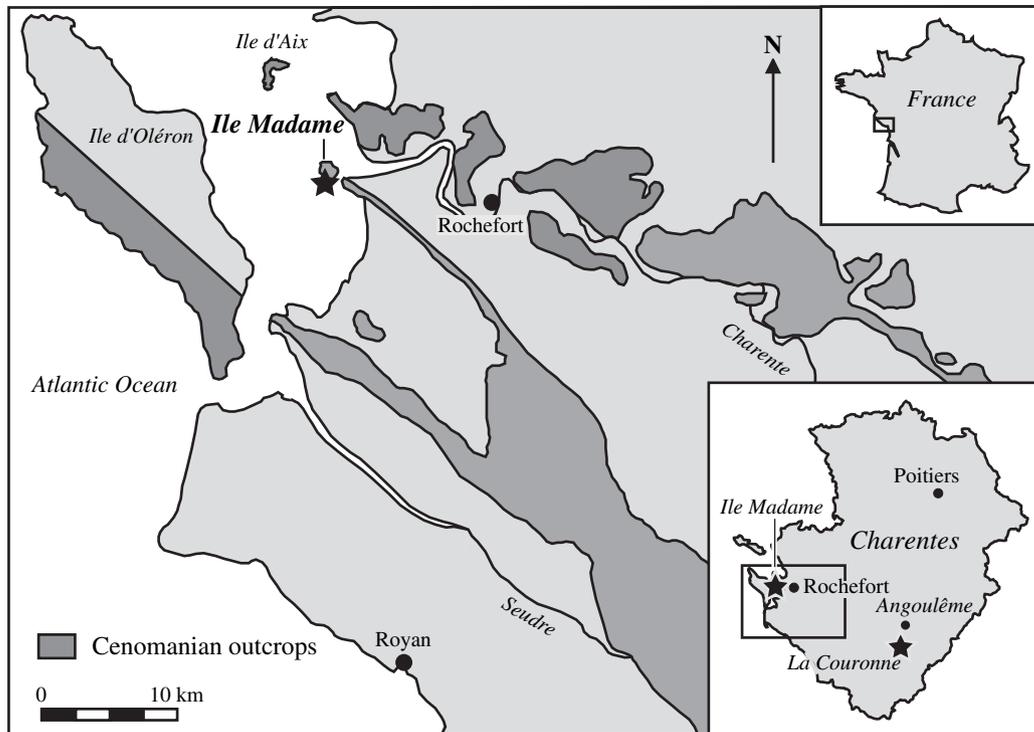


Fig. 1. Map showing localities (black stars) from where *Nucleopygus (Jolyclypus) jolyi* has been collected, on Ile Madame and at La Couronne near Angoulême.

common in fine sand as well as in silty and clayey deposits (Néraudeau and Moreau, 1989).

Gauthier (1898) failed to indicate the exact stratigraphic level in the Angoulême area from which he had collected his material of *Galeropygus jolyi*. However, judging from the associated echinoid fauna he listed, we assume that his material could not have come from the B3/C1 boundary (uppermost lower Cenomanian), but must have originated from unit F (upper Cenomanian). In addition, in the Angoulême area where Gauthier collected, the facies from which a new specimen (mentioned above) has recently been recovered, is considered to be unit F of the upper Cenomanian.

3. Systematic palaeontology

Repositories. The specimens mentioned below are housed at the following locations: MNHN-DHT, Collections du Domaine Sciences de la Terre du Muséum National d'Histoire Naturelle de Paris; Niort Museum.

Order: Cassiduloida Claus, 1880

Family: Cassidulidae Agassiz and Desor, 1847

Genus *Nucleopygus* Agassiz, 1840

Type species. *Nucleopygus minor* Desor, 1842, by subsequent designation of Lambert (1898).

Subgenus *Jolyclypus* Lambert, 1918

Type species. *Galeropygus jolyi* Gauthier, 1898, by monotypy.

Nucleopygus (Jolyclypus) jolyi (Gauthier, 1898)
Figs. 3–5

1898 *Galeropygus jolyi* Gauthier, pp. 837, 838.

1918 *Galeropygus (Jolyclypus) jolyi* Gauthier: Lambert, p. 26.

1920 *Jolyclypus jolyi* (Gauthier): Lambert, p. 166.

1921 *Galeropygus (Jolyclypus) jolyi* Gauthier: Lambert and Thiéry, p. 337.

1948 *Jolyclypus jolyi* (Gauthier): Mortensen, p. 110.

1962 *Jolyclypus jolyi* (Gauthier): Kier, p. 227.

1966 *Jolyclypus jolyi* (Gauthier): Kier, p. 523.

1966 *Jolyclypus jolyi* (Gauthier): Mintz, p. 32.

1968 *Jolyclypus jolyi* (Gauthier): Mintz, p. 1275.

Neotype. Specimen MNHN-DHT R65001 (see Figs. 3A, B; 5A, B) is here designated neotype. This definition meets the qualifying conditions specified in article 75 of the International Code of Zoological Nomenclature. We have attempted to trace the original material, and failed, which is why we considered the type to have been lost. The neotype clarifies the taxonomic status of *Nucleopygus (Jolyclypus) jolyi*, being supported by a phylogenetic analysis, and is consistent with what is known from the original description by Gauthier (1898) in having been collected from the same area and stratigraphic level as the original type.

Diagnosis. Test distinguished by low profile, with maximum height situated slightly anterior to centre, close to apical system. Anterior edge of test rounded and posterior margin acuminate and pointed upwards. Apical system eccentric

