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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.

Keywords: Echinoidea; *Nucleopygus* (*Jolyclypus*) *jolyi*; Cenomanian; France; Charentes; Phylogeny; Reversal; Sexual dimorphism; Neotype

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-myr 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 (*Terebratula 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 fleuriaui*), 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 holectypoids are well represented at both levels, in particular by small cassiduloids (*Catopygus*, *Nucleopygus*), which generally are