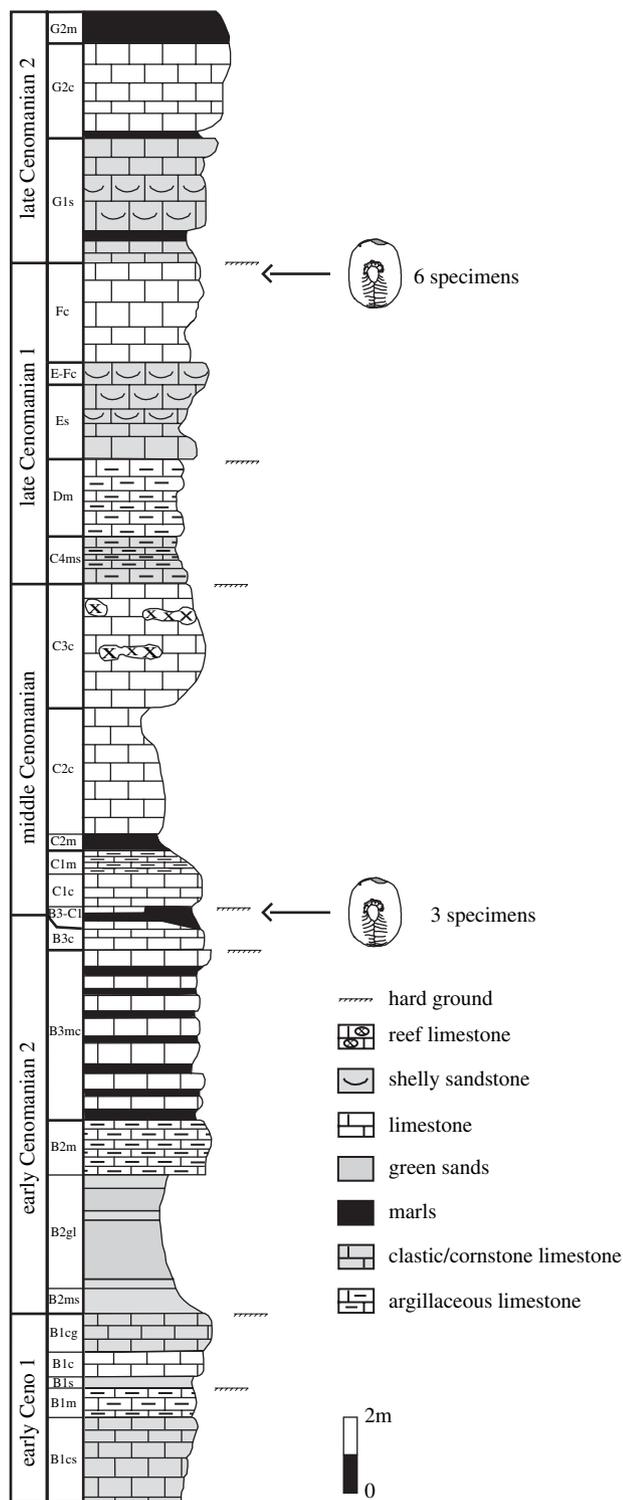


Fig. 2. Stratigraphic log of Cenomanian strata on Ile Madame (Charente-Maritime), showing the provenance of nine specimens of *N. (J.) jolyi*.

anteriorly; four genital plates of equal size, organised into arc around anterior edge of periproct. Ocular plates II, III and IV exsert, so that adjacent genital plates are in contact. All ocular plates of same size; posterior ocular plates I and V not elongated. No supplementary plates in apical disc. Important dimorphism in gonopore size (minimum and maximum diameters 0.06 and 0.45 mm, respectively). Periproct supramarginal, situated in

deep, narrow longitudinal groove, in contact with apical system anteriorly and extending backwards up to midway between apical system and posterior test margin.

Dimensions. Maximum length, width and height are 11.4, 9.4 and 4.4 mm, respectively.

Description. Test small, ranging between 7.1 and 11.4 mm in length (average 8.7 mm), between 5.8 and 9.4 mm in width (average 6.7 mm) and between 2.9 and 4.4 mm in height (average 3.4 mm). Width/length ratio ranges between 0.73 and 0.82 (mean 0.77) and height/length ratio between 0.34 and 0.42 (mean 0.38). Material (three specimens) from B3/C1 boundary are larger than material from unit F (Fig. 4).

Test elongated, with greatest width situated in posterior part. Margins smoothly rounded and slightly convergent towards anterior part of test when in plan view. Adoral surface depressed around peristome as well as in anterior and lateral portions, whereas posterior part shows wide, shallow sulcus leading to posterior edge. Test profile low, with greatest height situated slightly anterior to centre, close to apical system. Anterior edge rounded and ambitus low, whereas posterior margin is acuminate and points upwards (Fig. 5). This feature gives test an uncommon, flattened diamond-shaped profile, reminiscent of that of the disasterid *Grasia elongata*, except that in that species the posterior edge points downwards and the anterior upwards (Cotteau, 1867–1874).

Apical system positioned eccentric anteriorly; four genital plates of approximately same size, each of them perforated by one gonopore, and organised into an arc around anterior edge of periproct. Ocular plates II, III and IV exsert, so that adjacent genital plates are in contact; all ocular plates of same size; posterior ocular plates I and V not elongated. No supplementary plates present in apical disc (see Fig. 3).

Gonopore diameters were measured in seven specimens, showing significant variation (Fig. 5). Four specimens possess gonopores, with diameters ranging between 0.25 and 0.45 mm, several times larger than those of the three other specimens (diameters ranging from 0.06 to 0.09 mm) (Fig. 4). Large and small gonopores are present in specimens of both stratigraphic levels so that gonopore diameter appears independent of test size (Fig. 4). During growth, the pre-adult stage is characterised by a rapid acquisition of the full diameter of gonopores relative to a small increase in test size and is associated with low sample sizes over a wide size range (David, 1980; Ebert, 1982; David and Laurin, 1991; Néraudeau, 1991). Pre-adult specimens are generally so rare in the fossil record that all echinoids collected must be adults with gonopores fully opened. Moreover, in comparison to previous work dealing with sexual dimorphism in echinoids (e.g., Philip, 1963; Kier, 1969; David et al., 1988; Néraudeau, 1993), the difference we have measured between gonopore diameters is so pronounced that it can be interpreted as an expression of sexual dimorphism. In addition, we have noted a similar dimorphism with comparable values in associated material of *Nucleopygus similis*.

Periproct supramarginal, situated in a deep, narrow longitudinal groove, longer and narrower in largest specimens

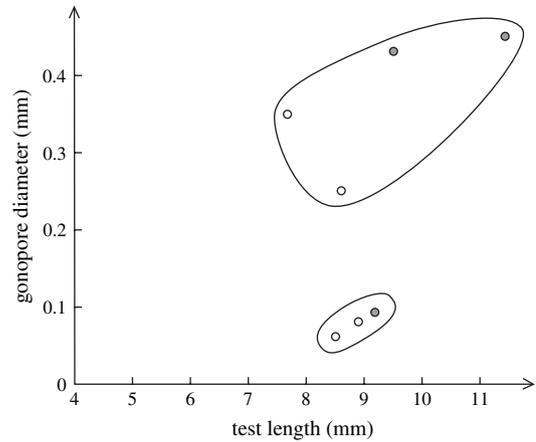
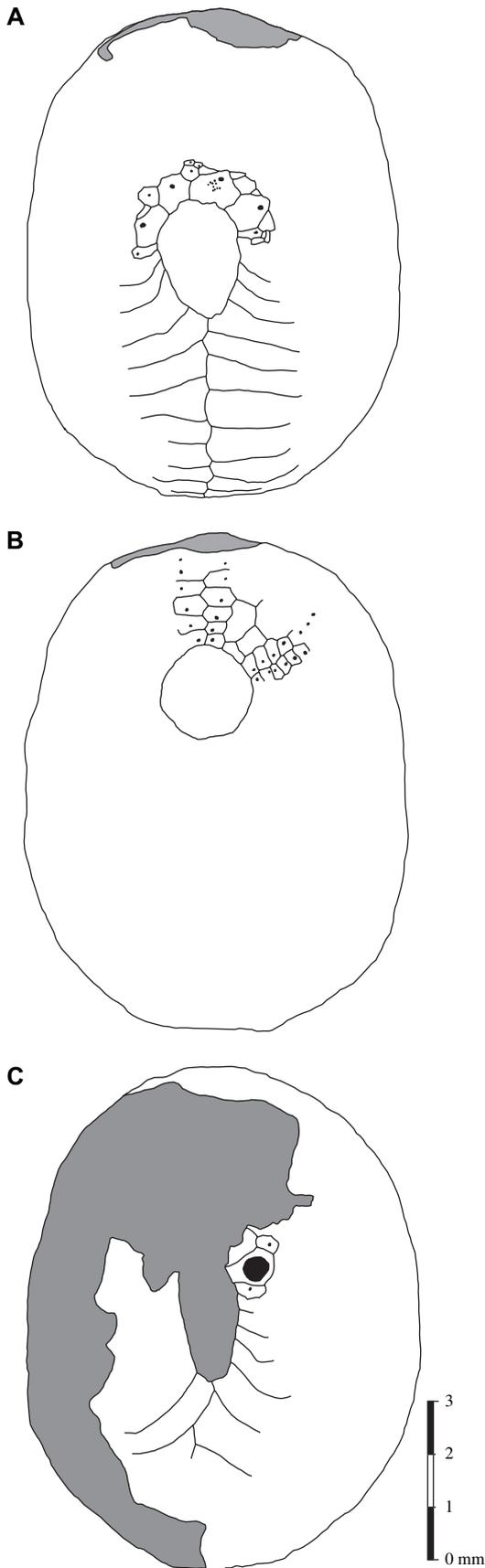


Fig. 4. Graphic plot of gonopore size versus test length for seven specimens of *N. (J.) jolyi* from the B3/C1 boundary (grey-infilled circles) and from unit F (open circles).

(Fig. 5), contacting apical system anteriorly and extending backwards up to midway between apical system and posterior test margin. Peristome anterior in position, subpentagonal in shape and slightly depressed. Ambulacral plates far smaller than interambulacra, pierced by pairs of round pores aborally, extremely reduced in size, and by single pores distal to petals. Petals are inconspicuous and flush with test. Phylloides narrow, organised in a single column of pores in each half ambulacrum. Buccal pores present, located closer to phylloides than to peristomial edge (Fig. 3); bourrelets weakly developed and flush with test. Tubercles characterised by sunken areoles, undifferentiated and regularly scattered over entire test, except for presence of a narrow naked area in interambulacrum 5 on oral side.

Remarks. Our specimens match both the description and the illustrations of Gauthier (1898) closely, except for the apical pattern of ocular plates. In the original description, ocular plates II and IV are stated to be insert, i.e., intercalated between the genital plates and in contact with the periproct, whereas they are exsert in our material. However, Gauthier noted that genital plates 1 and 4 are rather small, and this could result from an incorrect interpretation of boundaries between ocular and genital plates. As Kier (1962) and Mintz (1966) noted, Gauthier's specimens are presumed lost and we cannot therefore confirm his observations. Lambert bought Gauthier's Collection, but did not supply additional details (Lambert, 1918, 1920). Be that as it may, the apical pattern described by Gauthier was certainly similar to that of *Galeropygus* and must have led him to believe that he had discovered a new species of that genus. Actually, the apical system in *Galeropygidae* is quite different from that of our

Fig. 3. Camera-lucida drawings of two specimens of *N. (J.) jolyi* from the B3/C1 boundary on Ile Madame. A, B, male (neotype, MHNN-DHT R65001), aboral and oral views; length of test 9.2 mm. C, female (MHNN-DHT R65002), aboral view, length of test 9.5 mm. Note the marked difference in gonopore size between these specimens, despite the fragmentary nature of the female test.

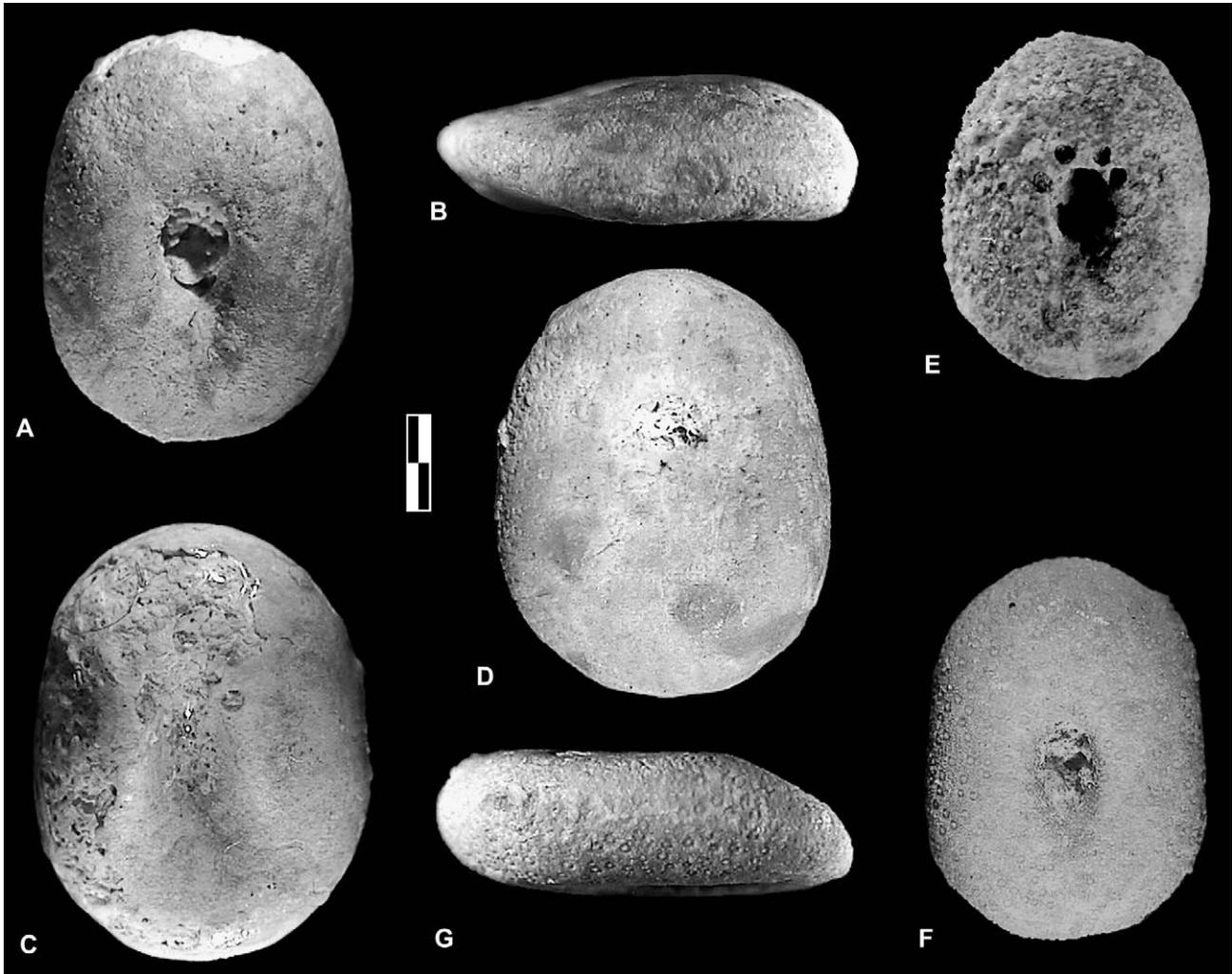


Fig. 5. *Nucleopygus (Jolychypus) jolyi* (Gauthier, 1898). A, B, male (neotype), B3/C1 boundary, Ile Madame (MNHN-DHT R65001), aboral and lateral views, test length 9.2 mm. C, D, female, B3/C1 boundary, Ile Madame (MNHN-DHT R65002), aboral and oral views, test length 9.5 mm. E, female, unit F, Ile Madame (Nicolleau Coll., Niort Museum, no. 8529), aboral view, test length 7.7 mm. F, G, male (MNHN-DHT A24552), unit F, Ile Madame, aboral and lateral views, test length 8.5 mm. Scale bar represents 2 mm.

specimens, as well as of that of Gauthier's material. It is endocyclic, i.e., apical plates completely enclose the periproct, and supplementary plates are present (Kier, 1962; Mintz, 1966, 1968), posterior ocular plates are elongated and genital plate 5 is present (Jesionek-Szymańska, 1963). All these characters are absent from our Cenomanian material.

Gauthier's description provides too few details on ambulacral pores, as well as on tubercle arrangement, so that the systematic position of his material could not be determined with certainty. In our specimens, the ambulacral plates bear single pores beyond the petals, the phyllodes are narrow and single pored, and buccal pores are present. The adoral and adapical tubercles are of approximately the same size and a very narrow naked area is present in interambulacrum 5. Such features are absent from both *Galeropygus* and other galeropygids (Kier, 1962, 1966) but occur in more derived groups of cassiduloids, particularly in *Nucleopygus* (Kier, 1962), which shares most characters with our specimens. According to Kier (1962),

this genus differs from *Nucleolites*, a primitive cassiduloid with plesiomorphic features, by having narrower petals, single-pored phyllodes and buccal pores. These are derived characters that are also present in our material. Nevertheless, the apical system of *Nucleopygus* and of our specimens is not identical: in *Nucleopygus*, the periproct does not abut the apical system, the posterior genital plates (1 and 4) are separated by genital plate 2, and the anal groove is less well developed than in our specimens.

Stratigraphic and geographic distribution. Material of *N. (J.) jolyi* is now known from the uppermost lower (B3/C1 boundary) and upper Cenomanian (unit F) of Ile Madame (Charente-Maritime, France), as well as from unit F at La Couronne, close to Angoulême (Charente). Specimens described by Gauthier (1898) are assumed to have been collected from unit F (upper Cenomanian), at three localities in the Angoulême area: Entre-Roches, Saint Michel and Les Tuileries.

4. Phylogenetic analysis

Previous work. Gauthier (1898) considered his material to represent a new species of *Galeropygus*, *G. jolyi*, and based his arguments on test shape, on the anterior position of the peristome, and on the plesiomorphic pattern displayed by the apical system, i.e., the organisation of genital plates into an arc that abuts the periproct. Comparing with congeneric forms, Gauthier hypothesised that supplementary plates were initially present in the apical system of *G. jolyi* but were not preserved. However, he did note that the posterior ocular plates were not elongated in *G. jolyi*, unlike congeners. To Lambert (1918), *G. jolyi* differed from other species of *Galeropygus* in having an elongated, depressed shape and relatively tall ambulacral plates. He erected the subgenus *Jolyclypus* to accommodate it, and later elevated this to generic rank (Lambert, 1920). Lambert and Thiéry (1921) considered *Jolyclypus* as a subgenus of *Galeropygus*, from which it differs by its small size, elongated and depressed shape, as well as tall ambulacral plates, whereas Mortensen (1948) regarded *Jolyclypus* as a distinct genus of galeropygid. Because of their small size, Kier (1962) assumed Gauthier's specimens possibly to have been immature, and he suspected that the age assignment given by Gauthier was incorrect because of their apparent primitive morphology. Following Lambert (1918), he accepted *Jolyclypus* as a possible cassiduloid but listed it as "incertae sedis" (Kier, 1966). Finally, Mintz (1966, 1968) also considered Gauthier's specimens to be juveniles of a primitive echinoid, and assigned *Jolyclypus* to the Galeropygidae.

Cladistic analysis. Phylogenetic affinities between our specimens and other cassiduloid echinoids have been studied using a cladistic approach. We have modified the data matrix published by Suter (1994), using 51 taxa and 31 morphological characters (see Appendix). All taxa included in our analysis belong to the ten main families of the order Cassiduloida and range stratigraphically from the Middle Jurassic to the Recent (see Appendix). Several studies suggest that the Cenozoic orders Clypeasteroidea, Oligopygoidea and Neolampadoidea arose from within the "cassiduloids" (Kier, 1974; Phelan, 1977; Mooi, 1990; Suter, 1994; Smith, 2001), and are therefore demonstrably not monophyletic. Nevertheless, representatives of these three orders have not been included in the analysis to minimise the probability of homoplastic changes and phenomena of long-branch attraction and character exhaustion (Stewart, 1993; Wagner, 1995, 2000; Smith, 2001).

Because of their basal stratigraphic position, the character states of *Hyboclypus* and *Galeropygus* have been considered plesiomorphic for coding, and *Hyboclypus* has been defined as outgroup in the analysis. The data matrix has been treated with computer program PAUP 3.1 (Swofford, 1993); we have been compelled to use the heuristic option because of the huge number of trees. Character states were unordered and all characters have been weighted equally.

The optimisation procedure computed 2239 most parsimonious trees with a minimum length of 153 steps. Completion of 100 replicates with random taxon addition sequences did

not reveal the existence of other trees of equal shortest length. A majority rule consensus tree (Fig. 6) was computed to visualise the best supported branches and clades.

As in Suter's analysis (1994), out of the ten families of cassiduloids recognised by Kier (1966), the Archiaciidae is the only one to form a complete clade in 100% of the 2239 trees. The robustness of this clade relies on its two synapomorphies, viz. the presence of an apical rostrum and the reduction of the anterior petal. All other families constitute paraphyletic or polyphyletic groups, the polyphyletic families being represented in part by several clades scattered in the cladogram (Fig. 6). The paraphyletic Galeropygidae is present at the base of the trees. This family has been recognised by most authors (Jesioneck-Szymańska, 1963; Mintz, 1966; Smith, 1984) as the stem-group of cassiduloids as well as of non-cassiduloid echinoids, the Disasteroidea, so that it can be considered a paraphyletic assemblage. The two families Clypeidae and Nucleolitidae were distinguished by Kier (1962) on the basis of test shape, pore arrangement in phyllodes and petal development. All of these characters show a high level of homoplasy (see below), which means that members of these families might be scattered into numerous different clades. In fact, as noted by Suter (1994), the Clypeidae and Nucleolitidae constitute the stem-groups of distinct cassiduloid clades (Fig. 6).

Jolyclypus jolyi and the genus *Nucleopygus* form a robust clade, present in 100% of the trees. The robustness of this clade relies on test characters other than periproct position. Hence, in the cladistic analysis, *J. jolyi* and *Nucleopygus* are closely related despite their different apical structures. This result supports the conclusion drawn from our morphological observations. Both taxa form a crown-group, rooted in the paraphyletic apatopygids, and are well separated from the Galeropygidae and from basal cassiduloids such as *Clypeus* and *Nucleolites*. However, *Nucleopygus*, as well as *Ochetes*, are not related to the clade formed by other Cassidulidae (Fig. 6), whereas they were included in that family by Kier (1962). In fact, the affinity between members of the Cassidulidae (after Kier, 1962) is not straightforward, and the same goes for eight other families of cassiduloids.

The ambiguity of phylogenetic relationships within cassiduloids results from the important rate of homoplasy displayed by numerous characters. A consequence of this is the relative low robustness of the trees (CI = 0.31; HI = 0.69; RI = 0.70; RC = 0.21), although similar to Suter's results. Seven characters display a homoplasy index (HI) higher than 0.8. These are: development of genital plate 2 (character 6), petal shape and development (characters 10 and 11), peristome shape and orientation (characters 19 and 20) and phyllode development (characters 25 and 27). All these characters involve ambulacral, apex and peristome specialisation, and are known to display parallel evolutionary trends in different taxa of cassiduloids (Kier, 1962).

On the other hand, six characters display a null rate of homoplasy (HI = 0). Two of them, presence of an apical rostrum (character 1) and reduction of the anterior petal (character 12)

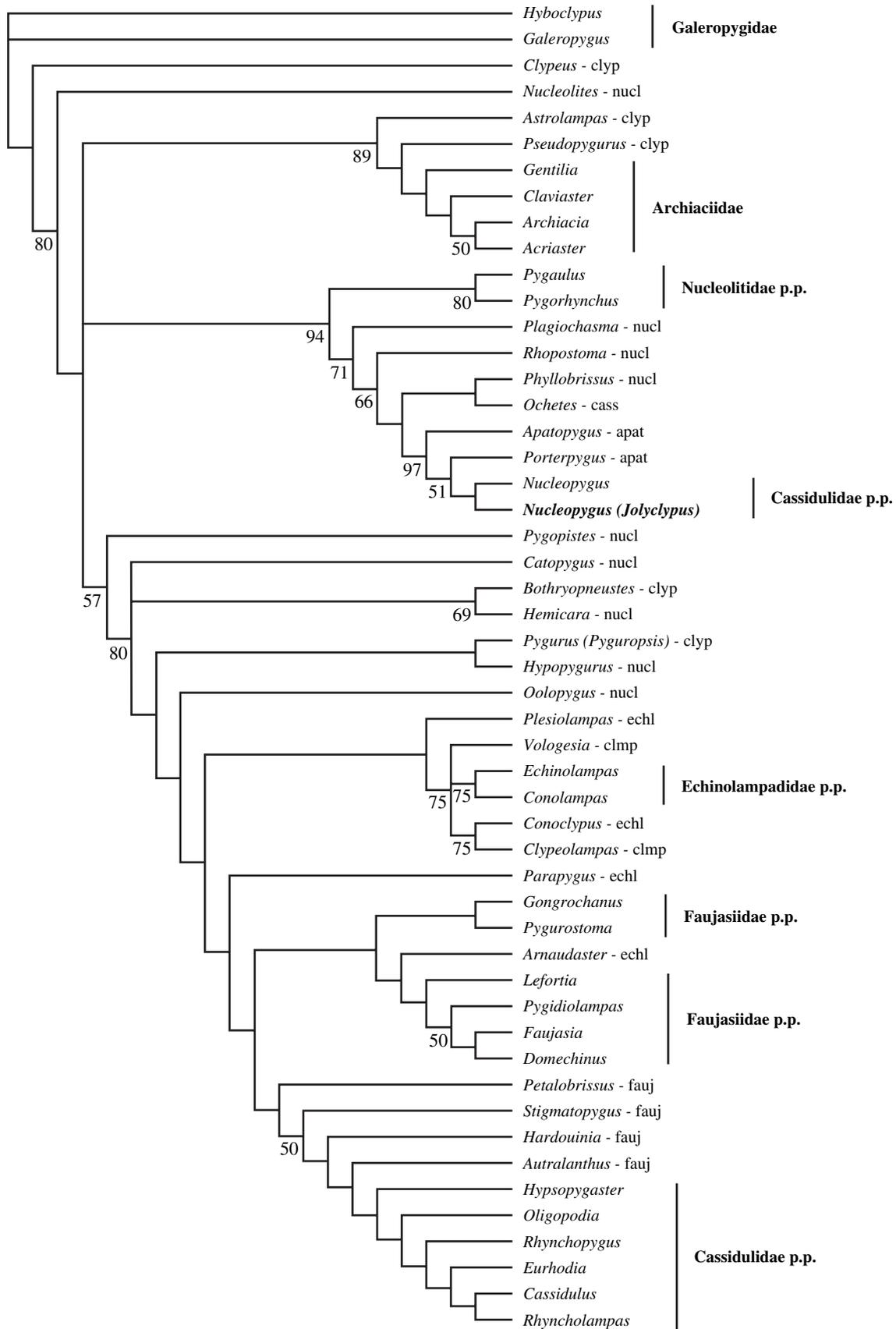


Fig. 6. Fifty-percent majority-rule consensus tree of the 2239 most parsimonious trees of 153 steps resulting from the cladistic analysis. Numbers show the frequency of nodes when they are present in less than 100% of trees. Other nodes are present in 100% of trees. Abbreviations: apat, apatopygids; cass, cassidulids; clyp, clypeids; clmp, clypeolampadids; echl, echinolampadids; fauj, faujasiids; nucl, nucleolitids.

correspond to synapomorphies of the Archiaciidae. The small size of the periproct (character 17) is the state supporting the clade Faujasiidae, pro parte (Fig. 6). The other characters are: presence of supplementary plates (characters 7 and 8) and elongation of posterior ocular plates (character 9). These characters have a plesiomorphic state expressed in the very first cassiduloids only, i.e., in taxa branched at the base of the trees: *Hyboclypus*, *Galeropygus*, *Clypeus* and *Nucleolites*.

Finally, two characters display a moderate rate of homoplasy (HI = 0.333). One involves the number of genital pores (character 2) and distinguishes the three genera *Porterpygus*, *Gongrochanus* and *Hypsopygaster*; the other is defined as periproct position with respect to apical disc (character 14), which is plesiomorphic (see Appendix) in basal cassiduloids (*Hyboclypus*, *Galeropygus* and *Clypeus*), as well as in *Jolyclypus jolyi*.

The high rate of homoplasy displayed by numerous characters was described and illustrated well by Kier (1962, 1966), who showed the importance of parallel evolution of traits within Cassiduloida. Kier (1962) used the evolutionary trends of the characters as well as the stratigraphic ranges of taxa to establish his phylogeny of cassiduloids. As a consequence, his systematics of cassiduloids implies the existence of parallel evolution among families. This certainly reflects true parallelism, but renders cassiduloid phylogeny a difficult topic to investigate by procedures based on parsimony.

Remarks. Characters of the apical system that have been considered to be of prime importance in taxonomy by Gauthier (1898) and Lambert (1918) carry far less weight in our interpretation of the species. In this species, the apical pattern mimics that of the first cassiduloids of the Jurassic (Galeropygidae) but differs in details; e.g., it has non-elongated ocular plates and lacks supplementary plates. Hence, it cannot be considered homologous with that of Galeropygidae, in view of the morphological and phylogenetic arguments above. The odd morphology of the periproct and apical system does not justify the creation of a new genus, and the generic rank given by Lambert (1918) to *Jolyclypus* is not retained herein. We do treat *Jolyclypus* as a subgenus, but transfer it to *Nucleopygus*, with which our species has the closest affinities.

5. Discussion

Convergence and parallelism are common phenomena among irregular echinoids, documenting adaptation of sea urchins to similar ecological conditions (Kier, 1962, 1974; Smith, 1978, 1981, 1984, 2001; Néraudeau and Moreau, 1989; Kanazawa, 1992; Suter, 1994; Wilkinson et al., 1996; Villier et al., 2004). This is also the case in cassiduloids, which evolved to colonise nearshore environments with sandy bottoms (Telford and Mooi, 1996). Specialisation of ambulacra for feeding (phyllodes) and gas exchange (petals), the evolution of shape, and location of the peristome are adaptive features which show the importance of parallelism in the history of cassiduloids (Suter, 1994). Convergence and

parallelism also characterise the evolution of apical system structure in irregular echinoids (Jesionek-Szymańska, 1963; Mintz, 1966; Kier, 1974; Saucède, 2002), although it is occasionally difficult to advance any obvious adaptive significance of such. When taxa separate early in their evolution, evolutionary trends initiated in the stem-group may continue progressively and in the same way in diverging subsets. This is the case in periproct migration that ended in exocyclism several times in the main subsets of irregular echinoids (Jesionek-Szymańska, 1963; Smith, 1984), while the onset of this migration had appeared earlier in the very first irregulars (Jesionek-Szymańska, 1970; Smith and Anzalone, 2000).

The uniqueness of *N. (J.) jolyi* lies in the reversal that applies to periproct position with respect to the apical system, and seemingly reproduces a pattern not seen since the end of the Jurassic. Finding the adaptive advantage of such a feature is not straightforward because other characters such as petals, phyllodes and tubercles suggest the same ecological requirements as other small species of *Nucleopygus*. *Nucleopygus similis* is well represented in strata of late early and late Cenomanian age, which have also yielded *N. (J.) jolyi*. The two species differ from congeners by their small size and their presence in fine sands and clayey deposits (Néraudeau and Moreau, 1989). Their small size is very likely related to the presence of clay, since larger species of cassiduloids feed in coarser and cleaner sands, mainly because they did not evolve the respiratory and feeding organs found in large irregular echinoids (such as spatangoids) for burrowing in clayey or silty deposits (Néraudeau and Moreau, 1989; Telford and Mooi, 1996). Moreover, small species of *Nucleopygus* possess numerous closely spaced tubercles that supported a dense cover of spines and allowed them to stabilise the walls of their minute burrows in marly sediments (Néraudeau and Moreau, 1989).

The fact that posterior ocular plates are not elongated in *N. (J.) jolyi* suggests that the onset of periproct migration differs from the mechanism present in basal cassiduloids such as *Galeropygus*, and follows the same process as in other derived cassiduloids, i.e. cassiduloids with a disjunct periproct/apical system. However, we assume that for some unknown reason periproct migration stopped early during growth in *N. (J.) jolyi*, and that the apical system and periproct remained in contact as seen in the very first stages of growth of other irregular echinoids (Gordon, 1926). Other examples of “paedomorphic” patterns are not rare in small species of echinoids, the most famous being the origin of the diamond-shaped cross-section of teeth in the Eognathostomata, inherited from the small opportunist “regular” species, *Eodiadema minutum*, which evolved a paedomorphic lantern from the standard aulodont one (Smith, 1981, 1984). Hence, our interpretation of the apical structure of *N. (J.) jolyi* as a paedomorphic pattern relates this uncommon feature to a well-known phenomenon in echinoid evolution. Moreover, this case study provides yet another example of the role played by extrinsic (i.e., adaptation to silty and clayey deposits) and intrinsic (i.e., heterochrony) factors in evolutionary trends, and also emphasises the importance of adaptive strategies in echinoid evolution (McNamara, 1990).

Together with *Hemiaster* (*Leymeriaster*) *similis* from the upper Cenomanian of southwest France (Néraudeau, 1993), *N. (J.) jolyi* represents the oldest example of secondary sexual dimorphism known in irregular echinoids. Indeed, sexually dimorphic echinoids were very rare prior to the end of the Cretaceous. Among the numerous species of mid-Cretaceous hemiasterid and related groups (e.g., *Mecaster*), secondary sexual dimorphism is highly exceptional and limited to *H. (L.) similis* and closely related species (e.g., the early Turoonian *H. (L.) leymeriei*; see Néraudeau, 1990). It seems that sexual dimorphism is just as exceptional in mid-Cretaceous cassiduloid echinoids because such gonopore size differentiation has been found only in sympatric *N. (J.) jolyi* and *N. similis*.

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References

- Agassiz, L., 1840. Catalogus systematicus ectyporum echinodermatum fossilium Musei Neocomensis, secundum ordinem zoologicum dispositus. O. Petitpierre, Neuchâtel, 20 pp.
- Agassiz, L., Desor, E., 1847. Catalogue raisonné des espèces, des genres, et des familles d'échinides. *Annales des Sciences Naturelles* 7 (3), 129–168; 8 (3), 5–35, 355–380.
- Claus, C.F.W., 1880. Grundzüge der Zoologie, I. N.G. Elwert'sche Universitäts-Buchhandlung, Marburg/Leipzig, 822 pp.
- Cotteau, G.H., 1867–1874. Paléontologie française, description des animaux invertébrés, Terrain jurassique 9, Échinides irréguliers. Masson, Paris, 551 pp.
- David, B., 1980. Un modèle d'ontogenèse: la croissance de *Toxaster granosus kiliani* (Lambert), échinide spatangoïde du Valanginien. *Geobios* 13, 903–929.
- David, B., Laurin, B., 1991. L'ontogenèse complexe du spatangue *Echinocardium cordatum*: un test des standards des trajectoires hétérochroniques. *Geobios* 24, 569–583.
- David, B., Laurin, B., de Ridder, C., 1988. How *Echinocardium cordatum* (Pennant) shows sexual dimorphism. In: Burke, R.D., et al. (Eds.), *Echinoderm Biology. Proceedings of the Sixth International Echinoderm Conference, Victoria 1987*. A.A. Balkema, Rotterdam, pp. 683–686.
- Desor, E., 1842. Des Galérites. In: Agassiz, L. (Ed.), *Monographie d'échinodermes vivants et fossiles* 3. O. Petitpierre, Neuchâtel, 94 pp.
- Ebert, T.A., 1982. Longevity, life history, and relative body size in sea urchins. *Ecological Monographs* 52, 353–394.
- Erwin, D.H., Droser, M.L., 1993. Elvis taxa. *Palaios* 8, 623–624.
- Gauthier, V., 1898. Contribution à l'étude des échinides fossiles. *Bulletin de la Société Géologique de France* 25 (3), 831–841.
- Gordon, I., 1926. The development of the calcareous test of *Echinocardium cordatum*. *Philosophical Transactions of the Royal Society of London B* 215, 255–313.
- Jablonski, D., 1986. Causes and consequences of mass extinctions. In: Elliott, D.K. (Ed.), *Dynamics of Extinction*. John Wiley, New York, pp. 183–229.
- Jesionek-Szymańska, W., 1963. Echinides irréguliers du Dogger de Pologne. *Acta Palaeontologica Polonica* 8, 293–414.
- Jesionek-Szymańska, W., 1970. On a new pygasterid (Echinoidea) from the Jurassic (middle Liassic) of Nevada, U.S.A. *Acta Palaeontologica Polonica* 15, 411–423.
- Kanazawa, K., 1992. Adaptation of test shape burrowing and locomotion in spatangoid echinoids. *Palaeontology* 35, 733–750.
- Kier, P.M., 1962. Revision of the cassiduloid echinoids. *Smithsonian Miscellaneous Collections* 144, 262 pp.
- Kier, P.M., 1966. Cassiduloids. In: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology, Part U, Echinodermata-Echinozoa-Echinoidea* 3(2). Geological Society of America, Boulder, and University of Kansas Press, Lawrence, pp. U492–U523.
- Kier, P.M., 1969. Sexual dimorphism in fossil echinoids. In: Westermann, G.E.G. (Ed.), *Sexual Dimorphism in Fossil Metazoa and Taxonomic Implications*. International Union of Geological Sciences A1, 215–222.
- Kier, P.M., 1974. Evolutionary trends and their functional significance in the post-Paleozoic echinoids. *The Paleontological Society, Memoir* 48, 1–96.
- Kier, P.M., 1977. Triassic echinoids. *Smithsonian Contributions to Paleobiology* 30, 1–88.
- Kier, P.M., 1984. Echinoids from the Triassic (St. Cassian) of Italy, their lantern supports, and a revised phylogeny of Triassic echinoids. *Smithsonian Contributions to Paleobiology* 56, 1–41.
- Lambert, J., 1898. Notes sur les Échinides de la craie de Cipro. *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie* 11 (for 1897), 141–190.
- Lambert, J., 1918. Considérations sur la classification des échinides atélostomes. *Mémoires de la Société et de l'Académie d'Aube* 3 (55), 9–54.
- Lambert, J., 1920. Sur quelques genres nouveaux d'échinides. *Mémoires de la Société et de l'Académie d'Aube* 3 (55), 145–172.
- Lambert, J., Thiéry, P., 1921. Essai de nomenclature raisonnée des échinides, 5. Librairie Septime Ferrière, Chaumont, pp. 321–384.
- McNamara, K.J., 1990. Echinoids. In: McNamara, K.J. (Ed.), *Evolutionary Trends*. University of Arizona Press, Tucson, pp. 205–231.
- Mintz, L.W., 1966. The origins, phylogeny, descendants of the echinoid family Disasteridae A. Gras 1848. Unpublished PhD thesis, University of California, Berkeley, 314 pp.
- Mintz, L.W., 1968. Echinoids of the Mesozoic families Collyritidae d'Orbigny 1853 and Disasteridae Gras 1848. *Journal of Paleontology* 42, 1272–1288.
- Mooi, R., 1990. Pedomorphosis, Aristotle's lantern, and the origin of the sand dollars (Echinodermata: Clypeasteroidea). *Paleobiology* 16, 25–48.
- Mortensen, T., 1948. A Monograph of the Echinoidea, IV(1). Holactypoida, Cassiduloida. C.A. Reitzel, Copenhagen, 371 pp.
- Néraudeau, D., 1990. Ontogenèse, paléoécologie et histoire des *Hemiaster*, échinides irréguliers du Crétacé. Unpublished PhD thesis, Université de Bourgogne, Dijon, 194 pp.
- Néraudeau, D., 1991. Lateral variations of size-frequency distribution in a fossil echinoid community and their palaeoecological significance. *Lethaia* 24, 299–309.
- Néraudeau, D., 1993. Sexual dimorphism in mid Cretaceous hemiasterid echinoids. *Palaeontology* 36, 311–317.
- Néraudeau, D., 1995. Diversité des échinides fossiles et reconstitutions paléoenvironnementales. *Geobios, Mémoire Spéciale* 18, 337–345.
- Néraudeau, D., Floquet, M., 1991. Les échinides Hemiasteridae: marqueurs écologiques de la plate-forme castillane et navarro-cantabre (Espagne) au Crétacé supérieur. *Palaeogeography, Palaeoclimatology, Palaeoecology* 88, 265–281.
- Néraudeau, D., Moreau, P., 1989. Paléoécologie et paléobiogéographie des faunes d'échinides du Cénomanien nord-aquitain (Charente-Maritime, France). *Geobios* 22, 293–324.
- Néraudeau, D., Goubert, E., Lacour, D., Rouchy, J.M., 2001. Changing biodiversity of Mediterranean irregular echinoids from the Messinian to the present-day. *Palaeogeography, Palaeoclimatology, Palaeoecology* 175, 43–60.

- Phelan, T.H., 1977. Comments on the water vascular system, food grooves, and the ancestry of the clypeasteroids. *Bulletin of Marine Science* 27, 400–422.
- Philip, G.M., 1963. Two Australian Tertiary neolampadids, and the classification of cassiduloid echinoids. *Palaeontology* 6, 718–726.
- Saucède, T., 2002. Origine et évolution vers l'extrême des échinides irréguliers. Un nouveau modèle d'homologie, l'Extraxial Axial Theory, clef d'interprétation de la structure des appareils apicaux. Unpublished PhD thesis, Université de Bourgogne, Dijon, 246 pp.
- Saucède, T., Mooi, R., David, B., 2003. Combining embryology and paleontology: origins of the anterior-posterior axis in echinoids. *Comptes Rendus Palevol* 2, 399–412.
- Smith, A.B., 1978. A comparative study of the life style of two Jurassic irregular echinoids. *Lethaia* 11, 57–66.
- Smith, A.B., 1981. Implications of lantern morphology for the phylogeny of post-Palaeozoic echinoids. *Palaeontology* 24, 779–801.
- Smith, A.B., 1984. *Echinoid Palaeobiology*. George Allen and Unwin, London, 190 pp.
- Smith, A.B., 1988. Echinoid evolution from the Triassic to early Liassic. *Cahiers de l'Université Catholique de Lyon, Séries des Sciences* 3, 79–117.
- Smith, A.B., 2001. Probing the cassiduloid origins of clypeasteroid echinoids using stratigraphically restricted parsimony analysis. *Paleobiology* 27, 392–404.
- Smith, A.B., Anzalone, L., 2000. *Loriolella*, a key taxon for understanding the early evolution of irregular echinoids. *Palaeontology* 43, 303–324.
- Sprinkle, J., 1983. Patterns and problems in echinoderm evolution. In: Jangoux, M., Lawrence, J.M. (Eds.), *Echinoderm Studies*, vol. 1. A.A. Balkema, Rotterdam, pp. 1–18.
- Stewart, C.-B., 1993. The powers and pitfalls of parsimony. *Nature* 361, 603–607.
- Suter, S.J., 1994. Cladistic analysis of cassiduloid echinoids: trying to see the phylogeny for the trees. *Biological Journal of the Linnean Society* 53, 31–72.
- Swofford, D.L., 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1. Computer program. Smithsonian Institution, Washington.
- Telford, M., Mooi, R., 1996. Podial particle picking in *Cassidulus caribaeorum* (Echinodermata: Echinoidea) and the phylogeny of sea urchin feeding mechanisms. *The Biological Bulletin* 191, 209–223.
- Videt, B., 2004. Dynamique des paléoenvironnements à huîtres du Crétacé supérieur nord-aquitain (SO France) et du Mio-Pliocène andalou (SE Espagne). *Mémoires des Géosciences de Rennes* 108, 1–261.
- Villier, L., Néraudeau, D., Clavel, B., Neumann, C., David, B., 2004. Phylogeny and early Cretaceous spatangoids (Echinodermata: Echinoidea) and taxonomic implications. *Palaeontology* 47, 265–292.
- Wagner, P.J., 1995. Stratigraphic tests of cladistic hypotheses. *Paleobiology* 21, 153–178.
- Wagner, P.J., 2000. Exhaustion of morphologic character states among fossil taxa. *Evolution* 54, 365–386.
- Wilkinson, M., Suter, S.J., Shires, V.L., 1996. The reduced cladistic consensus method and cassiduloid echinoid phylogeny. *Historical Biology* 12, 63–73.
4. Apical plating: 0: tetrabasal (at least in juveniles); 1: monobasal.
5. Posterior genital plates (1, 4) separated by 2: 0: no; 1: yes.
6. Posterior ocular plates (Oc1, Oc5) separated by 2: 0: no; 1: yes.
7. Catenal plates between posterior oculars and periproct: 0: yes, in at least some specimens; 1: no.
8. Supplementary plates present in apical disc: 0: yes, in at least some specimens; 1: no.
9. Relative size of ocular plates: 0: approximately equal; 1: posterior oculars (1, 5) larger, elongate.
10. Petal development: 0: pore zones not expanded; 1: pore zones expanded.
11. Petal shape: 0: open, tapering adapically; 1: bowed, tapering both directions.
12. Anterior petal (ambulacrum III) development: 0: normal, as developed as paired petals; 1: shorter petal III, with less elongate pores; 2: absent, ambulacrum III non petaloid.
13. Pore zones of individual petals differ in length: 0: no, not by more than a single pore pair; 1: yes, by two or more pore pairs (one pore zone is clearly longer).
14. Periproct position with respect to apical disc: 0: enclosed, between posterior oculars and genital 5; 1: contacts posterior oculars; 2: separate, free from apical system.
15. Periproct position on test surface: 0: supramarginal, opening upwards from above ambitus; 1: marginal, opening rearwards; 2: submarginal, at ambitus opening downwards; 3: inframarginal, on oral surface of test.
16. Periproct orientation: 0: longitudinal; 1: equant; 2: transverse.
17. Periproct size: 0: larger or same size as peristome; 1: smaller than peristome.
18. Anal sulcus: 0: absent, periproct flush with test; 1: narrow, with small posterior longitudinal groove widening to rear; 2: small subanal heel and adapical lip; 3: broad, well-developed longitudinal groove from apex.
19. Peristome shape: 0: round; 1: pentagonal.
20. Peristome orientation: 0: longitudinal; 1: equant; 2: transverse; 3: oblique;
21. Bourrelet elevation: 0: flush, not projecting into peristome or oral funnel; 1: rounded, but not strongly projecting; 2: strongly projecting over peristome, and/or toothlike.
22. Ambulacral pores beyond the petals: 0: double; 1: double, but adoral pore much reduced; 2: single.
23. Arrangement of adoral pores in the phyllodes: 0: triad arcs in each half ambulacrum; 1: two discrete columns in each half; 2: single column in each half; 3: two columns with additional pores scattered between them.
24. Shape of phyllodes: 0: narrow, uniform in width towards the peristome; 1: expanded, bowed outward beyond the bourrelets; 2: broad arcs, almost perpendicular to the ambulacra.
25. Relative development of columns of phyllode pores: 0: inner and outer series approximately equally developed; 1: inner series much shorter.
26. Buccal pores: 0: absent, no enlarged pores between phyllodes and peristome; 1: present, single enlarged pore in the first ambulacral plates.
27. Separation between buccal pores and phyllodes: 0: narrow, with buccal pores much closer to phyllodes; 1: wide, with buccal pores much closer to peristome.
28. Plating in ambulacra beyond petals: 0: normal; 1: pyrinid, with small triangular plates enclosed between two primary plates adradially, and regular castellation of perradial sutures.
29. Naked zone in ambulacrum III of oral surface: 0: absent; 1: present, medial region lacking primary and secondary tubercles.
30. Naked zone in interambulacrum 5 of oral surface: 0: absent, medial tuberculation not differing; 1: narrow, width of zone only 2–4 times tubercle separation; 2: wide, width of zone many times that of tubercle separation.
31. Surface of medial naked zone in interambulacrum 5: 0: granular; 1: pitted.

Appendix

Character states coded in the phylogenetic analysis (modified after Suter, 1994)

1. Apical rostrum: 0: absent; 1: present, apical disc and petals elevated forward.
2. Number of genital pores: 0: 4; 1: missing on 2; 2: missing on 3.
3. Relative size of genital plates: 0: approximately equal; 1: 2 enlarged.

Archiaciidae Cotteau and Triger

Archiacia sandalina Agassiz*Claviaster libycus* Gauthier*Acriaster sergipensis* Smith*Gentilia syriensis* Kier

Faujasiidae Lambert

Faujasia apicalis (Desor)*Australanthus longianus* (Gregory)*Domechinus chelonium* (Cooke)*Gongrochanus herschelianus* (M'Clelland)*Hardouinia mortonis* (Michelin)*Lefortia trojana* Cooke*Petalobrissus setifensis* (Cotteau)*Pygidiolampas eurynota* Clark*Pygurostoma morgani* Cotteau and Gauthier*Stigmatopygus lamberti* Besairie

Cassidulidae Agassiz and Desor

Cassidulus caribaeorum Lamarck*Eurhodia marrisii* d'Archiac and Haime*Hypsopygaster ungosensis* Bajarunas*Nucleopygus minor* Desor*Nucleopygus (Jolyclypus) jolyi* (Gauthier)*Ochetes morrisii* (Forbes)*Oligopodia epigonis* (von Martens)*Rhyncholampas pacifus* (Agassiz)*Rhynchopygus marmini* (Agassiz)

Echinolampadidae Gray

Echinolampas ovata Leske*Arnaudaster gauthieri* Lambert*Conolampas sigsbei* Agassiz*Parapygus coquandi* (Cotteau)*Plesiolampas saharae* Bather

Conoclypidae von Zittel

Conoclypus conoideus (Leske)

Clypeolampadidae Kier

Clypeolampas ovatus (Lamarck)*Vologesia ovatum* (de Grateloup)